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The effect of abandoned leaf-cutting ant nests on plant assemblage composition in a tropical rainforest of Costa Rica[1]

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Abstract: Leaf-cutting ant nests represent a potential source of disturbance within Neotropical forests that might favour selective establishment of some plant species. To test this hypothesis, I counted the number and determined the composition of plant species and individuals established in 10 abandoned *Atta cephalotes* nests and adjacent understory plots in an old-growth forest of Costa Rica. Specifically, I evaluated whether abandoned leaf-cutting ant nests differentially affect plant assemblages according to their 1) regeneration status, 2) seed size, and 3) dispersal mode. No differences were found in the relative abundance of species (and individuals) with different regeneration status, seed size, and dispersal mode between understory plots and abandoned *Atta* nests. Moreover, entire sites (abandoned ant nests and their nearby understory plots) were frequently grouped together according to those characteristics, suggesting that local effects were stronger than the effect of nests. Four non-mutually exclusive factors are discussed to explain the lack of a consistent effect of abandoned ant nests on plant assemblage composition: refuse dump location, spatial heterogeneity, dispersal limitation, and the local species pool. Chance events in the dynamics of both ant and plant species populations apparently restrict the effect of abandoned nests to an ecological time. Abandoned ant nests, however, might favour selective establishment of some plant assemblages if their refuse piles are located on the soil surface and if the potentially favoured plant species are locally available.

Keywords: *Atta cephalotes*, disturbances, recruitment limitation, regeneration niches, spatial heterogeneity, understory gaps.

Résumé : Les nids de fourmis coupeuses de feuilles représentent une source potentielle de perturbations dans les forêts tropicales des Amériques qui pourrait favoriser l'établissement sélectif de certaines espèces végétales. Pour tester cette hypothèse, j'ai compté le nombre et déterminé la composition des espèces de plantes et des individus établis dans 10 nids abandonnés de *Atta cephalotes* ainsi que dans des parcelles situées dans le sous-bois adjacent. L'étude s'est déroulée dans une vieille forêt du Costa Rica. J'ai voulu savoir si les nids abandonnés de fourmis affectent de façon différencielle les assemblages de plantes, et ce, en fonction de *i*) leur état de régénération, *ii*) la taille des graines et *iii*) leur mode de dissémination. Aucune différence n'a été trouvée au niveau de l'abondance relative des espèces et des individus entre les parcelles du sous-bois et les nids de fourmis abandonnés, malgré des différences dans l'état de régénération, la taille des graines et le mode de dissémination. De plus, des sites entiers, incluant des nids de fourmis abandonnés et des parcelles de sous-bois adjacentes, ont fréquemment été regroupés en fonction de ces caractéristiques, ce qui suggère que les caractéristiques locales des sites ont plus d'impacts sur les plantes que les nids de fourmis. Quatre hypothèses non mutuellement exclusives sont discutées pour expliquer l'absence d'un effet uniforme des nids de fourmis abandonnés sur la composition des assemblages de plantes : l'emplacement des déchets des fourmis, l'hétérogénéité spatiale, les limites à la dissémination et le bassin local d'espèces. Ce serait le hasard de la dynamique des populations de fourmis et des espèces de plantes qui minimiserait l'effet des nids abandonnés. Les nids de fourmis abandonnés peuvent toutefois favoriser un établissement sélectif de certains assemblages végétaux lorsque leurs amas de déchets sont situés sur la surface du sol et lorsque les espèces de plantes qui pourraient en bénéficier sont localement disponibles.

Mots-clés : *Atta cephalotes*, hétérogénéité spatiale, limites au recrutement, niches de régénération, perturbations, trouées dans le sous-bois.

`Nomenclature`

Nomenclature: Please provide reference(s) for nomenclature.

Introduction

Natural disturbances have long been accepted as one of the main factors maintaining high plant diversity in tropical rain forests (Clark, 1990). By increasing the spatial and temporal heterogeneity of limiting resources, disturbances provide conditions different from those of the surroundings that offer opportunities for regeneration and establishment of species that differ in resource use, thus enhancing niche separation. In tropical rain forests, treefall gaps are dominant examples of natural disturbances that promote the increase of species diversity (Denslow, 1987; Brokaw & Busing, 2000). When a tree falls there is an increase in light availability, providing opportunities for recruitment of species adapted to different light regimes (Denslow, 1980; Brokaw, 1985; Kobe; 1999; but see Hubbell *et al.*, 1999). However, apart from treefall gaps, there are other small-scale disturbances that also might be important for the maintenance of plant diversity in these systems.

Leaf-cutting ant nests (mainly *Atta* spp.) are considered to be understory, small-scale disturbances that affect

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plant species composition and dynamics in tropical rain forests (Farji-Brener & Medina, 2000; Farji-Brener & Illes, 2000; Hull-Sanders & Howard, 2003; Wirth *et al.*, 2003). When the colony is active, most leaf-cutting ant species maintain the nest area free of plants. However, once a colony dies or abandons a nest site, this area represents a set of opportunities for plant regeneration very different than either undisturbed understory or treefall gaps. A recently abandoned *Atta* nest is a space free of understory vegetation and litter, with higher nutrient concentrations and higher light availability than the adjacent forest understory (Farji-Brener & Illes, 2000; Wirth *et al.,* 2003). The new environmental conditions created by an abandoned *Atta* nest may be more important for some species assemblages than others. Specifically, it has been proposed that abandoned *Atta* nests may affect the establishment of plants according to their regeneration status, seed size, and dispersal mode. First, the higher light intensity at ground level in abandoned ant nests is expected to favour light-demanding species for establishment and initial growth, such as gap-dependent species or small-seeded plants with few energy reserves (Farji-Brener & Illes, 2000; Hull-Sanders & Howard, 2003; Wirth *et al.*, 2003). Second, the litter layer may act as an inhibitory light filter (Vazquez-Yanes *et al.,* 1990). Species with small seeds do not have the resources to emerge from underneath the leaf litter and often require litter-free sites for successful establishment (Guzmán-Grajales & Walker, 1991; Metcalfe & Turner, 1998). Indeed, many seeds from tropical plant species are capable of germinating when the litter layer is disrupted and the soil surrounding the seed is disturbed without simultaneous opening of the canopy (Metcalfe & Turner, 1998). Therefore, the lack of a leaf litter barrier on abandoned nests could favour species that need cleared soil for germination and/or establishment. Third, there may be limited dispersal of biotically dispersed species to an abandoned *Atta* nest because the absence of vegetation in the nest area reduces the availability of perch (*e.g.*, for birds) and refuge sites (*e.g.*, for mammals). Finally, the modified structure of the soil and the higher level of nutrients in the nest area may also affect which species assemblages are capable of germinating and becoming established. These factors, together with the high abundance and turnover rate of nest sites in several tropical rain forests (Perfecto & Vandermer, 1993; Farji-Brener & Illes, 2000; Wirth *et al.,* 2003) suggest that recently abandoned ant nests may serve as regeneration islands for shade-intolerant, nutrient-limited, small-seeded litter-gap demanders and/or abiotically dispersed species.

Although several authors (Farji-Brener & Illes, 2000; Farji-Brener & Medina, 2000; Hull-Sanders & Howard, 2003; Moutinho, Nepstad & Davidson, 2003; Wirth *et al.,* 2003) have proposed that the presence of abandoned leaf-cutting ant nests may favour the establishment of some plant species assemblages, this hypothesis has not been tested. The goal of this study was to evaluate the role of abandoned leaf-cutting ant nests on plant species with respect to their regeneration status, seed size, and dispersal mode in a tropical rain forest of Costa Rica. To test this idea, I measured the number of plant species and individuals established in abandoned *Atta cephalotes* nests and adjacent understory plots. If the environmental conditions of abandoned ant nests favoured the establishment of some species assemblages, I expected to find a consistent group of species assemblages on abandoned nests different from those in understory sites.

Methods

I conducted this study at La Selva Biological Station, operated by the Organization for Tropical Studies (10° 26' N, 83° 59' W) in the Atlantic lowlands of Costa Rica, in February 1999. The area is a wet premontane forest and receives a mean annual rainfall of 4,000 mm. La Selva Biological Station includes old-growth forest and patches of forest in different successional stages (McDade *et al.,* 1994). Colonies of leaf-cutting ants, mainly *Atta cephalotes*, are common within La Selva (Farji-Brener, 2001). To determine the effect of abandoned leaf-cutting ant nests on plant assemblages, I located 10 abandoned *Atta cephalotes* nests in the old-growth forest along the "**Camino circular lejano**" (CCL), "Camino experimental sur" (CES), "Sendero suroeste" (SSO), and "**Camino circular lejano**" (CCC) trails. The leaf-cutting ant nests located had been abandoned for 6 -12 months (O. Vargas, pers. comm.), and the mean ± SD size of the nests was 60 ± 15 m^2. The number of abandoned ant nests sampled ($n = 10$) was limited by their availability. However, this sample effort is similar to or larger than others made in similar studies (Garretson *et al.,* 1998; Farji-Brener & Illes, 2000; Hull-Sanders & Howard, 2003; Moutinho, Nepstad & Davidson, 2003; Wirth *et al.*, 2003).

Same name twice..

At each abandoned nest I established three plots of 1 m^2 around the centre of the area of disturbed soil to sample plant species richness and abundance. Since local characteristics of a site (*i.e.,* plant species availability) can affect plant community composition and structure, I also randomly established three plots of 1 m^2 at the forest understory 10-15 m away from colony centres as a site-control effect. The adjacent plots did not show tracks of the foraging trails leaving the nest when it was still active. In each case (abandoned nests and adjacent understory) data from the three plots were pooled for the analysis. Thus, each leaf-cutting ant nest and its adjacent understory (*i.e.,* a site) was considered to be a replicate (n = 10 sites). Each site was located at least 100 m away from the next site to avoid cross-influence among nests and adjacent plots.

All plants (< 1.5 m height) found in abandoned leaf-cutting ant nests and adjacent plots were identified to species and categorized according to their regeneration status (gap-dependent or shade-tolerant), seed size (< 2 mm, 2-10 mm, > 10 mm diameter), dispersal mode (biotic or abiotic), and life form when possible. Although tropical trees vary continuously in the light conditions they require for establishment (Lieberman *et al.,* 1995), two broad regeneration categories are generally recognized and widely used (Coley, 1983; 1987; Brokaw, 1985; Whitmore, 1989; Clark & Clark, 1992; Wright *et al.,* 2003; Uriarte *et al.,* 2004). Gap-dependent or pioneer species, also referred to as light-demanding or shade-intolerant, generally need high light environments to establish and grow, such as those found in treefall gaps. In contrast, shade-tolerant species, also called mature forest species, survive and grow in deep shade. I was able to assign 46 of a total of 60 species compiled (77%) to one of these two categories based on existing literature and on opinions of plant ecologists with extensive experience in Neotropical rainforest areas (Farji-Brener, 2001). The remaining 14 plant species did not fit readily into these categories: the opinions of experts were not in agreement and/or the plant was unidentified at the species level. Orlando Vargas and Bette Loiselle, two ecologists with extensive experience in the study area, assigned the seed size and dispersal mode categories of each species.

To evaluate whether abandoned leaf-cutting ant nests affect plant assemblage composition I used two different approaches. First, I used paired *t*-tests and contingency tables to compare the number of species between abandoned *Atta cephalotes* nests and adjacent understory according to their regeneration status, seed size, and dispersal mode. Second, I employed the *k*-means clustering method (Hartigan, 1975; Hartigan & Wong, 1978) to group sites according to their regeneration status, seed size, and dispersal mode. This procedure classifies objects into a user-specified number of clusters, and it is used when there is an *a priori* hypothesis concerning the number of clusters (as in the present study). To evaluate the appropriateness of the classification, within-cluster variability (small if the classification is good) and between-cluster variability (large if the classification is good) are compared; that is, a standard between-groups analysis of variance for each dimension is performed. Computationally, this analysis is similar to an analysis of variance "in reverse". The program starts with *k* random clusters, and then moves objects between clusters with the goal to minimize variability within clusters and maximize variability between clusters. Finally, the means of each cluster on each dimension is examined to assess how distinct the *k* clusters are. The magnitude of *F* values from the ANOVA performed on each dimension is an indication of how well the respective dimension (*i.e.*, variable) discriminates between clusters. Because in tropical rain forests the absolute number of plant species or individuals may be highly variable among sites (Denslow, 1987; Clark & Clark, 1992), I performed this analysis using relative frequencies.

If the presence of abandoned ant nests affects plant assemblages in a consistent way, species assemblages found in abandoned leaf-cutting ant nests should be similar to each other but different from those located in the undisturbed forest understory. **Therefore, I analyzed the data by forming two clusters as distinct as possible from each other,** expecting that one cluster would group plots mainly from abandoned ant nests and the other cluster would group plots mainly from the understory forest. I carried out this analysis to separately evaluate the effect of abandoned leaf-cutting ant nests on plant assemblages according to 1) regeneration status, 2) seed size, and 3) dispersal mode. I performed the analysis twice: first considering the number of species in each category (in %) and second considering the number of individual plants in each category (in %). OK?

Results

A total of 341 individuals from 60 plant species were recorded in this study. The most frequent species were *Geonoma* spp., *Hampea appendiculata*, *Philodendron* spp., *Prestoea decurrens*, and *Welfia regia* (Table I). The total number of species (41, Table I) and the mean number of species in abandoned *Atta cephalotes* nests were similar to those found in the forest understory (8.2 ± 1.0 *versus* 7.6 ± 0.8, respectively, mean ± SE, $t = 0.47$, $P = 0.65$, paired *t*-test).

The regeneration status, seed size, and dispersal mode of the plant species sampled were similar between abandoned nests and the forest understory. The mean numbers of gap-dependent, small-seeded, and abiotically dispersed plants were similar between abandoned ant nests and forest understory sites, considering both the number of species and the number of individuals (Table II). Furthermore, the relative abundance of species according to their regeneration status, seed size, and dispersal mode was independent of the presence of an abandoned ant nest ($\chi^2 = 0.45$, 0.10, and 1.62, respectively, all $P > 0.45$, Figure 1).

Likewise, the *k*-clustering method often grouped entire sites in different clusters rather than separating abandoned ant nests and understory plots into different clusters. Abandoned *A. cephalotes* nests did not show consistent differences with understory plots in their relative abundance of plant species (and individuals) with different regeneration status, seed size, or dispersal mode (Table III). In contrast, abandoned ant nests and their nearby understory (*i.e.*, the components of individual sites) were commonly grouped together according to those characteristics. For example, sites 5, 8, and 10 showed a high relative abundance of shade-tolerant species compared with sites 1, 2, 3, 4, and 9. Sites 8 and 10 also had a high number of species with seeds > 10 mm when compared to the rest of the sites, and site 5 had a large number of individuals with seeds between 2-10 mm. Finally, sites 5, 8, and 10 had more species with biotic dispersion than sites 1, 2, 3, and 4.

Discussion

The relative abundance of species (and individuals) of different regeneration status, seed size, and dispersal mode were more similar within sites than between different abandoned *Atta cephalotes* nests. This suggests that abandoned ant nests do not influence species composition in a consistent way, raising questions about their importance as a selective force on the establishment of plant species assemblages (Farji-Brener & Illes, 2000). **This absence of a strong effect may be attributable to the short period of time since nest abandonment in this study**. It is possible that 6-12 months is not a long enough time for significant seed dispersion and seedling establishment for many tree species. Thus, the lack of difference between abandoned ant nests and adjacent understory may be the result of samples that are not old enough to detect an impact of leaf-cutter nest abandonment on the seedling community. However, most tropical tree species produce seeds annually (Hartshorn, 1978; McDade *et al.*, 1994; OK?

TABLE I. Relative frequency (%) of plant species and their regeneration status (RS), seed size (SS), dispersal mode (DM), and life form (LF) in 10 abandoned *Atta cephalotes* nests (Nest) and 10 understory forest plots (Forest). P = Pioneer, gap-dependent, ST = shade-tolerant; S = small (< 2mm), M = medium (2-10 mm), L = large (> 10 mm); B = biotic, A = abiotic; H = herbs, L = lianas and vines, EP = epiphytes, S = shrubs, P = palms, T = trees, and CT = canopy trees.

	Relative abundance					
Species	Nest	Forest	RS	SS	DM	LF
Alchornea costaricensis	10		P	M	B	T
Anaxagorea crassipetala	10	10	ST	M	B	T
Anthurium spp.	10		ST	M	B	EP
Aphelandra storkii		10	ST	M	B	T
Ardisia nigropunctata	20	20	P	M	B	T
Aristolochia constricta		10	P	M	A	L
Asplundia spp.		10	ST	M	B	EP
Byrsonima crispa		10	P	M	B	CT
Calathea micans	20	10		M	B	H
Calathea spp.	10	30		M	B	H
Casearia arborea		10	P	M	A	T
Casearia corymbosa	20		P	M	B	CT
Cedrela odorata	30		P	L	A	CT
Cissus spp.		10	P	M	B	L
Costus spp.	10		P	M	B	H
Dendropanax arboreus		10	P	M	B	T
Dichorisandra hexandra		10	P	M	B	H
Dycranostiles ampla	10	20	ST	L	B	L
Euterpe precatoria		10		M	B	T
Faramea spp.		10	ST	M	B	
Ficus spp.	10			S	B	T
Geonoma spp.	70	80	ST	M	B	P
Geophila spp.	10		P	S	B	H
Guarea bullata	20	10	ST	L	B	T
Guarea spp.	30		ST	L	B	T
Hampea appendiculata	50	10	P	M	B	P
Heliconia irasa	10		ST	M	B	H
Inga spp.	20			L	B	T
Inga thibaudina	10		P	L	B	CT
Inga umbelifera	10		ST	L	B	CT
Jubelina wilburii	10		ST	L	A	L
Mabea occidentalis		10		M		S
Machaerium seenmanii		10	P	L	A	L
Mendoncia tonduzii		10	P	L	B	L
Mendoncia spp.		10		L	B	L
Miconia multispicata		10	P	S	B	T
Miconia spp.	20		P	S	B	T
Monstera spp.	10			M	B	EP
Myrcia splendens		10	P	M	B	T
Otoba novogranatensis		10	ST	L	B	CT
Paullinia spp.		10		M	B	L
Pentaclethra macroloba	20	20	ST	L	A	CT
Perebea hispidula	20		ST	M	B	T
Philodendron spp.	80	80		M	B	EP
Piper spp.	10	10		S	B	S
Piper trigonum	10	10	ST	S	B	S
Piper urostachyum	20	10	ST	S	B	S
Prestoea decurrens	20	30	ST	S	B	P
Protium pittieri	10		P	L	B	T
Protium spp.	10	10		L	B	T
Psychotria spp.	20	20		M	B	T
Rinorea deflexiflora		20	ST	M		T
Siparuna tonduziana	10		ST	M	B	S
Smilax spp.	20	20	P	M	B	L
Swartzia simplex	10		ST	L	B	T
Virola sebifera	20	20	ST	L	B	CT
Welfia regia	30	20	ST	L	B	P
Unknown spp1	50	60				
Unknown spp2	10	30				
Unknown spp3	10	10				
TOTAL NUMBER OF SPECIES	41	41				

TABLE II. Mean number ± SE of gap-dependent, small-seeded (seeds < 2 mm), and abiotically dispersed species and individuals in abandoned *Atta cephalotes* nests and adjacent forest understory (n = 10). Data were analyzed with paired t-tests. Mean number of species and individuals are given per 3 m^{-2} (see text for methodological details).

Variables	Abandoned ant nests	Forest understory	t	P
A) SPECIES				
Gap-dependent	2.0 ± 0.5	1.1 ± 0.4	**1.20**	0.26
Seeds < 2 mm	0.7 ± 0.4	0.5 ± 0.3	0.54	0.59
Abiotic dispersal	0.7 ± 0.2	0.4 ± 0.1	0.91	0.36
B) INDIVIDUALS				
Gap-dependent	4.0 ± 1.9	1.8 ± 0.6	**1.20**	0.26
Seeds < 2 mm	1.7 ± 0.9	1.2 ± 0.9	**0.60**	0.56
Abiotic dispersal	0.7 ± 0.2	0.7 ± 0.3	0	1

OK?

Loiselle, Ribbens & Vargas, 1996), and 6-12 months is considered long enough to allow the establishment of most tropical plant species from the seed bank (Dalling, Swaine & Garwood, 1994; Loiselle, Ribbens & Vargas, 1996; Farji-Brener & Medina, 2000). Therefore, I believe that the lack of a consistent effect of abandoned ant nests on plant assemblage composition is not only a matter of lack of time. Abandoned nests continue to be monitored in order to better understand this aspect. There are at least four other non-mutually exclusive factors that may explain why local effects were stronger than the nest effect on plant assemblage composition: refuse dump location and nest soil characteristics, spatial heterogeneity, dispersal limitation, and the local species pool.

Leaf-cutting ants concentrate large quantities of freshly cut vegetation from a large area into nest chambers where it is decomposed by a mutualistic fungus. The remains of the exhausted fungal material are deposited either on the soil surface outside the nest or in refuse chambers below the fungus chambers. Given that in Neotropical forests soil nutrients can limit plant growth (Vitousek, 1984; Sollins, 1998), the location of this nutrient-rich refuse should have an important effect on determining which plant species will establish in an abandoned ant nest site. The leaf-cutting ant species studied in this study (*Atta cephalotes*) deposits its organic refuse in underground chambers, which may be accessible only by roots of adult trees (Moutinho, Nepstad & Davidson, 2003), not by establishing seedlings (Farji-Brener & Medina, 2000). In addition, soil resistance to penetration could affect plant species composition. For example, **soil-nest** of *Atta cephalotes* in Amazonia is generally flat and shows a high resistance to penetration, resulting in additional limits for the establishment of some species' seedlings (Moutinho, Nepstad & Davidson, 2003). However, abandoned nests of other leaf-cutter species (*e.g.*, *Atta sexdens*) are usually a mound of soft soil. Thus, soil effects on plants probably depend on the leaf-cutting ant species studied. In summary, the lack of an effect of abandoned *A. cephalotes* nests on the establishment of nutrient-limited plant species in this study may be due to soil compactness and the absence of an external refuse pile in the ant nest sites, but the internal refuse heap may affect larger plants (Moutinho, Nepstad & Davidson, 2003).

Not nest soil?

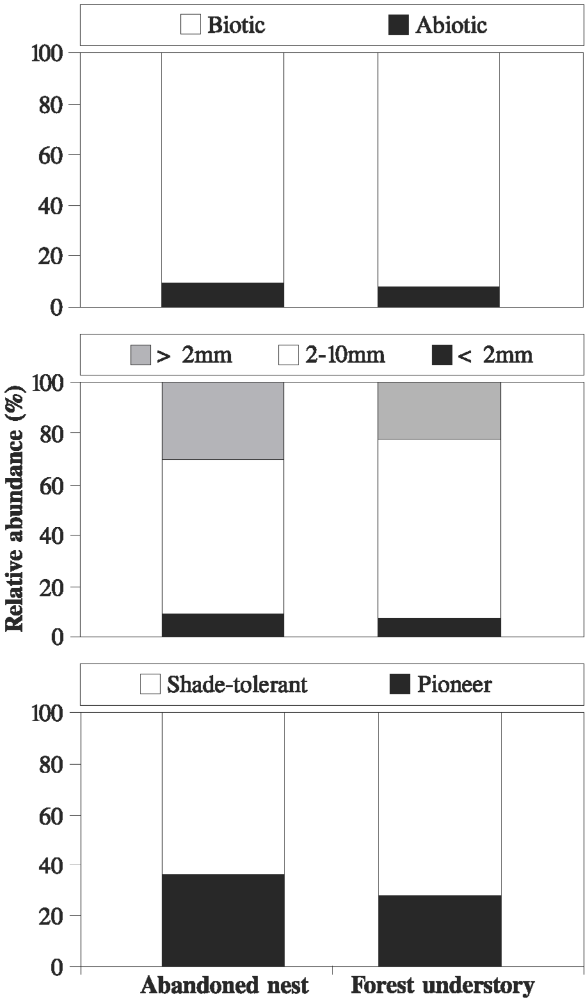

FIGURE 1. Relative abundance (in %) of species according to their dispersal mode, seed size, and regeneration status in abandoned ant nests and adjacent understory plots (χ^2 = 0.45, 0.10, 1.62, respectively, all P > 0.45).

Should Legend for seed size be < 2mm (grey), 2-10 mm (white) and > 10 mm (black) ?

It is known that the establishment of several plant species or species assemblages is affected by the characteristics of the microenvironment, such as soil type, topography, and light availability (Clark *et al.*, 1995; Clark, Clark & Read, 1998; Nicotra, Chazdon & Iriarte, 1999; Svenning, 1999). Several studies have demonstrated that many tropical plant species are distributed non-randomly with respect to microenvironmental variation, and the consensus is that these patterns reflect species-specific habitat preferences or life history variation (Gentry, 1988; Tuomisto & Ruokolainen, 1994; Clark *et al.*, 1995; Clark, Clark & Read, 1998; Terborgh & Mathews, 1999). Although this study was carried out in a relatively small area in the same type of forest, the differences between sites were stronger than the differences between abandoned nests and their adjacent forest understory. This means that, for the plant species found, the environmental modifications made by ant nests were less important than the environmental differences existing between sites.

TABLE III. Members of clusters, explanatory variables, and ANOVA results of the *k*-means clustering method, considering a) species and b) number of individual plants. The values belonging to the explanatory variables are means ± SD of species (a) or individuals (b) per $3 \cdot m^{-2}$. Statistically significant variables are in bold (see text for details).

	Cluster 1	Cluster 2	*F*	*P*
HYPOTHESIS 1. REGENERATION STATUS				
a) Variables				
Shade-tolerant	5.1 ± 1.3	2.1 ± 1.0	30.8	< 0.001
Gap-dependent	1.5 ± 1.5	1.5 ± 1.2	< 0.01	1
Cluster members				
Nest plots	5, 7, 8, 10	1-4, 6, 9		
Understory plots	5, 6, 8, 10	1-4, 7, 9		
b) Variables				
Shade-tolerant	41.0 ± 7.1	4.9 ± 3.2	183.9	< 0.001
Gap-dependent	2.5 ± 3.5	3.0 ± 4.7	0.02	0.87
Cluster members				
Nest plots	5	1-4, 6-10		
Understory plots	5	1-4, 6-10		
HYPOTHESIS 2. SEED SIZE				
a) Variables				
< 2 mm	0.9 ± 1.5	0.5 ± 0.9	0.5	0.47
2-10 mm	5.1 ± 1.6	4.2 ± 1.0	2.5	0.13
> 10 mm	3.7 ± 0.9	0.9 ± 0.9	44.5	< 0.001
Cluster members				
Nest plots	3,5,7,8,10	1,2,4,6,9		
Understory plots	8, 10	1-7, 9		
b) Variables				
< 2 mm	7.7 ± 2.1	0.3 ± 1.0	100	< 0.001
2-10 mm	36.0 ± 16	8.0 ± 3.0	56.2	< 0.001
> 10 mm	1.7 ± 0.6	2.3 ± 2.3	0.23	0.63
Cluster members				
Nest plots	5, 9	1-4, 6-8,10		
Understory plots	5	1-4, 6-10		
HYPOTHESIS 3. DISPERSION MODE				
a) Variables				
Biotic dispersion	4.4 ± 0.9	8.2 ± 1.2	65.4	< 0.001
Abiotic dispersion	0.4 ± 0.5	0.7 ± 0.7	0.6	0.45
Cluster members				
Nest plots	1-4	5-10		
Understory plots	1-4, 6-7, 9	5, 8, 10		
b) Variables				
Biotic dispersion	45.0 ± 15	9.5 ± 3.2	93.4	< 0.001
Abiotic dispersion	0.7 ± 1.1	0.7 ± 0.8	0.05	0.94
Cluster members				
Nest plots	5, 9	1-4, 6-8,10		
Understory	5	1-4, 6-10		

Dispersal limitation also potentially explains the lack of association between species composition and abandoned nest sites. Since gap-dependent, small-seeded trees are relatively scarce in old-growth forest, and abandoned ant nests provide differential conditions during a limited period of time (Perfecto & Vandermeer, 1993; Wirth *et al.*, 2003), the availability of propagules from nearby trees is likely to be central in controlling colonization. Several studies in tropical forests have shown the importance of dispersal limitation in controlling local composition of plant communities. In field work carried out in the same tropical forest studied here, Loiselle, Ribbens, and Vargas (1996) found that site was a better explanatory factor of composition than differences in seed rain between gap and understory. Another extensive study based on a 50-ha permanent plot in a tropical forest of Panama found that species composition in treefall gaps was not predictable from descriptors of treefall regime even for gap-dependent species, suggesting the potential importance of recruitment limitation, in which species fail to recruit in all sites favourable for germination, growth, and survival (Hubbell *et al.,* 1999; Brokaw & Busing, 2000; Dalling *et al.,* 2002). In support of this hypothesis, Grau (2002) found that aggregations of treefalls at scales of 1,000-2,500 m^2 in subtropical forests in northwestern Argentina increased species richness, probably by reducing the dispersal limitation of gap-dependent trees into newly formed treefall gaps. Given the dispersal limitation into abandoned ant nests and the reduced abundance of leaf-cutting ant nests in old-growth forests (Farji-Brener, 2001), the chance of nest-site recolonization by plant species that potentially could benefit from these understory disturbances may be low. This effect could explain both the low similarity of species assemblages between different abandoned *Atta cephalotes* nests and the high similarity within sites (*e.g.,* Loiselle, Ribbens & Vargas, 1996).

The composition of plant species at a particular site is often influenced by the pool of species in the surrounding area ("mass effect" or "vicinity", Shmida & Wilson, 1985; Van der Maarel, 1994; Grau, 2002; 2004). Therefore, the colonization of an abandoned nest may be strongly influenced by the composition of the surrounding forests. Recent studies in tropical (Dalling *et al.,* 2002), subtropical (Grau, 2002; 2004), and non-tropical environments (Tilman, 1997; Butaye *et al.,* 2002; Tofts & Silvertown, 2002) have shown the importance of the available species pool in regulating the capacity of gap-dependent species to colonize treefall gaps. For example, distance to secondary forests may be an important factor controlling the presence of gap-dependent trees in treefall gaps (Grau, 2004). Likewise, distance to secondary forests or disturbed areas (where the potential colonizers are more common) could control the composition of species in abandoned ant nests.

Although the results of this study suggest that abandoned *Atta cephalotes* nests are not acting as selective forces on the establishment of species assemblages, abandoned *Atta* nests may still affect vegetation patterns. As several authors have pointed out, abandoned nest areas of *Atta* spp. may represent an important regeneration site for plants, affecting seed bank abundance and composition (Farji-Brener & Medina, 2000) and plant density and richness (Garretson *et al.,* 1998; Farji-Brener & Illes, 2000). However, chance events in the dynamics of both ant and plant species populations apparently restrict the effect of abandoned nests to an ecological time. Nevertheless, abandoned ant nests may favour selective establishment of some plant groups if their refuse is located on the soil surface and if the potentially favoured plant assemblage is locally available. Therefore, the next step to elucidate the effect of abandoned nests on the composition of plant assemblages should focus on leaf-cutting ant species that have external refuse piles and are located in secondary forests or near disturbed areas in which both ant nests and the plant species that are likely to benefit most are more common (Farji-Brener, 2001).

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