

How leaf-cutting ants impact forests: drastic nest effects on light environment and plant assemblages

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Abstract Leaf-cutting ants (*Atta* spp.) have become a topical issue in Neotropical ecology, particularly because they are reaching hyper-abundance due to escalating levels of fragmentation in recent years. Yet, despite intensive research on their role as dominant herbivores, there is still insufficient documentation on the impacts of their large, long-lived nests on plant assemblage structure and ecosystem functioning. Our study aimed at investigating the magnitude, nature, and spatial extent of nest influence by assessing 11 attributes of ant nest, canopy structure, light environment and sapling assemblage for 20 colonies in four plots along nest-understorey gradients in a large remnant of Atlantic forest. We also monitored the performance of seeds and seedlings of *Chrysophyllum viride*, an abundant

shade-tolerant species. Previously unrecognized canopy gaps above ant nests (0.04–87.9 m²) occurred in 95% of all colonies surveyed. Overall, canopy openness and light availability at least doubled in ant nest plots compared with distant understorey plots. These drastic changes in the light environment paralleled those in plant assemblage: sapling density almost tripled (mean ± SE: 0.42 ± 0.1 saplings m⁻²) and sapling species richness doubled (0.16 ± 0.02 species m⁻²) in distant plots, as did shade-tolerant species. After a 1-year period, only 33 ± 15.6% of the seeds germinated and all seedlings died on nests, whereas seed germination reached 68 ± 5.1% in distant plots and 66.4 ± 7.6% of their seedlings survived after 12 months. Therefore, plot location was the most significant explanatory variable for predictable and conspicuous changes in the light environment and structure of sapling assemblages. Our findings greatly extend knowledge on the role played by leaf-cutting ants as ecosystem engineers by demonstrating that ant nest-mediated disturbance promotes environmental modifications in tens of meters around nests and is thus, strong enough to drive plant recruitment and consequently alter both the floristic and functional signature of plant assemblages.

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Introduction

Leaf-cutting ants (*Atta* spp. and *Acromyrmex* spp., Formicidae, Hymenoptera) are prevalent herbivores and dominant invertebrates of tropical and subtropical America (Weber 1972). Because of their multifarious effects on the vegetation, they have been denoted as key species (Fowler et al.

1989) and ecosystem engineers (Wirth et al. 2003), particularly in Neotropical forests. They are among the most polyphagous and voracious herbivorous insects, cutting up to 15% of the standing leaf crop (Wirth et al. 2003; Urbas et al. 2007) and up to 50% of the species of a given forest flora (Vasconcelos and Fowler 1990; Wirth et al. 2003) in their colony's territory each year. Their herbivorous impact has therefore received considerable research attention (Cherrett 1989; Rao et al. 2001; Wirth et al. 2003). Moreover, leaf-cutting ants opportunistically forage on fruit parts as substrate for the fungus they cultivate and have been shown to contribute to seed dispersal of certain forest plants (Dalling and Wirth 1997; Leal and Oliveira 1998; Silva et al. 2007).

The overall effects of leaf-cutting ant activity (especially *Atta* spp.) in tropical forests may go far beyond occasional seed dispersal and simple foliage removal. They are also largely associated with the construction and maintenance of their nests, which can reach 250 m² or more in surface area (Cherrett 1989). These prodigious structures: (1) enhance soil nutrient availability through the accumulation of nutrient-rich leaf material used to feed fungus gardens in underground chambers (Farji-Brener and Silva 1995; Sternberg et al. 2007); (2) substantially improve soil penetrability relative to non-nest soils (Moutinho et al. 2003); (3) promote active removal of leaf litter, resulting in bare ground on and in the vicinity of nests (Weber 1972); and (4) create “nest clearings” or vegetation gaps above and immediately around *Atta* nest sites, where understory vegetation growing on or overhanging the immediate nest surface is constantly cleared leading to an increased light availability (Farji-Brener and Illes 2000). Only quite recently, however, have investigations addressed nest-mediated alterations of edaphic and microclimatic forest conditions (Hull-Sanders and Howard 2003; Moutinho et al. 2003), with few and sometimes inconsistent findings regarding their implications for forest structure, composition and dynamics (e.g., Garrettson et al. 1998; Farji-Brener 2005).

Although smaller in scale (20–70 m²), nest clearings by *Atta* have been considered as analogous to tree fall gaps, as both are disturbance-generated openings in the understory and/or subcanopy vegetation layer beneath a canopy, where additional above- and below-ground resources become available due to the absence of a tree or part of a tree (e.g., Brokaw 1982; Connell et al. 1997 for treefall gaps, and Garrettson et al. 1998; Hull-Sanders and Howard 2003; Wirth et al. 2003; and Farji-Brener 2005 for *Atta* nests). Therefore, nests of *Atta* species have been hypothesized to present a set of conditions, which affect plant species composition and dynamics in tropical forest. Specifically, increased nutrient and light availability, which when combined with the absence of leaf litter, promote the regeneration of light-demanding, nutrient-limited, and small-seeded

litter-gap demanders, and thus, affect plant recruitment and plant assemblage structure above nests (Farji-Brener and Ghermandi 2000; Farji-Brener and Illes 2000; Farji-Brener 2005).

However, the bulk of research addressing nest effects on plant assemblages has targeted abandoned ant nests (with the exception of Garrettson et al. 1998 and Hull-Sanders and Howard 2003), motivated by the idea that open nest areas, while inhabited by ants, are probably not of significance for plants due to the ants' zealous clearing behavior (Wirth et al. 2003). Conversely, we expect that the effects of increased resource availability in forest areas inhabited by living *Atta* colonies are vastly under-appreciated because long-lasting, persistent clearing activities, accompanied by increased light availability, likely affect plant abundance and species richness, especially of light-sensitive shade-tolerant species on and around the nest mound. Considering the longevity of *Atta* colonies (life spans of up to 15 years; Weber 1972), these effects might be less transient than those of abandoned nests, especially with regard to light penetration. Fraver et al. (1998), for example, demonstrated that light levels in treefall gaps fell, and returned to pre-gap levels within 2 years.

The high density of leaf-cutting ants in forest patches and edges (Rao et al. 2001 and Wirth et al. 2007, respectively) is a reason to address the impact of active ant nests on plant assemblages and forest regeneration. We investigate the effects of active leaf-cutting ant (*Atta cephalotes*) colonies on forest structure, light availability, plant assemblages and seed/seedling performance along the edges of a large remnant of Atlantic forest in Northeast Brazil. We hypothesize that along a nest-forest understory gradient: (1) canopy openness and light decrease, (2) sapling stands of trees and shrubs become more dense and rich, (3) shade-tolerant species become more abundant, and (4) seed germination and seedling survivorship increase as ant activities decrease.

Materials and methods

Study site

This study was carried out at the Usina Serra Grande, a large, privately owned sugar-cane company located in the State of Alagoas, in northeastern Brazil (8°30'S, 35°50'W). This site still retains approximately 9,000 ha of forest cover assigned to a unique biogeographic zone of the Atlantic forest biota—the Pernambuco Center of Endemism; an 80-km-wide strip of tropical forest that once covered 56,400 km² along the Brazilian Atlantic coast (Santos et al. 2007). Sugar-cane cultivation in this landscape, which dates back to the nineteenth century or

earlier, provided the strongest incentive for clearing large tracts of pristine old-growth forests (Pôrto et al. 2006). Currently this hyper-fragmented landscape retains 9.2% of forest cover, including the Coimbra forest—the largest (3,500 ha) and best preserved patch of Atlantic forest in northeastern Brazil (Grillo et al. 2006). Coimbra still supports ecological groups that are believed to inhabit more continuous and undisturbed tracts of Atlantic forest, such as large-seeded trees and frugivorous vertebrates (Pôrto et al. 2006). The Coimbra forest is situated on a low-altitude plateau (300–400 m above sea level) covered by two similar classes of dystrophic and clay-laden soils: yellow-red latosol and yellow-red podzol according to the Brazilian system of soil classification (IBGE 1985). Annual rainfall is ~2,000 mm, with a 3-month dry season (<60 mm month⁻¹) from November to January, and the natural vegetation is a lower montane rain forest (Veloso et al. 1991). Regionally, Leguminosae, Lauraceae, Sapotaceae, Chrysobalanaceae, Euphorbiaceae and Lecythidaceae hit the highest scores of tree species richness [≥ 10 cm diameter at breast height (DBH); Grillo et al. 2006]. The Coimbra forest is embedded into a stable, relatively old (at least 60 years) and homogeneous matrix of sugar-cane fields. Its pioneer-dominated edge zone with a 20- to 25-m-tall upper canopy layer (Oliveira et al. 2004) has been shown to support impoverished plant assemblages, particularly in terms of shade-tolerant and large-seeded trees (Melo et al. 2006).

Atta cephalotes

Atta cephalotes is a leaf-cutting ant of Neotropical forests, with a continuous distribution from Mexico to Bolivia (Kempf 1972). The recently published record of the species in Coimbra marked its most southern occurrence in the Atlantic forest of northeast Brazil (Corrêa et al. 2005). Together with the co-occurring *Atta sexdens*, it was found to achieve increased densities of colonies along the edges as compared to the interior patches of the Coimbra forest (mean \pm SE: 1.70 ± 2.83 ha⁻¹ vs. 0.30 ± 1.41 ha⁻¹, respectively; Wirth et al. 2007). In this forest *A. cephalotes* builds compact nests, with nest clearings that frequently extend to the upper canopy layers, hereafter referred to as “canopy gaps above nests” (Corrêa 2006; Meyer 2008). These gaps are characterized by a pronounced proportion of dead stems (up to 5 cm diameter) compared to undisturbed forest, resulting from different activities of the ants including: (1) repeated defoliation of seedlings and saplings, (2) substantial damage by cutting of their stems, or (3) burial by excavated soil (Meyer 2008). Canopy openings occasionally result from the death of adult trees on nests, either through repeated defoliation or perhaps by root disturbance (Meyer 2008).

Canopy gaps above nests and light availability

In order to investigate the frequency, size and light environment in the canopy gaps above nests, we randomly selected 40 adult, active colonies of *A. cephalotes* with nest size varying from 9.4 to 184.8 m² (58.5 ± 7.04 m²). Colonies were located in both close edge (0–100 m) and distant edge habitats (100–250 m) across the ca. 40-km perimeter of Coimbra forest; habitats in which over 95% of all colonies have been concentrated (Wirth et al. 2007). As an indicator for the size of nest-associated canopy gaps, we measured the area of sun patches on the forest floor, when the sun was directly overhead (ca. 1145–1215 hours). These sunlit areas were distinctively detectable and assumed to adequately reflect the vertical projection of gap edges. We determined the nest size and the size of the sun patches >20 cm by measuring two perpendicular maximal and minimal diameters across the respective structure and calculating the area as an ellipsoid.

Moreover, for a random subset of 20 colonies (ten at the closest and ten at the distant edge), we assessed parameters of canopy structure and light environment at four locations above ant nests and adjacent areas. Each nest was assigned to a sampling unit consisting of a transect from the nest center towards the adjacent understorey, along which four square plots were set: one in the center of the nest clearing (hereafter referred to as the “nest plot”); one at the border of the ant nest (border plot); one 5 m distant from the border plot (close understorey plot), and one 20 m away from the close understorey plot (distant understorey plot). Within each sampling unit, plot sizes were equal to the size of the nest, which varied from 15.7 to 259.6 m² (mean \pm SE: 77.1 ± 13.3 m², 16 colonies were <100 m²). We are conscious that sampling plots of varying sizes have the potential to introduce some bias but this was required to address the same “habitats” across the colonies (i.e., ant nest, border, close and distant understorey plots) as ant nests greatly differed in size. Transects were set parallel to the nearest forest border in order to control for any influence of forest edge; thereby they exclusively covered an ant nest-forest understorey gradient.

Canopy structure and light availability in nest and understorey plots were characterized via hemispherical photographs at 1 m above ground level using a Nikon Coolpix 990 camera with a FC-E8 fisheye converter. Photos were taken at dawn before sunrise, at dusk after sunset, or during overcast sky conditions to avoid direct solar radiation in any part of the canopy. Five horizontally leveled photographs were taken in each plot, totaling 20 photographs per sampling unit. To identify the north/south orientation on each photo, we marked them at the time of exposure with a pointer protruding 5 mm above the front edge of the camera lens. Hemispherical photographs were

analyzed using the image analysis software Gap Light Analyzer (version 2.0; Frazer et al. 1999). Each photograph was analyzed twice to reduce the error in threshold selection for the distinction between visible sky and foliage. Descriptors of canopy structure and light regime derived from image analysis, including canopy openness (the percentage of open sky seen from beneath a forest canopy) and total light transmission (the fraction of radiation reaching the ground relative to that in the top-most canopy layer) are according to Frazer et al. (1999). Because spatial heterogeneity in light transmission in and around canopy gaps is largely due to variation in the amount of direct-beam radiation (Wirth et al. 2003), we separately estimated direct light transmission (the amount of direct solar radiation transmitted by the canopy) and diffuse light transmission (the amount of diffuse solar radiation transmitted by the canopy).

Plant assemblages on and around *Atta* nests

We used the same 20 colonies and their sampling units to describe some attributes of sapling assemblages colonizing ant nests and adjacent areas in the forest understorey. All saplings sizing 1.5–5.0 cm DBH (tree and shrub species) were recorded within the four plot locations. As *A. cephalotes* colonies at Coimbra forest have a life expectancy of ca. 8 years (Meyer et al. 2009), we believe that by using this particular range of DBH we avoided as much as possible including saplings that recruited before colony foundation. Saplings were identified at species level with the help of a local parataxonomist and via comparisons with specimens deposited: (1) at the Universidade Federal de Pernambuco Herbarium (voucher nos. 34,445–51,604 for the study site), and (2) at the Plant Ecology Laboratory (Serra Grande seedling and sapling collections) of the Universidade Federal de Pernambuco, Brazil. The checklist of Serra Grande flora is available in www.cepan.org.br and in Pôrto et al. (2006). Plant species were assigned to mutually exclusive categories of regeneration, which represent distinct functional groups: pioneer or shade-tolerant species, according to definitions provided by Hartshorn (1978) and information on life history traits provided by Oliveira et al. (2004) and Grillo et al. (2006).

The influence of ant nests on the recruitment of shade-tolerant plant species was also addressed around ant nests by monitoring seed germination and seedling mortality of a typical and locally abundant, large-seeded, shade-tolerant tree species, *Chrysophyllum viride* Mart. and Eichler (Sapotaceae). In the Coimbra forest, both seed delivery and recruitment of *Chrysophyllum* have been documented in forest edge and interior sites (Melo et al. 2006; Melo et al. 2007). In the rainy season of 2003, we collected 400 fresh seeds from different trees from the local population of

Chrysophyllum and buried ten single seeds (1 cm deep and at least 1 m apart) in the central portion of each plot, and across the sampling units of only ten randomly chosen colonies because of the limited number of available seeds. During a 1-year period (April 2004–March 2005), both seeds and seedlings were monitored weekly for germination and mortality. The mortality due to herbivory by leaf-cutting ants was quantified.

Based on these procedures, we described attributes of ant nests, forest structure, and the sapling assemblages across the sampling units (with their four plot locations) as follows:

1. Ant nest attributes: nest location in terms of distance from the forest edge, size of the nest, and sizes of the associated canopy gaps.
2. Forest structure and light environment attributes: canopy openness and light availability (direct, diffuse and total light transmission).
3. Sapling assemblage attributes: number of saplings and plant species (per m²), number of shade-tolerant saplings and species (per m²), and percentage of shade-tolerant saplings and species.

Ant nest attributes and plot location (i.e., nest, border, close and distant understorey plot) were considered as explanatory variables for the variation in forest structure, light environment, and sapling assemblage attributes (response variables). We also described *Chrysophyllum* seed and seedling performance across sampling units. The whole study was carried out between March 2003 and February 2006.

Data analysis

General linear mixed models (GLMMs) were used to detect any effect of ant nest attributes and plot location on the forest structure, light environment, and attributes of sapling assemblages across the sampling units and plot locations. We adopted a mixed approach (including interactions) to account for the potential lack of spatial independence of plot locations within sampling units and to assess natural variability among ant colonies (our replicates), including differences in plot sizes between colonies. GLMMs, via the residual maximum likelihood method, were fitted to nest location, nest size, gap size, and plot location as fixed effects, whereas forest structure, light environment, and sapling assemblage attributes were assumed to be nested within colonies, over which the random effects varied. Random effects were considered significant when “colony” explained >30% of the variance captured by GLMMs (i.e., variance ratio >0.7; see Grafen and Hails 2006). Both response and explanatory variables were checked for normality (Lilliefors tests; Sokal and

Rohlf 1995), and some of them were transformed to stabilize variance, improve data normality and consequently increase the explanatory power of models. GLMMs were followed by *t*-test post hoc comparisons as this test is less sensitive to increased variance within treatments (Sokal and Rohlf 1995). The JMP 7.0 (SAS Institute, N.C.) was used to fit the GLMMs.

Total sapling species richness (a community-level analysis) was estimated for all plot locations as well. We constructed mean species-area accumulation curves from which we obtained three estimates of richness: the number of species observed, and the non-parametric estimators Chao-1 and Chao-2 (see Colwell and Coddington 1994), all of them provided by the Estimates 7.5.0 program (Colwell 2005). Chao-1 and Chao-2 are based on the incidence of species and have been noted in the literature as reasonable indicators of true seedling richness in tropical forests (Benítez-Malvido and Martínez-Ramos 2003), in particular for datasets which do not reach a steady asymptote (Gotelli and Colwell 2001). Species accumulation curves were obtained after 1,000 randomizations within each group of 20 plots—the total sampling effort per location. Estimators were performed using patchiness 0 in order to eliminate any bias in the estimation of species richness due to species patchiness (Benítez-Malvido and Martínez-Ramos 2003). In order to control for differences in the total number of saplings sampled, we also obtained the expected number of sapling species across the four plot locations based on random sub-samples of 150 individuals via rarefaction curves. Rarefaction procedures were computed by the Ecological Methodology 5.1 software, Species Diversity program group (Krebs 1999).

We also performed an indicator species analysis (sensu Dufrière and Legendre 1997) based on two groups of sapling plots: one combining nest, border and close understorey plots ($n = 60$) and another one formed by the distant understorey plots ($n = 20$) in order to compare those habitats more influenced by ant activities to those with apparently less or no effects. This analysis offers an indicator value (IV) that may reach a maximum score of 100 and quantifies the extension to which the species is associated with a particular group. The mean IV scores obtained from 1,000 calculations on randomized data provide a benchmark to compare with IV scores for the real (observed) data obtained for each species (Dufrière and Legendre 1997). Finally, differences of seed germination and seedling mortality across plot locations within sampling units were analyzed via GLMMs; plot location as fixed effect and colony as random. A χ^2 -test was used to detect differences in the frequency of *Chrysophyllum* seedlings that were cut by ants across plot locations. These analyses were carried out using PC-Ord (McCune and Mefford 1999), JMP 7.0, and Systat (Wilkinson 1996), respectively.

Results

Canopy gaps above ant nests (as inferred from sun patches on the nest surface) were highly frequent in the study site as they were recorded in 38 (95%) out of the 40 ant colonies surveyed; these gaps ranged between 0.04 and 87.9 m² in size (mean \pm SE: 12.9 \pm 3.3 m²). Plot location was the most significant explanatory variable for changes in the light environment of ant nests and adjacent areas (Table 1). Overall, canopy openness (%) and the three measures of light availability at least doubled in ant nest plots as compared with distant understorey plots (Fig. 1). Remarkably, significant changes in canopy structure and light environment were detectable even at the border of nests. Total light transmission, for instance, dropped from 11.9% \pm 1.1 in ant nest plots to 4.9% \pm 0.3 in distant understorey plots; a 59% decrease. Light availability on ant nests and its gradual decline towards the forest understorey showed a cross-colony congruence as “colony” proved to be a non-significant explanatory variable (variance ratio <0.04).

A total of 1,351 saplings from 107 woody plant species were recorded in the plots across transects; most of them pioneer shrub and tree species (e.g., Euphorbiaceae, Melastomataceae, Rubiaceae and Malpighiaceae). GLMMs consistently pinpointed plot location as the key explanatory variable for the attributes of sapling assemblages inhabiting ant nests and adjacent areas (see Table 1). Nest location and nest size played a minor role, the former explaining sapling richness and shade-tolerant density, and the latter sapling density (see *F*-ratios in Table 1). Similar to the light environment, the majority of sapling assemblage attributes gradually changed along the ant nest-forest understorey gradient. Sapling density almost tripled from nest towards distant plots, where it reached 0.42 \pm 0.1 saplings m⁻² (Fig. 2a), while species richness of saplings doubled in distant plots as compared to ant nest plots (Fig. 2b). Shade-tolerant species were also more abundant as distance from ant nests increased; both abundance of saplings and species richness doubled in distant understorey plots (Fig. 3a, b). This significant and predictable pattern of sapling assemblage organization along the nest-forest gradient emerged regardless of the apparently limited influence of gap size and ant nest attributes (e.g., nest size and position); as well as of the fact that plant assemblage attributes largely varied across the 20 colonies as this variable (assigned as a random effect) explained over 50% of the variation in plant attributes (variation ratio >1.2). The proportion of both shade-tolerant saplings and species was similar across plot locations and ant nest attributes (see GLMMs in Table 1).

Total species richness in ant-plots ranged from 36.7–53.2 observed species (S_{obs}) to 54.6–114.4 species (estimated by Chao-2), whereas it varied from 66.4–87.5 species (S_{obs}) up to 96.6–172.1 species (Chao-2) in distant understorey

Table 1 Results from general linear mixed models examining light environment and sapling assemblage attributes of 20 *Atta cephalotes* nests and adjacent areas in the Coimbra forest, northeastern Brazil

Response variables ^a	Explanatory variables ^b	<i>df</i>	Sum of squares	<i>F</i> -ratio	<i>P</i>
Canopy openness (%)	Nest location	1	0.955	0.248	0.6195
	Nest size (sqrt)	1	1.062	0.275	0.6006
	Gap size (sqrt)	1	0.654	0.170	0.6811
	Plot location	3	151.41	13.137	<0.0001
Direct light (%)	Nest location	1	0.026	0.017	0.967
	Nest size (sqrt)	1	0.0005	0.000	0.995
	Gap size (sqrt)	1	5.668	0.3648	0.547
	Plot location	3	782.57	16.786	<0.0001
Diffuse light (%)	Nest location	1	1.493	0.241	0.624
	Nest size (sqrt)	1	2.43	0.392	0.532
	Gap size (sqrt)	1	4.986	0.805	0.372
	Plot location	3	357.43	19.242	<0.0001
Total light (%)	Nest location	1	0.432	0.046	0.830
	Nest size (sqrt)	1	0.58	0.063	0.802
	Gap size (sqrt)	1	5.45	0.585	0.446
	Plot location	3	554.148	19.80	<0.0001
Sapling density (m ⁻²)	Nest location	1	0.052	2.49	0.1204
	Nest size (sqrt)	1	0.264	12.57	0.0008
	Gap size (sqrt)	1	0.0003	0.017	0.894
	Plot location	3	0.8558	13.54	<0.0001
No. of species (m ⁻²)	Nest location	1	0.013	4.94	0.034
	Nest size (sqrt)	1	0.0001	0.0006	0.98
	Gap size (sqrt)	1	0.0002	0.0915	0.7634
	Plot location	3	0.0830	9.7912	<0.0001
Shade-tolerant sapling density (m ⁻²)	Nest location	1	0.0828	3.88	0.053
	Nest size (sqrt)	1	0.014	0.664	0.418
	Gap size (sqrt)	1	0.00004	0.0022	0.96
	Plot location	3	0.39	6.09	0.0012
No. of shade-tolerant species (m ⁻²)	Nest location	1	0.0002	0.1984	0.6578
	Nest size (sqrt)	1	0.0004	0.388	0.5359
	Gap size (sqrt)	1	0.0012	1.21	0.275
	Plot location	3	0.0311	9.72	<0.0001
Shade-tolerant saplings (%)	Nest location	1	27.03	0.193	0.66
	Nest size (sqrt)	1	4.2	0.03	0.86
	Gap size (sqrt)	1	0.53	0.003	0.95
	Plot location	3	294.5	0.702	0.55
Shade-tolerant species (%)	Nest location	1	4.8	0.035	0.85
	Nest size (sqrt)	1	0.77	0.005	0.94
	Gap size (sqrt)	1	0.035	0.003	0.98
	Plot location	3	75.4	0.183	0.9

Significant effects are shown in *bold*

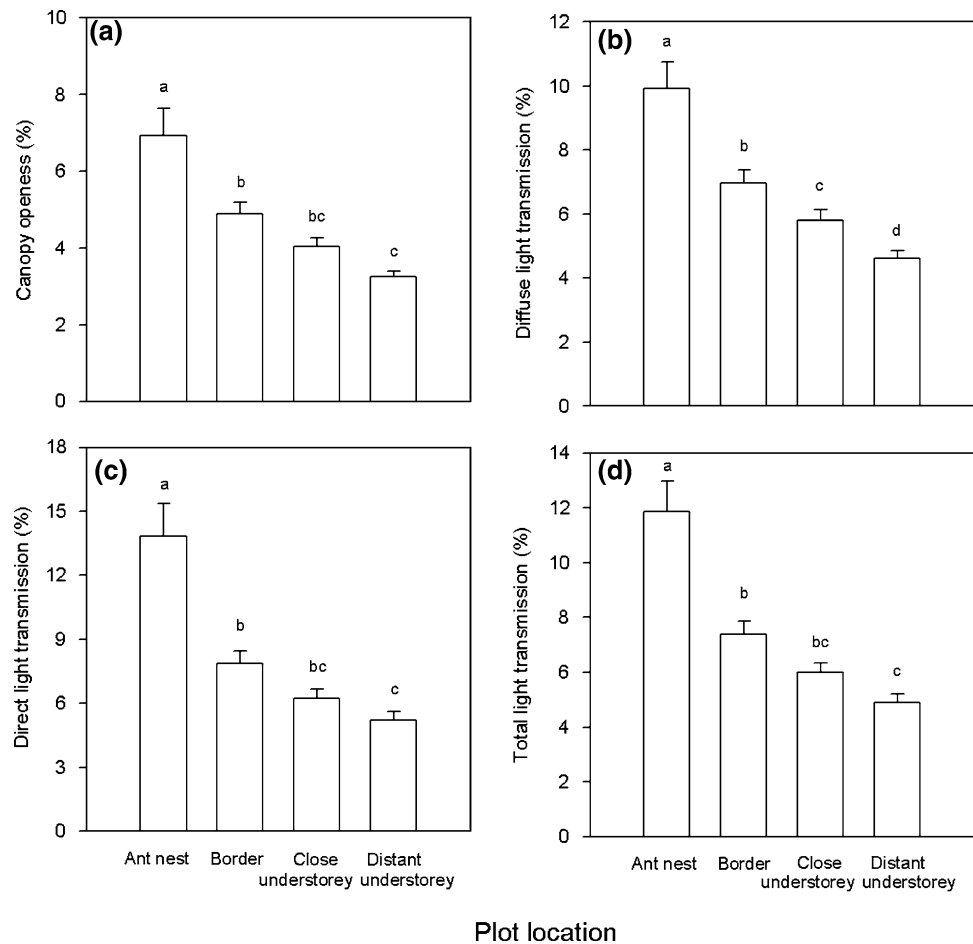
^a Response variables were arcsine transformed

^b Some explanatory variables were square root-transformed (*sqrt*) as indicated

plots (Table 2). Chao-1 offered intermediate scores, but reinforced the pattern of increasing species richness with distance from ant nests. Roughly, scores for total species richness in nest plots were 40% lower than those from distant understorey plots, but even border plots faced a 20% decrease in species richness as compared to distant plots. Likewise, the standardized richness by rarefying 150 saplings

confirmed slight but rather significant differences in the expected number of species across the four plot locations as described by 95% confidence limits: 43.1–43.4 plant species (ant nest plots) and up to 44.3–46.03 species in distant understorey plots. Finally, an indicator species analysis yielded a set of six short- and long-lived pioneer species (Table 3), which were significantly associated with distant understorey

Fig. 1 Mean (\pm SE) canopy openness (a), diffuse (b), direct (c), and total (d) light transmission estimated from hemispherical canopy photographs taken at 1 m above ground level across four plot locations within 20 *Atta* nest-understorey transects in the Coimbra forest, northeastern Brazil. Post hoc comparisons between plot locations (*t*-tests) are indicated by letters above the SE bars; general linear mixed models (GLMM) statistics are given in Table 1



plots (i.e., nest-undisturbed habitats), but no indicators were detected for the second sample group formed by ant nest, border and close understorey plots. In synthesis, ant nests and close adjacent areas were marked by increased light availability, low-density and impoverished sapling assemblages.

Chrysophyllum seeds germinated rapidly and synchronously across plot locations, with germination occurring exclusively in the first 2 months following seed burying. After a 1-year period, a conspicuous pattern emerged: germination and seedling survivorship increased from ant nest towards forest understorey plots. On ant nests, $33 \pm 15.6\%$ of the seeds germinated and all seedlings died in the first 6 months, but even border plots had decreased germination as compared to plots in the forest understorey (Fig. 4a, b); seed germination reached $68 \pm 5.1\%$ in distant plots and $66.4 \pm 7.6\%$ of their seedlings were still alive after 12 months ($df = 3$, $sq. = 2,756.95$, F -ratio = 5.56, $P = 0.003$ for germination, and $df = 3$, $sq. = 17,908.81$, F -ratio = 15.02, $P < 0.0001$, for survival). These patterns were largely congruent across colonies as this variable proved to be non-significant (variance ratio $< 1\%$). Herbivory by *Atta* ants accounted for all seedling deaths on ant nest plots, but their role as a source of seedling mortality drastically decreased across nest-understorey locations: 47.4% in

border, 22.7% in close and 36.4% in distant understorey plots ($\chi^2 = 40.04$, $P < 0.0001$).

Discussion

The nests of leaf-cutting ants (*Atta* spp.) are a conspicuous phenomenon of Neotropical rainforests, especially in fragmented or edge forests, where up to six of them may be found per hectare (Rao et al. 2001; Wirth et al. 2007). However, there is insufficient documentation on the impacts of leaf-cutting ants on plant assemblage structure and ecosystem functioning (Wirth et al. 2003). Here we adopted a replicable sample design which enabled us to assemble evidence that *A. cephalotes* ants are able to create substantial forest gaps, not only in the understorey, as recorded previously (e.g., Farji-Brener and Illes 2000; Hull-Sanders and Howard 2003), but also in the upper canopy layers above their nests. In the Coimbra forest, ant nests and their close periphery are light and homogeneous environments, which support low-density stands and impoverished sapling assemblages at local (i.e., colony) and patch level (a pool of colonies). Moreover, forest structure, light availability and plant assemblage attributes

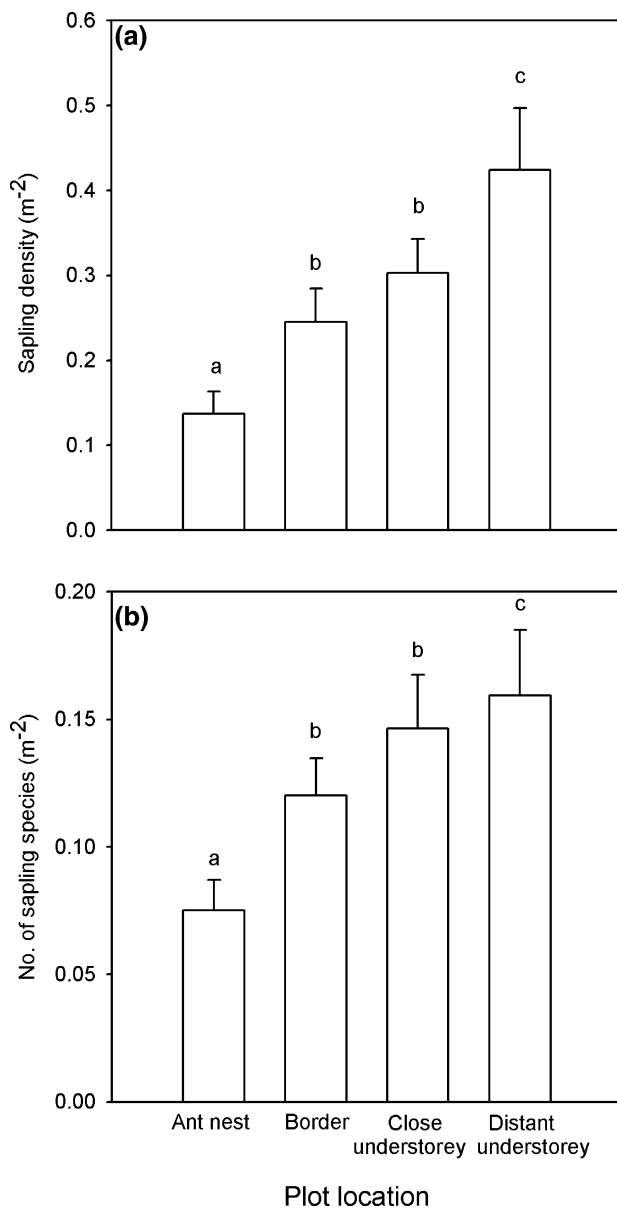


Fig. 2 Mean (\pm SE) sapling density (a) and species richness (b) across four plot locations within 20 *Atta* nest-understorey transects in the Coimbra forest, northeastern Brazil. Post hoc comparisons between plot locations (*t*-tests) are indicated by letters above the SE bars; GLMM statistics are given in Table 1

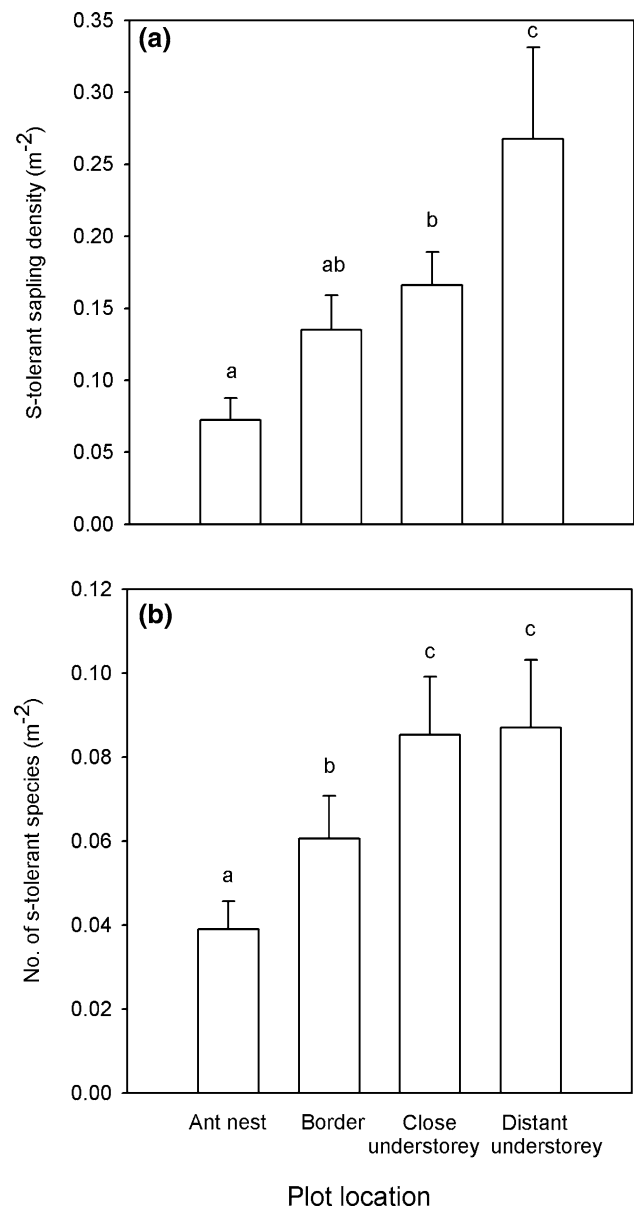


Fig. 3 Mean (\pm SE) density of shade-tolerant saplings (a) and species (b) across four plot locations within 20 *Atta* nest-understorey transects in the Coimbra forest, northeastern Brazil. Post hoc comparisons between plot locations (*t*-tests) are indicated by letters above the SE bars; GLMM statistics are given in Table 1

change gradually along the ant nest-forest understorey gradient; this implies that ant activities are strong enough to drive plant recruitment and consequently alter plant assemblages. In contrast to previous findings from a study focused on the area of an ant nest (Garrettson et al. 1998; Hull-Sanders and Howard 2003), our article is the first to document the pervasive effects that ant nests and their associated canopy gaps may impose in terms of the understorey environment and the functional structure of plant assemblages.

While understorey gap formation by leaf-cutting ants in tropical forests has received considerable attention (Farji-Brener and Illes 2000; Hull-Sanders and Howard 2003), gaps in the upper canopy layer above nests have been ignored. In this paper we documented small- to medium-sized canopy gaps, occurring in 95% of all *A. cephalotes* colonies surveyed, which were caused by intense and patchy removal of foliage used as substrate for the fungus garden, or to maintain the nest area free of plants and debris (Meyer 2008), just as described for nest-understorey gaps

Table 2 Variation in the total number of sapling species (expressed as 0.95 confidence intervals) according to four estimators across four plot locations within 20 *A. cephalotes* nest-understorey transects in the Coimbra forest, northeastern Brazil

Plot location	Sobs ^a	Chao-1 ^a	Chao-2 ^a	Rarefaction to 150 saplings
Ant nest	36.7–53.2	47.3–72.5	54.6–114.4	43.1–43.4
Border plots	53.5–72.4	71.1–128.2	76.9–144.3	48.6–49.7
Understorey plots	64.1–81.8	82.5–138.2	83.9–135.7	47.9–49.5
Distant understorey plots	66.4–87.5	97.01–99.9	96.6–172.1	44.3–46.03

^a Number of species observed (*Sobs*), Chao-1 and Chao-2 were obtained via species-area accumulation curves for a sample of 20 plots per location

Table 3 Indicator tree species (sensu Duf rene and Legendre 1997) found in distant understorey plots around 20 *A. cephalotes* nests in the Coimbra forest, northeastern Brazil

Indicator species	Family	Indicator value (IV) ^a	IV randomized groups (\pm SD)	<i>P</i>
<i>Thyrsodium spruceanum</i>	Anacardiaceae	44.3	33.2 \pm 5.1	0.038
<i>Cupania recemosa</i>	Sapindaceae	27.9	15.9 \pm 4.4	0.022
<i>Myrcia sylvatica</i>	Myrtaceae	23.4	7.4 \pm 3.07	0.005
<i>Erythroxylum squamatum</i>	Erythroxilaceae	21.5	12.6 \pm 4.2	0.03
<i>Hyeronima alchornioides</i>	Euphorbiaceae	15.7	9.1 \pm 3.5	0.06
<i>Byrsonima stipulacea</i>	Malpighiaceae	8.6	5.5 \pm 2.5	0.05

Significant *P*-values are shown in bold

^a Note that the IV scores obtained by this pool of species largely differed from those obtained by random species distributions between plot groups

(Cherrett 1989; Farji-Brener and Illes 2000). This foliage removal results in an elevated proportion of dead stems up to 5 cm diameter compared to undisturbed forest caused by: (1) repeated defoliation of seedlings and saplings, (2) substantial damage by cutting of their stems, or (3) burial by excavated soil (Meyer 2008). Moreover, several years of observations on *A. cephalotes* colonies at Coimbra forest (see Corr ea et al. 2005; Urbas et al. 2007; Wirth et al. 2007; Almeida et al. 2008; Silva et al. 2009) suggest that canopy openings occasionally result from the death of adult trees on nests, either through repeated defoliation or perhaps by root disturbance. Using sun patches at midday as an approximation, most nest-associated canopy gaps were found to be smaller (0.04–87.9 m²) than regular treefall gaps (typically ranging between 20 and 750 m²; cf. Brokaw 1982; Denslow and Hartshorn 1994), but about one-fifth had extensions similar to small treefall gaps (>25 m²; e.g., Pearson et al. 2002), which frequently account for the bulk of the total gap area in tropical forest, and have conspicuous impacts on plant recruitment and forest regeneration (Hubbell et al. 1999).

A. cephalotes nests of the Coimbra forest were associated with a pervasive pattern of increased light levels—by as much as 140%—on ant nests, but even areas adjacent to nests experienced a 50% increase. These values are considerably greater than those hitherto obtained by Hull-Sanders and Howard (2003), who reported a 49% increase at the

center of *Atta colombica* nests, probably because of the smaller nest size in comparison to *Atta cephalotes* (Herz 2001). The increased light levels above and in close vicinity to the ant nests reported here were even higher than those published for treefall gaps. For instance, while we found total light transmission above *Atta* nests to reach nearly 12% of full sunlight, Denslow et al. (1998) and Chazdon and Fetcher (1984) measured 11–13% in the center of 65–76-m² treefall gaps, and 9% in a 200-m² gap in a Costa Rican lowland tropical forest, respectively. We believe that this is due to a structural peculiarity of many *Atta* nests, whose ground is completely devoid of understorey vegetation (Farji-Brener and Illes 2000; Hull-Sanders and Howard 2003) and, thus, receive greater amounts of light than treefall gaps with a dense, rapidly encroaching second growth.

Regardless of their origins and final sizes, we demonstrated that canopy gaps above leaf-cutting ant nests, and the consequent increase in light availability, are positively correlated with conspicuous and predictable shifts in the attributes of plant assemblages on and around nests, particularly density and species richness. Briefly, sapling density almost tripled along the nest-forest understorey gradient, and sapling species richness doubled in distant plots as compared to ant nest plots. Even border plots faced a 30% decrease in species richness as compared with distant plots, and the abundance of shade-tolerant saplings steadily

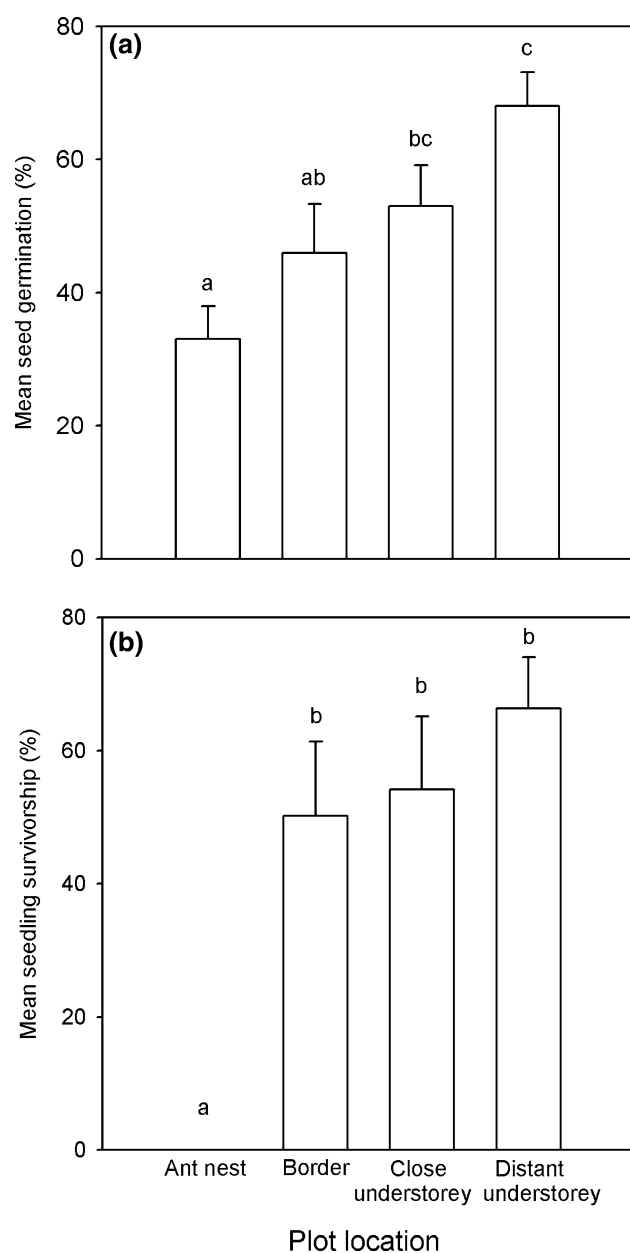


Fig. 4 Mean (\pm SE) seed germination (a) and survivorship (b) of *Chrysophyllum viride* seedlings across four plot locations within 20 *Atta* nest-understorey transects in the Coimbra forest, northeastern Brazil ($n = 100$ seeds per plot location, total 400 seeds). Post hoc comparisons between plot locations (t -tests) are indicated by letters above the SE bars

increased along the nest-forest understorey gradient. Moreover, species-area accumulation curves showed that species richness above nests was 40% lower than in the putatively undisturbed understorey habitat (distant plots), where we identified a small set of indicator tree species. Collectively, these findings constitute a clear sign that *A. cephalotes* nests significantly drive the structure of plant assemblages in their zone of influence, i.e., nest-affected habitats roughly

60–120 m², considering a mean nest size of 60 m² and an equal area of border plots in this study.

The underlying mechanisms driving these assemblage-level shifts probably involve depressed recruitment of sensitive trees and shrubs around ant nests (i.e., nest-sensitive plants), as suggested by the performance of *Chrysophyllum viride* recruitment at our study site. Precisely, seed germination and seedling survivorship of *C. viride* sharply increased from ant nests towards forest understorey plots, indicating that leaf-cutting ants directly or indirectly act as a filter for the establishment of particular species or ecological groups. In tropical forests, light availability drives plant recruitment and shapes the nature of tree and shrub assemblages as it is the primary limiting factor of seedling growth and survival (Kitajima 1996). Increased light availability usually results in the replacement of shade-tolerant species by pioneers as recorded in treefall gaps (Brokaw 1982) and forest edges (Laurance et al. 2006). Actually, several shade-tolerant species are light intolerant and their seedlings suffer physiological stress while exposed to high-irradiance, desiccated environments (Kitajima 1996). As increased light availability was the most striking abiotic nest effect in this study, it is plausible to hypothesize that it is an important factor for the limited recruitment of sensitive shade-tolerant species and the modifications of plant assemblages around nests. In addition, plant assemblages are likely to be affected by increased seedling herbivory by *Atta* ants around nests. Even those *C. viride* seedlings located away from the nests experienced considerable damage by ants. Complete defoliation of seedlings on leaf-cutting ant nests has been reported previously for *Protium heptaphyllum* (Burseraceae) in another site of the Atlantic forest (Silva et al. 2007). In fact, ant-seedling predation around nests suggests that nest-clearing activities potentially nullify the expected enhancement of seed germination and seedling growth by the nest-mediated increase in light and nutrient levels while colonies remain active (Haines 1975; Farji-Brener and Silva 1995).

Impacts of leaf-cutting ant nests on plant assemblages have been already documented in tropical forests. The ants are expected to inhibit the establishment of plants on active nests, reducing both plant density and species richness (Garrettson et al. 1998; Hull-Sanders and Howard 2003). However, this effect has been detected (Garrettson et al. 1998) or addressed (Hull-Sanders and Howard 2003) only at the immediate nest surface. Moreover, as a nest is abandoned or the colony dies, these vegetation-free areas represent available spots for plant colonization, thus influencing plant assemblages and forest regeneration dynamics, much like in the case of treefall gaps (Fowler et al. 1989; Farji-Brener and Illes 2000; Moutinho et al. 2003). For example, Farji-Brener and Illes (2000) and Farji-Brener (2005) suggested that inactive nests of *Atta* spp. could favor

light-demanding tree and shrub species or those whose seeds were carried to the nest by the leaf-cutting ants while colonies were still active. These ideas largely supported the notion that in undisturbed ecosystems, leaf-cutting ants promote environmental heterogeneity (see Wirth et al. 2003).

However, the ecological role of *Atta* nests may be context dependent. For the present scenario, we provide evidence that *Atta* nests and ant activity (particularly seedling cutting) represent a disturbance regime that may lead to the impoverishment of plant assemblages along forest edges of an exceptionally large and long-standing fragment of Atlantic forest by directly and indirectly reducing the recruitment of sensitive tree and shrub species. It is already known that proliferation of pioneers following the creation of forest edges is fueled by elevated rates of treefall gaps and the collapse of the emergent layer (Laurance et al. 2006). Peripheral treefall gaps and edge-related microclimatic changes then further promote suitable conditions (increased light) for a striking recruitment and growth of pioneers within 100 m of fragment margins (Laurance et al. 2002, 2006; Oliveira et al. 2004). By considerably increasing the level of canopy openness and light availability at the forest ground (via nest construction and maintenance), it is reasonable to hypothesize that ant nests favor the recruitment of light-demanding species, including pioneers and those shade-tolerants that respond positively to moderate increments in light availability. However, in contrast to our initial expectations, nest-affected habitats may represent an inhospitable environment for: (1) light-sensitive, shade-tolerant species; (2) plant species bearing ant-targeted seedlings; and (3) plant species whose seeds require undisturbed habitats for better germination. This complex process of ecological filtering is currently the best explanation for the ant nest-mediated shifts we documented for sapling assemblages, including the reduced recruitment (in the nest-affected habitats) of those six pioneer plant species that served as indicators of the whole habitat used by colonies.

Leaf-cutting ants have long been regarded as allogenic ecosystem engineers (sensu Jones et al. 1994) by growing fungus in prodigious subterranean nests, which locally redistribute soil particles, change the structure and composition of soil, produce microsite enrichment and alter the forest vegetation in Neotropical forests (see review in Wirth et al. 2003). Our findings greatly extend knowledge on the role played by leaf-cutting ants by demonstrating that *A. cephalotes*' nest construction and maintenance modulates light transmission, influencing the vegetation not only over the nest but in tens of meters around it. Considering that *A. cephalotes* colonies have reached unprecedented densities along the edges of Coimbra forest (Wirth et al. 2007), it is likely that the magnitude of their engineering effects may be much more intense than previously anticipated (see Wirth et al. 2003). In fact, the various consequences

of edge-driven accumulations of *Atta* colonies may achieve far-reaching consequences for edge-affected habitats in hyper-fragmented landscapes (see review in Wirth et al. 2008). In the light of the ever-increasing pervasiveness of edge habitats and a growing awareness of their significant impact on ecosystem processes (Laurance et al. 2002, 2006; Wirth et al. 2008), further studies should investigate the generality of the patterns described here. We hope our working hypotheses promote a new line of investigation about the role played by leaf-cutting ants as ecosystem engineers in human-disturbed habitats such as tropical fragmented landscapes.

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