

Leaf-cutting ants alter seedling assemblages across second-growth stands of Brazilian Atlantic forest

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Abstract: Secondary forests promote an increased abundance of leaf-cutting ants (LCA) but the consequences on forest dynamics have been poorly addressed. Here we examine seedling assemblage attributes, seed germination and seedling survival across foraging zones of *Atta cephalotes* colonies inhabiting 15 second-growth patches (25–47 y old) of Atlantic forest. Seeds and seedlings were monitored within foraging zones and control sites over 1 y, including spots around ant nests. Overall, 1862 seedlings from 108 plant species were recorded. Seedling density decreased by 53% in foraging-zone plots (3.31 ± 0.23 seedlings m^{-2}) when compared with control plots (7.02 ± 0.44 seedlings m^{-2}) and a similar decrease was observed for species richness. Ant-induced alterations in the seedling assemblage were further indicated by segregation between foraging-zone and control plots (NMDS), habitat effects on species similarity (ANOSIM), and indicator tree species associated with control plots. While seed germination and seedling survivorship were uncorrelated to either nest distance or age of second-growth stands (with the exception of *Tapirira guianensis*), defoliation by LCAs was a significant cause of seedling mortality. Our results suggest that LCAs interfere with successional trajectories of Atlantic forest as foraging zones filter seedling establishment, supporting less-dense, impoverished and convergent seedling assemblages.

Key Words: *Atta*, ecological filter, ecosystem engineering, herbivory, forest regeneration, plant recruitment, seed germination

INTRODUCTION

Leaf-cutting ants (*Atta* spp. and *Acromyrmex* spp., Formicidae, Hymenoptera) are prevalent herbivores and dominant invertebrates of tropical and subtropical America, as they are able to harvest up to 15% y^{-1} of the standing leaf crop in their foraging areas (Urbas *et al.* 2007, Wirth *et al.* 2003). In tropical forests, however, the overall effects of leaf-cutting ants (especially *Atta* spp.) may go far beyond occasional simple foliage removal. Much of their influence can be attributed to the construction and maintenance of their nests, which often reach more than 100 m^2 in surface area (Cherrett

1989). These prodigious structures has been argued to (1) enhance soil nutrient availability, (Farji-Brener & Silva 1995, Moutinho *et al.* 2003, Sternberg *et al.* 2007); (2) improve soil penetrability relative to non-nest soils (Moutinho *et al.* 2003); (3) promote active removal of leaf litter (Weber 1972); and (4) create 'nest clearings' or vegetation gaps above and immediately around *Atta* nest sites (Corrêa *et al.* 2010, Farji-Brener & Illes 2000). Because of their diverse effects on the vegetation, leaf-cutting ants have been denoted as keystone species (Fowler *et al.* 1989) and ecosystem engineers (Wirth *et al.* 2003).

Ecosystem engineering is a scale-dependent process generating shifts in the resource availability to other organisms, which, in the case of leaf-cutting ants (LCAs), has been well documented at the spatial scale of ant nests, particularly in terms of plant recruitment while colonies are active (Corrêa *et al.* 2010, Meyer *et al.* 2011a) or after nest abandonment (Bieber *et al.* 2011).

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In contrast, the broader spatial scale of the foraging area has been neglected. Through a well-formed system of foraging trails (e.g. covering up to 9050 m²; Silva *et al.* 2009), these ants harvest large quantities of plant material for cultivating their fungus garden (Wirth *et al.* 2003). By creating small foliage gaps through the removal of leaves in the canopy, LCA herbivory causes a patchy increase in light transmittance and thus an increased frequency/variability of light availability on the forest floor (Wirth *et al.* 2003). Such increased heterogeneity in the light regime has been proposed to affect plant recruitment and species coexistence via niche partitioning (Svenning 2000). This perspective is consistent with the fact that light availability is one of the most important ecological factors affecting the growth, survival and establishment of seedlings and saplings (Augsburger 1984, Nicotra *et al.* 1999).

In addition to herbivory in the forest canopy, LCA activities in their foraging areas frequently include both massive and occasional seed harvesting (Dalling & Wirth 1998, Silva *et al.* 2007), and seedling/sapling defoliation (Rao *et al.* 2001, Silva *et al.* 2007, Vasconcelos & Cherrett 1997), particularly close to foraging trails (Silva *et al.* 2007). In synthesis, many mechanisms allow us to expect that LCA activities impose effects at the scale of foraging areas, particularly in terms of plant recruitment. Such effects are likely to be more evident across regenerating forest patches, in which LCAs may attain increased density and reduced foraging range (Silva *et al.* 2009). Here we address seedling-assemblage attributes, seed germination and seedling survival across foraging sites of *Atta cephalotes* colonies inhabiting second-growth patches (25–47 y old) of Atlantic forest in order to identify potential effects from LCA activities on plant recruitment. In particular, we examine the hypothesis that seedling assemblages in foraging areas are impoverished and taxonomically distinct from those inhabiting forest areas free of ant activity. We also expected reduced seed germination and seedling survival in foraging areas.

METHODS

Study area

The study was carried out at Usina Serra Grande – a 667-km² privately held sugarcane plantation in the state of Alagoas, north-eastern Brazil (8°30'S, 35°50'W). Soils include yellow-red latosols and podzols. Annual rainfall is approximately 2000 mm, and the dry season (< 60 mm mo⁻¹ rainfall) extends from November to February (Santos *et al.* 2008). The Serra Grande landscape still retains nearly 9000 ha of evergreen and semi-deciduous lowland forests (< 400 m asl), including the 3500-ha Coimbra Forest – the largest and

best-preserved private forest patch in north-east Brazil (Santos *et al.* 2008). Fabaceae, Lauraceae, Sapotaceae, Euphorbiaceae, Chrysobalanaceae and Lecythidaceae are the most species-rich families (Grillo *et al.* 2006).

Seedling assemblages

We assessed *Atta cephalotes* colonies across 15 second-growth patches (ranging in size from 0.53 to 7.4 ha, with a total area of 43.3 ha), which consisted of formerly clear-cut sites within flat, core areas of the Coimbra Forest, our study spot (Figure 1). Although embedded in the same matrix of mature forest, these second-growth patches were apart from each other (i.e. spatially independent patches) and represented well-known 25–47-y-old chronosequence created by the abandonment of slash-and-burn gaps following 5–10 y of subsistence agriculture (maize, cassava, beans) as described elsewhere (Santos *et al.* 2008, Silva *et al.* 2009). Within each patch we selected a single *A. cephalotes* colony, resulting in a set of 15 similar-sized colonies (20.5 ± 2.7 m²; mean ± SE). The average distance between colonies was 1477 ± 94 m (range = 34–3400 m; Figure 1). Colony foraging areas were mapped via a single, monthly observation during the peak phase of daily harvesting activity by measuring compass bearings and lengths of all quasi-linear trail segments. This procedure was repeated throughout 1 y (2005), resulting in 12 estimates per colony, which were further collapsed into a single annual measure of foraging area per colony as described by Silva *et al.* (2009) and Kost *et al.* (2005). The resulting annual foraging area was 5870 ± 618 m² (mean ± SE) and tripled across the regeneration chronosequence ranging from 3010 m² in a 25-y-old to 9050 m² in a 47-y-old patch (Silva *et al.* 2009).

During a 1-y period (2006), seedlings were recorded at monthly intervals in 1-m² plots disposed within foraging zones and control areas, i.e. forest sites in the vicinity of, but clearly outside a given foraging zone (c. 30–50 m away). Control areas were pre-assigned based on the previous assessments of annual foraging areas (Silva *et al.* 2009) and monitored monthly to ensure that they remained LCA-free throughout the study period. Plot location in both habitats varied monthly. Foraging-zone plots were located at random distances from the ant nest, 1 m away from major active ant trails to avoid foraging sectors without ant activity (Wirth *et al.* 2003). Nest-to-plot distances averaged 46.0 ± 56.2 (mean ± SD) and mean inter-plot distance was 36 ± 55 m. Similarly, control plots were randomly placed into the corresponding control areas with a minimum distance of 20 m to each other. This design resulted in 12 plots per colony per treatment (foraging zone and control area), yielding a total sampling effort of 180 m² per

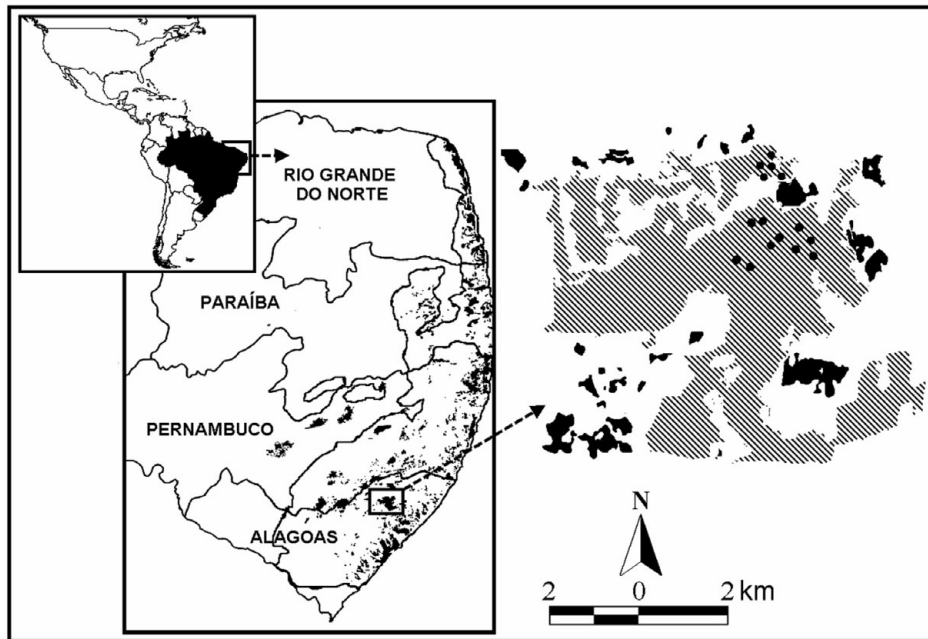


Figure 1. Map of the Usina Serra Grande landscape in north-east Brazil showing the location of 15 second-growth patches sampled to evaluate seedling assemblage attributes, seed germination and seedling survival across foraging sites of *Atta cephalotes* colonies. Within each patch we selected a single *Atta cephalotes* colony. The hatched polygon represents the Coimbra forest with the sampled second-growth patches (filled circles); white area indicates the matrix of sugar-cane monoculture.

treatment. Seedlings were defined as individuals up to 50 cm tall, including shrub, tree, liana and palm species. Individuals with evidence of resprouting or subterranean stems (stolons) were disregarded. Seedlings were assigned to species with the help of a local parataxonomist and through comparisons with specimens deposited in the Federal University of Pernambuco (Brazil), UFP Herbarium (voucher numbers 34,445–51,604 for the study site) and in the Serra Grande seedling and fruit/seed collection stored at the Plant Ecology Laboratory of the Federal University of Pernambuco as previously adopted by Santos *et al.* (2008).

Seed germination and seedling mortality

During the 2007 rainy season, we collected 3675 fresh seeds from three tree species in the Coimbra Forest: *Tapirira guianensis* Aubl. (Anacardiaceae, 1350 seeds), *Pouteria* sp. (Sapotaceae, 1200 seeds) and *Simarouba amara* Aubl. (Simaroubaceae, 1125 seeds). Seeds were buried individually (1 cm deep) across five distances from the nest edge (3, 6, 9, 12 and 15 m) of our 15 focal colonies. Seedling germination and seedling mortality were monitored during a 17-mo period based on weekly censuses. Dead seedlings were assigned to six sources of mortality: dried out, herbivory by LCAs, other herbivores, physical damage, failed radicle attachment and unknown reason.

Data analysis

Between-habitat differences of seedling density and species richness were examined using the following approach. We first ran analyses of covariance (ANCOVA; Sokal & Rohlf 1995), considering habitat as a factor and age of second-growth stands as covariate. As stand age proved to be not significant ($P > 0.05$), habitats were further compared via paired t-tests. We also estimated species richness of seedlings per habitat (i.e. foraging-zone plots vs. control plots) using mean species–area accumulation curves and Chao's non-parametric estimators: S_{obs} , Chao-1 and Chao-2, with 95% confidence intervals (Chazdon *et al.* 1998). These estimators are based on the incidence of species and have been described in the literature as the best estimators of species richness in tropical forests (Chazdon *et al.* 1998). Here we particularly adopted them to verify the consistency of between-habitat differences relative to species richness (foraging areas vs. control plots). Species accumulation curves were obtained by randomizing seedling records from 180 1-m² plots, which were obtained by sampling, once monthly over 1 y, 15 foraging zones and their respective control areas. We performed 1000 randomizations of the total dataset using the software EstimateS 8.2. We also conducted rarefaction analysis of total species richness considering a standard sample of 597 seedlings (i.e. the maximum number of seedlings recorded in one of the second-growth stands) in order to compare habitats based on the same number of individuals.

To examine species similarity among plots, we performed a non-metric multidimensional scaling (NMDS) ordination (via PRIMER software) of all 30 plots (collapsing all monthly records) using their Bray–Curtis similarity matrix of species composition (Krebs 1999). Species abundance data were square-root-transformed and standardized in order to avoid any bias resulting from highly abundant species and differences in sample sizes (i.e. seedling density per plot). To examine the relationships between habitat type and patterns of species similarity between plots, habitat was considered as a factor in the ANOSIM procedure. Additionally, we performed an indicator species analysis (Duf rene & Legendre 1997) based on two groups of seedling plots identified by both NMDS ordination and ANOSIM test: one consisting exclusively of foraging zone plots and another of control plots. The influence of indicator species on patterns of taxonomic similarity between habitats was investigated via a SIMPER analysis. Finally, differences in seed germination and seedling mortality relative to nest distance and age of second-growth stands were examined via Survival Analyses adopting Cox's proportional hazard models, while between-species differences in terms of seedling-mortality causes were examined via ANOVAs (one ANOVA per each source of mortality). All percentages were arcsine-transformed prior to analyses (Sokal & Rohlf 1995). NMDS, ANOSIM and SIMPER procedures were performed with PRIMER 5, ANCOVAs, ANOVAs and Survival Analyses via ESTADISTICA 8.0.

RESULTS

A total of 1862 seedlings from 108 plant species were recorded across both habitats – 597 (32%) seedlings and 74 (69%) species in foraging-zone plots and 1265 (68%) seedlings and 94 (87%) species in control plots. Seedling assemblage attributes (density and richness) were not affected by the age of second-growth stands ($F = 0.94$, $df = 1$, $P = 0.333$ and $F = 2.79$, $df = 1$, $P = 0.095$, respectively). However, average seedling density in foraging-zone plots ($3.31 \pm 0.23 \text{ m}^{-2}$; mean \pm SE) was half that in control plots ($7.02 \pm 0.44 \text{ m}^{-2}$; $t = 8.03$, $df = 17$, $P < 0.0001$), and average seedling richness also differed: 2.09 ± 0.10 species in foraging zones vs. 3.22 ± 0.13 species in control plots ($t = 8.37$, $df = 17$, $P < 0.0001$). At the community level, species–area accumulation curves revealed significant differences in terms of total species richness regardless of the estimator adopted (Figure 2). In foraging zones, total expected richness estimates varied from 74 (S_{obs}) to 139 (Chao-2); whereas it achieved 80.6 (S_{obs}) and 299 (Chao-2) in control sites; Chao-1 offered intermediate scores of species richness. However, the rarefaction method for a standard

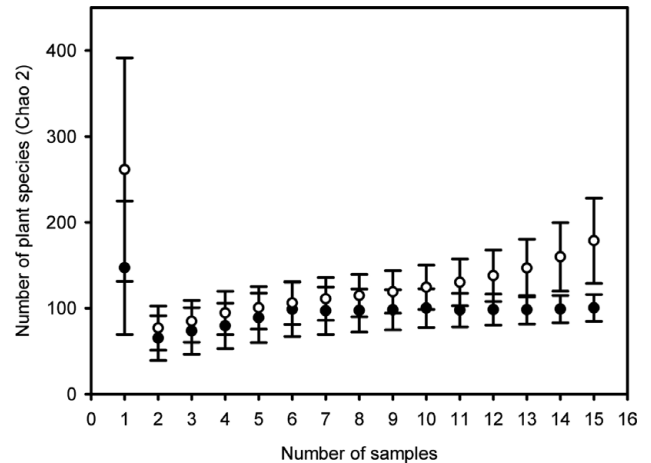


Figure 2. Species–area accumulation curves (Chao-2) in foraging zone plots of 15 *Atta cephalotes* colonies (filled circles) and in control plots (open circles) recorded at 15 second-growth stands of Atlantic forest in Serra Grande, north-east Brazil. 12 plots (1 m^2) were surveyed per colony and per treatment (foraging and control plots), yielding a total sampling effort of 180 m^2 for each group. Bars indicate 95% confidence intervals.

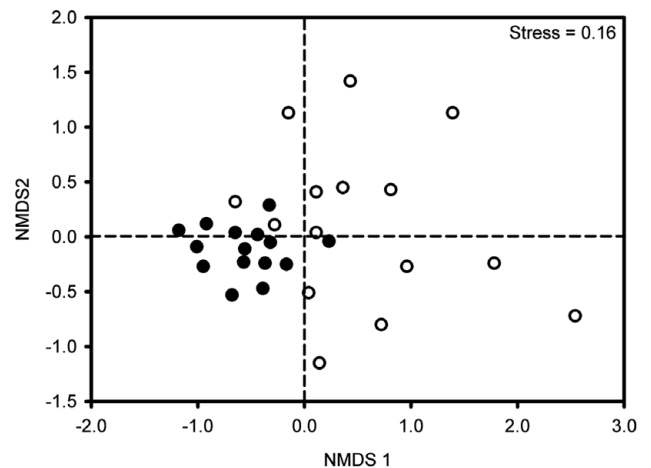


Figure 3. Non-metric multidimensional scaling ordination of seedling assemblages across 30 plots (360 m^2) based on Bray–Curtis similarity coefficients: 15 foraging-zone plots (filled circles) and 15 control plots (open circles) located in second-growth stands of Atlantic forest in Serra Grande, north-east Brazil.

set of 597 seedlings indicated a similar pattern of tree species in the two habitats.

NMDS ordination of seedling plots based on species similarity and abundance resulted in two consistent and clearly segregated clusters: one formed by the 15 foraging-zone plots and another formed by control plots (Figure 3). Plot ordination was well supported by low stress levels of 0.16 and the ANOSIM detected a significant effect of habitat type ($R = 0.372$, $P = 0.001$). Moreover, between-plot species similarity was much higher among those located in the foraging zones (87.3 ± 0.21) than in control plots (81.6 ± 0.31 ;

Table 1. Scores of a SIMPER analysis indicating the contribution of tree species to the average Bray–Curtis dissimilarity between foraging-zone plots (FZP) and control plots (CP) in Atlantic forests patches at Serra Grande, north-east Brazil. The following values are given: average abundance observed in foraging-zone and control plots, average dissimilarity \pm SD for each species and proportional contribution of each species to the dissimilarity index between FZP and CP. The list of species contains only the 10 tree species that contributed most to the dissimilarity between FZP and CP, accounting for 28.6% of the overall dissimilarity.

Species	Family	Average abundance		Average dissimilarity \pm SD	Contribution to dissimilarity index (%)
		FZP	CP		
<i>Tapirira guianensis</i> Aubl.	Anacardiaceae	6.17	12.77	0.85 \pm 1.32	4.72
<i>Erythroxylum mucronatum</i> Benth.	Erythroxylaceae	3.3	9.7	0.72 \pm 1.19	3.99
<i>Thyrsodium spruceanum</i> Benth.	Anacardiaceae	2.3	9.37	0.64 \pm 1.16	3.53
<i>Erythroxylum</i> sp.	Erythroxylaceae	4.1	8.1	0.58 \pm 1.04	3.22
<i>Ocotea glomerata</i> (Nees) Mez	Lauraceae	4.63	4.97	0.53 \pm 1.30	2.91
<i>Myrcia sylvatica</i> (G.Mey.) A.DC.	Myrtaceae	2.37	5.57	0.50 \pm 1.12	2.77
Unidentified species	Papilionaceae	2.1	2.3	0.37 \pm 1.31	2.04
<i>Vochysia oblongifolia</i> Warm.	Vochysiaceae	0.63	3.5	0.34 \pm 0.55	1.9
<i>Palicourea crocea</i> (Sw) Roem. & Schult	Rubiaceae	1.83	1.37	0.33 \pm 1.17	1.85
<i>Cupania oblongifolia</i> Mart.	Sapindaceae	1.7	1.83	0.31 \pm 1.22	1.69

F = 227, df = 1, P < 0.0001). The indicator species analysis generated a higher indicator value (IV) for three species in the control plots: *Thyrsodium spruceanum* Benth. (Anacardiaceae), *Myrcia sylvatica* (G.Mey.) A. DC. (Myrtaceae) and *Erythroxylum mucronatum* Benth. (Erythroxylaceae), while it failed to detect any indicator species across foraging-zone plots. These three species were among the ten best plot-discriminating species, which accounted for a cumulative contribution of 28.6% on average between-plot species similarity (Table 1, SIMPER analysis of Bray–Curtis dissimilarity).

After a 1-y period a total of 552 seeds germinated but total germination was highly variable among tree species, ranging from 15.3% in *Simarouba amara* to 43.2% in *Pouteria* sp. For these two tree species, seed germination did not correlate significantly to either distance from ant nests or age of second-growth stands, while in the case of *Tapirira guianensis* total germination correlated positively (Beta = 0.19, Wald statistic = 13.4, P = 0.0002) with distance from ant nests ($\chi^2 = 14.1$, df = 2, P < 0.001 for the whole model). After 1 y, total seedling mortality achieved c. 93% in *S. amara*, but lower scores were recorded in *T. guianensis* (57%) and *Pouteria* sp. (54%). Similar to germination, seedling mortality was not correlated to distance from nests or age of second-growth stands in the case of *S. amara* and *Pouteria* sp. However, mortality among *T. guianensis* seedlings correlated positively with distance from ant nests (Beta = 0.23, Wald statistic = 9.87, P = 0.016), but negatively with the age of second-growth stands ($\chi^2 = 15.5$, df = 2, P = 0.0001 for the whole model). Finally, tree species exhibited differential susceptibility to mortality factors in all studied species. In *T. guianensis* seedlings experienced high mortality caused by herbivores, probably gall-inducing arthropods, while most *S. amara* and *Pouteria* sp. seedlings died from desiccation (Figure 4). Moreover, LCAs killed a total of 76 seedlings through defoliation and were thus responsible for a proportional

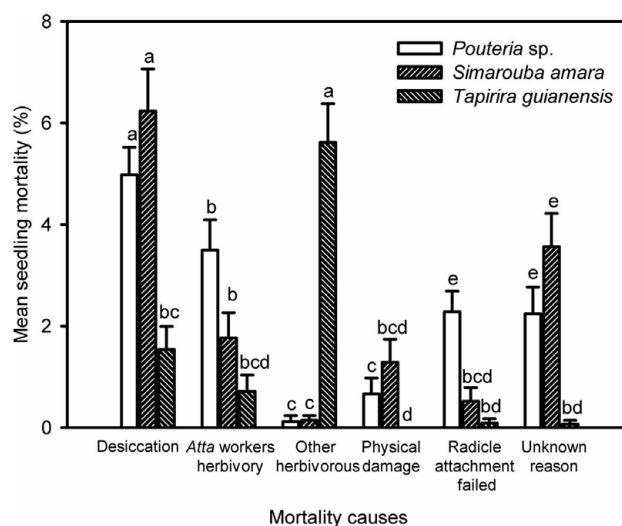


Figure 4. Average seedling mortality within six categories of death causes in the species *Tapirira guianensis*, *Simarouba amara* and *Pouteria* sp. across second-growth stands of Atlantic forest at Serra Grande, north-east Brazil. Letters above bars (\pm SE) denote significant differences at the 5% level (ANOVAs, LSD post hoc tests).

mortality of 3.1% in *T. guianensis* and 13.6% in *S. amara*.

DISCUSSION

Our results suggest that foraging zones of *A. cephalotes* ants in the Atlantic forest support less dense and impoverished seedling assemblages at local and habitat scale. With a reduction of one third of species richness, such assemblages are taxonomically distinct and lack species that are characteristic of ant-free forest zones (e.g. *Thyrsodium spruceanum*, *Myrcia sylvatica* and *Erythroxylum mucronatum*). In fact, seedling assemblages in ant foraging zones were floristically much more similar

to each other than in ant-free zones, and formed a discrete species cluster; i.e. a clear signal of floristic convergence. Finally, shifts in seedling assemblages across foraging zones may partially result from (1) seedling defoliation by ants, and (2) reduced seed germination close to ant nests as observed in *Tapirira guianensis*. We addressed seedling assemblages through a whole year by shifting plot location every month within each of the 15 foraging zones located in differently aged second-growth stands (25–47 y old) immersed in a single large forest remnant and exposed to the same pool of plant species. Thus, the patterns uncovered here, cannot be considered ephemeral or related to microhabitat selection by colony founding ant queens (Vieira-Neto & Vasconcelos 2010). In other words, our results suggest that leaf-cutting ants act as an important selective filter for seedling establishment, affecting seedling density, species richness and taxonomic composition.

LCAs are expected to interfere directly and indirectly on the nature of seedling assemblages via a large set of activities and processes: reduced seed production due to intense herbivory on adult trees (Rockwood 1973), seed harvesting (Silva *et al.* 2007, Wirth *et al.* 2003), seedling defoliation related to nest-clearing activities (Corrêa *et al.* 2010, Meyer *et al.* 2011b) or collection of plant material to feed the symbiotic fungus (Silva *et al.* 2007, Vasconcelos & Cherrett 1997). Leaf-cutting ants may directly cut the leaves and/or epicotyls of seedlings during foraging, particularly close to nests and in the vicinity of trunk trails (Silva *et al.* 2007, Vasconcelos & Cherrett 1997). In most *Atta* species this behaviour seems less common than foraging on large canopy trees (Wirth *et al.* 2003), but we observed seedling defoliation by *A. cephalotes* apparently in the context of foraging trail clearing activities at our study site. Likewise, *A. sexdens* has been considered the most important herbivore operating in abandoned pastures of the Amazon region by promoting defoliation with detectable impacts on seedling survivorship and growth (Nepstad *et al.* 1996), while Rao *et al.* (2001) attributed the reduced plant recruitment on small forest islands (0.3–3.0 ha) to high levels of *Atta* herbivory in Lago Guri, Venezuela. Massive defoliation of seedlings by LCA has also been reported from the Atlantic forest (Silva *et al.* 2007), where it was primarily concentrated on seedlings recruited close to nest entrances. Again, it is important to note that the ants do not necessarily use seedlings as fungus garden substrate but rather remove them while clearing newly established foraging trails (Wirth *et al.* 2003).

Although seedling defoliation imposed by LCAs partially explains the differences among seedling assemblages documented in this study, we would like to speculate about additional mechanisms that act complementarily. LCAs are largely associated with the construction and maintenance of their nests, which

can reach 100 m² or more in surface area (Cherrett 1989). These prodigious structures have been argued to promote the active removal of leaf litter, resulting in bare ground on and in the vicinity of nests, thus creating nest clearings or vegetation gaps above and immediately around *Atta* nest sites, where understorey vegetation growing on or overhanging the immediate nest surface is constantly cleared (Farji-Brener & Illes 2000). These gaps increase the amount of light passing through the foliage and reaching the understorey, and affect microclimatic conditions such as soil temperature, moisture (Corrêa *et al.* 2010, Meyer *et al.* 2011a) and soil penetrability (Bieber *et al.* 2011). Such intense physical alterations above the nests and their vicinities (Corrêa *et al.* 2010, Meyer *et al.* 2011a, 2011b) may potentially operate as a filter for seed germination and seedling recruitment; i.e. they represent an inhospitable environment for: (1) plant species bearing ant-preferred seedlings; (2) small-seeded tree species without resprouting abilities, (3) light-sensitive, shade-tolerant species; and (4) plant species whose seeds require undisturbed habitats for better germination and establishment (Corrêa *et al.* 2010, Meyer *et al.* 2011b, Silva *et al.* 2007).

Whatever the consequences of leaf-cutting ant activities on the nature of seedling assemblages, their intensity and spatial extent depends on both nest density and size of foraging zones. It has already been documented that several LCA species tend to proliferate in human-disturbed habitats such as second-growth stands or edge and road-affected habitats (Dohm *et al.* 2011, Meyer *et al.* 2009, Silva *et al.* 2009, Vasconcelos & Cherrett 1995, Vasconcelos *et al.* 2006, Wirth *et al.* 2007). But in addition to increased colony densities in disturbed habitats, the patterns of ant activities are expected to differ from those documented across undisturbed habitats due to a higher availability of palatable pioneer plants (Farji-Brener 2001, Peñaloza & Farji-Brener 2003, Wirth *et al.* 2003), and lower pressure imposed by natural enemies (Almeida *et al.* 2008, Rao 2000). For example, Wirth *et al.* (2007) and Urbas *et al.* (2007) observed that *A. cephalotes* colonies are able to multiply their nest density, scale down their foraging ranges by a factor of 2.5 (0.9 vs. 2.3 ha per colony y⁻¹), and more than double their herbivory pressure in Atlantic forest edge zones (14.3% vs. 7.8% of standing leaf crop). Furthermore, Silva *et al.* (2009) estimated that the ants accessed up to 100% of the area covered by early secondary patches (25 y old), whereas they explored only a small portion of the available forest (16–23%) in mid-successional patches (42–47 y old). It is thus not surprising considering the second-growth scenario of the present study that we documented shifts in seedling abundance, species richness and composition on those sites exposed to LCAs activities.

While manifold impacts of LCAs on plant assemblages have previously been documented in tropical forests, par-

ticularly on nest sites and their close vicinity (Bieber *et al.* 2011, Corrêa *et al.* 2010, Garrettson *et al.* 1998, Hull-Sanders & Howard 2003, Meyer *et al.* 2011a), this study is the first to document tangible shifts at the spatial scale of ant foraging areas as initially proposed by Wirth *et al.* (2003). In fact, our seedling plots were located between 2 and 414 m from nest mounds (46 m on average). Impoverished and floristically convergent seedling assemblages at such spatial scales reinforce the notion that LCAs can operate as ecosystem engineers at spatial scales far beyond ant nests (Meyer *et al.* 2011a, Wirth *et al.* 2003). In addition to seedling defoliation (Meyer *et al.* 2011b), it is reasonable to propose that environmental shifts resulting from nest-activities and foliage removal from the canopy alter resource availability (Corrêa *et al.* 2010, Meyer *et al.* 2011a) and may act as potential environmental filters for particular plant guilds (i.e. reduce the recruitment of sensitive tree and shrub species). Such a cascade has already been documented across nest vicinities in edge-affected habitats (Corrêa *et al.* 2010, Meyer *et al.* 2011b). In synthesis, our results suggest that LCAs modify seedling assemblages at broader spatial scale than previously reported. The consequences of such a disturbance regime still deserve further investigation as it may alter all attributes of plant assemblages attending to forest dynamic; i.e. impoverished and convergent assemblages. This is particularly relevant in the case of human-modified landscapes, where LCAs attain increased colony densities and their activities are able to cover the whole area of forest patches (Silva *et al.* 2009).

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