

Leaf-cutting ant populations profit from human disturbances in tropical dry forest in Brazil

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Abstract: Anthropogenic disturbance often results in the proliferation of native species of particular groups that leads to biotic homogenization. Leaf-cutting ants are an example of such winner organisms in tropical rain forests, but their response to disturbance in dry forests is poorly known. We investigated *Atta* colony density in areas of tropical dry forest in Brazil with different distance to roads and vegetation cover. *Atta* colonies were surveyed in 59 belt transects of 300 × 20 m, covering a total area of 35.4 ha. We found 224 *Atta* colonies, 131 of which were active and belonged to *Atta opaciceps* (87 colonies, 2.45 ha⁻¹), *A. sexdens* (35 colonies, 0.98 ha⁻¹) and *A. laevigata* (9 colonies, 0.25 ha⁻¹). The density of active colonies sharply decreased from 15 ± 2.92 ha⁻¹ in the 50-m zone along roads to only 2.55 ± 1.65 ha⁻¹ at distances up to 300 m. The reverse pattern was observed for inactive colonies. Active *Atta* colonies preferentially occur in areas with low vegetation cover, while inactive colonies prefer areas with high vegetation cover. We demonstrate for the first time that anthropogenic disturbances promote the proliferation of leaf-cutting ants in dry forest in Brazil, which may affect plant regeneration via herbivory and ecosystem engineering as demonstrated for rain forests.

Key Words: *Atta laevigata*, *Atta opaciceps*, *Atta sexdens*, chronic anthropogenic disturbance, colony density, ecological release, edge effect, roads, seasonally dry tropical forest

INTRODUCTION

In the tropics, anthropogenic disturbance often permits the proliferation of native species of particular groups (e.g. pioneer plants), contributing to functional and phylogenetic homogenization of assemblages (Lôbo *et al.* 2011, McKinney & Lockwood 1999, Tabarelli *et al.* 2012). One group of organisms that has proliferated in anthropogenic landscapes is generalist herbivores (Estes *et al.* 2011, Martinson & Fagan 2014, Wirth *et al.* 2008). In the Neotropics, leaf-cutting ants (LCA) of the genera *Atta* and *Acromyrmex* are dominant herbivores, removing up to 15% of the standing leaf crop in their foraging areas (Urbas *et al.* 2007, Wirth *et al.* 2003) to cultivate the symbiotic fungus upon which they feed (Hölldobler

& Wilson 1990). Moreover, these insects have been recognized as being among the most ‘successful’ species in anthropogenically modified tropical landscapes (Leal *et al.* 2014), inhabiting from forest to agricultural fields (Fowler 1983, Oliveira *et al.* 1998, Wirth *et al.* 2003). LCA directly profit from (1) increased availability of open areas for nesting sites (Vasconcelos 1990, Vieira-Neto & Vasconcelos 2010), (2) increased abundance of palatable pioneer plants (Coley & Barone 1996, Coley *et al.* 1985, Santos *et al.* 2008), which are preferred by LCA (Falcão *et al.* 2011, Farji-Brener 2001, Urbas *et al.* 2007), and (3) reduced populations of natural enemies such as predators (Terborgh *et al.* 2001, Wirth *et al.* 2008) and parasitoids (Almeida *et al.* 2008, Barrera *et al.* 2017).

Despite the large literature on LCA in Neotropical rain forests, grasslands and savannas (Leal *et al.* 2014), surprisingly little is known about the status and ecological role of these organisms in another major Neotropical

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biome: the seasonally dry tropical forest (hereafter dry forest) (but see Barrera *et al.* 2015). As in rain forests and savannas, dry forests have experienced high rates of habitat loss through deforestation (Leal *et al.* 2005, MMA & IBAMA 2010). However, the remaining habitat of dry forests is also typically subjected to high rates of chronic anthropogenic disturbance (*sensu* Singh 1998) in the form of livestock production, timber harvesting and extensive firewood collection in rural areas (Ribeiro *et al.* 2015, 2016). Moreover, dry forests naturally have a more open habitat structure, making it difficult to discern whether such chronic disturbance likely leads to a similar proliferation of LCA in these habitats. This is because causal mechanisms behind LCA proliferation (i.e. increased availability of suitable nesting sites and light-demanding pioneer plants) operate on the assumption that human disturbances lead to an opening of closed canopies as in rain forests.

In this study, we investigate the population responses of three species of *Atta* LCA to anthropogenic disturbance in areas of dry forest in Brazil. We specifically test the prediction that disturbance does not cause a similar proliferation of LCA as occurs in rain forests, because the dry forest naturally has a more open vegetation structure (Pennington *et al.* 2009). For example, edge effect on tree communities – one of the main drivers of LCA proliferation – has been found to be negligible in dry forest fragments (Oliveira *et al.* 2013). Moreover, dry forests are dominated by deciduous species, and it is plausible that the sparse availability of woody plant foliage is not capable of sustaining large populations of LCA during the dry season, especially in species and vegetation-poor disturbed sites (Ribeiro *et al.* 2015).

METHODS

Study area

The study was carried out in Catimbau National Park (8°24'00"–8°36'35" S, 37°0'30"–37°1'40" W), a 607-km² area located in Pernambuco state, Brazil. The climate is semi-arid, with annual temperature averaging 23°C, and mean annual rainfall varying from 480 to 1100 mm, concentrated between March and July, but with marked inter-annual variation (Sociedade Nordestina de Ecologia 2002). Deep sandy soils are predominant in the Park (quartzite sands, 70% of area), but planosols and lithosols are also present (15% each one; Sociedade Nordestina de Ecologia 2002). The vegetation is known as caatinga, a mosaic of seasonally dry tropical forest and thorn scrub (*sensu* Pennington *et al.* 2009) covering an area of 850 000 km² in north-eastern Brazil (Santos *et al.* 2011). Dominant families of woody plants are Fabaceae, Euphorbiaceae and Boraginaceae, and the

ground layer is dominated by Cactaceae, Bromeliaceae, Malvaceae, Asteraceae and Fabaceae (Rito *et al.* 2017a). The Park was only recently (2002) proclaimed, and its original inhabitants still live there, continuing to graze livestock, extract timber, collect firewood, harvest other plant material, and hunt (Rito *et al.* 2017a).

Atta survey

Atta colonies were surveyed in 59 belt transects of 300 × 20-m, covering a total area of 35.4 ha. Transects were established from roadside points, and ran perpendicular to the road. Distances between transects ranged from 1 to 4 km. All active, inactive and/or abandoned and/or dead colonies of *Atta* within the survey areas were located and recorded using a GPS with < 3-m resolution (Garmin Etrex 10). Most of the colonies were recorded by observing their large mounds, but foraging trails, standing leaves with tell-tale circular cuts, and cut material on the ground were also used to locate colonies (Wirth *et al.* 2007). Each colony was identified to species on the basis of mound structure and specimens collected for laboratory identification, and activity status was determined by (1) the presence of active foraging trails or their distinct physical structures, (2) fresh leaf fragments typically left over from nocturnal activity on foraging trails or around nest entrances and (3) appearance of workers after disturbing the colonies by poking a flexible 1-m pole into a nest entrance for 1 min (Almeida *et al.* 2008, Wirth *et al.* 2007). Colonies without apparent activity were categorized as 'inactive' (i.e. abandoned or dead colonies), although in a few cases colonies may have been alive, but in a longer phase of inactivity at the time of the censuses.

Characterization of anthropogenic disturbance

We used two independent indicators of intensity of anthropogenic disturbance, proximity to roads and vegetation cover. The 207 km of road that run through the Catimbau National Park are used by its inhabitants to travel between local communities and urban centres, to move their livestock, and to collect plant and animal resources. Transport occurs through small cars, 4 × 4 vehicles, tractors, ox- or horse-driven carts, horse-back and by foot. Many studies have shown that distance from the nearest road is a strong indicator of local human activity (Ahrends *et al.* 2010, Coffin 2007, Martorell & Peters 2005, Ribeiro *et al.* 2015), and it is a good predictor of loss of woody species in dry forest in Brazil due to use by people (Ribeiro *et al.* 2015). Similarly, vegetation cover is often used as an indicator of forest disturbance and regeneration (Jafari *et al.* 2007, Purevdorj *et al.* 1998), with decreasing forest

cover indicating increasing disturbance (Fahrig 2013, Gould 2000).

For each *Atta* colony we measured the shortest distance between the centre point of the colony and the nearest road using ArcGIS 10.1 (ESRI Environmental Systems Resource Institute 2012). Data for vegetation cover were obtained from a cover classification map derived from satellite imagery (RapidEye, 5-m resolution). Iso Cluster Unsupervised Classification in ArcGIS 10.1 was used to create four cover categories in the study area based on reflectance of soil and vegetation: (1) exposed soil (0–10% of vegetation cover) or agricultural field; (2) low vegetation cover (11–30%); (3) medium vegetation cover (31–50%); and (4) high vegetation cover (>51%). The locations of *Atta* colonies were plotted on the vegetation-cover map, and categorized according to a circular plot with a 200-m radius from the centre of each colony, corresponding to the approximate foraging area of a colony. To evaluate the accuracy of the classification, 69 points (50 × 20 m) were subsequently assessed in the field, and 80.2% were found to be correctly classified (Jain *et al.* 1999). We also calculated the percentage of land covered by vegetation in ImageJ software 1.50.

Data analysis

Each transect was divided into contiguous 10-m sections according to distance from a road (i.e. 0–10 m; 11–20 m, 21–30 m, etc.), and the number of colonies (active and inactive) within each section was counted. We used regression analysis to examine variation in colony density with distance to roads, considering all colonies combined as well as active and inactive colonies separately. We selected the best-fitting model from a set of regressions models for each response variable. We used chi-square tests (Zar 2010) to assess variation in the frequency of occurrence of total, active and inactive colonies among vegetation cover classes. We calculate the expected frequencies considering the percentage of areas cover by the vegetation cover classes (i.e. number of nests in high vegetation cover multiplied by the proportion of area cover by vegetation cover class). All analyses were performed using R software 3.0.1.

RESULTS

We recorded a total of 224 *Atta* colonies, 131 (58.48%) of which were active, giving an overall density of 3.7 active colonies ha⁻¹. Of the active colonies, 87 belonged to *Atta opaciceps* (2.45 ha⁻¹), 35 to *A. sexdens* (0.98 ha⁻¹) and nine to *A. laevigata* (0.25 ha⁻¹). The density of active colonies was very high (15 ± 2.92 ha⁻¹) for the first 50 m from a road, and decreased markedly thereafter to only

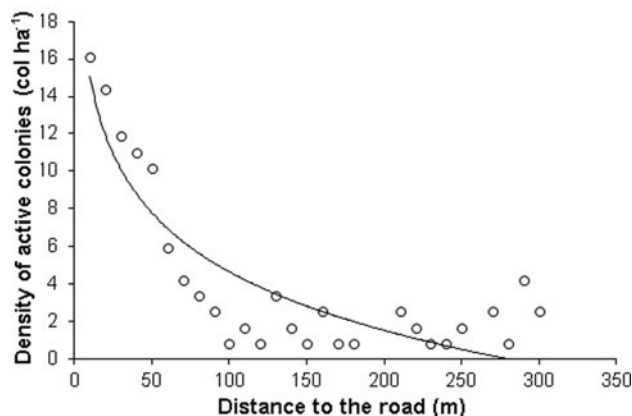


Figure 1. Relationship between distances to the road (m) and density of active colonies recorded in Catimbau National Park, Pernambuco, north-eastern Brazil. The black line is the fit of a logarithmic regression analysis ($y = -4.5\ln(x) + 2.60$, $R^2 = 0.78$, $P < 0.0001$).

2.55 ± 1.65 ha⁻¹ at a distance of 300 m (Figure 1). Such a pattern of high colony density for the first 50 m and low density thereafter was shown for both *A. opaciceps* (Figure 2a) and *A. sexdens* (Figure 2b). For *A. laevigata*, high colony density was restricted to the first 20 m, and no colonies were recorded beyond 80 m (Figure 2c). The density of inactive colonies averaged at 2.63 ha⁻¹ and showed a reverse pattern to that of active colonies, with lowest densities in the first 50 m (Figure 3).

The frequency of occurrence of active *Atta* colonies varied significantly among the vegetation cover categories, and was lower than expected in sites with high vegetation cover (Figure 4, Table 1). The reverse pattern occurred for inactive colonies, which were far less abundant than expected where vegetation cover was high (Figure 4, Table 1). When assessing the frequency of occurrence for different *Atta* species separately (Figure 4), species exhibited different patterns. For *A. opaciceps* and *A. laevigata*, the most abundant and the rarer species, respectively, there was no difference between the observed and expected frequency of occurrence (Figure 4, Table 1). Colonies of *A. sexdens* were more abundant than expected in areas of high vegetation cover (Figure 4, Table 1).

DISCUSSION

Leaf-cutting ants of the genus *Atta* commonly proliferate after anthropogenic disturbance in Neotropical rain forests due to their preference for open habitats and the lack of population control in those disturbed areas. However, their response to human disturbance in more open and less productive dry forests has received little research attention (but see Barrera *et al.* 2015). Our study tests the hypothesis that *Atta* abundance does not

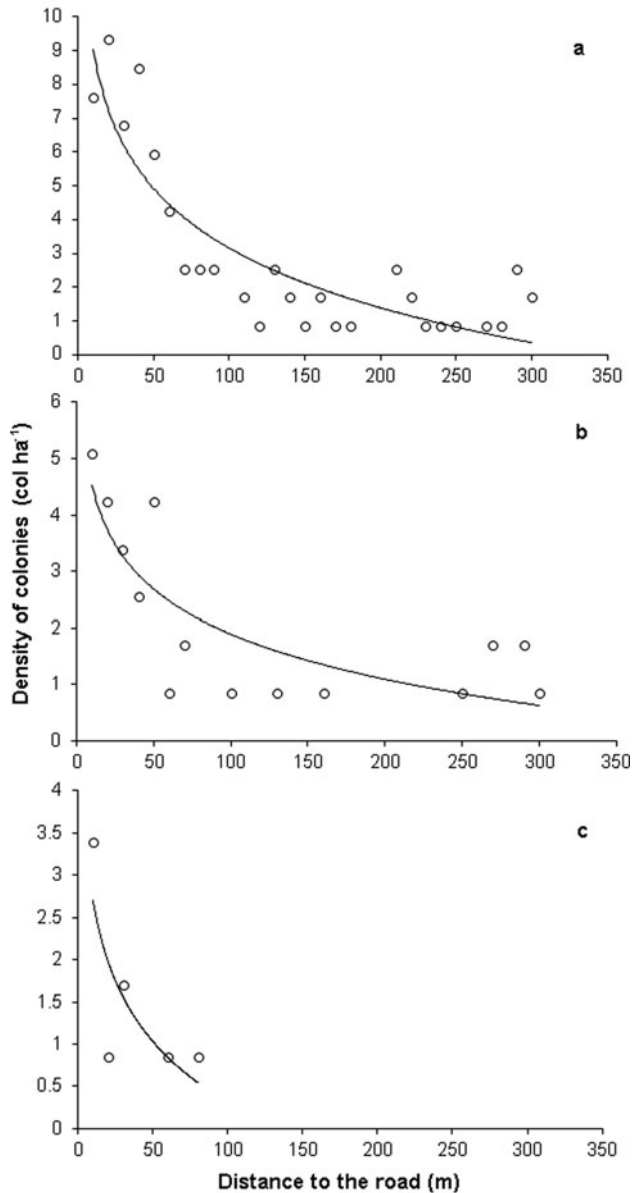


Figure 2. Relationship between distance to the road (m) and colony density of *Atta opaciceps* (a), *A. sexdens* (b), and *A. laevigata* (c) recorded in Catimbau National Park, Pernambuco, north-eastern Brazil. The black line is the fit of a logarithmic regression analysis (*A. opaciceps* $y = -2.6\ln(x) + 14.9$, $R^2 = 0.77$, $P < 0.0001$, *A. sexdens* $y = -1.1\ln(x) + 7.2$, $R^2 = 0.66$, $P = 0.0004$, *A. laevigata* $y = -1.0\ln(x) + 5.1$, $R^2 = 0.62$, $P = 0.115$).

increase with disturbance in dry forest in Brazil because it naturally has more open-structured vegetation, which is dominated by deciduous species, and the reduced foliage availability of woody plants at disturbed sites might not be capable of sustaining large populations of LCA. Yet, contrary to this prediction, our findings indicate that the density of active *Atta* colonies sharply increases in a 50-m-wide zone along roads and that colonies preferentially

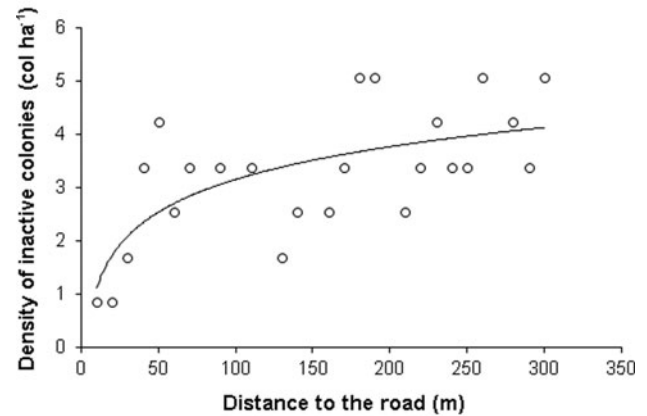


Figure 3. Relationship between distances to the road (m) and density of inactive colonies recorded in Catimbau National Park, Pernambuco, north-eastern Brazil. The black line is the fit of a logarithmic regression analysis ($y = 0.9\ln(x) - 0.9$, $R^2 = 0.45$, $P = 0.0003$).

occur in areas with low vegetation cover, while the density of inactive colonies was negatively correlated with road proximity and higher in areas with high vegetation cover. Such a contrasting pattern/response has been rarely documented and can shed some light on the potential mechanisms for the spatial distribution of LCA in the dry forest. This is especially interesting considering that queen preference for open habitats (Vasconcelos 1990) is unable to explain the positive relationship between vegetation cover and inactive nests. Moreover, although the genus *Atta* as a whole benefited from the presence of roads and habitats with low vegetation cover, the responses to vegetation cover were clearly species-specific.

Several studies have reported an increased density of LCA near roads (Vasconcelos *et al.* 2006, Vieira-Neto *et al.* 2016), near forest edges of large fragments (Dohm *et al.* 2011, Wirth *et al.* 2007), in small fragments dominated by edge habitats (Rao 2000, Terborgh *et al.* 2001) and in early-successional forests (Farji-Brener 2001, Silva *et al.* 2009, Vasconcelos & Cherrett 1995), where plant assemblages are functionally and taxonomically similar to forest edge (Santos *et al.* 2008). Few studies, however, demonstrated that the density of inactive colonies decrease with human disturbance, suggesting reduced mortality in these habitats (Meyer *et al.* 2009). While LCA density has been shown to be unaffected by vegetation types (Costa & Vieira-Neto 2015) and negatively correlated with categories of decreasing vegetation complexity (Fowler 1983), the influence of vegetation cover remained essentially uninvestigated. We suggest that the preference of active colonies for low vegetation cover, combined with the predominance of inactive colonies in areas with dense vegetation, supports the idea that LCA proliferate in or benefit from human-modified habitats (Leal *et al.* 2014).

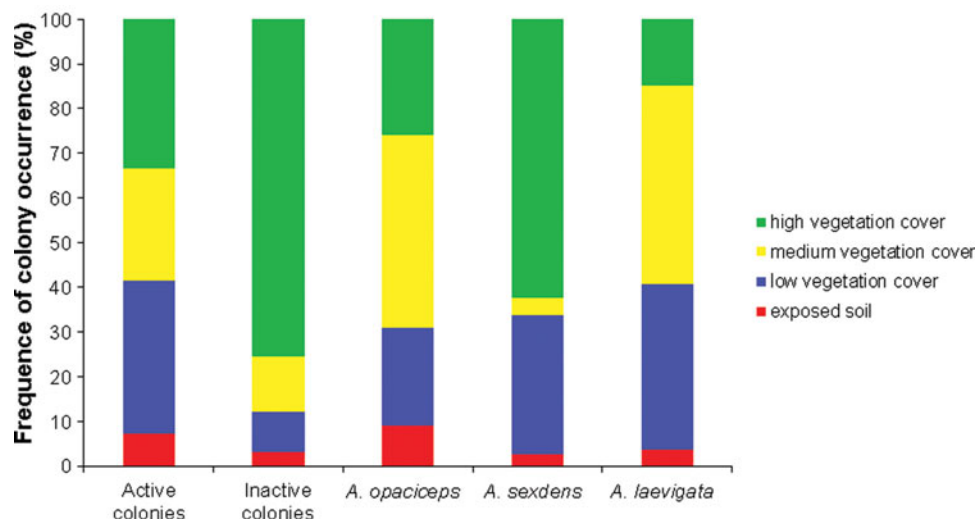


Figure 4. Frequency of occurrence of *Atta* colonies: active colonies, inactive colonies, *Atta opaciceps*, *A. sexdens* and *A. laevigata* in four categories of vegetation cover (exposed soil, low, medium, and high vegetation cover) in Catimbau National Park, Pernambuco, north-eastern Brazil.

Table 1. Chi-square analyses of the frequency of occurrence of *Atta* colonies (active and inactive) in different categories of vegetation cover (exposed soil, low, medium and high vegetation cover) recorded in Catimbau National Park, Pernambuco, north-eastern Brazil.

Colony type	Df	χ^2	P
Active	3	8.1	0.0432
<i>Atta laevigata</i>	3	1.5	0.691
<i>Atta opaciceps</i>	3	2.7	0.444
<i>Atta sexdens</i>	3	12.3	0.0064
Inactive	3	12.4	0.0061

Cross-species differences in terms of disturbance tolerance or preference for specific types of habitat structure (here represented by vegetation cover) is not an unexpected result. In our focal landscape, *A. opaciceps* and *A. laevigata* occurred equally across all classes of vegetation cover, while *A. sexdens* was more abundant in areas of high vegetation cover. *Atta opaciceps* is the only species endemic to the dry forest in Brazil (Brandão 1995, Ulysséa & Brandão 2013) and was the most abundant species in the Catimbau landscape. In view of the high variability of the vegetation cover, ranging from seasonally dry forests with higher vegetation cover to more open areas with scrub vegetation (Pennington *et al.* 2009), it is reasonable that this species is able to exist across the natural range of dry forest habitats. In contrast, *Atta laevigata* and *A. sexdens* are widely distributed throughout South American rainforests and savannas. While both species do occur in closed forests, they predominate in savannas and open habitats and are strong indicators of forest degradation, road and edge creation (Costa & Vieira-Neto 2015, Dohm *et al.* 2011, Fowler *et al.* 1986, Vasconcelos 1990). In this regard, the

preference of *A. sexdens* for areas with high vegetation cover is a pattern rarely described in the literature.

The increased density of LCA near roads has been associated with more open habitat conditions. This has been explained by the facts that founding ant queens are attracted to areas of high light reflectance (Forys *et al.* 2002), exposed soils are preferred nesting sites (Vasconcelos *et al.* 2006), and colonies founded in areas of greater exposure to sunlight are more productive (Weber 1972, Vieira-Neto *et al.* 2016). However, direct road effects appear to be limited to relatively short distances. For example, Vieira-Neto *et al.* (2016) showed that such effects were limited to the first 15 m in a Brazilian savanna, where more than a third of all adult colonies occurred. In contrast, we found elevated colony densities as far as 50 m from roads, suggesting that additional disturbance factors associated with roads or forest edges in general are at play.

The reverse pattern of decreased density of inactive colonies near the 50-m edge zones may provide additional cues for other processes controlling LCA colony density in edge habitats. Several studies have demonstrated or suggested that both bottom-up and top-down population control are relaxed near forest edges, small fragments and early successional forests compared with the interior of continuous forest (Almeida *et al.* 2008, Terborgh *et al.* 2001, Urbas *et al.* 2007). In this context, a decrease of inactive nests in areas near edges may be explained by the higher availability of palatable food sources, such as herbs and pioneer/colonizing plants (i.e. reduced bottom-up control). Indeed, several Euphorbiaceae shrubs have been reported to proliferate in disturbed areas of Brazil's dry forest (e.g. *Croton*, *Jatropha* and *Cnidocolus*, Ribeiro *et al.* 2015, 2016, Ribeiro-Neto *et al.* 2016, Rito *et al.* 2017b). These species are often succulent with very

conservative leaf-economy and seem to be able to withstand disturbances, including soil degradation and desiccation (Rito *et al.* 2017b). The fact that light is probably not a limiting resource in dry forests suggests however, that LCA proliferation is not driven by increased light availability (opposed to edge-induced pioneers of humid forests). Nevertheless, these species make up a large portion of the diet of LCA (F.F.S. Siqueira, unpubl. data), and may therefore represent a resource advantage in near road environments or sites with low cover of mature-forest vegetation. Herbs also proliferate in disturbed habitats in the dry forest (L.A.F. Vieira, unpubl. data) and we have already documented a frequent use of herbs (e.g. *Portulaca elatior* Mart. ex Rohrb and *Sida galheirensis* Ulbr.) by LCA in our focal landscape (F.F.S. Siqueira, unpubl. data). In addition, it is possible that LCA colonies of disturbed areas experience reduced pressure by parasitoid flies (Diptera: Phoridae), because this group is susceptible to open environments with reduced vapour pressure (Morrison *et al.* 2000, Wuellner & Saundres 2003). Decrease in populations or behavioural avoidance of vegetation edges by vertebrate predators such as armadillos and anteaters are also common in dry forests (Melo *et al.* 2014, Superina & Abba 2014). It is thus entirely reasonable that the same mechanisms that release LCA from population control at rain-forest edges are also operating along road-affected or other disturbed areas of dry forest.

In synthesis, our findings document for the first time a case of drastic *Atta* proliferation associated with human-disturbances (roads and changes in vegetation cover) in the tropical dry forest of north-east Brazil. This population growth is likely driven by a combination of mechanisms including a preference of founding queens for open habitats and a relaxation of population control forces. However, in contrast to other neotropical ecosystems, these changes are probably not induced by increased light availability as the ultimate causality behind disturbance-induced LCA proliferation. Our study provides not just another instance in which *Atta* proliferates, but rare evidence that some LCA species are able to persist and even benefit from human disturbance in a very harsh environment (i.e. severe annual and inter-annual droughts), in which evergreen woody plants can represent less than 1% of all stems (Lima & Rodal, 2010). As herbivores (Urbas *et al.* 2007) and ecosystem engineers (Corrêa *et al.* 2010, 2016; Meyer *et al.* 2011, 2013) these ants have far-reaching effects on plant recruitment and the successional trajectory of forest patches (Bieber *et al.* 2011, Corrêa *et al.* 2010, Farji-Brener & Illes 2000, Meyer *et al.* 2011). With the human-induced spread of these ants, such activities and their cascading impacts on ecosystem functions have proliferated across the Neotropics and turned LCA into an emerging key player of human modified landscapes (Leal *et al.* 2014). We therefore urge

further studies aimed at exploring the forces driving LCA proliferation near roads and disturbed habitats, and its consequences for the regeneration of dry forests to maintain the functions and services of this ecosystem, which now faces a future of increased aridity (Magrin *et al.* 2014).

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LITERATURE CITED

- AHRENDTS, A., BURGESS, A. N. D., MILLEDGE, S. A. H., BULLING, M. T., FISHER, B., SMART, J. C. R., CLARKE, G. P., MHORO, B. E. & LEWIS, S. L. 2010. Predictable waves of sequential forest degradation and biodiversity loss spreading from an African city. *Proceedings of the National Academy of Sciences USA* 107:14556–14561.
- ALMEIDA, W. R., WIRTH, R. & LEAL, I. R. 2008. Edge-mediated reduction of phorid parasitism on leaf-cutting ants in a Brazilian Atlantic forest. *Entomologia Experimentalis et Applicata* 129:251–257.
- BARRERA, C. A., BUFFA, L. M. & VALLADARES, G. 2015. Do leaf-cutting ants benefit from forest fragmentation? Insights from community and species-specific responses in a fragmented dry forest. *Insect Conservation and Diversity* 8:456–463.
- BARRERA, C. A., BECKER, E. L., ELIZALDE, L. & QUEIROZ, J. M. 2017. Parasitoid phorid flies of leaf-cutting ants are negatively affected by loss of forest cover. *Entomologia Experimentalis et Applicata* 164: 66–77.
- BIEBER, A. G. D., OLIVEIRA, M. A., WIRTH, R., TABARELLI, M. & LEAL, I. R. 2011. Do abandoned nests of leaf-cutting ants enhance plant recruitment in the Atlantic forest? *Austral Ecology* 36: 220–232.
- BRANDÃO, C. R. F. 1995. *Formigas dos Cerrados e Caatingas. Habilitation thesis*, Universidade de São Paulo, 147 pp.
- COFFIN, A. W. 2007. From roadkill to road ecology: a review of the ecological effects of roads. *Journal of Transport Geography* 15:396–406.
- COLEY, P. D. & BARONE, J. A. 1996. Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics* 27:305–335.

- COLEY, P. D., BRYANT, J. P. & CHAPIN, F. S. 1985. Resource availability and plant anti-herbivore defense. *Science* 230:895–899.
- CORRÊA, M., SILVA, P., WIRTH, R., TABARELLI, M. & LEAL, I. R. 2010. How leaf-cutting ants impact forests: drastic nest effects on light environment and plant assemblages. *Oecologia* 162:103–115.
- CORRÊA, M., SILVA, P. S. D., WIRTH, R., TABARELLI, M. & LEAL, I. R. 2016. Foraging activity of leaf-cutting ants changes light availability and plant assemblage in Atlantic forest. *Ecological Entomology* 41:442–450.
- COSTA, A. N. & VIEIRA-NETO, E. H. M. 2015. Species turnover regulates leafcutter ant densities in environmental gradients across the Brazilian Cerrado. *Journal of Applied Entomology* 140:474–478.
- DOHM, C., LEAL, I. R., TABARELLI, M., MEYER, S. T. & WIRTH, R. 2011. Leaf-cutting ants proliferate in the Amazon: an expected response to forest edge? *Journal of Tropical Ecology* 27:645–649.
- ESTES, J. A., TERBORGH, J., BRASHARES, J. S., POWER, M. E., BERGER, J., BOND, W. J., CARPENTER, S. R., ESSINGTON, T. E., HOLT, R. D., JACKSON, J. B. C., MARQUIS, R. J., OKSANEN, L., OKSANEN, T., PAINE, R. T., PIKITCH, E. K., RIPPLE, W. J., SANDIN, S. A., SCHEFFER, M., SCHOENER, T. W., SHURIN, J. B., SINCLAIR, A. R. E., SOULÉ, M. E., VIRTANEN, R. & WARDLE, D. A. 2011. Trophic downgrading of planet Earth. *Science* 333:301–306.
- FAHRIG, L. 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. *Journal of Biogeography* 40:1649–1663.
- FALCÃO, P. F., PINTO, S. R. R., WIRTH, R. & LEAL, I. R. 2011. Edge-induced narrowing of dietary diversity in leaf-cutting ants. *Bulletin of Entomological Research* 101:305–311.
- FARJI-BRENER, A. G. 2001. Why are leaf-cutting ants more common in early secondary forests than in old-growth tropical forests? An evaluation of the palatable forage hypothesis. *Oikos* 92:169–177.
- FARJI-BRENER, A. G. 2001. Why are leaf-cutting ants more common in early secondary forests than in old-growth tropical forests? An evaluation of the palatable forage hypothesis. *Oikos* 92:169–177.
- FARJI-BRENER, A. G. & ILLES, A. E. 2000. Do leaf-cutting ant nests make “bottom-up” gaps in Neotropical rain forests? A critical review of the evidence. *Ecology Letters* 3:219–227.
- FORYS, E. A., ALLEN, C. R. & WOJCIK, D. P. 2002. Influence of proximity and amount of human development and roads on the occurrence of the red imported fire ant in the lower Florida Keys. *Biological Conservation* 108:7–33.
- FOWLER, H. G. 1983. Distribution patterns of Paraguayan leaf-cutting ants (*Atta* and *Acromyrmex*) (Formicidae: Attini). *Studies on Neotropical Fauna Environment* 18:121–138.
- FOWLER, H. G., PEREIRA, V. S. & FORTI, L. C. 1986. Population dynamics of leaf-cutting ants: a brief review. Pp. 123–145 in Lofgren, C. S. & Vander Meer, R. K. (eds). *Fire ants and leaf-cutting ants: biology and management*. Westview Press, London.
- GOULD, W. 2000. Remote sensing of vegetation, plant species richness, and regional biodiversity hotspots. *Ecological Applications* 10:1861–1870.
- HÖLDOBLER, B., & WILSON, E. O. 1990. *The ants*. Harvard University Press, Cambridge. 732 pp.
- JAFARI, R., LEWIS, M. M. & OSTENDORF, B. 2007. Evaluation of vegetation indices for assessing vegetation cover in southern arid lands in South Australia. *Rangeland Journal* 29:39–49.
- JAIN, A. K., MURTY, M. N. & FLYNN, P. J. 1999. Data clustering: a review. *ACM Computing Surveys* 31:265–323.
- LEAL, I. R., SILVA, J. M. C., TABARELLI, M. & LACHER, T. E. 2005. Changing the course of biodiversity conservation in the Caatinga of Northeastern Brazil. *Conservation Biology* 19:701–706.
- LEAL, I. R., WIRTH, R. & TABARELLI, M. 2014. The multiple impacts of leaf-cutting ants and their novel ecological role in human-modified neotropical forests. *Biotropica* 46:516–528.
- LIMA, A. L. A. & RODAL, M. J. N. 2010. Phenology and wood density of plants growing in the semi-arid region of northeastern Brazil. *Journal of Arid Environment* 74:1363–1373.
- LÔBO, D., LEÃO, T., MELO, F. P. L., SANTOS, A. M. M. & TABARELLI, M. 2011. Forest fragmentation drives Atlantic forest of northeastern Brazil to biotic homogenization. *Diversity and Distributions* 17:287–296.
- MAGRIN, G. O., MARENGO, J. A., BOULANGER, J. P., BUCKERIDGE, M. S., CASTELLANOS, E., POVEDA, G., SCARANO, F. R. & VICUÑA, S. 2014. Central and South America. Pp. 1499–1566 in Barros, V. R., Field, C. B., Dokken, D. J., Mastrandrea, M. D., Maach, K. L. & Bilir, T. E. (eds). *Climate change 2014: impacts, adaptation, and vulnerability. Part b: regional aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge and New York.
- MARTINSON, H. M. & FAGAN, W. F. 2014. Trophic disruption: a meta-analysis of how habitat fragmentation affects resource consumption in terrestrial arthropod systems. *Ecology Letters* 17:1178–1189.
- MARTORELL, C. & PETERS, E. M. 2005. The measurement of chronic disturbance and its effects on the threatened cactus *Mammillaria pectinifera*. *Biological Conservation* 124:199–207.
- MCKINNEY, M. L. & LOCKWOOD, J. L. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution* 14:450–453.
- MELO, F. P., SIQUEIRA, J. A., SANTOS, B. A., ALVARES-DA-SILVA, O., CEBALLOS, G. & BERNARD, E. 2014. Football and biodiversity conservation: Fifa and Brazil can still hit a green goal. *Biotropica* 46:257–259.
- MEYER, S. T., LEAL, I. R. & WIRTH, R. 2009. Persisting hyperabundance of leaf-cutting ants (*Atta* spp.) at the edge of an old Atlantic forest fragment. *Biotropica* 41:711–716.
- MEYER, S. T., LEAL, I. R., TABARELLI, M. & WIRTH, R. 2011. Ecosystem engineering by leaf-cutting ants: nests of *Atta cephalotes* drastically alter forest structure and microclimate. *Ecological Entomology* 36:14–24.
- MEYER, S. T., NEUBAUER, M., SAYER, E. J., LEAL, I. R., TABARELLI, M. & WIRTH, R. 2013. Leaf-cutting ants as ecosystem engineers: topsoil and litter perturbations around *Atta cephalotes* nests reduce nutrient availability. *Ecological Entomology* 38:497–504.
- MMA & IBAMA. 2010. *Monitoramento do desmatamento nos biomas brasileiros por satélite: Monitoramento do Bioma Caatinga 2002 a 2008*. Ministério do Meio Ambiente, Instituto Brasileiro do Meio Ambiente e Recursos Naturais Renováveis, Brasília. 46 pp.
- MORRISON, L. W., KAWAZOE, E. A., GUERRA, R. & GILBERT, L. E. 2000. Ecological interactions of *Pseudacteon parasitoids* and *Solenopsis* ant hosts: environmental correlates of activity and effects on competitive hierarchies. *Ecological Entomology* 25:433–444.

- OLIVEIRA, D. G., PRATA, A. P. D. N., SOUTO, L. S. & FERREIRA, R. R. A. 2013. Does the edge effect influence plant community structure in a tropical dry forest? *Revista Arvore* 37:311–320.
- OLIVEIRA, M. A. DE, DELLA-LUCIA, T. M. C., ANJOS, N. DOS, DE OLIVEIRA, M. A. & DOS ANJOS, N. 1998. Occurrence and nest density of leaf-cutting ants in eucalypt plantations in southern Bahia. *Revista Brasileira de Entomologia* 42:17–21.
- PENNINGTON, R. T., LAVIN, M. & OLIVEIRA-FILHO, A. 2009. Woody plant diversity, evolution, and ecology in the tropics: perspectives from seasonally dry tropical forests. *Annual Review of Ecology, Evolution, and Systematics* 40:437–457.
- PUREVDORJ, T., TATEISHI, R., ISHIYAMA, T. & HONDA, Y. 1998. Relationships between percent vegetation cover and vegetation indices. *International Journal of Remote Sensing* 19:3519–3535.
- RAO, M. 2000. Variation in leaf-cutter ant (*Atta* sp.) densities in forest isolates: the potential role of predation. *Journal of Tropical Ecology* 16:209–225.
- RIBEIRO, E. M. S., ARROYO-RODRÍGUEZ, V., SANTOS, B. A., TABARELLI, M. & LEAL, I. R. 2015. Chronic anthropogenic disturbance drives the biological impoverishment of the Brazilian Caatinga vegetation. *Journal of Applied Ecology* 52:611–620.
- RIBEIRO, E. M. S., SANTOS, B. A., ARROYO-RODRÍGUEZ, V., TABARELLI, M., SOUZA, G. & LEAL, I. R. 2016. Phylogenetic impoverishment of plant communities following chronic human disturbances in the Brazilian Caatinga. *Ecology* 97:1583–1592.
- RIBEIRO-NETO, J. D., ARNAN, X., TABARELLI, M. & LEAL, I. R. 2016. Chronic anthropogenic disturbance causes homogenization of plant and ant communities in the Brazilian Caatinga. *Biodiversity and Conservation* 25:943–956.
- RITO, K. F., ARROYO-RODRÍGUEZ, V., QUEIROZ, R. T., LEAL, I. R. & TABARELLI, M. 2017a. Precipitation mediates the effect of human disturbance on the Brazilian Caatinga vegetation. *Journal of Ecology*. doi: 10.1111/1365-2745.12712.
- RITO, K. F., TABARELLI, M., & LEAL, I. R. 2017b. Euphorbiaceae responses to chronic anthropogenic disturbances in Caatinga vegetation: from species proliferation to biotic homogenization. *Plant Ecology* 218: 749–759.
- SANTOS, B. A., PERES, C. A., OLIVEIRA, M. A., GRILLO, A., ALVES-COSTA, C. P. & TABARELLI, M. 2008. Drastic erosion in functional attributes of tree assemblages in Atlantic forest fragments of northeastern Brazil. *Biological Conservation* 141:249–260.
- SANTOS, J. C., LEAL, I. R., ALMEIDA-CORTEZ, J. S., FERNANDES, G. W. & TABARELLI, M. 2011. Caatinga: the scientific negligence experienced by a dry tropical forest. *Tropical Conservation Science* 4:276–286.
- SILVA, P. S. D., WIRTH, R., TABARELLI, M. & LEAL, I. R. 2009. Decreasing abundance of leaf-cutting ants across a chronosequence of advancing Atlantic forest regeneration. *Journal of Tropical Ecology* 25:223–227.
- SINGH, S. P. 1998. Chronic disturbance, a principal cause of environmental degradation in developing countries. *Environmental Conservation* 25:1–2.
- SOCIEDADE NORDESTINA DE ECOLOGIA. 2002. *Projeto Técnico para a Criação do Parque Nacional do Catimbau/PE*. Secretaria de Ciência, Tecnologia e Meio Ambiente de Pernambuco – SECTMA, Recife. 151 pp.
- SUPERINA, M., & ABBA, A. M. 2014. What do we know about armadillos? An analysis of four centuries of knowledge about a group of South American mammals, with emphasis on their conservation. *Mammal Review* 44:69–80.
- TABARELLI, M., PERES, C. A. & MELO, F. P. L. 2012. The ‘few winners and many losers’ paradigm revisited: emerging prospects for tropical forest biodiversity. *Biological Conservation* 155:136–140.
- TERBORGH, J., LOPEZ, L., NUÑEZ, P., RAO, M., SHAHABUDDIN, G., ORIHUELA, G., RIVEROS, M., ASCANIO, R., ADLER, G. H., LAMBERT, T. D. & BALBAS, L. 2001. Ecological meltdown in predator-free forest fragments. *Science* 294:1923–1926.
- ULYSSEÁ, M. A. & BRANDÃO, C. R. F. 2013. Ant species (Hymenoptera, Formicidae) from the seasonally dry tropical forest of northeastern Brazil: a compilation from field surveys in Bahia and literature records. *Revista Brasileira de Entomologia* 57:217–224.
- URBAS, P., ARAÚJO, M. V., LEAL, I. R. & WIRTH, R. 2007. Cutting more from cut forests: edge effects on foraging and herbivory of leaf-cutting ants in Brazil. *Biotropica* 39:489–495.
- VASCONCELOS, H. L. 1990. Foraging activity of two species of leaf-cutting ants (*Atta*) in a primary forest of the Central Amazon. *Insectes Sociaux* 37:131–145.
- VASCONCELOS, H. L. & CHERRETT, J. M. 1995. Changes in leaf-cutting ant populations (Formicidae: Attini) after the clearing of mature forest in Brazilian Amazonia. *Studies on Neotropical Fauna and Environment* 30:107–113.
- VASCONCELOS, H. L., VIEIRA-NETO, E. H. M., MUNDIM, F. M. & BRUNA, E. M. 2006. Roads alter the colonization dynamics of a keystone herbivore in neotropical savannas. *Biotropica* 38:661–665.
- VIEIRA-NETO, E. H. M. & VASCONCELOS, H. L. 2010. Developmental changes in factors limiting colony survival and growth of the leaf-cutter ant *Atta laevigata*. *Ecography* 33:538–544.
- VIEIRA-NETO, E. H. M., VASCONCELOS, H. L. & BRUNA, E. M. 2016. Roads increase population growth rates of a native leaf-cutter ant in Neotropical savannas. *Journal of Applied Ecology* 53:983–992.
- WEBER, N. A. 1972. *Gardening ants, the attines*. The American Philosophical Society, Philadelphia. 146 pp.
- WIRTH, R., HERZ, H., RYEL, R. J., BEYSCHLAG, W. & HOLDOBLER, B. 2003. *Herbivory of leaf-cutting ants: a case study on Atta colombica in the tropical rainforest of Panama*. Springer-Verlag, Berlin. 230 pp.
- WIRTH, R., MEYER, S. T., ALMEIDA, W. R., ARAÚJO, M. V., BARBOSA, V. S. & LEAL, I. R. 2007. Increasing densities of leaf-cutting ants (*Atta* spp.) with proximity to the edge in a Brazilian Atlantic forest. *Journal of Tropical Ecology* 23:501–505.
- WIRTH, R., MEYER, S., LEAL, I. R. & TABARELLI, M. 2008. Plant herbivore interactions at the forest edge. *Progress in Botany* 69:423–448.
- WUELLNER, C. T. & SAUNDRES, J. B. 2003. Circadian and circannual patterns of activity and territory shifts: comparing a native ant (*Solenopsis geminata*, Hymenoptera: Formicidae) with its exotic, invasive congener (*S. invicta*) and its parasitoids (*Pseudacteon* spp., Diptera: Phoridae) at a Central Texas site. *Annals of the Entomological Society of America* 96:54–60.
- ZAR, J. H. 2010. *Biostatistical analysis*. Prentice Hall, Upper Saddle River. 663 pp.