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Human disturbance promotes herbivory by leaf-cutting ants in the Caatinga dry forest

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ABSTRACT

Anthropogenic disturbances are known to modify plant–animal interactions such as those involving the leaf-cutting ants, the most voracious and proliferating herbivore across human-modified landscapes in the Neotropics. Here, we evaluate the effect of chronic anthropogenic disturbance (*e.g.*, firewood collection, livestock grazing) and vegetation seasonality on foraging area, foliage availability in the foraging area, leaf consumption and herbivory rate of the leaf-cutting ant *Atta opaciceps* in the semiarid Caatinga, a mosaic of dry forest and scrub vegetation in northeast Brazil. Contrary to our initial expectation, the foraging area was not affected by either disturbance intensity or the interaction between season and disturbance intensity. However, leaf consumption and herbivory rate were higher in more disturbed areas. We also found a strong effect of seasonality, with higher leaf consumption and herbivory rate in the dry season. Our results suggest that the foraging ecology of leaf-cutting ants is modulated by human disturbance and seasonality as these two drivers affect the spectrum and the amount of resources available for these ants in the Caatinga. Despite the low productivity of Caatinga vegetation, the annual rates of biomass consumption by *A. opaciceps* are similar to those reported from other leaf-cutting ants in rain forests and savannas. This is made possible by maintaining high foraging activity even in the peak of the dry season and taking benefit from any resource available, including low-quality items. Such compensation highlights the adaptive capacity of LCA to persist or even proliferate in human-modified landscapes from dry to rain forests.

Abstract in Portuguese is available with online material.

Key words: ant–plant interactions; *Atta opaciceps*; chronic anthropogenic disturbance; foraging ecology; human-modified landscapes; leaf consumption; plant selection; seasonally dry tropical forests.

In tropical forests, changes in land use invariably cause habitat loss and fragmentation, including the resulting creation of forest edges (Laurance *et al.* 2014). This type of disturbance has been referred to as acute human disturbance and currently represents the main cause of species extinction, disruption in species interactions, reorganization of communities and depletion of ecosystem functions and services (Hansen *et al.* 2013). Additionally, the remaining vegetation in such human-modified landscapes experiences a more subtle disturbance known as chronic anthropogenic disturbances (*sensu* Singh 1998, hereafter chronic disturbances). In contrast to acute, chronic disturbance is sometimes imperceptible, because it refers to periodic but continuous removals of small portions of biomass (no habitat loss), such as firewood collection, exploitation of non-timber forest products, fodder for livestock and hunting (Singh *et al.* 1984, Martorell & Peters 2005). In addition to changes in vegetation structure and the physical environment (such as light levels), chronic disturbances may cause taxonomic, functional and phylogenetic impoverishment of woody plant communities (Ribeiro *et al.* 2015, 2016) and drive assemblages toward biotic homogenization due to the proliferation of disturbance-adapted species and the collapse of populations of sensitive species (Wiegmann & Waller 2006, Ribeiro-Neto *et al.* 2016).

Some leaf-cutting ant species (LCA; fungus-growing ants of the genus *Atta*) have been reported to respond positively to human disturbances, proliferating across several habitats in human-modified landscapes such as pastures, crop fields, roads, regenerating forest patches, small forest fragments and forest edges (Wirth *et al.* 2007, Meyer *et al.* 2009, Vieira-Neto *et al.* 2016). Such proliferation has been proposed to result from a combination of several processes, including (1) a higher

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availability of nesting sites in open areas (Vasconcelos *et al.* 2006), and (2) reduced population control via the relaxation of both bottom-up (increased availability of pioneer plant species, largely preferred by LCA; Farji-Brener 2001, Falcão *et al.* 2011) and top-down (less parasitoid phorid flies and predators such as armadillos and anteaters; Rao 2000, Almeida *et al.* 2008) forces. LCA may affect plant assemblages directly through foliage removal and seed dispersal, and indirectly via decreasing topsoil fertility and increasing light levels in nest and foraging areas (see reviews in Leal *et al.* 2014, Farji-Brener & Werenkraut 2015, Tabarelli *et al.* 2017). The net outcomes of these effects negatively affect plant regeneration, reduce seed germination and seedling/sapling recruitment of shade-tolerant and disturbance-sensitive species and alter the dynamic and structure of tree assemblages (Wirth *et al.* 2003, Corrêa *et al.* 2010, 2016, Meyer *et al.* 2011, Costa *et al.* 2016).

Regarding their role as herbivores, LCA are key organisms capable of harvesting *ca.* 70 to 500 kg of dry weight/colony/yr (Wirth *et al.* 2003, Herz *et al.* 2007, Costa *et al.* 2008). Area-based herbivory rates of LCA vary from 2.1% of the available foliage in an undisturbed late-successional forest in Panama (0.52 *A. colombica* colonies/ha, Herz *et al.* 2007) to 36% at the edge of human-modified Atlantic forest (2.79 *A. cephalotes* colonies/ha, Urbas *et al.* 2007, Wirth *et al.* 2007). The latter value greatly exceeds the overall rate of herbivory estimated for tropical forests (5–15%, Coley & Barone 1996). Accordingly, LCA herbivory impacts plant fitness, demography and community structure (Corrêa *et al.* 2010, 2016, Leal *et al.* 2014). Most research on LCA herbivory has been conducted in tropical rain forests and savannas (*e.g.*, Cherrett 1968, Blanton & Ewel 1985, Vasconcelos *et al.* 2006, Urbas *et al.* 2007, Costa *et al.* 2008, Corrêa *et al.* 2010), but little is known about their plant consumption (Rockwood 1975) and how populations are affected by human disturbances in other Neotropical biomes such as seasonally dry tropical forest (but see, Barrera *et al.* 2015 and Tabarelli *et al.* 2017).

Brazil's dry forest—the Caatinga—is mosaic of seasonally dry tropical forests and scrub vegetation (*sensu* Pennington *et al.* 2009) originally covering 884,453 km² of northeastern Brazil (Leal *et al.* 2005). It supports dense (26 inhabitants/km², Medeiros *et al.* 2012) and low-income human populations (Ab'Saber 2000) that are strongly dependent on natural resources for their subsistence (Vergles *et al.* 2015). Resource use typically includes grazing of native vegetation by livestock (Leal *et al.* 2003), firewood collection (Cavalcanti *et al.* 2015), exploitation of bark and leaves for medicinal use (Albuquerque *et al.* 2007), hunting (Alves *et al.* 2009) and slash-and-burn agriculture (Pereira *et al.* 2001), all chronic disturbances considered potential forces driving species interactions (Leal *et al.* 2017, Câmara *et al.* 2018) and the ecology of LCA in Caatinga human-modified landscapes (Tabarelli *et al.* 2017). In fact, acute impacts such as edge effects on tree assemblages—one of the main drivers of LCA proliferation in tropical rain forests—have been found to be negligible in Caatinga dry forest due to its low stature and reduced canopy cover (Oliveira *et al.* 2013). Consequently, all light-related mechanisms influencing LCA populations and their herbivory levels in tropical rain forest are expected to have less of an effect in the Caatinga vegetation (Siqueira *et al.* 2017). On the other hand, LCA achieve extremely high densities in chronically disturbed habitats in this biome (Siqueira *et al.* 2017). Therefore, depending on their herbivory under variable disturbance levels, these ants may represent a driver of regeneration dynamics and the successional trajectory experienced by Caatinga vegetation.

In this study, we investigate the effect of chronic disturbance on herbivory rate of the LCA *A. opaciceps* in the Caatinga dry forest. In view of the pronounced seasonality of this vegetation, we also evaluated the variation in herbivory rates of this species between rainy and dry season. As the Caatinga is more open and has a higher proportion of deciduousness than tropical rain forests (Pennington *et al.* 2009), we hypothesize a decrease in the herbivory rate with increasing disturbance and during the dry season. Thus, we predict that, with increasing disturbance, *A. opaciceps* colonies will have (1) larger forging areas (under the assumption that foraging effort is increased due to reduced food plant availability), (2) reduced foliage availability in the foraging areas, (3) decreased leaf consumption, (4) decreased herbivory rate, and (5) that these changes in foraging patterns will be more pronounced during the dry season.

METHODS

STUDY SITE.—This work was carried out in the Catimbau National Park (8°24′00′′ and 8°36′35′′ S; 37°0′30′′ and 37°1′40′′ W), located in the state of Pernambuco, northeastern Brazil (hereafter Catimbau). The climate is semiarid, with annual temperature averaging 23°C, and mean annual rainfall varying from 480 to 1100 mm, concentrated between March and July (Sociedade Nordestina de Ecologia 2002). Deep sandy soils are predominant in Catimbau (quartzite sands, 70% of area), but planosols and lithosols are also present (15% each one; Sociedade Nordestina De Ecologia 2002). Vegetation is dominated by low-statured trees with Fabaceae, Euphorbiaceae and Boraginaceae as the predominant plant families, while the ground layer is composed of Cactaceae, Bromeliaceae, Malvaceae, Asteraceae and Fabaceae (Rito *et al.* 2017a).

STUDY SPECIES.—Three *Atta* species occur in Catimbau: *A. laevigata* (Smith, 1985), *A. opaciceps* (Borgmeier, 1939) and *A. sexdens* (L. 1758) (Siqueira *et al.* 2017). *Atta opaciceps*, the focal species in this study, is considered to be endemic to the Caatinga region (Ulysséa & Brandão 2013) and is thus tolerant to low humidity and high temperatures. In Catimbau, *A. opaciceps* achieves a high population density (2.45 colonies/ha) and ranges from open habitats (*e.g.*, abandoned field crops) to forest patches (Siqueira *et al.* 2017). The deposition of soil above nests is quite irregular, formed either by a single large mound similar to *A. laevigata* or, less frequently, by several small mounds similar to that of *A. sexdens*. They have external refuse dumps, which are annually renewed in the beginning of the rainy season, when nest cleaning and maintenance is increased.

Study design and methods.—To test whether the LCA foraging behavior is affected by disturbance intensity, eight adult and active colonies of *A. opaciceps* were selected in vegetation patches exposed to different levels of disturbance. Mean nest size was 38.67 m^2 (±5.04, mean ± SD), and nests were on average 2.25 km (±1.70) apart, occupying a total area of 9.33 km^2. Around each colony, disturbance was computed as a global multi-metric index (hereafter disturbance index) using the method adapted by Arnan *et al.* (2018). The disturbance index integrates nine disturbance indicators related to the two main sources of chronic disturbance at Catimbau: livestock and human pressure via collection of forest products (Rito *et al.* 2017a). Taking into account these main sources of disturbance, we adopted the following groups of descriptors: (1) descriptors correlated with the disturbance by livestock, (2) descriptors related to firewood and timber collection and (3) descriptors associated with human pressure in general (i.e., exploitation of non-timber forest products, hunting). For the first two groups, the following descriptors were measured in a 100-m buffer around each colony: (1) animal dung density (goats, sheep, horses and cattle); (2) the number of trails of goats and sheep; and (3) the number of cut stumps (indicative of stem cutting at low height). For the third group of descriptors, we considered the following: (1) the distance to the farms' headquarters (Fazenda Brejo or Fazenda Angico), (2) distance to roads (BR-232 or PE-270, two highways at the region), (3) distance to vicinal unpaved roads that give access to the farms and (4) distance to the nearest town (Arcoverde or Buíque) (Ribeiro *et al.* 2015). It was assumed that natural resources near human settlements tend to be exploited first, producing 'sequential waves of forest degradation' (Ahrends *et al.* 2010). We then calculated the disturbance index as the sum of the nine descriptors using the following formula proposed by Legendre and Legendre (1998): $\mathrm{DI} = \frac{\sum_{i=1}^{n}(y_i - y_{\min})/(y_{\max} - y_{\min})}{n} \times 100$, where DI is the disturbance index, y_i is the observed value for one descriptor in colony i, $y_{\min}$ is the minimum observed value for the descriptor considering all colonies, $y_{\max}$ is the maximum observed value for the descriptor considering all colonies and n is the number of individual descriptors considered in the index. By this, the formula first standardizes the values of each disturbance descriptor to a range between 0 and 1 in order to weigh them equally. The overall disturbance index varies from 0 (zero values for all component metrics) to 100 (maximum values of all component disturbance metrics) (for more details on chronic disturbance index see Arnan *et al.* 2018).

To investigate LCA foraging and herbivory, the daily activity pattern of a subset of five of our eight *A. opaciceps* colonies was assessed prior to data collection. For this, the colonies' foraging activity was examined via 24-h censuses in May and December as representative months for the rainy and dry season, respectively (see details in Electronic supplementary material—Daily foraging activity—and Wirth *et al.* 1997). We found a stable circadian foraging rhythm throughout the year (Fig. S1), which allowed us to make standardized measurements of foraging characteristics for all eight focal *A. opaciceps* colonies between 8 pm and 10 pm—the peak times of their foraging activity during the rainy (March–July) and dry (August–February) season, respectively. In the following, we provide details on the assessment of (1) foraging area, (2) foliage availability in the foraging areas, (3) consumption rate, (4) herbivory rate and (5) dietary composition.

Foraging area.—Our foraging area estimates for the eight focal colonies were based on trunk trails (cleared foraging trails >5 cm width), which describe the colony's main, long-term foraging zones (Wirth *et al.* 2003). Trunk trails were examined during the time of peak daily foraging activity 1 d a month from March to July (5 mo) in the rainy season and from August to February (7 mo) in the dry season. All active foraging trails were followed from the nest entrance to the place where the ants were cutting plant material, and trails were mapped with a GPS (Global Positioning System, Garmin e-Trex 10), which resulted in an error of less than 3 m. Maps of foraging trails were generated using Corel Draw 8.0 software (Corel Corporation, Ottawa, Canada). To determine the seasonal foraging area of the colonies, we delimited a zone of 20 m around all trails and superimposed the monthly maps of the trails of rainy (March–July) and dry (August–February) months. This 20-m zone has been considered a reasonable proxy for LCA foraging areas (see Wirth *et al.* 2003, Urbas *et al.* 2007 for more details).

Foliage availability.—To estimate the foliage availability across the foraging areas of the eight LCA colonies, we calculated the leaf area index (LAI, total one-sided area of leaves per unit ground surface area) by means of digital hemispherical photographs (Urbas *et al.* 2007). Hemispherical photographs capture the light obstruction/penetration patterns in the canopy and supply gap fraction data that calculate LAI by mathematical inversion of a light interception model (Norman & Campbell 1989). We sampled the LAI within the foraging area of the colonies adopting a 100 × 80 m grid, with the nest occupying the central position. The grid was split into two pairs of parallel; north-to-south-oriented transects set up 20 m west and east of the nest, respectively, to avoid the influence of nest clearings (Farji-Brener & Illes 2000). Along the four transects, we took pictures at 20-m intervals, totalling 20 pictures per colony. We took the photographs on eight consecutive days (1 d for each colony) at about 1 m aboveground with a Nikon DX 3000 equipped with fisheye converter FC-E8. The photographs were taken under diffuse light conditions during morning (05:00–06:30 h) and evening (16:00–17:30 h) hours to avoid image contrast and errors from foliage reflection of direct sun light in the canopy (Whitmore *et al.* 1993). LAI estimation was performed during May and December as representative months for the rainy and dry season, respectively. The average values of the LAI were multiplied by the foraging area of each colony for both rainy (March–July) and dry (August–February) season, obtaining the amount of foliage (in m^2) per season available to the colonies.

Consumption rate.—To estimate plant consumption by LCA, we sampled each month (March–July as rainy months and August–February as dry) all ants carrying plant fragments (leaves, flowers and seeds) at 5-min intervals during the peak of daily activity on trunk trails (Urbas *et al.* 2007). Plant fragments were packed in plastic bags, and later placed on a scanner for size measurement (Epson Ecotank L375). The surface area of the collected fragments was obtained using Image J software (Abràmoff *et al.* 2004). After measuring the area, the fragments were placed in a stove and dried to a constant weight at approximately 70°C for dry weight determination.

Based on these measurements, foliage removal was calculated by predicting daily totals from previously established regression equations relating 24-h counts of leaf fragments (F_{24d}) to the respective 5-min counts at the daily foraging peak (F_{5d}) during the two seasons; dry season totals: $F_{24d} = 334.76 + (-56.75) \times F_{5d} + (2.48) \times F_{5d}^{2}$; ($R^2 = 0.7186$, $P = 0.0037$, $N = 5$); rainy season: $F_{24w} = 117.84 + (-\ 8.79) \times F_{5w} + (0.82) \times F_{5w}^{2}$; ($R^2 = 0.6319$, $P = 0.0113$, $N = 5$). Then, to obtain area- and biomass-based consumption rates per day, we replaced the respective value of number of fragments in 5 min by the average area or biomass calculated for the whole samples. These daily estimates were extrapolated to achieve monthly and annual consumption rates. To avoid disproportionate contribution of the season length, we calculated mean monthly consumption rate of rainy (March–July) and dry (August–February) months.

Herbivory rate.—We defined herbivory rate as the leaf area harvested by a colony relative to the leaf area available in its respective foraging area and calculated it through the following equation: $\mathrm{HR} = \frac{\mathrm{LC}}{(\mathrm{LC+AVC})} \times 100$, where HR is the herbivory rate, LC is leaf area consumption and AVC is the available foliage area after consumption (*sensu* Wirth *et al.* 2003). As for consumption, the daily herbivory rate was extrapolated to obtain monthly values, which were presented as mean monthly herbivory rate of rainy (March–July) and dry (August–February) months to avoid disproportional contribution of season length.

Dietary composition.—To characterize the dietary composition of *A. opaciceps*, we identified plant species and parts carried into the nest during monthly surveys throughout the study year. For this, foraging ants of the eight focal colonies were followed from the nest to the cutting spots. Samples of the cut plant material were taken from the ants and from the harvested plant species to facilitate identification in the field when possible. Undetermined species were morphotyped and later identified at the lowest possible taxonomic level with the help of taxonomists.

Statistical analysis.—To test the hypothesis that CAD and seasonality affect herbivory of *A. opaciceps*, we used full factorial generalized linear mixed models (GLMM) with Poisson error distribution as adopted by Bates *et al.* (2015), with the disturbance index as a continuous fixed predictor, season (rainy and dry) as a categorical fixed predictor, and LCA colony as a random factor. The dependent variables consisted of colony foraging area, leaf area index, vegetation availability in the foraging area, consumption rate (in biomass and leaf area) and herbivory rate. All analyzes were performed using the package lme4 (Bates *et al.* 2015) for the R statistical programming language (R Development Core Team 2015).

RESULTS

The average foraging area of the eight focal colonies was nearly five times larger in the dry ($18{,}242.5\ m^2 \pm 15{,}749.13$, mean ± SD) compared to rainy ($4645\ m^2 \pm 2820.92$) season (Fig. 1A; Table 1). Contrary to our prediction, the foraging area was not affected by either disturbance or the interaction between season and disturbance intensity (Fig. 1A; Table 1). The available foliage was highly variable across foraging areas and reached in average $2189.45\ m^2$ (±2289.32) in the dry season and $3284.18\ m^2$ (±3433.98) in the rainy season (Fig. 1B-C; Table 1). This 1.5-fold difference was due to the low average LAI in the dry season (0.12 ± 0.11) compared to rainy season (0.18 ± 0.16, Fig. 1B; Table S1). Foliage availability declined with increasing disturbance, and this effect was particularly strong in rainy season (Fig. 1B; Table 1).

LCA colonies consumed significantly more plant material during the dry season in terms of both biomass (Fig. 1D; Table 1) and leaf area (Fig. 1E; Table 1). Precisely, colonies consumed 19.19 kg (±7.18) of biomass per month during the dry season but only 15.97 kg (±6.24) of biomass per month in the rainy season (Table S2). The same pattern was observed for leaf area as it reached $135.62\ m^2$ (±41.62) consumed per month in the dry season vs. $46.18\ m^2$ (±14, 79) in the rainy season (Table S2; Table 1). Scaling up these season-adjusted monthly rates, the annual harvest of *A. opaciceps* colonies amounts to 243.79 kg (±96.61) of plant biomass/colony/yr or $1170.74\ m^2$ (±357.66) of foliage/colony/yr. Vegetation consumption measured as biomass increased with increasing disturbance intensity (Fig. 1D; Table 1), but this effect was not observed for leaf area consumption (Fig. 1E; Table 1). In neither case was there an interaction between season and disturbance intensity (Table 1).

Colony herbivory rate was highly variable in both seasons, ranging from 9.1% to 98.8% in the dry season, and 1.6% to 93.4% in the rainy season. Overall, however, LCA removed twice as much foliage in the dry season (45.2% ± 31.56) as compared to the rainy season (22.2% ± 31.03, Fig. 1F). The rate of herbivory also increased with increasing disturbance (Fig. 1F), and there was no interaction between season and disturbance (Table 1).

A total of 11,696 fragments (leaves, flowers and seeds) from 38 different resource types, were collected in the annual diet of focal colonies. Among these resources, a total of 36 plant species within 12 families were recorded (Table 2). The woody species *Croton argyrophylloides* (18%), *Cenostigma microphylla* (10%) and *C. pyramidalis* (7%) were the most frequent species in the *A. opaciceps* diet (Table 2). However, non-tree items represented around 30% of the plant material harvested by *A. opaciceps* colonies, with

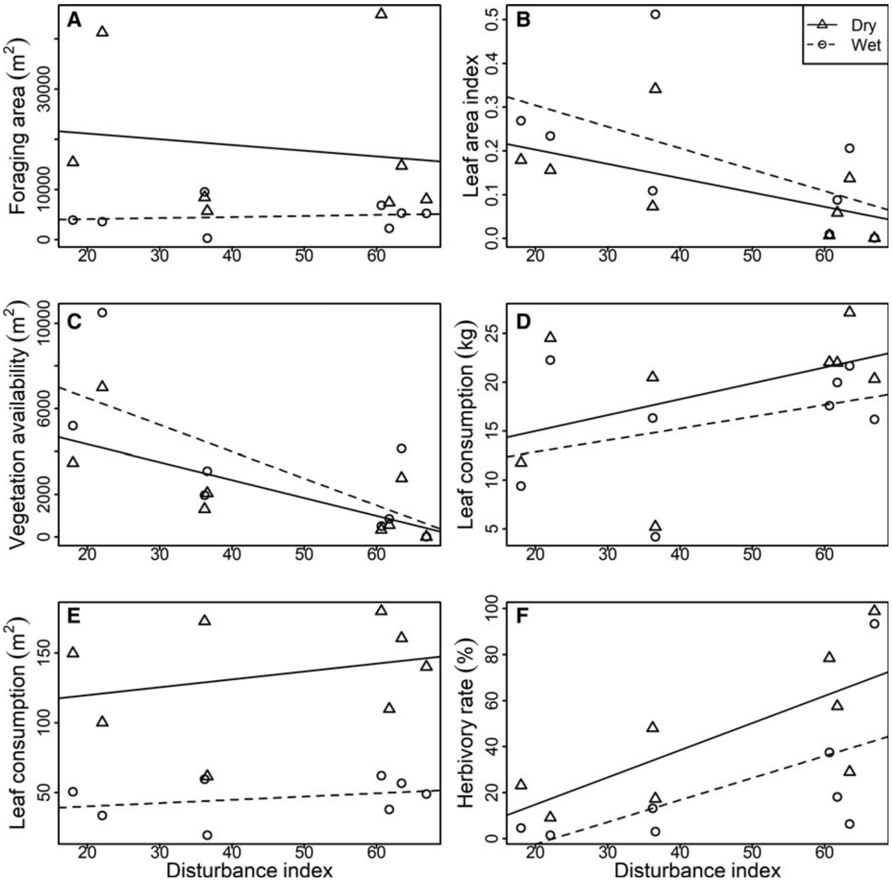

FIGURE 1. Mean values of foraging area (A), leaf area index in the foraging area (B), vegetation availability (C) monthly biomass of leaf consumption (D), monthly area of leaf consumption (E) and herbivory rate (F) of eight colonies of *Atta opaciceps* during dry and rainy season plotted along a chronic anthropogenic disturbance gradient (disturbance index) in the Catimbau National Park, state of Pernambuco, Northeast Brazil.

two species of herbs, *Portulaca elatior* and *Sida galheirensis*, accounting for 10% of the fragments collected, while several cacti species collectively represented almost 17%. LCA were also recorded to use dry leaves on the ground below trees, biological soil crusts and fecal pellets of goats and lizards (Table 2).

DISCUSSION

By demonstrating that LCA harvest biomass from Caatinga vegetation at similar levels to those reported in tropical rain forests (*e.g.*, 266 kg/colony/yr in *A. colombica*, Herz *et al.* 2007) and savannas (*e.g.*, 173 kg/colony/yr in *A. laevigata* and *A. sexdens*, Costa *et al.* 2008), our study (244 kg/colony/yr) extends the key ecological role of LCA into the dry forest biome. Based on a single year, but exhibiting regular dry and wet season, our results suggest that both disturbance and seasonality affect the available vegetation and the foraging behavior of *A. opaciceps* in Caatinga. Briefly, (1) the foraging area is larger during the dry season, but it is not affected by disturbance, (2) the available vegetation in foraging areas is lower during the dry season, and it is negatively affected by disturbance, (3) LCA consume more vegetation in terms of both biomass and leaf area during the dry season, particularly in more disturbed sites and (4) herbivory rate is higher during the dry season and increases in response to disturbance. Although highly variable across colonies and seasons, LCA are able to harvest a substantial proportion of the available vegetation, including a large spectrum of resources.

These findings reinforce the notion that human disturbances affect many aspects of the ecological relationship between LCA and their environments as well documented in tropical rain forests, such the Atlantic and Amazonian forests (Vasconcelos 1988, Rao 2000, Corrêa *et al.* 2010, Dohm *et al.* 2011, Meyer *et al.* 2013, respectively), and Cerrado savanna (Costa *et al.* 2008, Vieira-Neto *et al.* 2016). But in contrast to rain forests, in which LCA concentrate plant harvesting on tree species, in the Caatinga other plant resources are apparently crucial such as herbs (annual dicotyledonous species) and perennial Cactaceae, in addition to litter and feces. Such polyphagia and opportunistic behavior has been considered a crucial aspect of LCA ecology, which allows them to inhabit and proliferate across a large range of habitats, including those disturbed/created by human activities such as pastures, plantation, roads, secondary forest patches, small forest

TABLE 1. *Effects of season, disturbance index and their interaction on foraging area, vegetation availability, consumption rate (kg and* m^2*), and herbivory rate of colonies of* Atta opaciceps *in the Catimbau National Park, state of Pernambuco, Northeast Brazil. Significant effects are in bold (*$P < 0.05$*) of the full factorial generalized linear mixed models.*

Response variable	Effect	df	*F*	*P*
Foraging area	Season	1.6	6.65	**0.04**
	Disturbance index	1.6	0.07	0.80
	Season*Disturbance index	1.6	0.28	0.77
Leaf area index	Season	1.6	11.75	**0.01**
	Disturbance index	1.6	6.65	**0.04**
	Season*Disturbance index	1.6	3.03	0.13
Vegetation availability	Season	1.6	13.14	**0.01**
	Disturbance index	1.6	6.57	**0.04**
	Season*Disturbance index	1.6	6.57	**0.04**
Consumption rate (Kg)	Season	1.6	35.35	**0.01**
	Disturbance index	1.6	6.64	**0.04**
	Season*Disturbance index	1.6	0.22	0.66
Consumption rate (m^2)	Season	1.6	83.12	**0.01**
	Disturbance index	1.6	0.55	0.49
	Season*Disturbance index	1.6	0.45	0.53
Herbivory rate	Season	1.6	20.40	**0.01**
	Disturbance index	1.6	5.54	**0.05**
	Season*Disturbance index	1.6	0.65	0.45

fragments and forest edges (Vasconcelos *et al.* 2006, Wirth *et al.* 2007, Dohm *et al.* 2011). Our findings in the Caatinga amplify the perspective that LCA benefit and tend to become human commensals as natural landscapes are converted into human-modified landscapes.

It is not surprising that LCA exhibit larger foraging areas during the dry season as the deciduous Caatinga vegetation has much less to offer per unit of area compared to the rainy season. Note that, during the dry season, most of the Caatinga patches support just few evergreen trees or shrubs (Machado *et al.* 1997). Such scarcity probably forces LCA to compensate by accessing extra areas and other sources to obtain the amount of vegetation needed to sustain the fungus garden. We refer, for example, to transient herbaceous resources (*e.g.*, *Portulaca elatior* and *Sida galheirensis*), flowers from several species, Cactaceae cladodes, dry leaves on the ground and scavenging on animal feces, as observed in our study. Therefore, in view of the scarcity and scattered distribution of resources in the dry season, the spatial extension of the foraging area is consistent with predictions of the optimal foraging theory (Pyke *et al.* 1977).

In contrast, it seems surprising that LCA collected in absolute terms more material in the dry season than in the rainy season, resulting in higher herbivory rates. In fact, the rates estimated here (45% in dry season vs 22% in rainy season) are substantially higher than stand-level herbivory rates reported from other systems such as tropical rain forests: 12.5% and 14%

TABLE 2. *Plant species and other food items collected by eight colonies of* Atta opaciceps *in Catimbau National Park, Pernambuco state, Northeast Brazil. The overall frequency of use (%) and the plant parts collected by the ants are presented. *We treated cladodes in Cactaceae species as leaves.*

Families/Species	Leaf	Flower	Seed	Frequency of use (%)
Anacardiaceae				
Schinopsis brasiliensis Engl.	X			1.13
Spondias tuberose Arruda	X			0.55
Boraginaceae				
Cordia bullata Jacq.	X	X	X	3.31
Cactaceae				
Cereus jamacaru DC.		X	X	2.76
Melocactus zehntneri Britton & Rose		X	X	2.27
Pilosocereus gounellei A. Weber		X	X	1.7
Pilosocereus pachycladus Ritter		X	X	2.76
*Tacinga inamoema** K. Schum	X		X	6.08
*Tacinga palmodora** Britton & Rose	X		X	0.55
Capparaceae				
Colicodendron yco Mart.	X			0.55
Convolvulaceae				
Ipomoeae sp.1	X	X		0.55
Euphorbiaceae				
Cnidoscolus obtusifolius Pohl	X	X		6.08
Cnidoscolus quercifolius Pohl	X	X		2.76
Croton argyrophylloides Müll. Arg	X	X	X	17.12
Croton grewioides Baill.	X	X	X	0.55
Croton micans Swartz	X	X		0.55
Jatropha mollissima Pohl	X	X		1.1
Jatropha mutabilis Pohl (Baill)	X	X		2.76
Jatropha ribifolia Pohl (Baill)	X	X		1.66
Fabaceae				
Fabaceae sp.1			X	0.55
Cenostigma microphyllum (Mart. ex G. Don) E. Gagnon & G. P. Lewis	X	X		9.39
Cenostigma pyramidale (Tul.) Gagnon & G. P. Lewis	X	X		7.18
Peltogyne pauciflora Benth.	X			0.55
Peltophorum dubium Spreng.	X	X		0.55
Pityrocarpa moniliformes Benth	X		X	2.21
Prosopis juliflora Sw.	X	X		0.55
Senegalia bahiensis Benth	X			0.55
Senna spectabilis DC.	X	X		1.1
Lianas				
Liana sp.1	X		X	1.34
Malvaceae				
Sida galheirensis Ulbr.	X	X		7.18
Poaceae				
Poaceae sp.1	X			1.1
Portulacaceae				
Portulaca elatior Mart.	X	X		6.08

(continued)

Table 2 *(continued)*

Families/Species	Leaf	Flower	Seed	Frequency of use (%)
Rhamnaceae				
Ziziphus joazeiro Mart.	X	X	X	1.1
Verbenaceae				
Verbenaceae sp.1	X		X	0.55
Others				
Biological soil crusts				0.55
Feces of goat				0.55
Feces of lizard				0.55

according to Wirth *et al.* (2003) and Urbas *et al.* (2007), respectively, and 17% in Brazilian savannas (Costa *et al.* 2008). This is probably largely due to the high proportion of herbs, cacti, litter, feces, and other non-tree materials in the LCA harvest and the fact that hemispheric photographs (at 1 m above the ground according to the standard protocol for LAI estimates) were not able to capture these materials, resulting in a considerable underestimate of the foliage availability. In fact, if we remove the 30% of fragments that come from these materials not captured by LAI estimates, herbivory rate is reduced to 37% in the dry season and 17% in the rainy season, showing that herbs, cacti and other non-tree materials are more commonly harvested during the dry season. Accordingly, future studies should consider measuring foliage availability on the ground and in the herb layer, as it is now clear that even forest species of LCA access non-tree materials as unexpectedly reported here for *Atta opaciceps*, but also observed for *A. laevigata* and *A. sexdens* in the study area (F. Siqueira pers. obs.).

Such high proportion of herbs, cacti and other non-tree materials is not common for the dietary composition of *Atta* ants, particularly in forest species, which are well known to prefer arboreal or liana life forms (Cherrett 1968, Blanton & Ewel 1985, Wirth *et al.* 2003, Falcão *et al.* 2011). For example, herbs made up less than 2% of the overall leaf harvest of *A. colombica* in Central American rain forest (Wirth *et al.* 2003). As a working hypothesis to explain the high dry-season consumption of *A. opaciceps*, we suggest that LCA compensate for low-quantity/-quality foliage by harvesting more materials, particularly in the dry season. We refer to litter and conservative/tough leaves, which the symbiotic fungus is not able to properly metabolize due to high contents of lignin and cellulose (in fibers and cell wall components) (Bucher *et al.* 2004). In other words, only a small fraction of all material transported to nests is consumed/metabolized in comparison to fresh tissues available in the rainy season, explaining why LCA collect more. In this perspective, low leaf quality during the dry season may also result from water deficits in plant tissues, which increase the concentration of secondary compounds (Gershenzon 1984) with LCA-repellent or fungicidal effects (*e.g.*, terpenoids, Howard 1988). However, the effects of drought on plant defensive compounds are complex, highly dependent on plant species, and basically unstudied for Caatinga plants.

Biomass consumption in absolute terms was also positively associated with disturbance, suggesting that although disturbance negatively affects woody vegetation availability (as measured by hemispherical photographs), it may (1) somehow increment the availability of palatable, light-demanding woody plants as documented across edge-affected habitats of Neotropical rain forests (Santos *et al.* 2008) or (2) increment the availability of light-demanding herbs (Lima *et al.* 2015). In fact, human disturbance in the Caatinga vegetation is positively associated with the proliferation of light-demanding herbaceous species (Vieira 2017) and disturbance-adapted woody species such as *Croton*, *Jatropha* and *Cenostigma* genera (Ribeiro *et al.* 2015, 2016); *that is,* the winner species *sensu* Tabarelli *et al.* (2012). In addition to *Croton* and *Jatropha*, other Euphorbiaceae species are regarded as good colonizers that proliferate in disturbed areas of Caatinga (*e.g.*, Ribeiro *et al.* 2015, Ribeiro-Neto *et al.* 2016, Rito *et al.* 2017b); some of them apparently preferred by LCA as the two *Cnidoscolus* species documented here. The two herbs most frequently used by LCA, *Portulaca elatior* and *Sida galheirensis*, are also very abundant and widely distributed in the Catimbau, especially in disturbed areas (Vieira 2017). This selectivity for more abundant plants that are good colonizers is already known for other species of leaf-cutting ants in tropical rain forests (Farji-Brener 2001, Wirth *et al.* 2003, Urbas *et al.* 2007, Falcão *et al.* 2011).

While LCA harvest in terms of biomass was higher in more disturbed sites, this was not the case for leaf area-based consumption rates. Relationship among leaf area, toughness, thickness and dry biomass are important traits concerning plant resistance to drought (Westbrook *et al.* 2011), and this rather than light, as in tropical rain forests, must drive leaf suitability to LCA in dry forests as the Caatinga. More specifically, the higher the environmental temperature and water deficit, the smaller, thicker and tougher the leaves, leading to a high foliar mass per area (Poorter *et al.* 2009). Again, this is the case for some woody Euphorbiaceae species (genera *Croton*, *Jatropha* and *Cnidoscolus*) already mentioned here to proliferate in disturbed Caatinga (Ribeiro *et al.* 2015, 2016, Rito *et al.* 2017b) and frequently harvested by LCA in these areas, although thick leaves have not been considered the most palatable resources for LCA (Nichols-Orians & Schultz 1989). These species present very different leaf sizes, but a common trait is that leaves are thick, helping to explain the fact that we found a relationship between disturbance and leaf biomass consumed, but failed to find such a relationship between disturbance and leaf area consumed.

This argument is in accordance with our perception that overall the available vegetation in the Caatinga has low quality and is particularly scarce in the dry season, forcing LCA to opportunistically collect what is available in high quantities, but with low substrate-use efficiency of the symbiotic fungus. Concretely, the non-deciduous dry forest vegetation is generally characterized by high degree of sclerophylly (thick, tough leaves with a high cell wall: cytoplasm ratio of the tissues; Loveless 1961) and there is considerable evidence that sclerophylly constitutes a plant mechanical defense against chewing herbivores (Coley 1983, Lowman & Box 1983). Even those herbs and woody species that proliferate in disturbed habitats supporting the harvest increments can be considered low-quality resources as compared to the soft leaves frequently found in rain forests (Westbrook *et al.* 2011). The degradation of such recalcitrant plant material by the mutualist fungus may be limited (Aylward *et al.* 2013) and may explain the conspicuous deposition of external refuse during the beginning of the rainy season, as we have observed not only for *Atta opaciceps*, but also for the two other species occurring in Catimbau *A. laevigata* and *A. sexdens* both well known so far as species with internal refuse dumps in other ecosystems (Leal *et al.* 2014). This represents an additional explanation to the hypothesis proposing external refuse dumps as less costly than internal refuse chambers, but it is only possible in pathogen-free environments such as the semiarid zones (Farji-Brener *et al.* 2016).

Moving to applied implications, we shall mention that the Caatinga vegetation is a naturally harsh environment for seedling recruitment and growth due to water scarcity imposed by the dry season and frequent long droughts (Machado *et al.* 1997). LCA proliferation in disturbed Caatinga patches (Siqueira *et al.* 2017, Tabarelli *et al.* 2017) and the ability of LCA to harvest substantial quantities of foliage throughout the year, including leaves considered of low quality for the symbiotic fungus, naturally raise the question about ecosystem-level impacts or engineering processes as described elsewhere (Wirth *et al.* 2003, Meyer *et al.* 2013). Particularly relevant is the question whether seedlings have chances of long-term survival while inhabiting LCA foraging areas, particularly of evergreen species. There have been plenty of anecdotal reports calling attention to the scarcity of woody species seedlings in the Caatinga vegetation and the omnipresence of LCAs might play a key role in the arrested succession experienced by Caatinga patches following land abandonment (Tabarelli *et al.* 2017).

In synthesis, the foraging ecology of LCA is modulated by human disturbance and climatic seasonality as these two drivers affect the spectrum and the amount of resources available for LCA in the Caatinga. It is worth emphasizing that, despite the low productivity of dry forests, *A. opaciceps* LCA are able to achieve annual rates of biomass consumption similarly high to those reported from other LCA in rain forests (Wirth *et al.* 2003, Herz *et al.* 2007, Urbas *et al.* 2007). Probably, this is made possible by maintaining high foraging activity even in the peak of the dry season and taking benefit from any resource available, including low-quality items. Such compensation via increased harvesting highlights the adaptive capacity of LCA to persist or even proliferate in human-modified landscapes from dry to rain forests, but long-term monitoring is required to confirm the season-related trends we documented in the Caatinga. The potential and probably complex synergy between human disturbances, in this case chronic disturbances, proliferation of key resources (*e.g.*, light-demanding herbs, native woody winner species) and vegetation regeneration dynamic deserves further investigation.

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DATA AVAILABILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.00000 (Siqueira *et al.* 2018).

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

FIGURE S1. Daily foraging activity assessed in 2 h-intervals over 24 h in five *Atta opaciceps* colonies in the Catimbau National Park, state of Pernambuco, Northeast Brazil.

TABLE S1. *Values of leaf area index (LAI) recorded in the foraging area of eight colonies of Atta opaciceps in the dry and wet season in the Catimbau National Park, state of Pernambuco, Northeast Brazil.*

TABLE S2. *Amount of monthly vegetation harvested by eight colonies of Atta opaciceps in the dry and wet season in the Catimbau National Park, state of Pernambuco, Northeast Brazil.*

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