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INFLUÊNCIA DE PERTURBAÇÕES ANTRÓPICAS CRÔNICAS SOBRE AS INTERAÇÕES ENTRE PLANTAS E FORMIGAS CORTADEIRAS NA CAATINGA

Recife, 2017

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Tese apresentada ao Programa de Pós-Graduação em Biologia Vegetal da Universidade Federal de Pernambuco como um dos requisitos necessários para obtenção do título de Doutor em Biologia Vegetal.

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Coorientadores: Prof. Dr. Rainer Wirth

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“Buliram muito com o planeta
e o planeta como um cachorro eu vejo,
se ele já não aguenta mais as pulgas,
se livra delas num sacolejo.”

Raul Seixas

RESUMO

Alterações na composição de espécies ocasionadas por perturbações antrópicas são conhecidas por modificarem as interações entre espécies. As formigas cortadeiras (especialmente do gênero *Atta*) são um exemplo de organismos que proliferam com perturbações antrópicas. Devido às suas atividades de herbivoria e de alterações nas propriedades do solo e no regime de luz devido à construção e manutenção dos ninhos, as formigas cortadeiras provocam mudanças na composição de espécies de regenerantes e na dinâmica e estrutura da comunidade vegetal nas áreas do ninho e de forrageamento. A proliferação das formigas cortadeiras e sua influência nas comunidades de plantas são bastante conhecidas para florestas úmidas como Amazônia e floresta Atlântica, mas ainda não se tem informações sobre estas questões em áreas de Caatinga. O objetivo principal desta tese foi investigar o efeito das perturbações antrópicas crônicas sobre as populações de formigas cortadeiras do gênero *Atta* (Capítulo 1) e sobre as taxas de herbivoria da única espécie endêmica da Caatinga, *Atta opaciceps* (Capítulo 2). No primeiro capítulo encontramos que a densidade de colônias ativas aumentou (de 2,55 ± 1,65 ha^{-1} para 15 ± 2,92 ha^{-1}) com a proximidade de estradas. O inverso foi encontrado para as colônias inativas. As colônias ativas ocorreram preferencialmente em áreas com baixa cobertura vegetal, enquanto as colônias inativas em áreas com alta cobertura vegetal. Com isso, demonstramos pela primeira vez que distúrbios antrópicos promovem a proliferação de formigas cortadeiras em florestas secas como a Caatinga. Adicionalmente, perturbações antrópicas crônicas tem um efeito positivo sobre as taxas de herbivoria de colônias de *Atta opaciceps* (de 5,34 % ± 5,32 para 96.09 % ± 3,87). Nós também encontramos um forte efeito da estação do ano em todas as variáveis relacionadas ao forrageamento das colônias (i.e. área de forrageamento das colônias, vegetação disponível na área de forrageamento, consumo foliar em biomassa e em área foliar), levando a maiores taxas de herbivoria na estação seca (45,18% ± 31,56) do que na chuvosa (22,24% ± 31,03), ocasionadas sobretudo pela menor disponibilidade de vegetação na estação seca. Esses resultados corroboram os padrões descritos para florestas úmidas, que indicam que áreas mais perturbadas têm vegetação mais palatável e proporcionam maior herbivoria por parte das colônias. A alta densidade de formigas cortadeiras aliada com alto consumo foliar, podem afetar a regeneração da vegetação de Caatinga via seu papel como herbívoro dominante e engenheiro de ecossistema como já relatado para florestas úmidas e savanas. Essa retirada de vegetação pode amplificar as mudanças ambientais ocasionadas por perturbações antrópicas crônicas, uma vez que valores altos de herbivoria aumentam a penetração de luz e a temperatura do ar e do solo, ao mesmo tempo em que reduzem a umidade do ar e do solo. Esses resultados suportam a ideia de que as formigas cortadeiras são um dos grupos vencedores de paisagens modificadas por atividades humanas na Caatinga.

Palavras-chave: Florestas tropicais sazonalmente secas. Paisagens humanas. Efeitos de estradas. Sazonalidade. Herbivoria. Seleção de plantas cortadas. *Atta laevigata*. *Atta opaciceps*. *Atta sexdens*.

ABSTRACT

Changes in species composition caused by anthropogenic disturbances are known to modify interactions between species. Leaf-cutting ants (especially of the genus *Atta*) are an example of organisms that proliferate with anthropogenic disturbances. Because their activities of herbivory and physical alterations of soil and light regime due to the construction and maintenance of the nests, leaf-cutting ants promote changes in plant recruitment and in the dynamics and structure of the plant assemblages in the nest area and foraging sites. The proliferation of leaf-cutting ants and its influence on plant communities are well known in rainforests as Amazon and Atlantic forest, but these questions have been completely neglected for Caatinga dry forest, although the strong role of leaf-cutting as key-species. The main objective of this thesis was to investigate the effect of chronic anthropogenic disturbances on populations of leaf-cutting ants (Chapter 1) and on the herbivory rate of the endemic species *Atta opaciceps* (Chapter 2). In the first chapter we find that the density of active colonies increases (from 2.55 ± 1.65 ha^{-1} to 15 ± 2.92 ha^{-1}) with the proximity of the road. The inverse pattern was found for inactive colonies. Active colonies occurred preferentially in areas with low vegetation cover, while inactive colonies were more frequent in areas with high vegetation cover. With this, we demonstrate for the first time that the anthropogenic disturbances promote the proliferation of leaf-cutting ants in dry forests as the Caatinga. Additionally, chronic anthropogenic disturbances positively influenced the herbivory rate of *Atta opaciceps* colonies (from 5.34 % ± 5.32 to 96.09 % ± 3.87). We also found a strong effect of the season on all variables related to foraging (i.e. foraging area of the colonies, vegetation available in the foraging area, foliar consumption in biomass and leaf area), leading to higher herbivory rate in the dry season (45.18% ± 31.56) as compared to the wet season (22.24% ± 31.03), mainly due to the lower availability of vegetation in the dry season. These results corroborate the patterns described for rainforests, which indicate that more disturbed areas have more palatable vegetation and proportionate higher herbivory rate by the colonies. The high density of leaf-cutting ants allied with high leaf consumption can affect the regeneration of the Caatinga vegetation through its role as dominant herbivore and ecosystem engineer as already reported for rainforests and savannas. This removal of vegetation can amplify the environmental shifts caused by chronic anthropogenic disturbances, since high values of herbivory increase light penetration and air and soil temperature, while reducing the humidity of the air and soil. These results support the idea that leaf-cutting ants are one of the winning groups of human modified landscapes in the Caatinga.

Key-words: Seasonally dry tropical forests. Human landscapes. Road effect. Seasonality. Herbivory. Plant selection. *Atta laevigata*. *Atta opaciceps*. *Atta sexdens*.

SUMÁRIO

1 APRESENTAÇÃO

Paisagens modificadas pela ação humana são tão antigas quanto à própria existência humana na Terra. O efeito dessas perturbações antrópicas, cada vez mais intensas, sobre a perda de biodiversidade e de serviços ecossistêmicos tem sido o foco de estudos há décadas. De maneira geral, tem-se registrado um declínio nas populações de espécies sensíveis à perturbação (LEES; PERES, 2006; PERES; PALACIOS, 2007; LAURANCE et al., 2011; RIBEIRO et al., 2015, 2016), perda não aleatória de diversidade taxonômica, funcional e filogenética (SILVA; TABARELLI, 2000; GIRÃO et al., 2007; SANTOS et al., 2010) e homogeneização biótica das comunidades de organismos em nível regional (Lôbo et al. 2011; Ribeiro et al. 2016). Essa é uma realidade também para as áreas de Caatinga, onde em torno de 54% da vegetação original, encontra-se distribuída em fragmentos de diferentes tamanhos e com diferentes graus de isolamento (MMA; IBAMA, 2011). Além disso, a vegetação remanescente sofre com perturbações crônicas como coleta de lenha, exploração de produtos florestais não madeireiros, caça e criação extensiva de animais domésticos (SAMPAIO, 1995; LEAL et al.; 2005; RIBEIRO et al., 2015). Embora o processo de alteração da paisagem natural da Caatinga tenha se acelerado nas últimas décadas, não se conhece ainda suas consequências para a perda da biodiversidade (para mais detalhes ver, RIBEIRO NETO et al., 2012; RIBEIRO et al., 2015; OLIVEIRA et al., 2016), muito menos para a dinâmica das interações entre espécies e suas implicações no estabelecimento e estrutura final das populações vegetais (CASTELETTI et al., 2004; LEAL et al., 2005). Sendo assim, é de fundamental importância entender como as perturbações antrópicas afetam as interações entre plantas e animais.

As formigas cortadeiras (gêneros *Atta* e *Acromyrmex*) são herbívoros dominantes dispersores/predadores de sementes e engenheiros de ecossistemas (i.e. organismos que alteram a disponibilidade de recursos para outras espécies *sensu* JONES; LAWTON; SHACHAK, 1994), sendo considerado organismos chave em florestas e savanas neotropicais (VASCONCELOS; CHERRETT, 1995; WIRTH et al., 2003; LEAL; WIRTH; TABARELLI, 2014). Além disso, sabe-se que formigas cortadeiras são um dos poucos grupos de organismos que se beneficiam do processo de perda e fragmentação de habitat em florestas, savanas e campos agrícolas (VASCONCELOS et al. 2006; URBAS et al., 2007; MEYER; LEAL; WIRTH, 2009; SILVA et al., 2009; DOHM et al., 2011). Será que em áreas de Caatinga essas formigas também são beneficiadas por perturbações antrópicas? Se sim, será que sua atividade de herbivoria é afetada por perturbações? Respostas a essas questões são de fundamental importância para o entendimento de como a pressão antrópica modifica algumas das interações planta-animal (e.g. planta-herbívoros e planta-dispersores de sementes), a dinâmica e estrutura da comunidade vegetal e a regeneração da vegetação da Caatinga, temas ainda pouco conhecidos pela comunidade científica. Dessa forma, o objetivo desse trabalho foi investigar o efeito de perturbações antrópicas crônicas sobre a interação entre plantas e formigas cortadeiras na Caatinga. Este trabalho é composto por dois capítulos estruturados em forma de artigos cientificos. O Capítulo I, intitulado "Leaf-cutting ant populations profit from human disturbances in dry forests in Brazil", que foi submetido ao periódico *Journal of Tropical Ecology*, teve como objetivo principal verificar como perturbações antrópicas afetam as populações de formigas cortadeiras em uma área de Caatinga. Já o Capítulo II, "Seasonality and human disturbances shape the foraging behavior and herbivory rate of the leaf-cutting ant *Atta opaciceps* in the Caatinga dry forest", a ser enviado ao periódico *Oecologia*, investigou o efeito de perturbações antrópicas crônicas sobre o consumo de vegetação e as taxas de herbivoria da formiga cortadeira típica da Caatinga, *Atta opaciceps*.

2 FUNDAMENTAÇÃO TEÓRICA

2.1 *Perturbações antrópicas*

Os seres humanos há aproximadamente 60.000 anos migraram da África e colonizaram todas as florestas tropicais (MELLARS, 2006) atualmente, cerca de 1 a 1,5 bilhão de pessoas dependem de florestas tropicais para alimentação, obtenção de madeira, medicamentos e outros serviços ecossistêmicos (VIRA et al., 2015). O uso dos recursos naturais dessas florestas tropicais pelos humanos tem influenciado a homeostase, funções e serviços ecossistêmicos (KREMEN, 2005; RAUDSEPP-HEARNE et al., 2010). Os impactos humanos podem ser divididos historicamente em quatro fases: (1) a caça e as extinções da megafauna nos primórdios da civilização, (2) o início da agricultura de baixa intensidade com os primeiros assentamentos, (3) a agricultura intensiva, exploração madeireira, incêndio florestal e perda e fragmentação dos habitats dos tempos modernos e (4) a intensificação do uso do solo, poluição da água, solo e ar juntamente com a intensificação das mudanças climáticas globais, em conjunto, as ações antrópicas, degradam severamente os ecossistemas naturais e levando a homogeneização global da biota (LEWIS et al., 2015).

Uma estimativa recente sugere que 24% das florestas tropicais existentes ainda estejam intactas, 46% estejam fragmentadas e 30% estejam degradadas (HANSEN et al., 2013). Mesmo as florestas estruturalmente intactas sofrem perturbações antrópicas como a caça, inclusive em áreas protegidas (LAURANCE et al., 2012). Os principais efeitos antrópicos podem ser divididos em agudos e crônicos (SINGH, 1998). A perturbação aguda consiste na mudança do uso do solo devido à conversão de áreas de floresta em terras agrícolas (GIBBS et al., 2010), áreas de mineração (EDWARDS et al., 2014), rodovias e cidades (RICHARD et al., 2000; TROMBULAK; FRISSELL, 2000). Neste cenário de paisagens fragmentadas, tem sido reportado uma limitação na distribuição e/ou redução nas populações de espécies como plantas tolerantes à sombra (LAURANCE et al., 2001), plantas do estrato emergente (OLIVEIRA et al., 2004), que dependem de vertebrados para sua polinização (GIRÃO et al., 2007) e dispersão de sementes (STONER et al., 2007; SANTOS et al., 2008), bem como de grandes mamíferos (PERES; PALACIOS, 2007), aves de sub-bosque (LEES; PERES, 2006), besouros rola-bosta (FILGUEIRAS et al., 2011, 2015, 2016), formigas especialistas (GOMES et al., 2010; LEAL et al., 2012) e outros grupos de invertebrados. Em contrapartida, espécies e/ou grupos que são adaptados às perturbações, como as espécies de plantas pioneiras (OLIVEIRA et al., 2004; SANTOS et al., 2008; TABARELLI et al., 2012) tornam-se cada vez mais dominantes nas paisagens fragmentadas e grupos de animais generalistas (LEES; PERES, 2006; LEAL et al., 2012; RIBEIRO et al., 2016). Dessa forma, apenas um subgrupo de espécies originalmente do ecossistema deve suportar as novas condições ambientais impostas pelas perturbações antrópicas, culminando em biotas mais homogêneas em termos taxonômicos, filogenéticos e funcionais (SANTOS et al., 2010; LÔBO et al., 2011; RIBEIRO et al., 2015; RIBEIRO-NETO et al., 2016).

Alterações na extensão da floresta influenciam os ciclos biogeoquímicos e as propriedades biofísicas da superfície da Terra (GATTI et al., 2014). Por exemplo, simulações de desmatamento em áreas tropicais geram um aumento da temperatura global de 0,9°C, devido principalmente a alterações no ciclo do carbono (ANDERSON et al., 2011). A atividade humana não só remove seletivamente as espécies das florestas, mas pode adicioná-las também (CLAVERO; GARCÍA-BERTHOU, 2005). Um conjunto de espécies invasoras e doenças foram introduzidos nas florestas tropicais, particularmente em ilhas oceânicas, conduzindo extinções de espécies que afetaram as funções de polinização, dispersão de sementes, herbivoria e predação (ALLENDORF; LUNDQUIST, 2003; VAN KLEUNEN et al., 2010).

Em contraste às perturbações agudas, as perturbações antrópicas crônicas (SINGH, 1998, daqui em diante, PAC) são consideradas mais sutis, às vezes imperceptíveis, porém duradouras, que podem ocorrer em remanescentes de floresta já degradada (i.e. por perturbação aguda) ou iniciar em uma floresta intacta (SINGH, 1998). As PAC ocorrem através da remoção regular de pequenas quantidades de biomassa de vegetação na forma de caça (PARRY et al., 2009), extração seletiva de madeira (EDWARDS et al., 2014), exploração de produtos florestais não madeireiros (CAVALCANTI et al., 2015), incêndio para agriculta familiar (COCHRANE, 2003), criação extensiva de animais domésticos (REID et al., 2008) e introdução de espécies forrageiras para a criação dos animais domésticos (ALMEIDA; PEIXOTO, 2012).

Nas últimas décadas tem crescido a atenção para o efeito das PAC sobre as áreas remanescentes de floresta. Embora os efeitos dessas perturbações sejam aparentemente gradativos, eles podem afetar a diversidade biológica em diferentes níveis (MARTORELL; PETERS, 2005, 2009). No nível de individuo, efeito negativo no sucesso reprodutivo (VAN LENT et al., 2014), decréscimo nas taxas de crescimento e reprodução (JIMÉNEZ-VALDÉS et al., 2010). Ao nível populacional, decréscimos no tamanho das populações (TABUTI, 2007). Níveis intermediários de PACs podem promover aumento no tamanho das populações de espécies de cactos (e.g. *Mammillaria pectinifera*, MARTORELL; PETERS, 2005), e aumento da taxa de crescimento populacional (URETA; MARTORELL, 2009). No entanto, níveis altos de PAC reduzem a taxa de crescimento populacional (MARTORELL; PETERS, 2005; URETA; MARTORELL, 2009). Efeitos para o nível de comunidade estão relacionados com a diminuição da área basal, altura da copa e cobertura nas florestas (MAREN et al., 2013), dominância de pequenas espécies arbóreas (SHANKAR et al., 1998) e conversão de comunidades maduras para estádios iniciais de sucessão (SOUZA et al., 2012). Com isso, os efeitos das PAC podem resultar em simplificação e homogeneização das comunidades biológicas, alterando o funcionamento do ecossistema e sua capacidade de prover bens e serviços (SINGH, 1998; ALVES et al., 2009; BLACKIE et al., 2014).

Durante o decorrer do século XXI ocorrerá um aumento na demanda por produtos oriundos do uso das florestas tropicais (GIBSON et al., 2011). Assim, as maiores ameaças provavelmente continuarão a serem conversão e degradação dos habitats, mas serão cada vez mais combinadas com os impactos das PAC e das rápidas mudanças climáticas (LAURANCE, 2013; FRISHKOFF et al., 2016). Essas ameaças para as florestas são impulsionadas por fatores socioeconômicos que vão desde uso local até os mercados internacionais, e ocorrem de forma legal e/ou ilegalmente, o que torna a mitigação complexa (LEWIS et al., 2015). Além disso, as soluções para a conservação das florestas dependerão de sua resiliência natural, aliado com as intervenções de manejo (LEWIS et al., 2015).

2.2 *As florestas tropicais sazonalmente secas*

Definir as florestas tropicais sazonalmente secas (*sensu* MURPHY; LUGO, 1986; PENNINGTON et al., 2009, daqui em diante FTSS) é uma questão complexa, principalmente porque as FTSS ocorrem dentro de outros tipos de vegetação como florestas úmidas e savanas (FOLEY, 2005). As FTSS diferem-se das savanas por apresentarem um dossel mais continuo e não possuírem um estrato gramináceo abundante, contínuo e tolerante ao fogo (BULLOCK et al., 1995). As FTSS podem ser definidas como florestas que ocorrem em regiões tropicais caracterizadas por uma forte sazonalidade na distribuição das chuvas, resultando em extensos períodos de secas. As florestas que se desenvolvem sob tais condições climáticas compartilham uma estrutura e fisionomia amplamente semelhantes, muitas também ocorrem em solos mesotróficos (PENNINGTON; PRADO; PENDRY, 2000; MILES et al., 2006).

Em ambientes áridos e semi-áridos, os quais abrigam 16 dos remanescentes das FTSS, as perturbações antrópicas crônicas são mais comuns que agudas (MARTORELL; PETERS, 2005; MARTORELL; PETERS, 2009). Isso se dá devido à presença de populações humanas densas e de baixa renda, as quais usam os recursos naturais das FTSS para a sua subsistência, mas sem a substituição da vegetação por outro tipo de uso do solo (SINGH 1998, HIROTA; HOLMGREN, 2011; RIBEIRO et al., 2015). Estas populações não apenas criam animais domésticos de forma extensiva, mas também introduzem espécies forrageiras para complementar a vegetação nativa (NASCIMENTO et al., 2014; ALMEIDA et al., 2015), dois dos mais frequentes e deletérios tipos de PAC (ALMEIDA et al., 2014; RIBEIRO et al., 2015; SCHULTZ et al., 2016). Isso ocorre porque nas áreas de clima seco a menor estatura da vegetação proporciona um clima mais adequado para a criação de animais e fazem com que os rebanhos sejam muito grandes e os animais criados de forma extensiva (MURPHY; LUGO, 1986; REID et al., 2008).

Assim, as PAC em FTSS têm sido documentadas no México (MARTORELL; PETERS 2005), Índia (SAGAR et al., 2003; SHAHABUDDIN; KUMAR 2006), e no Brasil em vegetação de Caatinga (LEAL; ANDERSEN; LEAL, 2014; RIBEIRO et al., 2015; RIBEIRO-NETO et al., 2016). Recentemente, pesquisas em florestas secas têm tentado responder como as PAC mudam as comunidades de plantas e animais (QUESADA et al., 2009). Porém, pouco se sabe sobre como interações ecológicas são alteradas por estas perturbações. Esse é o caso da Caatinga, que apresenta uma população humana densa (26 habitantes/km², MEDEIROS et al., 2012) e de baixa renda (AB’SABER, 2000), a qual tipicamente dependente dos recursos oriundos da floresta para a sua subsistência (VERGLES et al., 2015). A coleta de lenha (CAVALCANTI et al., 2015), exploração de cascas e folhas para uso medicinal (ALBUQUERQUE et al., 2007), pastejo de animais domésticos (LEAL et al., 2003) e caça (ALVES et al., 2009) são exemplos de usos crônicos típicos que as populações humanas fazem da Caatinga. Como consequência, algumas alterações na biota da Caatinga já foram reportadas, como redução da diversidade taxonômica e filogenética das comunidades lenhosas (RIBEIRO et al., 2015, 2016), proliferação de espécies adaptadas a perturbação levando à homogeneização em comunidades de plantas e formigas (OLIVEIRA et al., 2016; RIBEIRO-NETO et al., 2016; RITO et al., 2016), perda de serviços de dispersão de sementes e de proteção anti-herbivoria providos pelas formigas às plantas (LEAL; ANDERSEN; LEAL, 2014, 2015) e até redução nos estoques de nutrientes devido ao sobrepastejo de caprinos (SCHULZ et al., 2016).

2.3 *Formigas*

As formigas (Formicidae, Hymenoptera), com aproximadamente 13 000 espécies descritas para uma fauna estimada em cerca de 20.000 espécies (BOLTON, 2016), são consideradas o maior grupo de insetos eussociais na face da Terra (GORDON, 2009). A dominância numérica destes insetos sociais pode ser surpreendente: no Japão, por exemplo, uma super colônia de *Formica yessensis* Wheeler (Formicinae) foi estimada em 306 milhões de operárias e mais de um milhão de rainhas em 45 000 ninhos interconectados dispersos em uma área de 2,7 km^2; essa é considerada a maior sociedade animal conhecida (ITO, 1973). Com uma estimativa aproximada de mais de cem quadrilhões de indivíduos (100.000.000.000.000.000), as formigas equivalem à biomassa humana global (HÖLLDOBLER; WILSON, 2009). O fator chave de sucesso são as inúmeras interações que as formigas realizam com indivíduos da própria colônia, com outras espécies de formigas, outros insetos, plantas, microrganismos (endossimbiontes) e fungos (i.e. agricultura) (OLIVER; LEATHER; COOK, 2008; GORDON; GORDON, 2010; CHOMICKI; RENNER, 2017).

As interações das formigas com outros organismos são mediadas por semioquímicos cuticulares de hidrocarbonos (i.e. substâncias químicas envolvidas na comunicação entre seres vivos) que fazem parte da cutícula da maioria dos insetos (PEETERS, 1995). Entre os insetos solitários, a principal forma de comunicação é realizada durante o período de reprodução para auxiliar no encontro de parceiro sexual (WYATT, 2014). Já as formigas e outros insetos sociais apresentam sociedades auto-organizadas, nas quais indivíduos comunicam-se trocando informações entre eles para melhorar a divisão de trabalho, a utilização coletiva de recursos e as ações defensivas coletivas (ESTES et al., 2011). Desse ponto, as principais formas de comunicação das formigas são: (1) indivíduos da mesma colônia (cooperativismo) (WONG et al., 2013); (2) diferentes colônias (antagonismo) (BOOMSMA; FRANKS, 2006); (3) outros organismos, como por exemplo, hemípteros (mutualismo) (DEL-CLARO et al., 2006) e díptera (parasitismo) (ALMEIDA; WIRTH; LEAL, 2008).

2.4 *Interações planta-formiga*

Existe uma gama de interações entre formigas e plantas, incluindo o mutualismo de proteção mediado pela presença de domácias ou pela oferta de recursos alimentares como nectar extrafloral (NEFs) ou corpúsculos lipídicos (mirmecofitismo), polinização (mirmecofilia), dispersão de sementes (mirmecocoria), a nutrição de plantas que ocorre nos jardins de formigas ou em domácias presentes nas raízes das plantas (mirmecotrofismo) e a herbivoria por formigas cortadeiras via sua simbiose com fungos cultivados dentro dos seus ninhos que degradam os compostos vegetais e dos quais as formigas se alimentam (BEATTIE, 1985; HÖLLDOBLER; WILSON, 1990; HUXLEY; CUTLER, 1991). As formigas ainda são presas de plantas insetívoras, como *Nepenthes* (GAUME et al., 2016). Defesas mediadas por NEFs e dispersão são difundidas tanto nas regiões tropicais como em regiões temperadas, enquanto o mirmecotrofismo é limitado aos trópicos (GORDON, 2009). A herbivoria é limitada à região neotropical (para mais detalhes ver o subtópico, *herbivoria)*.

2.5 *As formigas cortadeiras*

A agricultura é uma forma especializada de simbiose que evoluiu apenas quatro vezes dentro do reino Animalia: humanos, besouros da casca da arvore, cupins e formigas (SCHULTZ; BRADY, 2008). Nas formigas, a agricultura se desenvolveu nos membros da tribo Attini (Myrmicinae, Formicidae, Hymenoptera), recentemente incluída dentro da tribo Pheidolini, mas ainda considerada um grupo monofilético (para mais detalhes ver,WARD et al., 2015), e por isso mantida como tribo neste documento. A tribo Attini teve uma única origem há aproximadamente 50 milhões de anos (SCHULTZ; BRADY, 2008; CHOMICKI; RENNER, 2017), provavelmente nas florestas da América do Sul após o seu isolamento da África (SCHULTZ; BRADY, 2008; WARD et al., 2015). A agricultura é um produto de uma relação antiga simbiótica entre três mutualistas, as formigas, os seus cultivares de fungos (Leucocoprineae e Pterulaceae) e uma bactéria filamentosa do gênero *Pseudonocardia* (Actinomycetes) que cresce sobre os tegumentos das formigas. Um parasita evoluiu conjuntamente aos três mutualistas, um fungo do gênero *Escovopsis* (Ascomycetes), que infecta os jardins de fungos de forma similar as pragas agrícolas das plantações humanas, pelo qual é controlado em parte por antibióticos produzidos por *Pseudonocardia* (MUELLER et al., 2005; SCHULTZ; BRADY. 2008). Além das formigas Attini, a fungivoria ocorre em *Euprenolepis procera* Emery, uma espécie de formiga especializada em se alimentar de cogumelos (WITTE; MASCHWITZ, 2008), e em formigas especialistas em predar o fungo cultivado pelas Attini, como *Gnamptogenys hartmani* Wheeler e espécies de *Megalomyrmex* (CURRIE et al., 1999). Além disso, outras formigas podem utilizar as hifas dos fungos para reforçar a parede de seus ninhos, como é o caso de *Azteca brevis* Forel (MAYER; VOGLMAYR, 2009).

Com base nas associações entre os grupos filogenéticos das Attini, seus cultivares de fungos e na disposição de sítios para *Escovopsis*, podemos dividir a agricultura em cinco sistemas biológicos distintos: (1) agricultura inferior, praticada pela maioria dos gêneros basais de Attini (76 espécies), os quais cultivam uma ampla gama de espécies de fungos da tribo Leucocoprineae ainda ocorrentes em vida livre (i.e. não exclusivamente associados às formigas); (2) agricultura de fungos de coral, praticada por espécies de um subgrupo (*pilosum*) do gênero *Apterostigma* (34 espécies), que cultivam um clado das Pterulaceae (outras espécies de *Apterostigma* pertencem ao sistema da agricultura inferior); (3) agricultura de leveduras, praticado por um subgrupo de espécies do gênero *Cyphomyrmex* (18 espécies), que cultivam um clado distinto de fungos Leucocoprineae derivados dos fungos da agricultura inferior; (4) agricultura superior generalizada, praticado por espécies dos gêneros *Sericomyrmex*, *Trachymermex* (63 espécies), as quais cultivam outro clado distinto de fungos Leucocoprineae que são derivados da agricultura inferior; e (5) agricultura das formigas cortadeiras, uma subdivisão da agricultura superior generalizada, com um maior grau de especialização, praticada por espécies dos gêneros *Acromyrmex* e *Atta* (40 espécies) (MIKHEYEV et al., 2007; SCHULTZ; BRADY 2008).

O desenvolvimento da agricultura foi o diferencial evolutivo para as formigas cortadeiras, que são os herbívoros dominantes na região Neotropical (HÖLLDOBLER; WILSON, 1990; WIRTH et al., 2003). Ao contrario dos membros mais basais das Attini que forrageiam e cultivam o seu jardim de fungos sobre detritos orgânicos (LEAL; OLIVEIRA, 1998), as formigas cortadeiras adquiriram a habilidade de coletar e processar material vegetal fresco para serem utilizados como substrato rico em nutrientes para seus cultivares de fungos (HÖLLDOBLER; WILSON, 1990). Esta associação natural é considerada o estômago externo das formigas que digerem celulose (HÖLLDOBLER; WILSON, 1990), a qual permitiu um alto grau de polifagia (NORTH; JACKSON; HOWSE, 1997) e possibilitou a exploração de recursos que de outra forma não estariam disponíveis, sobretudo folhas, por isso o nome formigas cortadeiras de folhas, ainda que flores, frutos e sementes também sejam utilizados quando presentes nas áreas de forrageamento das colônias (HÖLLDOBLER; WILSON, 1990; WIRTH et al., 2003). Esta inovação revolucionaria permitiu a uma colônia madura de *Atta* ter um papel ecológico equivalente a grandes mamíferos herbívoros em termos de coleta de biomassa, longevidade e quantidade de material vegetal (HÖLLDOBLER; WILSON, 1990).

As cerca de 40 espécies de formigas cortadeiras são restritas ao Novo Mundo, desde o Sul dos Estados Unidos seguindo pela América Central (exceto em algumas ilhas das Antilhas) e continuando por todos os países da América do Sul até o centro da Argentina (HÖLLDOBLER; WILSON, 1990; FARJI BRENER; RUGGIERO, 1994). No Brasil, os primeiros registros dessas espécies datam da época do descobrimento e, desde então, são alvo de estudo de muitos pesquisadores os quais já determinaram diversos aspectos de sua biologia, ecologia e evolução (MARICONI, 1981).

O gênero *Atta* é o mais estudado dentre as formigas cortadeiras, o qual apresenta o centro de diversidade no Brasil (CHERRETT, 1989), não sendo registrado apenas no arquipélago de Fernando de Noronha-PE (SCHOEREDER; COUTINHO 1990). As espécies de *Atta* constroem ninhos grandes subterrâneos e eminentes, os quais podem suportar populações contendo cerca de um milhão de indivíduos (MOREIRA et al., 2004). Seus ninhos são facilmente reconhecidos como uma pequena e uniforme abertura com grandes grãos de terra escavados nas redondezas da entrada e/ou de substrato vegetal seco, com a parte interna do ninho composta por câmaras e túneis conectados (SOARES et al., 2006). As câmaras são utilizadas para o cultivo do fungo simbionte, onde também são colocados os ovos, larvas, pupas e adultos. Outras câmaras são utilizadas para os resíduos orgânicos que contêm formigas mortas, fungo exaurido e material vegetal seco que ficam localizadas longe das câmaras para o cultivo do fungo, evitando assim a contaminação da colônia (SOARES et al., 2006; OLIVEIRA et al., 2007; FARJI-BRENER; WERENKRAUT, 2015). As colônias da maioria das espécies atingem a maturidade reprodutiva com cerca de 3 a 4 anos e seus ninhos apresentam, então, vários murundus grandes que cobrem uma superfície de mais de 250 m^2 (HÖLLDOBLER; WILSON, 1990; RAO, 2000; WIRTH et al., 2003). As rainhas possuem uma expectativa de vida que varia de 8 a 20 anos (FOWLER; SILVA; FORTI, 1986; MEYER; LEAL; WIRTH, 2009).

A grande importância das formigas cortadeiras se deve à influência que esses organismos desempenham sobre grande número de organismos e em diferentes escalas, desde populações de plantas até todo o ecossistema (WIRTH et al., 2003, LEAL;

WIRTH; TABARELLI, 2014). Ao nível populacional, afetam o sucesso reprodutivo de indivíduos tanto diretamente através da dispersão ou predação de sementes (LEAL; OLIVEIRA, 1998, 2000), quanto indiretamente através da sua atividade de herbivoria (WIRTH et al., 2003). As formigas podem induzir a mortalidade até mesmo de árvores inteiras através do corte de um percentual elevado de suas folhas (VASCONCELOS; CHERRETT, 1997). Modificações nas populações de plantas podem levar a mudanças na composição e estrutura da comunidade (GARRETTSON et al., 1998; FARJI-BRENER, 2001) e até mesmo "frear" a regeneração natural da floresta, pelo corte de espécies pioneiras, mantendo os ambientes abertos e não permitindo o avanço da sucessão (RAO; TERBORGH; NUÑEZ, 2001; CORRÊA et al. 2010). A dinâmica de sucessão da comunidade também pode ser afetada por mudanças no regime de luz da floresta e no microclima, devido à criação de clareiras sobre seus ninhos e nas suas adjacências (GARRETTSON et al., 1998; CORRÊA et al., 2010; MEYER et al., 2011). Além disso, as formigas cortadeiras causam mudanças na dinâmica da ciclagem de nutrientes, por carregar para dentro de suas colônias uma grande quantidade de matéria orgânica para o cultivo do fungo simbionte (FARJI-BRENER; WERENKRAUT, 2015).

2.5.1 Herbivoria

O aspecto mais importante relacionado às formigas cortadeiras é a sua posição como herbívoro dominante em ecossistemas neotropicais (MIKHEYEV et al., 2008), uma vez que uma única colônia pode consumir anualmente, uma grande diversidade plantas e centenas de quilogramas de material vegetal por ano (WIRTH et al., 2003; HERZ; BEYSCHLAG; HÖLLDOBLER, 2007; COSTA et al., 2008). Os efeitos da herbivoria em plantas variam de uma escala pequena a uma catastrófica, dependendo da parte da planta removida, da intensidade de remoção e do efeito desse ataque no desenvolvimento da planta (CRAWLEY, 1983). Altos níveis de herbivoria por formigas cortadeiras, frequentemente afetam negativamente as plantas coletadas, reduzindo a taxa de crescimento, o desempenho reprodutivo ou até mesmo levando a morte (TERBORGH et al., 2001). Afetando a aptidão dos indivíduos, as formigas cortadeiras podem influenciar a demografia e dinâmica das populações e a estrutura das comunidades de plantas (WIRTH et al., 2003, LEAL; WIRTH; TABARELLI, 2014, CORRÊA et al., 2016).

Apesar das formigas cortadeiras serem consideradas polífagas, elas apresentam uma seletividade notável dentro do espectro de plantas disponíveis (LEAL; WIRTH;

TABARELLI, 2014). Muitos estudos enfocaram a seleção de plantas coletadas por formigas cortadeiras para o cultivo do fungo simbionte e já foi registrada uma preferência por: (1) folhas de grandes árvores (WIRTH et al., 2003; FALCÃO et al., 2011); (2) folhas jovens (MUNDIM et al., 2009), embora se flores e frutos estiverem disponíveis, elas tendem a coletar esses recursos que são mais energéticos (WIRTH et al., 2003; FALCÃO et al., 2011); (3) indivíduos ou folhas sob estresse hídrico e/ou com maior teor de nutrientes (VASCONCELOS; CHERRETT, 1996; MEYER; ROCES; WIRTH, 2006; MUNDIM; COSTA; VASCONCELOS, 2009; RIBEIRO-NETO et al., 2012); (4) indivíduos sem defesas induzidas (KOST et al., 2011); (5) plantas pioneiras, com menos defesas químicas (FARJI-BRENER, 2001; WIRTH et al., 2003; FALCÃO et al., 2011); (6) plantas com menos defesas físicas (NICHOLS-ORIANS; SCHULTZ, 1989; HOWARD, 1990); (7) espécies de plantas pela as quais as operárias não tenham histórico de uso (SAVERSCHEK et al., 2010) e (8) folhas com baixa densidade de fungos endofíticos foliares (ESTRADA et al., 2013). Adicionalmente, os fatores abióticos são considerados essenciais para determinar o padrão da atividade de forrageamento. A temperatura do ar e a umidade relativa, por exemplo, são geralmente descritas como os principais fatores determinantes do comportamento diário das formigas (HÖLLDOBLER; WILSON, 1990; CALDATO et al., 2016). Em síntese, a seleção de plantas por formigas cortadeiras é um sistema complexo de tomada de decisão, envolvendo a avaliação de variados tipos de plantas, fatores induzidos pelo ambiente, o histórico de forrageamento individual e a homeostase das formigas e seu fungo (para mais detalhes ver LEAL; WIRTH; TABARELLI, 2014).

A taxa de herbivoria de uma colônia de *Atta* varia de acordo com a escala estudada. Por exemplo, Wirth et al., (2003) verificou que colônias de *Atta colombica* na ilha de Barro Colorado, Panamá, apresentam taxas de herbivoria de até 40% de plantas individuais, na escala da área de forrageamento as taxas são em torno de 12%, na escala de paisagem onde o estudo foi realizado o valor cai para 2,5% e na escala da ilha como um todo a taxa de herbivoria é praticamente desprezível. Na escala da área de forrageamento das colônias, mais adequada para refletir o quanto as formigas removem da produção de folhas, a taxa de herbivoria varia entre 12 e 17% em áreas de floresta (WIRTH et al., 2003, URBAS et al., 2007), 17% em Cerrado (COSTA et al., 2008) e uma estimativa de 6% para pastagens (CALDATO et al., 2016).

2.5.2 Dispersão de sementes

Devido as suas altas taxa de herbivoria, as formigas cortadeiras são consideradas prejudiciais à vegetação; entretanto, estudos em florestas tropicais têm demonstrado benefícios das formigas cortadeiras para a dispersão de sementes de plantas (LEAL; OLIVEIRA, 1998; ZAVALA-HURTADO, 2000; LIMA; OLIVEIRA; SILVEIRA, 2013). Elas atuam principalmente como agentes dispersores secundários de plantas dispersas primariamente por vertebrados (LEAL; OLIVEIRA, 1998; LEAL; WIRTH; TABARELLI, 2014). Em alguns casos raros, as LCA podem até atuar como dispersores primários (DALLING; WIRTH, 1998). Aos dispersarem os diásporos, elas redistribuem as sementes nos solos e consequentemente modificam a dinâmica do banco de sementes, influenciam a germinação de sementes, estabelecimento de plântulas e a estrutura espacial das populações (KASPARI, 1993; LEAL; OLIVEIRA, 1998; ZAVALA-HURTADO, 2000).

Os frutos e sementes utilizados por formigas cortadeiras são normalmente bagas e drupas dispersos primariamente por aves e morcegos (LEAL; OLIVEIRA, 1998; WIRTH et al., 2003; COSTA et al., 2014). Estruturas no diásporo (e. g. pedúnculo, tricomas, espinhos, carúncula e arilo) auxiliam na dispersão (LEAL; OLIVEIRA, 1998; PIZO, OLIVEIRA 1998). Em alguns casos ocorre a limpeza das sementes (i.e. remoção da polpa do fruto ou arilo) antes de serem carregadas para o ninho (TAVARES; ALVES-JUNIOR, 2016). Sementes completamente limpas são frequentemente encontradas nas lixeiras externas próximas a entrada do ninho especialmente em *Acromyrmex* (LEAL; OLIVEIRA, 1998)em disso a retirada da polpa dos frutos diminui o ataque de fungos às sementes (LEAL; OLIVEIRA, 1998; PIZO; OLIVEIRA, 1998). Durante o transporte para ninho pode acontecer que as sementes caiam ao longo da trilha, sendo depositadas em habitats com condições favoráveis à germinação das sementes, tais como solos mais aerados, com maior umidade e maior quantidade de nutrientes (LEAL; OLIVEIRA 1998; LEAL et al., 2003). As formigas cortadeiras do gênero *Atta*, no entanto, são consideradas dispersores de baixa qualidade (LEAL; ANDERSEN; LEAL, 2014), porque apesar do seu tamanho corporal relativamente grande, com capacidade de transportar sementes por longas distâncias, elas geralmente cortam ou soterram as plântulas que germinam em seus ninhos ou próximo a eles (SILVA et al., 2007; LEAL; ANDERSEN; LEAL, 2014).

2.5.3 Modificações na estrutura e qualidade do solo

O efeito das formigas cortadeiras no solo ocorre devido aos tamanhos colossais dos seus ninhos que podem ter mais de 250 m² em área, 7 m de profundidade e conter até 8000 câmaras subterrâneas (HOLLDOBLER; WILSON, 2011). Durante a construção, manutenção e expansão dos ninhos, as formigas podem (1) mover mais de 40 toneladas de solo (MOREIRA et al., 2004), depositando uma grande quantidade de solo mineral na superfície do solo (MEYER et al., 2013), (2) reduzir a serapilheira em uma área de até 40 m em torno do ninho (MEYER et al., 2013), e (3) acumular uma enorme quantidade de resíduos orgânicos resultantes do material vegetal não utilizado para o cultivo do fungo (daqui em diante “lixeira”) que são acumulados em câmaras internas do ninho ou na superfície do solo (FARJI-BRENER; MEDINA, 2000). Ninhos de formigas cortadeiras são considerados um dos mais importantes agentes de perturbação do solo, afetando a disponibilidade de nutrientes com efeitos concomitantes sobre as plantas ao nível de individuo, população e comunidade (WIRTH et al., 2003; MEYER et al., 2011; LEAL; WIRTH; TABARELLI, 2014; FARJI-BRENER; WERENKRAUT, 2015) e seus efeitos podem durar até 15 anos após a morte da colônia (FARJI-BRENER, 2005; BIEBER et al., 2011).

As lixeiras são consideradas as fontes de nutrientes através das quais as formigas cortadeiras aumentam a fertilidade do solo (HAINES, 1978; FARJI-BRENER; GHERMANDI, 2008; HUDSON et al., 2009). Por exemplo, uma lixeira pode ter 80 vezes mais nutrientes do que os solos adjacentes (FARJI-BRENER; MEDINA, 2000). Entretanto, alguns estudos têm relatado redução na disponibilidade de nutrientes no solo superficial dos ninhos e seus entornos (MOUTINHO et al., 2003; FARJI-BRENER; LESCANO; GHERMANDI, 2010; MEYER et al., 2013). Isso se dá porque, em espécies cujas lixeiras são internas, as formigas movem grandes quantidades de solo mineral com baixo teor de nutrientes das camadas inferiores para as camadas superficiais. Neste sentido, o solo enriquecido pelas lixeiras fica a grandes profundidades, não accessíveis para as plantas jovens (ALVARADO; BERISH; PERALTA, 1981; MEYER et al., 2013; LEAL; WIRTH; TABARELLI, 2014; FARJI-BRENER; WERENKRAUT, 2015). Outro ponto relevante é que as formigas coletam quase todas as plantas dentro de suas áreas de forrageamento e principalmente em torno dos ninhos, reduzindo a quantidade de serapilheira que cai sobre o solo ao redor do ninho e, consequentemente, reduzindo a entrada de nutrientes via serapilheira (HULL-SANDERS HOWARD, 2003; MEYER et al., 2013).

Lixeiras que estão localizadas no exterior dos ninhos têm maior influência na fertilidade dos solos sobre os murundus que lixeiras internas (FARJI BRENER; SILVA, 1995a,b). Além disso, tendem a ter maior quantidade de nutrientes do que as lixeiras internas (FARJI-BRENER; WERENKRAUT, 2015) devido à biota do solo ser mais ativa e abundante em camadas de solo superficiais do que nas mais profundas (Sousa-Souto et al. 2012). Por fim, lixeiras externas recebem nutrientes da serapilheira que representam uma entrada extra de nutrientes (FARJI-BRENER; WERENKRAUT, 2015). Este fator é possivelmente o que faz com que áreas em torno dos ninhos de *Acromyrmex* tenham maior concentração de nutrientes quando comparadas às áreas em torno dos ninhos de *Atta,* visto que a maioria dos ninhos de *Acromyrmex* possuem lixeiras externas enquanto que os ninhos de *Atta,* em sua maioria, possuem lixeiras internas (FARJI-BRENER; WERENKRAUT, 2015, 2017).

Ninhos em zonas subtropicais apresentam uma maior concentração de cátions do que em zonas tropicais, isso se deve a diferenças no teor de cátion da vegetação, onde folhas de áreas temperadas apresentam maiores concentrações de íons de cátion do que em áreas tropicais (LOVELOCK et al., 2007). Por outro lado, temperaturas extremas podem limitar a atividade das formigas cortadeiras, limitando o período de forrageamento e reduzindo o crescimento do ninho, e como consequência, reduzindo no seu efeito na estrutura e qualidade do solo (TADEY; FARJI-BRENER, 2007).

Colônias mortas ou abandonadas permanecem com baixa concentração de nutrientes em comparação com áreas florestais adjacentes por muito tempo (BIEBER et al., 2011, para *Atta cephalotes*). Além disso, os solos dos ninhos podem se tornar compactos e impenetráveis devido à exposição contínua à radiação e às chuvas, reduzindo o recrutamento de plantas até 15 anos após o abandono do ninho (BIEBER et al., 2011). Mesmo no caso de colônias com lixeiras internas ou externas. As concentrações de nutrientes diminuem rapidamente em ninhos abandonados há mais de 1 ano (HUDSON et al., 2009, para *Atta colombica*), provavelmente devido à lixiviação. Todos esses resultados reforçam a noção de que as atividades de construção e manutenção dos ninhos alteram as propriedades do solo e atuando como potenciais filtros ecológicos (BELYEA, 2004).

2.5.4 Modificações na estrutura da vegetação e regime de luz

Nas florestas tropicais, as formigas do gênero *Atta* são consideradas um dos principais agentes formadores de clareiras, principalmente devido à constante remoção da vegetação que cresce sobre os ninhos durante a construção, manutenção e expansão dos mesmos (CORRÊA et al., 2010). As clareiras oriundas de formigas cortadeiras são menores que as clareiras formadas pela queda de arvores nas florestas (HULL-SANDERS; HOWARD, 2003), mas ambas são aberturas de luz oriundas de distúrbios gerados na camada do sub-bosque ou do dossel (FARJI-BRENER; ILLES, 2000). Essas clareiras provocam mudanças nas condições microclimáticas, principalmente aumentos na disponibilidade de luz e temperatura do ar e do solo e diminuição no potencial de água do solo (MEYER et al., 2011). Durante a vida da colônia, as condições mais abertas e dessecadas sobre os ninhos diminuem o recrutamento de plântulas (CORRÊA et al., 2010; MEYER et al., 2011). Ninhos de *Atta cephalotes* na Floresta Atlântica, por exemplo, apresentam clareiras conspícuas que vão até o dossel da floresta em cerca de 95% das colônias (CORRÊA et al., 2010). Estas clareiras são causadas pela constante remoção da vegetação para utilização de substrato para o cultivo no seu jardim de fungo ou para manutenção da área do ninho livre de plantas e detritos (MEYER et al., 2011). Como consequência, há uma redução no recrutamento de espécies tolerantes à sombra ou em espécies suscetíveis à desfolha constante pelas colônias, provocando mudanças na estrutura da assembleia de plantas sobre os ninhos e nas suas adjacências (CORRÊA et al., 2010; MEYER et al., 2011). Por outro lado, espécies exigentes de luz, incluindo pioneiras e outras espécies que respondem positivamente a incrementos moderados na disponibilidade de luz, são beneficiadas pelas clareiras dos ninhos aumentando seu recrutamento (CORRÊA et al., 2010, 2016). Em função disso, colônias de *Atta cephalotes* agem como um filtro ecológico para o recrutamento de algumas espécies de plantas ou certos grupos ecológicos (SILVA et al., 2007; CORRÊA et al., 2010; MEYER et al., 2001).

A partir do momento em que uma colônia morre ou migra, o ninho fica abandonado, e pode tornar-se uma ilha de recrutamento para plântulas e plantas de sub-bosque (FARJI-BRENER, 2005), devido à ausência da desfolha por parte das formigas (MEYER et al., 2011) e a baixa densidade ou ausência de plantas competidoras na área ocupada antes pela colônia (FARJI-BRENER, 2005). Além disso, durante um curto período após a morte ou migração da colônia, a maior intensidade de luz na área do ninho (FARJI-BRENER; ILLES, 2000) pode favorecer o recrutamento de alguns grupos específicos (FARJI-BRENER, 2005). Mas em menos de um ano os níveis de luz retornam aos níveis de áreas não ocupadas por formigas cortadeiras (BIEBER et al., 2011).

2.5.5 Proliferação de formigas cortadeiras em áreas perturbadas e perspectiva para Caatinga

As formigas cortadeiras são um dos poucos grupos de organismos que se proliferam em paisagens tropicais modificadas pelo o homem. Vários estudos já reportaram aumento na densidade de colônias de várias espécies de formigas cortadeiras em áreas perturbadas, tais como: (1) pastagens (FOWLER, 1983), (2) plantações (DELLA LUCIA et al., 2014), (3) florestas em estádios iniciais de sucessão (FARJI-BRENER, 2001; SILVA et al., 2009), (4) remanescentes de florestas inseridas em matrizes (RAO; TERBORGH; NUÑEZ, 2001), (5) pequenos fragmentos de floresta (TERBORGH et al., 2001; MEYER; LEAL; WIRTH, 2009), (6) bordas de grandes fragmentos (WIRTH; LEAL, 2007; MEYER; LEAL; WIRTH, 2009; DOHM et al., 2011), (7) estradas não pavimentadas em áreas de florestas úmidas (WINSTON; HERZ, 2015) e savanas (VASCONCELOS et al., 2006; VIEIRA-NETO et al., 2016). Como visto, a maioria dos trabalhos que relataram a proliferação de formigas cortadeiras foram feitos em florestas úmidas ou savanas, exceto Barrera et al., (2015), que demonstrou a primeira evidência que a fragmentação em FTSS afeta a comunidade de formigas cortadeiras (i.e. *Acromyrmex* spp), relacionando efeitos de espécie-área e borda a mudanças na riqueza de formigas, abundância de colônias e composição taxonômica. As razões para tal proliferação também já foram bastante investigadas principalmente paras as florestas úmidas e savanas, e incluem maior quantidade de sítios para nidificação em áreas abertas (VASCONCELOS, 1990; VASCONCELOS et al., 2006) e relaxamento dos controles populacionais ascendentes (mais recurso alimentar na forma de plantas pioneiras, FARJI-BRENER 2001, URBAS et al., 2007, FALCÃO et al., 2011) e descendentes (menos inimigos naturais como moscas parasitoides da família Phoridae e predadores como tatus e tamanduás, ALMEIDA et al., 2008, WIRTH et al., 2008).

Apesar das formigas cortadeiras serem um grupo relativamente bem estudado nas florestas da região Neotropical (e.g. florestas úmidas, campos agrícolas e savanas) (DELLA-LUCIA et al., 2014; LEAL; WIRTH; TABARELLI, 2014), praticamente nada se sabe a respeito da ecologia e historia natural destes organismos em FTSS como a Caatinga (para mais detalhes, ver BARRERA; BUFFA; VALLADARES, 2015). Como visto acima, as FTSS estão sujeitas a perturbações antrópicas como as florestas úmidas. Contudo, ainda não se conhece o efeito das PAC sobre as populações de formigas cortadeiras na Caatinga, apesar de serem registradas três espécies de *Atta* e várias de

Acromyrmex neste ecossistema (ULYSSÉA; BRANDÃO, 2013), as quais podem ter um papel relevante na herbivoria, dispersão de sementes e nas mudanças nas condições edáficas e de luz como registrado para vários ecossistemas neotropicais (ver revisão em LEAL; WIRTH; TABARELLI, 2014).

Para o contexto da Caatinga, pressuponho que as perturbações antrópicas não ocasionariam uma proliferação das formigas cortadeiras como ocorre nas florestas úmidas, porque a vegetação de Caatinga é naturalmente mais aberta e com menor biomassa que as florestas úmidas. Isso ocorreria porque alguns dos mecanismos por trás da proliferação de formigas cortadeiras (i.e. maior disponibilidade de locais de nidificação e mais recursos alimentares na forma de plantas pioneiras), se tornam mais frequentes quando florestas úmidas são perturbadas e se tornam mais abertas. A vegetação da Caatinga é dominada por espécies caducifólias (RODAL; SAMPAIO, 2002), e poucas espécies mantém suas folhas na estação seca, tais como *Cynophalla hastata* Jacq., *Erythroxylum pungens* Schulz e *Ziziphus joazeiro* Mart. (ANDRADE-LIMA, 1981). Além disso, existem grandes variações fisiológicas interespecíficas e sazonais (ARAÚJO et al., 2005). Nesse sentido, áreas mais perturbadas de Caatinga teriam uma biomassa de vegetação lenhosa ainda menor (RIBEIRO et al., 2015), e não seriam capazes de manter uma população grande de formigas cortadeiras, especialmente durante a estação seca.

Aliado a isso, em regiões semiáridas da América do Sul, caprinos, bovinos e formigas utilizam as espécies mais nutritivas e podem interagir e competir pela exploração destes recursos (BUCHER, 1987; TADEY; FARJI-BRENER, 2007). Consequentemente, uma intensidade de pastejo elevada pode inibir o forrageio das formigas cortadeiras sobre plantas mais palatáveis (PILATI et al., 1997). Estudos prévios demonstram que mudanças na composição e abundância da comunidade de plantas afetam significativamente os recursos alimentares da dieta das formigas cortadeiras (FRANZEL; FARJI-BRENER, 2000). Por outro lado, a diminuição da cobertura vegetal aumenta a proporção de solo exposto, no qual eleva a temperatura do solo, aumentando o consumo de oxigênio e a perda de água, os quais reduzem as atividades diárias das formigas cortadeiras (JOHNSON; GIBBS, 2004; TADEY; FARJI-BRENER, 2007; CALDATO et al., 2016). Portanto, uma redução na disponibilidade de plantas devido às perturbações antrópicas, com um aumento associado de áreas com solo exposto, são possíveis candidatos para explicarem uma redução na atividade de formigas cortadeiras em áreas de Caatinga. Nesse contexto, as formigas cortadeiras seriam negativamente afetadas por perturbações antrópicas.

3 LEAF CUTTING ANT POPULATIONS ALSO PROFIT FROM HUMAN DISTURBANCES IN DRY FORESTS

MANUSCRIPT ACCEPTED IN THE *JOURNAL OF TROPICAL ECOLOGY*

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

Running title: Human disturbance benefits leaf-cutting ants

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

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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, 0.98 ha^{-1}) and *A. laevigata* (9, 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 in 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.

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, 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 1985, Coley & Barone 1996, 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 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 (8º24'00" and 8º36'35" S; 37º0'30" and 37º1'40" W), a 607-km^2 area located in Pernambuco state, Brazil. The climate is semi-arid, with annual temperature averaging 23ºC, 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 km^2 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 analyzes 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 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 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 occur in areas with low vegetation cover, while the density of inactive colonies were 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 *et al.* 2000, Terborg *et al.* 2001) and in early-successional forests (Farji-Brener 2001, Silva *et al*. 2009, Vasconcelos & Cherreett 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).

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 to 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 *Cnidoscolus*, 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

AHRENDS, 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 of the United States of America* 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.

ARAÚJO, F. S., MARTINS, S. V., NETO, J. A. A. M., LANI, J. L. & PIRES, I. E. 2006. Estrutura da vegetação arbustiva-arbórea colonizadora de uma área degradada por mineração de caulim, Brás Pires, MG. *Revista Arvore* 30:107-116.

BACH, C. E. & KELLY, D. 2004. Effects of forest edges on herbivory in a New Zealand mistletoe, *Alepis flavida*. *New Zealand Journal of Ecology* 28:195-205.

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.

BRANDÃO, C. R. F. 1995. *Formigas dos Cerrados e Caatingas. Habilitation thesis*, Universidade de São Paulo, 147 pp.

CADENASSO, M. L. & PICKETT, S. T. A. 2000. Linking forest edge structure to edge function: mediation of herbivore damage. *Journal of Ecology* 88:31-44.

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.

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.

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.

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. & ILLES, A. E. 2000. Do leaf-cuttin 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.

HÖLLDOBLER, B., & WILSON, E. O. 1990. *The ants*. Havard 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.

JAFFE, K. & VILELA, E. 1989. On nest densities of the leaf-cutting ant *Atta cephalotes* in tropical primary forest. *Biotropica* 21:234-236.

JAIN, A. K., MURTY, M. N. & FLYNN, P. J. 1999. Data clustering: a review. *ACM Computing Surveys* 31:265-323.

KIE, J. G., BOWYER, R. T., NICHOLSON, M. C., BOROSKI, B. B. & LOFT, E. R.

2002. Landscape heterogeneity at differing scales: effects on spatial distribution of mule deer. *Ecology* 83:530-544.

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 hyper-abundance 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.

OZANNE, C. M. P., SPEIGHT, M. R., HAMBLER, C. & EVANS, H. F. 2000. Isolated trees and forest patches: Patterns in canopy arthropod abundance and diversity in *Pinus sylvestris* (Scots Pine). *Forest Ecology and Management* 137:53-63.

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.

RAO, M., TERBORGH, J. & NUÑEZ, P. 2001. Increased herbivory in forest isolates: Implications for plant community structure and composition. *Conservation Biology* 15:624-633.

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-RODRÍGUES, 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.

ULYSSÉA, 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 savannahs. *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. & HOLLDOBLER, 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.

WRIGHT, S. J. 2005. Tropical forests in a changing environment.*Trends in Ecology and Evolution* 20:553-560.

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.

Table 1. Chi-square analyses of the frequency of occurrence of *Atta* colonies (actives and inactives) 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
Atta laevigata	3	1.5	0.691
Atta opaciceps	3	2.7	0.444
Atta sexdens	3	12.3	0.0064
Inactive	3	12.4	0.0061

Legends to figures

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 ($y = -4.5\ln(x) + 2.60$, $R^2 = 0.78$, $P < 0.0001$).

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* $y = -1.0\ln(x) + 5.1$, $R^2 = 0.62$, $P = 0.1155$).

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 ($y = 0.9\ln(x) + -0.9$, $R^2 = 0.45$, $P = 0.0003$).

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.

Figure 1.

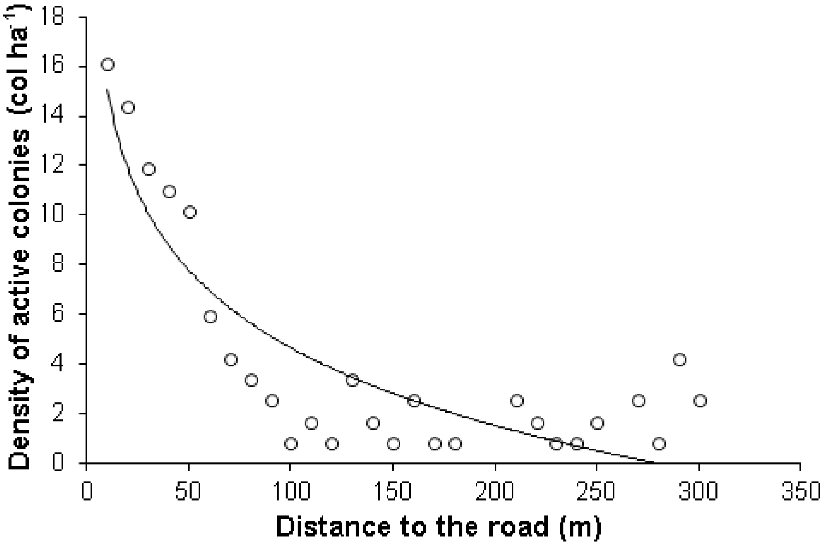

Density of active colonies (col ha^{-1})
18
16
14
12
10
8
6
4
2
0
0
50
100
150
200
250
300
350
Distance to the road (m)

Figure 2.

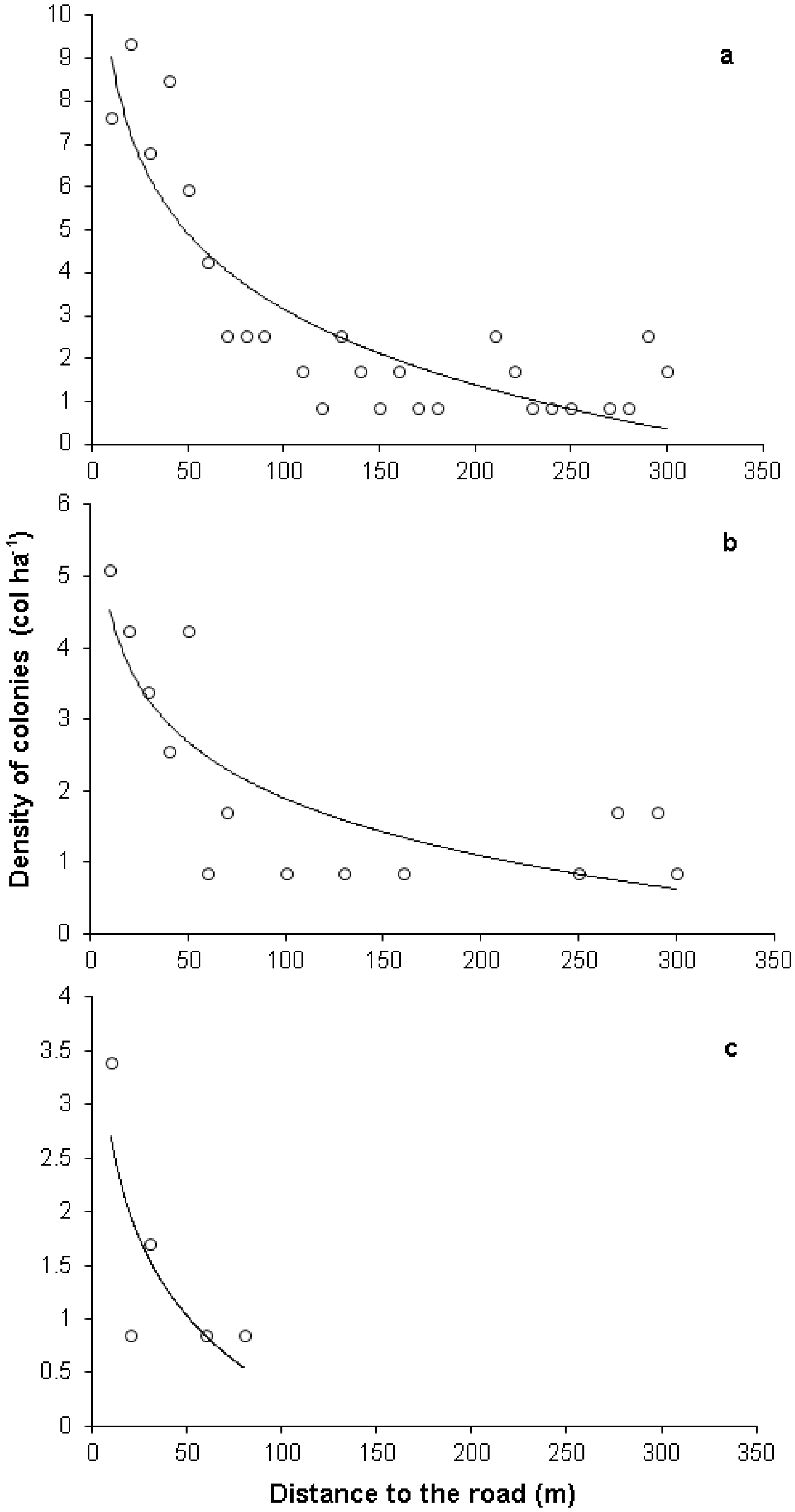

a
b
c
Density of colonies (col ha-1)
Distance to the road (m)
0
50
100
150
200
250
300
350
0
1
2
3
4
5
6
7
8
9
10
0.5
1.5
2.5
3.5

Figure 3.

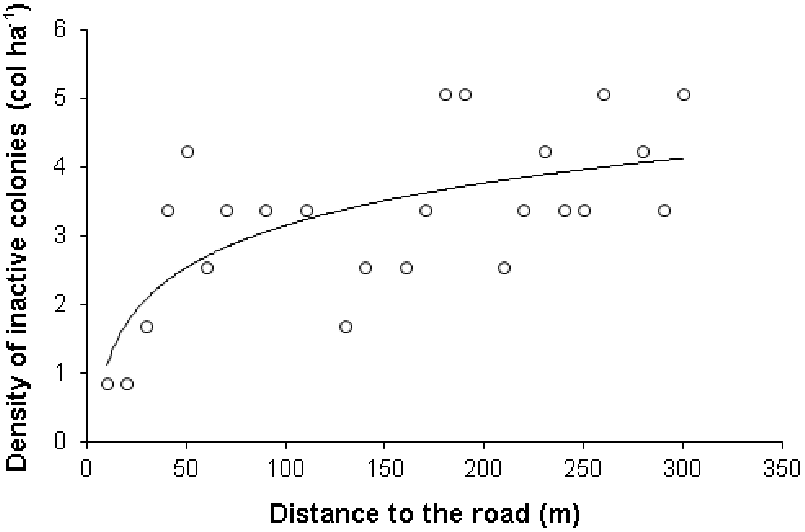
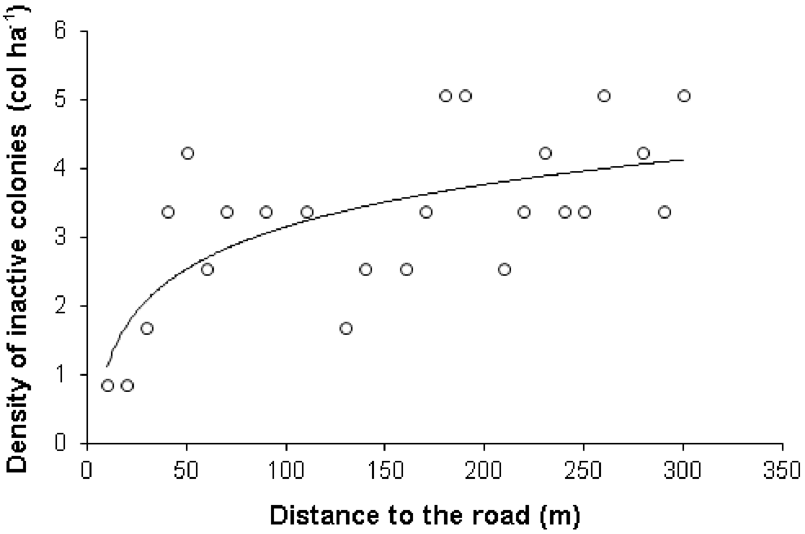

Density of inactive colonies (col ha^{-1})
6
5
4
3
2
1
0
0
50
100
150
200
250
300
350
Distance to the road (m)

Figure 3.


Density of inactive colonies (col ha^{-1})
0
1
2
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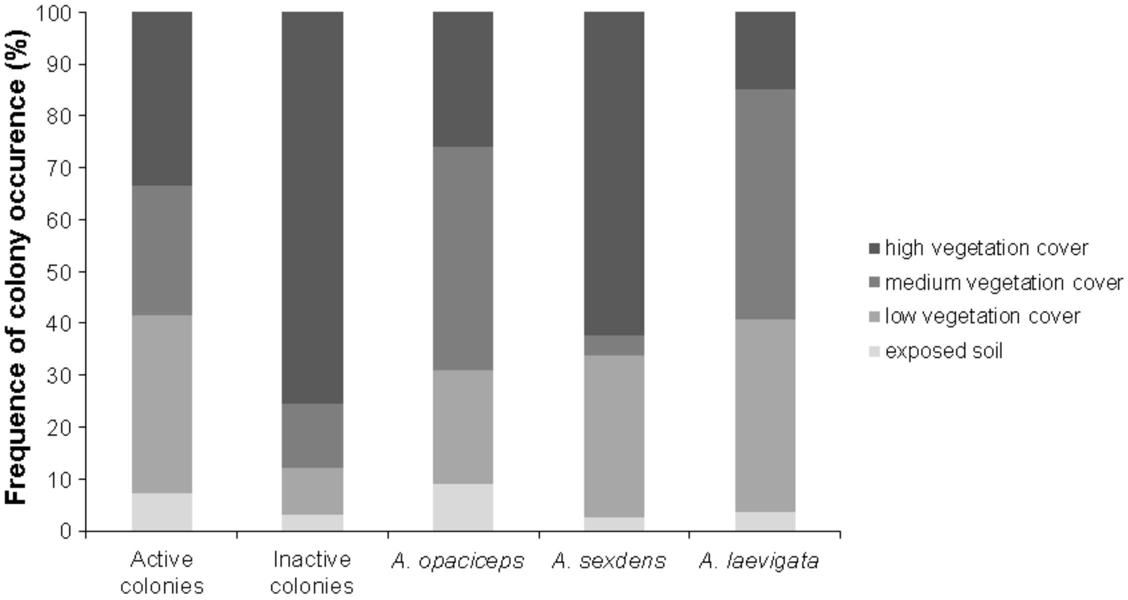
4
5
6
0
50
100
150
200
250
300
350
Distance to the road (m)

Figure 4.


Frequence of colony occurence (%)
100
90
80
70
60
50
40
30
20
10
0
Active colonies
Inactive colonies
A. opaciceps
A. sexdens
A. laevigata
high vegetation cover
medium vegetation cover
low vegetation cover
exposed soil

4 HERBIVORY BY THE LEAF CUTTING ANT *Atta opaciceps* IN BRAZILIAN CAATINGA: anthropogenic disturbance increases herbivory rate

MANUSCRITO A SER ENVIADOAO PERIÓDICO *OECOLOGIA*

Herbivory by the leaf cutting ant *Atta opaciceps* in Brazilian Caatinga: anthropogenic disturbance increases herbivory rate

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ABSTRACT

Changes in species composition caused by anthropogenic disturbances are known to modify interactions between organisms. Leaf-cutting ants are the most voracious herbivore of the Neotropical region and are known to proliferate in human modified landscapes. We evaluate the effect of chronic anthropogenic disturbance on the herbivory rates of the leaf-cutting ant *Atta opaciceps* in Caatinga areas. Due to the strong deciduousness of Caatinga vegetation, we also evaluated the variation in herbivory rates of this species in the dry and wet season. We assessed the foraging data (foraging area, foliage availability, leaf consumption and herbivory rate) of *A. opaciceps* colonies in areas of Caatinga with different levels of chronic anthropogenic disturbance. Herbivory rates ant leaf consumption were affected by chronic disturbance, with higher values of herbivory collected by the colonies located in more disturbed areas. We also found a strong effect of the season on all variables related to the foraging and herbivory of *A. opaciceps* with great values for the dry season. These results indicate that more disturbed areas in Caatinga may have more palatable vegetation and provide greater foliar consumption/herbivory by leaf-cutting ants. The increase of human activities are positively related with high values of herbivory by leaf cutting ants, which is more intense in the dry season. In this sense, human disturbances and herbivory by leaf cutting-ants in the Caatinga be also related to changes in microclimatic conditions, regeneration and dynamics of plants communities, nutrient stocks and cycling promoting the maintenance of vegetation in early stages of succession.

Key words: foraging ecology, foraging effort, foraging trails, plant selection, seasonally dry tropical forests.

Introduction

In the tropical forests, changes in land use invariably causes habitat loss and fragmentation, including the consequent creation of forest edges (Laurance et al. 2001 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 (Foley et al. 2005; Laurance et al. 2011; Hansen et al. 2013). Additionally, the remaining vegetation in such human-modified landscapes remains exposed to a more subtle disturbance known as chronic anthropogenic disturbances (CAD, *sensu* Singh et al. 1998). In contrast to acute disturbances, the CAD is sometimes imperceptible, because it refers to periodic but continuous removals of small portions of biomass such as firewood collection, exploitation of non-timber forest products, fodder for livestock, and hunting (Singh et al. 1984; Singh and Barbier 1996; Sagar et al. 2003; Martorell and Peters 2005). In addition to changes in vegetation structure and physical environment (i.e. increment of light habitats), CAD may causes taxonomic, functional and phylogenetic impoverishment of woody plant communities (Sagar et al. 2003; Ribeiro et al. 2015, 2016) and drive assemblages towards biotic homogenization due to the proliferation of disturbance-adapted species and the collapse of sensitive species populations (Smart et al. 2006; Wiegmann and Waller 2006; Ribeiro-Neto et al. 2016, Oliveira et al. 2017).

Some leaf-cutting ant species (LCA; Formicidae, Attini) have been reported to respond positively to human disturbances and thus to proliferate across several habitats in human-modified landscapes such as pastures, crop fields, roads, regenerating forest patches, small forest fragments and forest edges (Fowler 1983; Jaffe and Vilela 1989; Terborgh et al. 2001; Vasconcelos et al. 2006; Wirth et al. 2007; Meyer et al. 2009; Dohm et al. 2011). Proliferation has been proposed to result from a combination of several processes, including (1) a greater amount of nesting sites in open areas (Vasconcelos 1990; Vasconcelos et al. 2006), and (2) the relaxation of both bottom-up (increased availability of pioneer plants species, a high quality food resource Farji-Brener 2001; Urbas et al. 2007; Falcão et al. 2011) and top-down (less parasitoid phorid flies and predators such as armadillos and anteaters, Almeida et al. 2008; Wirth et al. 2008) population controls. LCA may affect plant assemblages directly through foliage removal (Wirth et al. 1997; Urbas et al. 2007), seed dispersal services (Dalling and Wirth 1997, Leal and Oliveira 1998, Costa et al. 2014), and indirectly decreasing in topsoil fertility (Meyer *et al*. 2013) and increasing in light environment in nest (Corrêa *et al*. 2010, Meyer et al. 2011a) and foraging areas (Corrêa et al. 2016). The net outcomes of these effects negatively affect plant regeneration, reducing seedling germination and sapling recruitment of shade-tolerant and disturbance-sensitive species (Corrêa et al. 2010; Meyer et al. 2011b), and altering the dynamic and structure of tree assemblages, especially in edge-affected forest patches (see review in Leal et al. 2014a and Tabarelli et al. 2017).

Whatever the LCA impact from plant population level to ecosystem dynamics it is mediated or regulated by the herbivory activity; i.e. LCA are able to harvest ca. 70 to 500 kg of dry weight/per colony/per year (Wirth et al. 2003; Herz et al. 2007; Costa et al. 2008; Falcão et al. 2011). As a consequence, forest area-based herbivory rates of LCA vary from 2.1% of the available foliage area in an undisturbed late-successional forest in Panama (0.52 *Atta colombica* colonies/ha, Herz et al. 2007) to 36% at the edge of human-modified Atlantic forest (2.79 *A. cephalotes* colonies/ha, Wirth et al. 2007; Urbas et al. 2007; Meyer et al. 2009). The latter value greatly exceeds the overall rate of herbivory estimated for tropical forests (5-15%, Schowalter et al. 1986; Landsberg and Ohmart 1989; Coley and Barone 1996). Accordingly, LCA herbivory impacts plant fitness, demography and community structure (Wirth et al. 2003; Leal et al. 2014a; Corrêa et al. 2010, 2016). It is important to point that most research on this topic has been developed in tropical rainforests and savannahs (e.g. Urbas et al. 2007; Costa et al. 2008; Corrêa et al. 2010) and little is known about how LCA population and herbivory rates relate to forest disturbances on seasonally dry tropical forests (SDTF; but see Barrera et al. 2015 and Tabarelli et al. 2017). For example, edge effects on tree assemblages - one of the main drivers of LCA proliferation in tropical rainforests - have been found to be negligible in Caatinga (a Brazilian SDTF) fragments due to its low stature and open-vegetation structure (Oliveira et al. 2013). Consequently, all light-related mechanisms concerning LCA population release and herbivory rates in tropical rainforest is expected to be of secondary importance in the Caatinga dry forest.

Caatinga is a mosaic of seasonally dry tropical forests and shrub, xerophytic vegetation (Pennington et al. 2009) which occupies 884,453 km² of northeastern Brazil (Sampaio 1995; Leal et al. 2005). It presents a dense (26 inhabitants / km², Medeiros et al. 2012) and low income human population (Ab'Saber 2000), which is typically dependent on natural resources for their subsistence (Vergles et al. 2015). We refer to firewood collection (Cavalcanti et al. 2015), exploitation of bark and leaves for medicinal use (Albuquerque et al. 2007), grazing of native vegetation by livestock (Leal et al. 2003), hunting (Alves et al. 2009) and slash-and-burn agriculture (Pereira et al. 2001), all activity typically leading to CAD and considered potential forces driving species interactions and the ecology of LCA in Caatinga human-modified landscapes.

In this study we investigate how seasonality and CAD affect vegetation availability and the foraging behavior of the LCA *Atta opaciceps* in a Caatinga dry forest, including herbivory rate through the whole year. As Caatinga vegetation is seasonal and CAD imposes biomass loss, available vegetation for LCA is expected to be lower in the dry season and in the most disturbed sites. Accordingly, LCA colonies set larger foraging areas during dry season and in the most disturbed sites, but with lower per capita consumption and herbivory rate.

METHODS

Study site

This work was carried out in the Catimbau National Park (8º24'00" and 8º36'35" S; 37º0'30" and 37º1'40" W), located in the state of Pernambuco, northeastern Brazil (hereafter Catimbau, Figure 1). The climate is semi-arid, with annual temperature averaging 23ºC, 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; Rito et al. 2017). 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). Vegetation is mostly a low-stature dry forest with Fabaceae, Euphorbiaceae and Boraginaceae as the predominant plant families, while the ground layer is dominated by Cactaceae, Bromeliaceae, Malvaceae, Asteraceae and Fabaceae (Rito et al. 2017).

Studied species

Three *Atta* species occur at the Catimbau: *A. laevigata* (Smith, 1985), *A. opaciceps* (Borgmeier, 1939), and *A. sexdens* (L. 1758) (Siqueira et al. in press). *Atta opaciceps*, the focal species in this study, is considered to be endemic to the Caatinga region (Ulysséa and Brandão 2013) and thus it is tolerant to reduced humidity and high temperatures. In the Catimbau, *A. opaciceps* achieves a high population density (2.45 col ha^{-1}; Siqueira et al. in press), and it has been recorded from open habitats (e.g. abandoned field crops) to forest patches. The deposition of soil above nests is quite irregular, formed by several small mounts, similar to that of *A. sexdens*, but can sometimes be constituted by a single large mound similar to *A. laeviagta*. They have external refuse dumps, which are annually renewed in 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 CAD intensity, eight adult and active colonies of *A. opaciceps* were selected in vegetation patches exposed to different levels of disturbance. These colonies were spread in to an area of 9.33 km^2 and were disposed at least 2.25 ± 1.70 km apart each other. Around each colony, CAD was computed as a global multi-metric index (hereafter disturbance index) using the method adapted by Arnan et al. (in revision). The disturbance index integrates nine disturbance indicators related to the two main sources of CAD at Catimbau: livestock and human pressure via collection of forest products (Rito et al. 2017). Taking into account these main sources of CAD, we adopted the following groups of descriptors: (1) descriptors correlated with the disturbance exerted by the livestock activity, (2) descriptors related firewood and timber collection, and (3) descriptors associated human pressure in general (i.e. exploitation of non-timber forest products, hunting). For the two first groups of descriptors, it was considered a 100-m buffer around each colony, and within this zone the following descriptors were measured: (1) animal dungs density (goats, sheep, horses and cattle); (2) the number of trails of goats and sheeps; and (3) the number of cut trunks (indicative of shallow cutting in vegetation). For the last group of descriptors, we considered: (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) (Leal et al. 2014b, Ribeiro et al. 2015). It was assumed that natural resources near human settlements tend to be exploited firstly, producing a “sequential waves of forest degradation” (Ahrends et al. 2010). Then we calculate the disturbance index as the sum of the nine descriptors using the following formula proposed by Legendre & Legendre (1998) and subsequently by other authors (Herzog et al. 2006; Blüthgen et al. 2012): $I = \frac{\sum_{i=1}^{n}(y_i - y_{min})/(y_{max} - y_{min})}{n} \times 100$, where I 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 descriptor considered in the index. Thus, this formula first standardizes the values of each disturbance descriptor between 0 and 1, and so they are weighted 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 disturbance index calculation, see Arnan et al. in revision).

To estimate LCA herbivory rate in the Catimbau, we first estimated the time peak of daily activity examining five of our eight focal colonies, which covered the whole CAD gradient as measured by the disturbance index. Each colony was examined twice (one on dry and one on wet season) via a 24-h survey, in which the number of leaf fragments carried into the nest by the ants were counted during a 5-min period every 2 hours (see Appendix 1 and Wirth et al. 1997). After determined the peak activity, we estimated (1) foraging areas, (2) vegetation availability in foraging areas, (3) consumption rate, (4) herbivory rate, and (5) harvested plants for all the eight focal colonies during the dry and wet seasons always throughout observation during the 5-min peak activity as detailed below.

Foraging area

Our foraging area estimates for the eight focal colonies took into account the activity concentrated on the trunk trails, which cover only a part of the area addressed by ants around the nest (Wirth et al. 2003; Kost et al. 2011). Foraging trails were examined monthly during a single day and at the peak of foraging activity and covering both season (dry and wet). All active foraging trails were followed to the spot where the ants were cutting the plant material and mapped with a GPS (Global Positioning System, Garmin e-Trex 10), which resulted in an error of less than 3 m. Foraging trail system maps 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 superimpose the monthly maps of the trails of dry (January-February and August-December) and wet (March-July) months. This 20-m zone has been considered a reasonable proxy for LCA foraging areas (see Wirth et al. 2003 for more details on the foraging area of LCA).

Vegetation availability

To estimate the vegetation availability across the foraging areas of the eight LCA colonies, we adopted the leaf area index (LAI, total one-sided area of leaves per unit ground surface area), by means of digital hemispherical photographs (Frazer et al. 2001; Urbas et al. 2007; Chianucci and Cutini 2012). 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 and Campbell 1989; Chen and Black 1992). We sampled the LAI within the foraging area of the colonies adopting a 100 m x 80 m grid, with the colony nest occupying the central position. The grid was split into four parallel transects north-to-south oriented, two of which set 20 m westward and two set 20 m eastward from the colony. It was necessary to set the transects 20 m apart from the colonies to avoid the influence of clearing above nests (Farji-Brener and Illes 2000). Along the four transects, we took pictures each 20 m, totalizing 20 pictures per colony. We took the photographs on eight consecutive days at about 1 m above ground with a Nikon DX 3000 equipped with fisheye converter FC-E8 at 05:00 to 06:30, in the morning, and 16:00 to 17:30, at the evening, avoiding the periods of greater solar intensity and direct solar radiation in the canopy. LAI estimation was performed during both dry (December 2014) and wet (May 2015) seasons. The average values of the LAI were multiplied by the foraging area of each colony for both dry (January-February and August-December) and wet (March-July) season, obtaining the amount of available vegetation (in m^2) per season.

Consumption rate

To estimate plant consumption by LCA, we sampled all ants loaded with plant fragments (leaves, flowers and seeds) considering an interval of five minutes at the peak of daily activity in the trunk trail (Wirth et al. 2003; Urbas et al. 2007). Plant fragments were packed in properly labeled plastic bags, and later placed on a scanner for size measurement (Epson Ecotank L375). The average size of the collected fragments was obtained (in cm^2) using Image J software (Abràmoff et al. 2004). After measuring the area, the fragments were placed in a stove with a temperature between 60-70°C for approximately 72 hours and then measured the dry weight.

Based on these parameters, the foliage removal was calculated by extrapolating the values obtained across the 5-min samples to 24 hours through two different equations (for dry and wet season). In the dry season: $F_{24d} = 334.76 + (-56.75) \text{ X } F_{5d} + (2.48) \text{ X } F_{5d}{}^2$, where F_{5d} is the number of fragments collected in five minutes during the dry season. For the wet season: $F_{24w} = 117.84 + (- 8.79) \text{ X } F_{5w} + (0.82) \text{ X } F_{5w}{}^2$, where F_{5w} is the number of fragments collected during five minute periods in wet season. Then, to obtain the foliage removal (area and biomass) in a single day, we replaced the respective value of number of fragments in five minutes by the average area or biomass calculated for the whole samples. These daily estimates were further used to obtain monthly and seasonal consumption rate. To avoid disproportional contribution of the season duration, we calculate mean monthly consumption rate of dry (January-February and August-December) and wet (March-July) months.

Herbivory rate

The herbivory rate for every colony was obtained through the following equation: Herbivory Rate = LC/(LC+AVC)X100, where, LC is the total foliage consumed by ants (leaf consumption) and AVC is the available vegetation after consumption (*sensu* Wirth et al. 2003). Similarly to consumption, the daily herbivory rate was extrapolated to reach monthly and seasonal values; the former were presented as mean monthly herbivory rate of dry (January-February and August-December) and wet (March-July) months to avoid disproportional contribution of the season duration.

Plants and other resources harvested

In order to identify the plant species and parts used as substrate for the cultivation of the symbiotic fungus, workers 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 harvest plant species, which were identified in the field when possible. Undetermined species were morphotyped and later identified at the lowest possible taxonomic level with the help of taxonomist.

Statistical analysis

To test the hypothesis that CAD affect herbivory of *A. opaciceps*, we adopted full factorial generalized linear mixed models (GLMM), with season (dry and wet) as a categorical fixed predictor, the disturbance index as a continuous fixed predictor, and LCA colony as a random factor. The dependent variables consisted of: colony foraging area, vegetation availability in the foraging area, consumption rate (in biomass and leaf area) and herbivory rate. We used Student's t-test for dependent samples to examine the differences in LCA foraging activity peak between dry and wet season. All analyzes were done using software R (R Development Core Team 2015).

RESULTS

Foraging area

Considering the eight focal colonies, the average foraging area was 4.7 times larger in dry season as compared to wet season (Table 1), as it ranged from 5700 to 44900 m² in dry to 320 to 9540 m² in wet season. Contrarily to our initial expectation, foraging area was not affected by either CAD intensity or the interaction between season and CAD intensity (Figure 2a; Table 1).

Vegetation availability

Available vegetation across foraging areas was highly variable and it reached in average 2189.45 m² ± 2289.32 (mean ± SD) in the dry season and 3284.18 m² ± 3433.98 in the wet season (Figure 2b-c; Table 1). This marked difference of almost 1.5 fold was due to the low average LAI in the dry season (0.12 ± 0.11, Figure 2b, Appendix 2). Moreover, vegetation availability was negatively affected by CAD intensity, and this effect was particularly strong in wet season (Figure 2b, Table 1).

Consumption rate

LCA colonies consumed more foliage during dry season concerning both biomass (Figure 2d, Table 1) and leaf area (Figure 2e, Table 1). Precisely, colonies consumed 19.19 kg ± 7.18 kg of biomass per month during dry season but only 15.96 kg (± 6.25) per month in the rainy season

(Appendix 3). The same pattern was observed for leaf area as it reached 134.29 m² ± 40.62 per month in the dry season vs. 46.13 m² ± 14, 66 consumed per month in the wet season (Appendix 3; Table 1). Additionally, vegetation consumption measured as biomass was positively affected by CAD intensity (Figure 2d, Table 1), but this effect was not observed on leaf area consumption (Figure 2e, Table 1). In both cases (kg and m²), there was no interaction between season and CAD intensity (Table 1).

Herbivory rate

Colony herbivory rate was highly variable in both seasons, ranging from 9.10% to 98.83% in dry season, while it ranged from 1.57% to 93.36% in wet season. However, LCA removed about twice as much foliage in dry season (45.18% ± 31.56) as compared to wet season (22.24% ± 31.03, Figure 2f). Herbivory rate was also higher in more disturbed sites (i.e. higher CAD index) (Figure 2f) and there was no interaction between season and CAD intensity (Table 1).

Plants and other resources harvested

A total of 11696 fragments (leaves, flowers and seeds) from 38 different resource items, were collected in the annual diet of focal colonies. Among these resources, a total of 36 plant species within 12 families was recorded. The woody species *Croton argyrophylloides* (18%), *Cenostigma microphylla* (10%) and *C. pyramidalis* (7%) were the most frequent species in diet (Table 2). However, herbs accounted for 10% of the fragments collected, while several cacti species represented almost 17%. LCA were also recorded to use biological soil crusts and dungs of goats and lizards (Table 2).

DISCUSSION

Overall, our results suggest that CAD and seasonality affect both the available vegetation and the foraging behavior of *A. opaciceps* in the Caatinga dry forest. Briefly, available vegetation (i.e. leaf-area index) is lower during the dry season and it is negatively affected by CAD. According to our expectation, foraging area is larger during the dry season but it is not affected by CAD. However, contrary to our prediction, LCA consume more vegetation in terms of both biomass and leaf area during dry season, particularly in more disturbed sites. Thereby, herbivory rate is higher during the dry season and increment in response to disturbance. Although highly variable across colonies and seasons, LCA are able to harvest an expressive portion of the available vegetation, including a large spectrum of resources.

These findings reinforce the notion that climate seasonality but also human disturbances affect many aspects of the relationship between LCA ecology and their environments as well documented in moist neotropical forests such the Atlantic and Amazonian forests and Cerrado savanna (Vasconcelos 1990; Vasconcelos et al. 2006; Corrêa et al. 2010, 2016; Meyer 2011a, 2011b, 2013). But in contrast to humid forests, in which LCA concentrates plant harvesting on tree species, in the Caatinga dry forest other plant resources are apparently crucial such as herbs (annual 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 allow 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 fragments and forest edges (Fowler 1983; Jaffe and Vilela 1989; Terborgh et al. 2001; Vasconcelos et al. 2006; Wirth et al. 2007; Dohm et al. 2011). Our findings in 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 surprisingly that LCA exhibit larger foraging areas during the dry season since the deciduous Caatinga vegetation has much less to offer per unit of area compared to the rainy season. Note that during dry season most of the Caatinga patches do not support a single evergreen tree or shrub (Sampaio 1995; Machado et al. 1997). Such a scarcity probably forces LCA to compensate by accessing extra areas and other sources to obtain the amount of vegetation need to keep the fungus garden. We refer, for example, to the transient herbaceous resources (e.g. *Sida galheirensis* and *Portulaca elatior*), flowers from several species, Cactaceae cladodes and scavenging on animal feces.

However, it is apparently surprising that LCA collect 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 wet season) are tightly higher than herbivory rates in other systems such as tropical rainforests: 12.5% and 14% according to Wirth et al. (2003) and Urbas et al. (2007), respectively, and 17% in Brazilian savannahs (Costa et al. 2008). It is true that hemispheric photographs (the standard protocol for LAI estimate) were not able to capture the herbaceous layer, resulting into an underestimate of available vegetation. Additionally, LCA shall compensate for low quantity/quality foliage available by harvesting more materials, particularly in dry season. We refer to litter and conservative/though leaves, which the symbiotic fungus is not able to properly degrade due to high contents of lignin and cellulose (major constituents of plant tissues) (Abril and Bucher 2002). In other words, only a small fraction of all material transported to nests is consumed/degraded in comparison to fresh tissues available in the rainy season, explaining why LCA collect more. In this perspective, as water deficit increases, the concentration of secondary compounds (e.g. terpenoids and tannins) in plant tissues may increase (Selmar 2008), and these compounds are ant repellent as they difficult the symbiotic fungus use (Hölldobler and Wilson 1990; Wirth et al. 2003). In contrast, as water deficit increases it has been reported that tissue concentration of proline and carbohydrates may increase (Meyer et al. 2006), and these drought-stressed plant parts or individuals are preferred by LCA (Vasconcelos and Cherret 1996; Meyer et al. 2006; Ribeiro-Neto et al. 2012). However, this preference may be relevant in the context of rainforests where LCA have a diverse flora and plenty of plant material to select.

Leaf biomass consumption in absolute terms was also positively associated with CAD, suggesting that although CAD negatively affect available woody vegetation (as measured by photos) it may (1) somehow increments the availability of palatable, light-demanding woody plants as documented across edge-affected habitats of humid neotropical forests (Oliveira et al. 2004; 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 (Silva et al. 2009; Vieira 2017) and woody disturbance-adapted species such as those from *Croton*, *Jatropha* and *Cenostigma* genera (Ribeiro et al. 2015, 2016; Ribeiro-Neto et al. 2016; Rito et al. 2017); i.e. 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. 2017); some of them apparently preferred by LCA as the two *Cnidoscolus* species documented here. The two herbs most frequently used by LCA, *Sida galheirensis* and *Portulaca elatior*, are also very abundant and widely distributed in the Catimbau, specially in disturbed areas (Vieira 2017). This selectivity by plants more abundant and that are good colonizers are already known for other species of leaf-cutting ants in tropical rainforests and savannas (Wirth *et al*. 2003; Facão et al. 2011; Leal et al. 2014a).

However, the leaf area consumption was not higher in more disturbed sites. Relationship among leaf area, toughness, thickness and dry biomass are important traits concerning plant resistance to drought (Vile et al. 2005; Westbrook et al. 2011), and this rather than light, as in tropical rainforests, must drive leaf suitability to LCA in dry forests as 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). This again is the case of some Euphorbiaceae woody species (genera *Croton*, *Jatropha* and *Cnidoscolus*) already mentioned here to proliferate in disturbed areas of Caatinga (Ribeiro et al. 2015, 2016; Ribeiro-Neto et al. 2016; Rito et al. 2017) and frequently harvested by LCA in these areas, although thick leaves have not been considered the most palatable resources for LCA (Howard 1988; Nichols-Orians and 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 CAD and leaf biomass consumed, but failed to find such a relationship between CAD and leaf area consumed.

This argument is in accordance with our perception that overall the available vegetation in the Caatinga has low quality and it is particularly scarce in the dry season, forcing LCA to opportunistically collect what is available in high quantities, but with low use by the symbiotic fungus. Even those herb and woody species that proliferate in disturbed habitats supporting increments in plant collection can be considered low-quality resources as compared to the soft leaves frequently found in humid forests (Vile et al. 2005; Westbrook et al. 2011). This 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 (Mundim et al. 2008; Leal et al. 2014a).

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 (Sampaio

1995; Machado et al. 1997). The LCA proliferation in Caatinga disturbed patches (Tabarelli et al. 2017; Siqueira *et al*. in press) and LCA ability to harvest reasonable portions across a large material through the whole year, including those 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; Corrêa et al. 2010, 2016; Meyer et al. 2011a, 2011b, 2013). Particularly relevant is the question whether seedlings have chance of long-term survival while inhabiting LCA foraging areas, particularly those evergreen. There have been plenty of anecdotal reports calling attention to the scarcity of woody species seedlings in the Caatinga vegetation and the LCA polyvalence might play a part in arrested succession experienced by Caatinga patches following land abandonment (Tabarelli et al. 2017).

In synthesis, foraging ecology of LCA is modulated by climatic seasonality and human disturbance as these two drivers affect the spectrum and the amount of resources available for LCA. This is worth mention the ability of LCA in maintaining foraging activity even in the peak of 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 humid forests. The potential and probably complex synergy between human disturbances, in this case chronic disturbances, proliferation of key resources (e.g. light-demanding herbs, native winner woody species) and vegetation regeneration dynamic deserves further investigation.

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LITERATURE CITED

AB’SABER (2000) Spaces occupied by the expansion of dry climates in South America during the quaternary ice ages. Rev do Inst Geológico 21:71–78

Abràmoff MD, Magalhães PJ, Ram SJ (2004) Image processing with image J. Biophotonics Int 11:36–41

Abril AB, Bucher EH (2002) Evidence that the fungus cultured by leaf-cutting ants does not metabolize cellulose. Ecol Lett 5:325–328

Agrawal, AA (2007) Macroevolution of plant defense strategies. Trends Ecol Evol 22:103–109

Ahrends A, Burgess ND, Milledge SAH, Bulling MT, Fisher B, Smart JCR, Clarke JP, Mhoro BE, Lewis SL (2010) Predictable waves of sequential forest degradation and biodiversity loss spreading from an African city. Proc Natl Acad Sci USA 107:14556–61

Albuquerque UP et al (2007) Medicinal plants of the caatinga (semi-arid) vegetation of NE Brazil: A quantitative approach. J Ethnopharmacol 114:325–354

Almeida WR, Wirth R, Leal IR (2008) Edge-mediated reduction of phorid parasitism on leaf-cutting ants in a Brazilian Atlantic forest. Entomol Exp Appl 129:251–257

Alves RRN, Mendonça LET, Confessor MVA, Vieira WLS, Lopez LCS (2009) Hunting strategies used in the semi-arid region of northeastern Brazil. J Ethnobiol Ethnomed. doi:10.1186/1746-4269-5-12

Amorim IL, Sampaio EVSB, Araújo EDL (2005) Flora e estrutura da vegetação arbustivo-arbórea de uma área de caatinga do Seridó, RN, Brasil. Acta Bot Brasilica 19:615–623

Barrera CA, Buffa LM, Valladares G (2015) Do leaf cutting-ants benefit from forest fragmentation? Insights from community and species-specific responses in a fragmentation Dry forest. Insect Conserv Divers. doi: 10.1111/icad.12125

Cavalcanti MCBT, Ramos MA, Araújo EL, Albuquerque UP (2015) Implications from the use of non-timber forest products on the consumption of wood as a fuel source in human-dominated semiarid landscapes. Environ Manage 56:389–401

Chianucci F, Cutini A (2012) Digital hemispherical photography for estimating forest canopy properties: Current controversies and opportunities. IForest 5:290–295

Coley PD, Barone JA (1996) Herbivory and plant defenses in Tropical Forests. Annu Rev Ecol Syst 27:305–335

Coley PD, Bryant JP, Chapin FS (1985) Resource availability and plant antiherbivore defense. Science 230:895–899

Corrêa MM, Silva PSD, Wirth R, Tabarelli M, Leal IR (2010) How leaf-cutting ants impact forests: Drastic nest effects on light environment and plant assemblages. Oecologia 162:103–115

CORRÊA MM, SILVA PSD, WIRTH R, TABARELLI M, LEAL IR (2016) Foraging activity of leaf-cutting ants changes light availability and plant assemblage in Atlantic forest Ecol Entomol 41:442–450

Costa RC, Araújo FS, Lima-Verde LW (2007) Flora and life-form spectrum in an area of deciduous thorn woodland (caatinga) in northeastern, Brazil. J Arid Environ 68:237–247

Costa AN, Vasconcelos HL, Vieira-Neto EHM, Bruna EM (2008) Do herbivores exert top-down effects in Neotropical savannas? Estimates of biomass consumption by leaf-cutter ants. J Veg Sci 19:849–8544

Costa UAS, Pinto SRR, Silva FA, Oliveira M, Agra DB, Marques E, Leal IR (2014) O papel das formigas como dispersores secundários de sementes na Floresta Atlântica Nordestina. In Tabarelli M, Aguiar Neto AV, Leal IR, Lopes AV (eds) Serra Grande: uma floresta de ideias 415–438. Editora Universitária da UFPE, Recife, Brazil.

Dalling JW, Wirth R. (1998) Dispersal of *Miconia argentea* seeds by the leaf-cutting ant *Atta colombica*. J Trop Ecol 14:705-710

Dohm C, Leal IR, Tabarelli M, Meyer ST, Wirth R (2011) Leaf-cutting ants proliferate in the Amazon: an expected response to forest edge? J Trop Ecol 27:645–649

Dorigo WA, Zurita-Milla R, Wit AJW, Brazile J, Singh R, Schaepman, MEA (2007) A review on reflective remote sensing and data assimilation techniques for enhanced agroecosystem modeling. International Journal of Applied Earth Observation and Geoinformation 9:165-193

Falcão PF, Pinto SRR, Wirth R, Leal IR (2011) Edge-induced narrowing of dietary diversity in leaf-cutting ants. Bull Entomol Res 101:305–311

Farji-Brener AG (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 AG, Illes AE (2000) Do leaf-cutting ant nests make “bottom-up” gaps in neotropical rain forests?: A critical review of the evidence. Ecol Lett 3:219–227

Foley JA et al (2005) Global consequences of land use. Science 309:570–4

Ford RG (1983) Home range in a patchy environment: Optimal foraging predictions. Integr

Comp Biol 23:315–326

Forti LC, Moreira AAA, Andrade APP, Castellani MA, Caldato N (2011) Nidificação e arquitetura de ninhos de formigas-cortadeiras. In: Della-Lucia TMC (eds) Formigas-cortadeiras da bioecologia ao manejo. Editora UFV, Viçosa, Brazil.

Frazer GW, Fournier RA, Trofymow JA, Hall RJ (2001) A comparison of digital and film fisheye photography for analysisof forest canopy structure and gap light transmission. Agric For Meteorol 109:249–263

Griffiths H, Parry MAJ, Hsiao T (2002) Plant responses to water stress. Annu Rev Plant Physiol 89:801–802

Hansen MC et al (2013) High-resolution global maps of 21st-century forest cover change. Science 342:850–3

Hölldobler B, Wilson EO (1990) The ants. Springer, Berlin.

Howard JJ (1988) Leaf-cutting ant diet selection: relative influence of leaf-chemistry and physical features. Ecology 69:250–260.

Hsiao TC (1973) Plant responses to water stress. Annu Rev Plant Physiol 24:519–70.

Kost C, Tremmel M, Wirth R (2011) Do leaf-cutting ants cut undetected? testing the effect of ant-Induced plant defences on foraging decisions in *Atta colombica*. PLoS One 6:e22340

Jorge MSP, Peres CA (2005) Population density and home range size of red-rumped agoutis (*Dasyprocta leporina*) within and outside a natural Brazil nut stand in southeastern Amazonia. Biotropica 37:317-321

Laurance WF et al (2011) The fate of Amazonian forest fragments: A 32-year investigation. Biol Conserv 144:56–67

Laurance WF et al (2001) Rain forest fragmentation and the structure of Amazonian liana communities. Ecology 82:105–116

Laurance WF, Sayer J, Cassman KG (2014) Agricultural expansion and its impacts on tropical nature. Trends Ecol Evol 29:107–116

Leal IR, Oliveira PS (1998) Interactions between fungus-growing ants (Attini), fruits and seeds in Cerrado vegetation in Southeast Brazil1. Biotropica 30:170–178

Leal IR, Oliveira PS (2000) Foraging ecology of attine ants in a Neotropical savanna: seasonal use of fungal substrate in the cerrado vegetation of Brazil. Insectes Soc 47:376–382

Leal IR, Silva JMC, Tabarelli M, Lacher TE (2005) Changing the course of biodiversity conservation in the caatinga of northeastern Brazil. Conserv Biol 19:701–706

Leal IR, Tabarelli M, Silva JMC (2003) Ecologia e Conservação da Caatinga. Editora Universitária da UFPE, Recife

Leal IR, Wirth R, Tabarelli M (2014a) The multiple impacts of leaf-cutting ants and their novel ecological role in human-modified Neotropical forests. Biotropica 46:516–528

Leal LC, Andersen AN, Leal IR (2014b) Anthropogenic disturbance reduces seed-dispersal services for myrmecochorous plants in the Brazilian Caatinga. Oecologia 174:173–181

Leal LC, Andersen AN, Leal IR (2015) Disturbance winners or losers? Plants bearing extrafloral nectaries in Brazilian Caatinga. Biotropica 47:468–474.

Lima PB, Lima LF, Santos BA, Tabarelli M, Zickel CS (2015) Altered herb assemblages in fragments of the brazilian Atlantic Forest. Biol Conserv 191:588–595

Machado IC, Barros LM, Sampaio EVSB (1997) Phenology of Caatinga species at Serra Talhada, PE, Northeastern Brazil. Biotropica 29:57-68

Martorell C, Peters EM (2005) The measurement of chronic disturbance and its effects on the threatened cactus *Mammillaria pectinifera*. Biol Conserv 124:199–207

Medeiros SS et al (2012) Sinopse do censo demográfico para o Semiárido Brasileiro.

Meyer ST, Leal IR, Tabarelli M, Wirth R (2011a) Ecosystem engineering by leaf-cutting ants:

Nests of *Atta cephalotes* drastically alter forest structure and microclimate. Ecol Entomol 36:14–24

Meyer ST, Leal IR, Tabarelli M, Wirth R (2011b) Performance and fate of tree seedlings on and around nests of the leaf-cutting ant *Atta cephalotes*: Ecological filters in a fragmented forest. Austral Ecol 36:779–790

Meyer ST, Leal IR, Wirth R (2009) Persisting hyper-abundance of leaf-cutting Ants (*Atta* spp.) at the edge of an old atlantic forest fragment. Biotropica 41:711–716

Meyer ST et al (2013) Leaf-cutting ants as ecosystem engineers: Topsoil and litter perturbations around *Atta cephalotes* nests reduce nutrient availability. Ecol Entomol 38:497–504

Meyer ST, Roces F, Wirth R (2006) Selecting the drought stressed: Effects of plant stress on intraspecific and within-plant herbivory patterns of the leaf-cutting ant *Atta colombica*. Funct Ecol 20:973–981

MMA (2004) Áreas Prioritárias para Conservação. Portaria no. 126 2–3.

Mundim FM, Costa AN, Vasconcelos HL (2008) Leaf nutrient content and host plant selection by leaf-cutter ants, *Atta laevigata*, in a Neotropical savanna. Entomol. Exp App 130:47–54.

Murphy PG, Lugo AE (1986) Ecology of Tropical Dry Forest. Annu Rev Ecol Syst 17:67–88

Nichols-Orians CM, Schultz JC (1989) Leaf-toughness affects leaf harvesting by the leaf-cutter ant, *Atta cephalotes* (L.) (Hymenoptera: Formicidae). Biotropica 21:80–83

Oliveira MA, Grillo AS, Tabarelli M (2004) Forest edge in the Brazilian Atlantic forest: drastic changes in tree species assemblages. Oryx 38:389–394

Oliveira FMP, Ribeiro-Neto JD, Andersen AN, Leal IR (2017) Chronic anthropogenic disturbance as a secondary driver of ant community structure: interactions with soil type in Brazilian Caatinga. Enviromental Conservation 44:115–123

Pennington RT, Prado DE, Pendry CA (2000) Neotropical seasonally dry forests and Quaternary vegetation changes. J Biogeogr 27:261–273

Pennington RT, Lavin M, Oliveira-Filho A (2009) Woody plant diversity, evolution, and ecology in the tropics: perspectives from seasonally dry Tropical Forests. Annu Rev Ecol Evol Syst 40:437–457

Pereira IM, Andrade LA, Costa JRM, Dias JM (2001). Regeneração natural em um remanescente de Caatinga sob diferentes níveis de perturbação, no agreste paraibano. Acta Botanica Brasilica, 15:413-426. doi:10.1590/S0102-33062001000300010

Quinn RM, Gaston KJ, Roy DB (1997) Coincidence between consumer and host occurrence: Macrolepidoptera in Britain. Ecol Entomol 22:197–208

R Core Team (2015) R: a language and environment for statistical computing. R Foundation for statistical computing, Vienna

Reid RS, Galvin KA, Kruska RS (2008) Global significance of extensive grazing lands and pastoral societies: An introduction. In: Reid RS, Galvin KA, Kuska RS (eds) Fragmentation in Semi-Arid and Arid Landscapes: Consequences for Human and Natural Systems, Springer, Berlin, pp. 1–24

Ribeiro-Neto JD, Pinho BX, Meyer ST, Wirth R, Leal IR (2012) Drought stress drives intraspecific choice of food plants by *Atta* leaf-cutting ants. Entomol Exp Appl 144:209–215

Ribeiro EMS, Arroyo-Rodríguez V, Santos BA, Tabarelli M, Leal IR (2015) Chronic anthropogenic disturbance drives the biological impoverishment of the Brazilian Caatinga vegetation. J Appl Ecol 52:611–620

Ribeiro EMS, Santos BA, Arroyo-Rodrigues V, Tabarelli M, Souza G, Leal IR (2016) Phylogenetic impoverishment of plant communities following chronic human disturbances in the Brazilian Caatinga. Ecology 96:1583–1502

Ribeiro-Neto JD, Arnan X, Tabarelli M, Leal IR (2016) Chronic anthropogenic disturbance causes homogenization of plant and ant communities in the Brazilian Caatinga. Biodivers Conserv 25:943–956

Rito KF, Arroyo-Rodrigues V, Queiroz RT, Leal IR, Tabarelli M (2017) Precipitation mediates the effect of human disturbance on the brazilian Caatinga vegetation. J Ecology 105:828–838

Rito KF, Tabarelli M, Leal IR (2017) Euphorbiaceae responses to chronic anthropogenic disturbances in Caatinga vegetation: from species proliferation to biotic homogenization. Plant Ecology 218:749-759

Rodal MJN, Sampaio EVSB (2002) A vegetação do bioma caatinga. In: Sampaio EVSB, Giulietti AM, Virgínio J, Gamarra-Rojas CFL (Eds)Vegetação e flora da caatinga, EMBRAPA, pp. 141–153

Sagar R, Raghubanshi AS, Singh JS (2003) Tree species composition, dispersion and diversity along a disturbance gradient in a dry tropical forest region of India. For Ecol Manage 186:61–71

Sampaio EVSB (1995) Overview of the Brazilian Caatinga In: Mooney HA, Bullock SH, Medina E (eds.) Dry tropical forest. Cambridge University Press, Cambridge, pp. 35-63

Santos BA, Peres CA, Oliveira MA, Grillo A, Alves-Costa CP, Tabarelli M (2008) Drastic erosion in functional attributes of tree assemblages in Atlantic forest fragments of northeastern. Brazil. Biol Conserv 141:249–260

Santos SA, Correia MF, Aragão MRS, Silva PKO (2005) Aspectos da Variabilidade Sazonal da Radiação, Fluxos de Energia e CO2 em Área de Caatinga. Rev Bras Geogr Física 04:761–773

Santos-Ribeiro E (2011) Influencia de perturbacoes antropicas sobre populações de cactáceas em áreas de caatinga. Master dissertation, Universidade Federal de Pernambuco, Recife, Brazil.

Selmar D (2008) Potential of salt and drought stress to increase pharmaceutical significant secondary compounds in plants. Landbauforsch. Volkenrode 58:139–144

Shahabuddin G, Kumar R (2006) Influence of anthropogenic disturbance on bird communities in a tropical dry forest: role of vegetation structure. Anim Conserv 9:404–413

Silva KA, Araújo EL, Ferraz EMN (2009) Estudo florístico do componente herbáceo e relação com solos em áreas de caatinga do embasamento cristalino e bacia sedimentar, Petrolândia, PE, Brasil. Acta bot bras 23:100–110

Singh JS, Pandey U, Tiwari AK (1984) Man and forests: A central Himalayan case study. Ambio 13:80–87

Singh SP, Barbier EB (1996) Chronic disturbance, a principal cause of environmental degradation in developing countries. Environ Conserv 24:1–2

Smart SM, Thompson K, Marrs RH, Le Duc MG, Maskell LC, Firbank LG (2006) Biotic homogenization and changes in species diversity across human-modified ecosystems. Proc R Soc B 273:2659–2665

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.

Tabarelli M, Siqueira FFS, Backe J, Wirth R, Leal IR (2017) Ecology of leaf-cutting ants in human-modifiedlandscapes. In: Oliveira SP. Koptur S (eds) Ant-plant interaction, impacts of human in terrestrial ecosystems. Cambridge University Press, Cambridge, pp73-90

Tadey M, Farji-Brener AG (2007) Indirect effects of exotic grazers: Livestock decreases the nutrient content of refuse dumps of leaf-cutting ants through vegetation impoverishment. J Appl Ecol 44:1209-1218

Terborgh et al (2001) Ecological meltdown in predator-free forest fragments. Science 30:1923-1926

Tonhasca JA, Bragança MAL (2000) Effect of leaf toughness on the susceptibility of the leaf-cutting ant Atta sexdens to attacks of a phorid parasitoid. Insectes Soc 47:220–222

Ulysséa MA, Brandão CRF (2013) Ant species (Hymenoptera, Formicidae) from the seasonally dry tropical forest of northeastern Brazil: A compilation from field surveys in Bahia and literature records. Rev Bras Entomol 57:217–224

Urbas P, Araújo MV, Leal IR, 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 HL, Cherrett JM. (1996) The effect of wilting on the selection of leaves by the leafcutting ant *Atta laevigata*. Entomol Exp Appl 78:215–220

Vasconcelos HL (1990) Foraging activity of two species of leaf-cutting ants (*Atta*) in a primary forest of the Central Amazon. Insectes Soc 37:131–145

Vasconcelos HL, Vieira-Neto EHM, Mundim FM, Bruna EM (2006) Roads alter the colonization dynamics of a keystone herbivore in neotropical savannas. Biotropica 38:661–665

Vergles EHD, Blackie RR, Koame CK, Gautier D (2015) Dry Forests, livelihoods and poverty alleviation: Understanding current trends. Int For Rev 17:54–69

Vieira LAF (2017) Comunidades de plantas herbáceas em um gradiente de precipitação e perturbação crônica na Caatinga. Master thesis, Universidade Federal de Pernambuco, Recife.

Wiegmann SM, Waller DM (2006) Fifty years of change in northern upland forest understories: Identity and traits of “winner” and “loser” plant species. Biol Conserv 129:109–123

Wirth R, Beyschlag W, Ryel RJ, Hölldobler B (1997) Annual foraging of the leaf-cutting ant Atta colombica in a semideciduous rain forest in Panama. J Trop Ecol 13:741–757

Wirth R, Herz H, Ryel RJ, Beyschlag W, Holldobler B (2003) Herbivory of leaf-cutting ants: a case study on *Atta colombica* in the tropical rainforest of Panama.Ecological Studies 164, Springer - Verlag, Berlin

Wirth R, Meyer S, Leal IR, Tabarelli M (2008) Plant herbivore interactions at the forest edge. Prog Bot 69:423–448

Wirth R, Meyer ST, Almeida WR, Araújo MV, Barbosa VS, Leal IR (2007) Increasing densities of leaf-cutting ants (Atta spp.) withproximity to the edge in a Brazilian Atlantic forest. J Trop Ecol 23:501

Zappi D (2008) Fitofisionomia da Caatinga associada à cadeia do Espinhaço. Megadiversidade 4:34–38

Table 1. Effects of season, disturbance index and their interaction on foraging area, vegetation availability, consumption rate (kg and m²) and herbivory rate of the colonies of *Atta opaciceps*in the Catimbau National Park, state of Pernambuco, Northeast Brazil. Significant effects are in bold ($p < 0.05$).

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 (m²)	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

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

Families/Species	Leaf	Flower	Seed	Frequency of total use (%)
Anacardiaceae				
Schinopsis brasiliensis Engl.	X			1.13
Spondias tuberosa 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

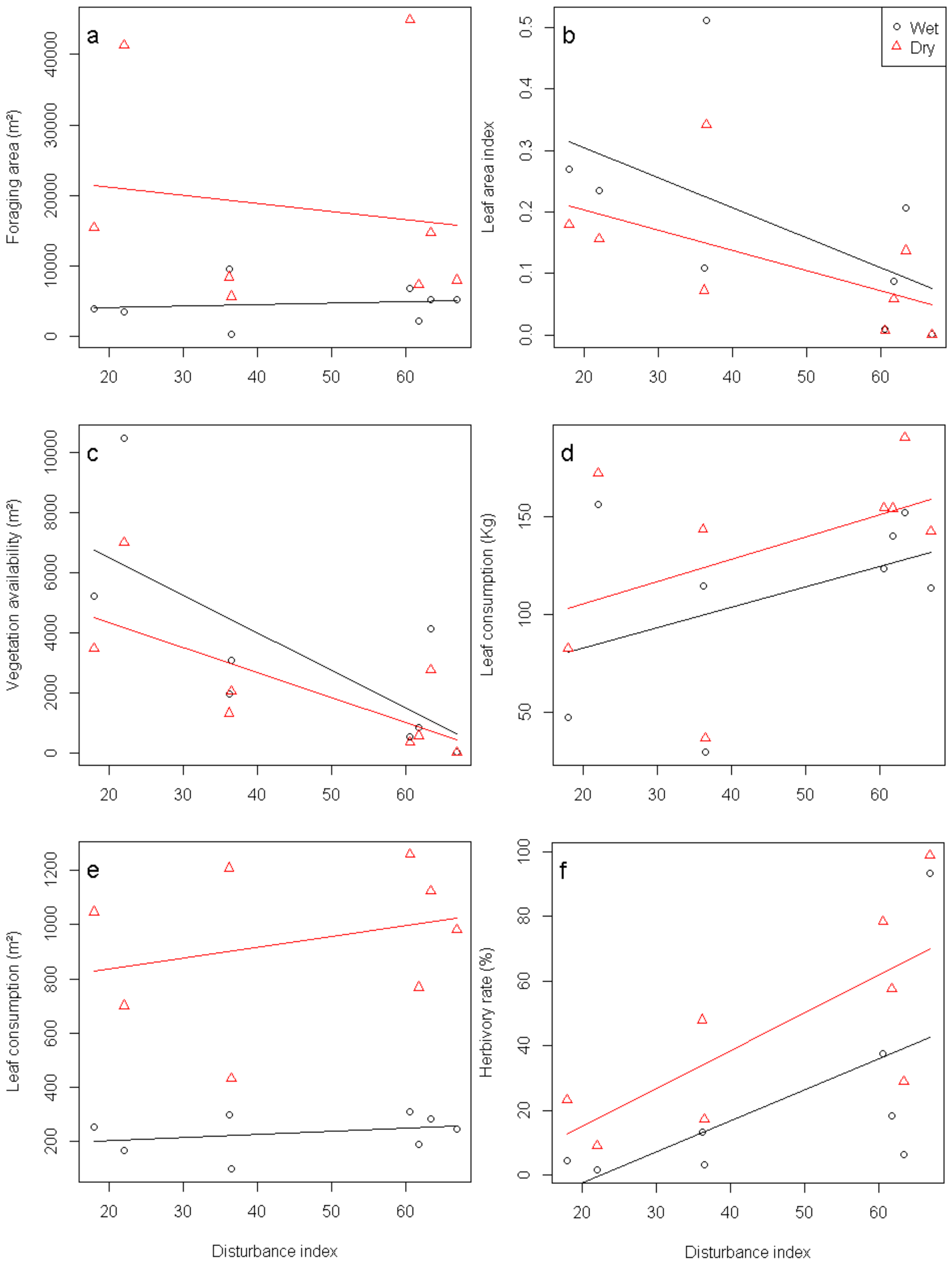
Euphorbiaceae				
Cnidoscolus obtusifolius Pohl	X	X		6.08
Cnidoscolus quercifolius Pohl	X	X		2.76
Croton argyrophylloides Müll. Arg	X	X	X	17.12
Croton grewioides Baill.	X	X	X	0.55
Croton micans Swartz	X	X		0.55
Jatropha mollissima Pohl	X	X		1.1
Jatropha mutabilis Pohl (Baill)	X	X		2.76
Jatropha ribifolia 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
Rhamnaceae				
Ziziphus joazeiro Mart.	X	X	X	1.1
Verbenaceae				
Verbenaceae sp.1	X		X	0.55
Others				
Biological soil crusts				0.55
Faeces of goat				0.55
Faeces of lizard				0.55

FIGURE LEGEND

Figure 1. Mean values of foraging area (a), leaf area index (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* plotted along an chronic anthropogenic disturbance gradient (disturbance index)in the Catimbau National Park, state of Pernambuco, Northeast Brazil.

Figure 1


a
Foraging area (m²)
0
10000
20000
30000
40000
b
Leaf area index
0.0
0.1
0.2
0.3
0.4
0.5
○ Wet
△ Dry
c
Vegetation availability (m²)
0
2000
4000
6000
8000
10000
d
Leaf consumption (Kg)
50
100
150
e
Leaf consumption (m²)
200
400
600
800
1000
1200
f
Herbivory rate (%)
0
20
40
60
80
100
20
30
40
50
60
Disturbance index
Disturbance index

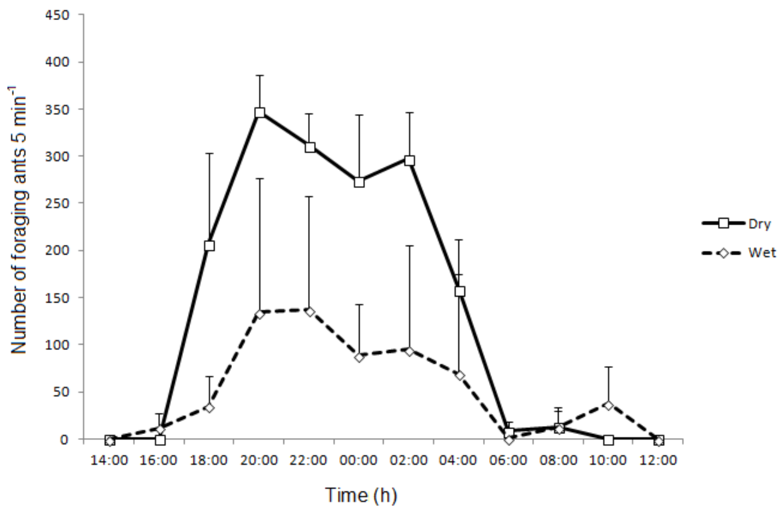
SUPPORTING INFORMATION

Appendix 1

Peak daily activity

In order to identify the time of the day of greatest activity of colonies of *A. opaciceps*, five of the eight colonies marked for a period of 24h were monitored. Every two hours the number of plant fragments carried by the ants into the colonies was counted for five minutes on all the active trails of the colony. To investigate the seasonal variations in the ant activity pattern, this method was applied to the same colonies in the dry seasons (December 2014) and wet season (May 2015). Thus, a regression was made between the number of fragments collected for 5 min at the peak of colony activity and the daily total (number of fragments collected during the day) (Wirth et al., 1997). A significant regression indicated that the amount of vegetation collected during the day is a function of the amount collected at peak colony activities. Thus, after the identification of the peak of activities and the significance of the regression, the herbivory rates of the colonies were estimated by counting the number of fragments collected only during that five-minute period at peak activities for all eight colonies over 12 months.

Peak daily activity calculated during five minutes in each two hours over 24 hours by eight colonies of *Atta opaciceps* in the Catimbau National Park, state of Pernambuco, Northeast Brazil.



Appendix 2.

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

Colony	Disturbance Index	Dry season	Wet season
1	18.00	0.19	0.27
2	22.06	0.16	0.23
3	36.20	0.07	0.10
4	36.58	0.34	0.51
5	60.63	0.007	0.01
6	61.74	0.06	0.09
7	63.44	0.14	0.21
8	66.87	0.0006	0.001
Total sum		0.12 ± 0.11	0.18 ± 0.17

Appendix 3.

Amount of vegetation removed (mean ± standard deviation) by eight colonies of *Atta opaciceps* in one month in the dry and wet seasons in the Catimbau National Park, state of Pernambuco, Northeast Brazil.

		Dry season		Wet season	
Colony	Disturbance Index	Kg	m^2	Kg	m^2
1	18.00	11.78 ± 0.93	149.69 ± 18.07	9.44 ± 1.05	50.76 ± 20.53
2	22.06	20.48 ± 0.38	172.63 ± 15.08	16.35 ± 2.39	59.59 ± 12.53
3	36.20	22.05 ± 0.79	179.87 ± 21.21	17.61 ± 2.65	62.47 ± 27.91
4	36.58	21.98 ± 0.51	109.85 ± 17.07	19.98 ±0.47	37.88 ± 15.99
5	60.63	5.22 ± 1.19	61.57 ± 24.50	4.21 ± 9.34	19.58 ± 15.53
6	61.74	24.53 ± 0.38	100.80 ± 18.53	22.30 ± 0.34	33.63 ± 17.55
7	63.44	27.15 ± 0.62	170.51 ± 16.06	21.68 ± 3.19	56.61 ± 28.90
8	66.87	20.33 ± 1.59	140.03 ± 8.87	16.20 ± 2.50	48.93 ± 29.98
Average		19.19 ± 7.18	135.62 ± 41.62	15.97 ± 6.24	46.18 ± 14.79

5 CONSIDERAÇÕES FINAIS

Nas últimas décadas tem crescido a atenção para o efeito das perturbações antrópicas sobre degradação dos ecossistemas naturais (BRESSANE et al., 2016). Principalmente devido ao suprimento das necessidades de alimento e moradia de uma população humana que cresce a taxas cada vez mais altas, as áreas de vegetação natural, especialmente florestas tropicais úmidas e secas (SINGH, 1998), foram transformadas em outros tipos de uso do solo fazendo com que a perda e fragmentação de habitats sejam consideradas as principais causas da perda de biodiversidade e de funções e serviços ecossistêmicos (LAURANCE et al., 2014). As formigas cortadeiras estão presentes em praticamente todos os ecossistemas tropicais e subtropicais no continente Americano, proliferando em áreas perturbadas. Pesquisas sobre as causas e consequências da proliferação de formigas cortadeiras à comunidade de plantas tem sido realizadas em florestas úmidas, savanas, campos agrícolas e em menor proporção para as florestas secas. Neste trabalho buscamos contribuir para o conhecimento dos efeitos das perturbações antrópicas sobre a interação entre plantas e formigas cortadeiras na Caatinga. Especificamente, os dois capítulos desta tese avaliaram como perturbações antrópicas afetam as populações (Capítulo 1) e as taxas de herbivoria (Capítulo 2) das formigas cortadeiras em áreas de Caatinga no Parque Nacional do Catimbau.

Ao contrário das nossas expectativas, os resultados do Capítulo 1 indicaram que as três espécies de formigas cortadeiras presentes no Parque, *A. laevigata*, *A. opaciceps* e *A. sexdens*, são beneficiadas por perturbações antrópicas, havendo um aumento na densidade populacional de colônias ativas em áreas mais perturbadas, enquanto colônias inativas foram mais frequentemente observadas em áreas mais conservadas. Reforçando este padrão, observamos que colônias ativas ocorrem preferencialmente em áreas com baixa cobertura vegetal, enquanto as colônias inativas em áreas com alta cobertura vegetal. Os processos responsáveis por este padrão podem incluir (1) maior quantidade de sítios favoráveis para a nidificação e estabelecimento das colônias nas proximidades das estradas, (2) aumento na quantidade de recursos alimentares (i.e. plantas palatáveis como Euphorbiaceae e espécies herbáceas) e (3) diminuição de inimigos naturais (i.e. moscas Phoridae parasitoides e predadores) (ALMEIDA et al., 2008; WIRTH et al., 2008). Esses resultados em conjunto confirmam os padrões descritos para florestas úmidas e savanas (MEYER; LEAL; WIRTH, 2009; LEAL; WIRTH; TABARELLI, 2014; VIEIRA-NETO et al., 2016), suportando a ideia de que formigas cortadeiras são um dos grupos vencedores de paisagens modificadas por atividades humanas.

Os resultados do Capítulo 2 também foram contrários aos padrões preditos, pois observamos maiores taxas de consumo de vegetação e de herbivoria em colônias de *A. opaciceps* localizadas em áreas mais perturbadas e durante a estação seca. Estes valores mais altos de taxa de herbivoria são devidos à combinação de grande quantidade de vegetação consumida em áreas e estações com baixa quantidade de vegetação disponível nas áreas de forrageamento das colônias. Este padrão de maiores taxas de herbivoria em áreas perturbadas já haviam sido reportadas para áreas de borda da Floresta Atlântica (URBAS et al., 2007) devido à alta proporção de plantas pioneiras nestas zonas (FARJI-BRENER, 2001; URBAS et al., 2007; FALCÃO et al., 2011). Os valores encontrados para as taxas de herbivoria, cerca de 45% (na estação seca) e 22% (na estação chuvosa) da vegetação presente nas áreas de forrageamento das colônias, são extremamente altos para uma floresta tropical seca com a Caatinga, e, mais surpreendentes, são muito maiores do que as taxas de herbivoria em outros sistemas menos sazonais que a Caatinga como florestas tropicais úmidas (de 12.5% a 17%, WIRTH et al., 2003; URBAS et al., 2007) e de savanas (17%, COSTA et al., 2008).

A alta densidade de formigas cortadeiras aliada com alto consumo foliar, podem afetar a regeneração da vegetação de Caatinga via seu papel como herbívoro dominante e engenheiro de ecossistema como já relatado para florestas úmidas e savanas (VASCONCELOS et al., 2006; MEYER et al., 2013; LEAL; WIRTH; TABARELLI, 2014). Essa retirada de vegetação pode amplificar as mudanças ambientais ocasionadas por perturbações antrópicas crônicas, uma vez que valores altos de herbivoria aumentam a penetração de luz e a temperatura do ar e do solo, ao mesmo tempo em que reduzem a umidade do ar e do solo (FARJI-BRENER, 2007; CORRÊA et al., 2010; MEYER et al., 2011a, 2011b, 2013; TADEY). Tais efeitos aliados com: (1) o uso de grande quantidade de frutos e sementes, onde as formigas podem atuar como dispersoras e/ou predadoras de sementes (LEAL; OLIVEIRA, 1998; SILVA et al., 2007), (2) modificações na estrutura da vegetação, regime de luz e condições microclimáticas e (3) modificações nas características físicas e químicas dos solos, estes dois últimos devido à construção e manutenção dos ninhos colossais (CORRÊA et al., 2010; MEYER et al., 2011, 2013) fazem das formigas cortadeiras espécies-chave e engenheiras do ecossistema em florestas tropicais sazonalmente secas com a Caatinga. E esse papel importante das formigas cortadeiras não é efêmero, se levarmos em conta a expectativa de vida das colônias que varia de 8 a 20 anos (MEYER et al., 2009) e ao fato de que seus efeitos podem durar até depois da morte da colônia (FARJI-BRENER, 2005; BIEBER et al., 2011). Finalmente, com o aumento da atividade humana em áreas de Caatinga (coleta de lenha e madeira, uso de produtos florestais não-madeireiros, criação extensiva de animais domésticos, caça) (ALVES et al., 2009; LEAL; TABARELLI; SILVA, 2003; ALBUQUERQUE et al., 2007; CAVALCANTI et al., 2015), podemos esperar um efeito cada vez maior destas formigas no recrutamento de jovens ao redor dos ninhos, mas também na reprodução de adultos, no estoque e ciclagem de nutrientes no solo, o aumento das condições estressantes da Caatinga e contribuindo para a manutenção da vegetação em estádios iniciais de sucessão como já registrado na Floresta Atlântica (FARJI-BRENER, 2001; SILVA et al., 2009).

Neste contexto, sugerimos para pesquisas futuras em áreas de Caatinga: (1) verificar o efeito da alta densidade de colônias sobre regeneração natural da vegetação de Caatinga, (2) avaliar os efeitos desta proliferação de formigas cortadeiras sobre serviços ecossistêmicos como redução nos estoques de nutrientes, nas plantas medicinais e em outras plantas usadas como fonte de alimento pelas comunidades locais, (3) elucidar a dinâmica edáfica e ecohidrológica mediada pelos ninhos das formigas cortadeiras, via fundação, manutenção expansão dos ninhos e depósito de nutriente em lixeiras internas e externas, (4) caracterizar importância agrícola e o nível de dano econômico por *A. opaciceps* e, por fim, (5) prever as respostas das formigas cortadeiras aos efeitos das mudanças climáticas e a sinergia entre a redução da precipitação e aumento das perturbações antrópicas. Paralelamente a estas pesquisas mais aplicadas, é importante conhecer a história natural das diferentes espécies de formigas cortadeiras para que se possa estabelecer mais precisamente como cada uma delas responde às diversas pressões antrópicas que atuam nas florestas tropicais sazonalmente secas. No PARNA Catimbau ocorrem três espécies do gênero *Atta* (*A. laevigata*, *A. opaciceps* e *A. sexdens*), tendo o conhecimento da historia natural destas espécies e das suas respostas a perturbações antrópicas e mudanças climáticas, conseguiremos elaborar planos de manejo para a conservação da Caatinga e mitigar os efeitos negativos para a vegetação mediados por formigas cortadeiras.

REFERÊNCIAS

AB'SABER. Spaces occupied by the expansion of dry climates in South America during the quaternary ice ages. **Revista do Instituto Geológico,** v. 21, n. 1, p. 71-78, 2000.

ALBUQUERQUE, U. P.; et al. Medicinal plants of the caatinga (semi-arid) vegetation of NE Brazil: A quantitative approach. **Journal of Ethnopharmacology**, v. 114, n. 3, p. 325-354, 2007.

ALLENDORF, F. W.; LUNDQUIST, L. L. Introduction: population biology, evolution, and control of invasive species. **Conservation Biology**, v. 17, p. 24-30, 2003.

ALMEIDA, W. R.; WIRTH, R.; LEAL, I. R. Edge-mediated reduction of phorid parasitism on leaf-cutting ants in a Brazilian Atlantic forest. **Entomologia Experimentalis et Applicata**, v. 129, n. 3, p. 251-257, 2008.

ALMEIDA, J.; PEIXOTO, C. P. **Caracterização do sistema de produção e utilização da palma forrageira na região semiárida do estado da Bahia**. (Nota técnica), 2012.

ALMEIDA, W. R.; et al. The alien flora of Brazilian Caatinga: deliberate introductions expand the contingent of potential invaders. **Biological Invasions**, v. 17, p. 51-56, 2015.

ALVARADO, A.; BERISH, C. W.; PERALTA, F. Leaf-cutter ant (*Atta cephalotes*) influence on the morphology of Andepts in Costa Rica. **Soil Science Society of America Journal**, v. 45, p. 790-794, 1981.

ALVES, R. R. N.; et al. Hunting strategies used in the semi-arid region of northeastern Brazil. **Journal of ethnobiology and ethnomedicine**, v. 5, n. 1, p. 5-12, 2009.

ANDERSON, R. G.; et al. Biophysical considerations in forestry for climate protection. **Frontiers in Ecology and the Environment**, v. 9, n. 3, p. 174-182, 2011.

ANDRADE-LIMA, D. The Caatingas dominium**. Revista Brasileira de Botânica**, v. 4, p. 149-153, 1981.

ARAÚJO, F.; RODAL, M. J. N.; BARBOSA, M. R. DE V. **Análise das variações da biodiversidade do bioma caatinga: suporte a estratégias regionais de conservação**. Brasília, DF: MMA, Secretária de Biodiversidade e Florestas, 2005.

BARRERA, C. A.; BUFFA, L. M.; VALLADARES, G. Do leaf-cutting ants benefit from forest fragmentation? Insights from community and species-specific responses in a fragmented dry forest. **Insect Conservation and Diversity**, v. 8, n. 5, p. 456-463, 2015.

BEATTIE, A. J. **The evolutionary ecology of ant plant mutualism**. Cambridge University Press, Cambridge, 1985

BIEBER, A. G. D.; et al. Do abandoned nests of leaf-cutting ants enhance plant recruitment in the Atlantic Forest? **Austral Ecology**, v. 36, n. 2, p. 220-232, 2011.

BLACKIE, R.; et al. **Tropical dry forests: The state of global knowledge and recommendations for future research**. Center for International Forestry Research, 2014.

BELYEA, L. R. Beyond ecological filters: feedback networks in the assembly and restoration of community structure. pp. 115–131 (In V. M. Temper- ton, R. J. Hobbs, T. Nuttle, and S. Halle, eds.). **Assembly rules and restoration ecology – Bridging the gap between theory and practice**. Island Press, Washington, DC, U.S.A, 2004.

BOOMSMA, J. J.; FRANKS, N. R. Social insects: from selfish genes to self organisation and beyond. **Trends in Ecology and Evolution**, v. 6, n. 6, p. 303-308, 2006.

BOLTON, B. **An online catalog of the ants of the world**. Disponível em: <http://antcat.org> Acesso em: 9 de agosto de 2016.

BUCHER, E. H. Herbivory in arid and semi-arid regions of Argentina. **Revista Chilena de Historia Natural**, v. 60, p. 265-273, 1987.

BUCHER, E. Chaco and Caatinga South American arid savannas, woodlands and thickets. pp. 48-79 (In: B. Huntley & B. Walker, eds). **Ecology of Tropical Savannas**. Springer-Verlag, Berlin, 1982.

BULLOCK, S. H.; MOONEY, H. A; MEDINA, E. Seasonally Dry Tropical Forests. **Biomass**, v. 78, n. Ma 2003, p. 0-450, 1995.

CALDATO, N.; et al. Foraging activity pattern and herbivory rates of the grass-cutting ant *Atta capiguara*. **Insectes Sociaux**, v. 63, n. 3, p. 421-428, 2016.

CAVALCANTI, M. C. B. T.; et al. Implications from the use of non-timber forest products on the consumption of wood as a fuel source in human-dominated semiarid landscapes. **Environmental Management**, v. 56, n. 2, p. 389-401, 2015.

CHERRETT, J. M. Leaf-cutting ants. In: H. LIETH, & M. J. A. WERGER, eds. **Ecosystems of the world**. Elsevier, 1989.

CHOMICKI, G.; RENNER, S. S. The interactions of ants with their biotic environment. **Proceedings of the Royal Society B: Biological Sciences**, v. 284, p. 20170013, 2017.

CLAVERO, M.; GARCÍA-BERTHOU, E. Invasive species are a leading cause of animal extinctions. **Trends in Ecology and Evolution**, v. 20, n. 3, p.110, 2005.

COCHRANE, M. A. Fire science for rainforests. **Nature**, v. 421, n. 6926, p. 913-919, 2003.

CORRÊA, M. M.; et al. How leaf-cutting ants impact forests: Drastic nest effects on light environment and plant assemblages. **Oecologia**, v. 162, n. 1, p. 103-115, 2010.

CORRÊA, M. M.; et al. Foraging activity of leaf-cutting ants changes light availability and plant assemblage in Atlantic forest. **Ecological Entomology**, v. 41, n. 4, p. 442-450, 2016.

COSTA, A. N.; et al. Do herbivores exert top-down effects in Neotropical savannas?

Estimates of biomass consumption by leaf-cutter ants. **Journal of Vegetation Science**, v. 19, n. 6, p. 849-863, 2008.

COSTA, U. A. S.; et al. O papel das formigas como disper- sores secundários de sementes na Floresta Atlântica Nordestina. In M. Tabarelli, A. V. Aguiar Neto, I. R. Leal, & A. V. Lopes eds. **Serra Grande: uma floresta de ideias**. Editora Universitária da UFPE, Recife, Brazil. 2014

CURRIE, C. R.; MUELLER, U. G.; MALLOCH, D. The agricultural pathology of ant fungus gardens. **Ecology**, v. 96, n. 14, p. 7998-8002, 1999.

DALLING, J. W.; WIRTH, R. Dispersal of *Miconia argentea* seeds by the leaf-cutting ant *Atta colombica*. **Journal of Tropical Ecology**, v. 14, n. 5, p. 705-710, 1998.

DEL-CLARO, K.; et al. Conservative benefits in an ant-hemipteran association in the Brazilian tropical savanna. **Sociobiology**, v. 47, n. 2, p. 415-421, 2006.

DELLA LUCIA, T. M.; GANDRA, L. C.; GUEDES, R. N. Managing leaf-cutting ants: Peculiarities, trends and challenges. **Pest Management Science**, v. 70, n. 1, p. 14-23, 2014.

DOHM, C.; et al. Leaf-cutting ants proliferate in the Amazon: an expected response to forest edge? **Journal of Tropical Ecology**, v. 27, n. 6, p. 645-649, 2011.

EDWARDS, D. P.; et al. Mining and the African environment. **Conservation Letters**, v. 7, n. 3, p. 302-311, 2014.

ESTES, J. A.; et al. Trophic downgrading of planet Earth. **Science**, v. 333, n. 6040, p. 301-306, 2011.

ESTRADA, C.; WCISLO, W. T.; VAN BAEL, S. A. Symbiotic fungi alter plant chemistry that discourages leaf-cutting ants. **New Phytologist**, v. 198, n. 1, p. 241-251, 2013.

FALCÃO, P. F.; et al. Edge-induced narrowing of dietary diversity in leaf-cutting ants. **Bulletin of Entomological Research**, v. 101, n. 3, p. 305-311, 2011.

FARJI BRENER, A. G.; RUGGIERO, A. leaf-cutting Ants (*Atta* and *Acromyrmex*) inhabiting Argentina: Patterns in species richness and geographical range sizes. **Journal of Biogeography**, v. 21, n. 4, p. 391-399, 1994.

FARJI BRENER, A. G.; SILVA, J. F. Leaf-cutting ants and forest groves in a tropical parkland savanna of Venezuela: facilitated succession? **Journal of Tropical Ecology**, v. 11, n. 4, p. 651, 1995.

FARJI-BRENER, A. G.; SILVA, J. F. Leaf-cutting ant nests and soil fertility in a well-drained savanna in western Venezuela. **Biotropica**, v. 27, n. 2, p. 250-254, 1995.

FARJI-BRENER, A. G.; ILLES, A. E. Do leaf-cutting ant nests make “bottom-up” gaps in neotropical rain forests?: A critical review of the evidence. **Ecology Letters**, v. 3, n. 3, p. 219-227, 2000.

FARJI-BRENER, A. G.; MEDINA, C. A. The importance of where to dump the refuse: seed banks and fine roots in nests of the leaf-cutting ants *Atta cephalotes* and *A. colombica*. **Biotropica**, v. 32, n. 1, p. 120-126, 2000.

FARJI-BRENER, A. G. 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**, v. 92, n. 1, p. 169-177, 2001.

FARJI-BRENER, A. G. The effect of abandoned leaf-cutting ant nests on plant assemblage composition in a tropical rainforest of Costa Rica. **Ecoscience**, v. 12, n. 4, p. 554-560, 2005.

FARJI-BRENER, A. G.; GHERMANDI, L. Leaf-cutting ant nests near roads increase fitness of exotic plant species in natural protected areas. **Proceedings. Biological sciences/The Royal Society**, v. 275, n. 1641, p. 1431-1440, 2008.

FARJI-BRENER, A. G.; LESCANO, N.; GHERMANDI, L. Ecological engineering by a native leaf-cutting ant increases the performance of exotic plant species. **Oecologia**, v. 163, n. 1, p. 163-169, 2010.

FARJI-BRENER, A. G.; WERENKRAUT, V. A meta-analysis of leaf-cutting ant nest effects on soil fertility and plant performance. **Ecological Entomology**, v. 40, n. 2, p. 150-158, 2015.

FOLEY, J. A. Global Consequences of Land Use. **Science**, v. 309, n. 5734, p. 570-574, 2005.

FOWLER, H. G. Distribution patterns of Paraguayan leaf-cutting ants (*Atta* and *Acromyrmex*) (Formicidae: Attini). **Studies on Neotropical Fauna and Environment.**, v. 18, n. 3, p. 121-138, 1983.

FOWLER H. G.; SILVA V. P.; FORTI L. C. S. N. Population dynamics of leaf-cutting ants: a brief review. (In: C. S., Lofgren & R. K. Vander Meer, eds) **Fire ants and leaf-cutting ants: biology and management.** Westview Press. 1986.

FRANZEL, C.; FARJI-BRENER, A. G. Oportunistas o selectivas? Plasticidad en la dieta de la hormiga cortadora de hojas Acromyrmex lobicornis en el noroeste de la Patagonia. **Ecologia Austral**, v. 10, n. 2, p. 159-168, 2000.

FRISHKOFF, L. O.; et al. Climate change and habitat conversion favour the same species. **Ecology Letters**, v. 19, n. 9, p. 1081-1090, 2016.

FURLEY, P.A., PROCTOR, J. & RATTER, J.A. **Nature and dynamics of forest–savanna boundaries**. Chapman and Hall. 1992.

GARRETTSON, M. et al. Diversity and abundance of understorey plants on active and abandoned nests of leaf-cutting ants (*Atta cephalotes*) in a Costa Rican rain forest. **Journal of Tropical Ecology**, v. 14, n. 1, p. 17-26, 1998.

GATTI, L. V.; et al. Drought sensitivity of Amazonian carbon balance revealed by atmospheric measurements. **Nature**, v. 506, n. 7486, p. 76-80, 2014.

GAUME, L.; et al. Different pitcher shapes and trapping syndromes explain resource partitioning in *Nepenthes* species. **Ecology and Evolution**, v. 6, n. 5, p. 1378-1392, 2016.

GIBBS, H. K.; et al. Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. **Proceedings of the National Academy of Sciences**, v. 107, n. 38, p. 16732-16737, 2010.

GIBSON, L.; et al. Primary forests are irreplaceable for sustaining tropical biodiversity. **Nature**, v. 478, n. 7369, p. 378-381, 2011.

GIRÃO, L. C.; et al. Changes in tree reproductive traits reduce functional diversity in a fragmented Atlantic forest landscape. **PLoS one**, v. 2, n. 9, 2007.

GORDON, D. M. **Ant encounters: interaction networks and colony behavior**. Princeton University Press. 2010.

HAINES, B. L. Element and energy flows through colonies of the leaf-cutting ant, *Atta colombica*, in Panama. **Biotropica**, v. 10, n. 4, p. 270-277, 1978.

HANSEN, M. C.; et al. High-resolution global maps of 21st-century forest cover change. **Science**, v. 342, n. 2013, p. 850-3, 2013.

HERZ, H.; BEYSCHLAG, W.; HÖLLDOBLER, B. Herbivory rate of leaf-cutting ants in a tropical moist forest in Panama at the population and ecosystem scales. **Biotropica**, v. 39, n. 4, p. 482-488, 2007.

HIROTA, M.; HOLMGREN, M. Global Resilience of Tropical Forest. **Science**, v. 334, n. October, p. 232-235, 2011.

HÖLLDOBLER, B.; WILSON, E. O. **The Ants**. Springer. 1990.

HÖLLDOBLER, B.; WILSON, E. O. **The superorganism: the beauty, elegance, and strangeness of insect societies**. W. W. Norton & Company, 2009.

HÖLLDOBLER, B.; WILSON, E.O. **The leafcutter ants: civilization by instinct**. W.W. Norton and Company, 2011.

HOWARD, J. J. Infidelity of leafcutting ants to host plants: resource heterogeneity or defense induction? **Oecologia**, v. 82, n. 3, p. 394-401, 1990.

HUDSON, T. M. et al. Temporal patterns of nutrient availability around nests of leaf-cutting ants (*Atta colombica*) in secondary moist tropical forest. **Soil Biology and Biochemistry**, v. 41, n. 6, p. 1088-1093, 2009.

HULL-SANDERS, H. M.; HOWARD, J.J. Impact of *Atta colombica* colonies on understory vegetation and light availability in a neotropical forest. **Biotropica**, v. 35, n. 3, p. 441-445, 2003.

HUXLEY, C. R.; CUTLER, D. F. **Ant-plant interactions**. Oxford University Press, 1991.

ITO, M. Seasonal population trends and nest structure in a polydomous ant, *Formica* (Formica) *yessensis* Forel. **Journal of Faculty of Science**, v. 19, n. 1, p. 270-293, 1973.

JIMÉNEZ-VALDÉS, M.; et al. Population dynamics of *Agave marmorata* Roezl. under two contrasting management systems in Central Mexico. **Economic Botany**, v. 64, n. 2, p. 149-160, 2010.

JOHNSON, R. A.; GIBBS, A. G. Effect of mating stage on water balance, cuticular hydrocarbons and metabolism in the desert harvester ant, *Pogonomyrmex barbatus*. **Journal of Insect Physiology**, v. 50, n. 10, p. 943-953, 2004.

KASPARI, M. Removal of seeds from Neotropical frugivore droppings - Ant responses to seed number. **Oecologia**, v. 95, n. 1, p. 81-88, 1993.

KELLER, L.; GORDON, E. **The Lives of Ants**. Oxford University Press, 2009.

KOST, C.; TREMMEL, M.; WIRTH, R. Do leaf cutting ants cut undetected? testing the effect of ant-induced plant defences on foraging decisions in *Atta colombica*. **PLoS one**, v. 6, n. 7, 2011.

KREMEN, C. Managing ecosystem services: What do we need to know about their ecology? **Ecology Letters**, v. 8, n. 5, p. 468-479, 2005.

LAURANCE, W. F.; et al. Rain forest fragmentation and the structure of Amazonian liana communities. **Ecology**, v. 82, n. 1, p. 105-116, 2001.

LAURANCE, W. F.; et al. Averting biodiversity collapse in tropical forest protected areas. **Nature**, v. 489, n. 7415, p. 290-294, 2012.

LAURANCE, W. F. Emerging threats to tropical forests. (In: M. Margaret, S. Devy & T. Ganesh, eds) **Treetops at Risk: Challenges of Global Canopy Ecology and Conservation**. Springer. 2013.

LEAL, I. R.; OLIVEIRA, P. S. Interactions between fungus-growing ants (Attini), fruits and seeds in cerrado vegetation in Southeast Brazil1. **Biotropica**, v. 30, n. 2, p. 170-178, 1998.

LEAL, I. R.; OLIVEIRA, P. S. Foraging ecology of attine ants in a Neotropical savanna: seasonal use of fungal substrate in the cerrado vegetation of Brazil. **Insectes Sociaux**, v. 47, n. 4, p. 376-382, 2000.

LEAL, I. R.; TABARELLI, M.; SILVA, J. M. C. **Ecologia e Conservação da Caatinga**. Editora Universitária da UFPE**.** 2003.

LEAL, I.; WIRTH, R.; TABARELLI, M. The multiple impacts of leaf-cutting ants and their novel ecological role in human-modified neotropical forests. **Biotropica**, v. 46, n. 5, p. 516-528, 2014.

LEAL, L. C.; et al. Myrmecochores can target high-quality disperser ants: Variation in elaiosome traits and ant preferences for myrmecochorous Euphorbiaceae in Brazilian Caatinga. **Oecologia**, v. 174, n. 2, p. 493-500, 2014.

LEAL, L. C.; ANDERSEN, A. N.; LEAL, I. R. Anthropogenic disturbance reduces seed-dispersal services for myrmecochorous plants in the Brazilian Caatinga. **Oecologia**, v. 174, n. 1, p. 173-181, 2014.

LEAL, L. C.; ANDERSEN, A. N.; LEAL, I. R. Disturbance winners or losers? Plants bearing extrafloral nectaries in Brazilian Caatinga. **Biotropica**, v. 0, n. 0, p. 1-7, 2015.

LEES, A. C.; PERES, C. A. Rapid avifaunal collapse along the Amazonian deforestation frontier. **Biological Conservation**, v. 133, n. 2, p. 198-211, 2006.

LEWIS, S. L.; EDWARDS, D. P.; GALBRAITH, D. Increasing human dominance of tropical forests. **Science**, v. 349, n. 6250, 2015.

LIMA, M. H. C.; OLIVEIRA, E. G.; SILVEIRA, F. A. O. Interactions between Ants and Non-myrmecochorous Fruits in *Miconia* (Melastomataceae) in a Neotropical Savanna. **Biotropica**, v. 45, n. 2, p. 217-223, 2013.

LÔBO, D.; et al. Forest fragmentation drives Atlantic forest of northeastern Brazil to biotic homogenization. **Diversity and Distributions**, v. 17, n. 2, p. 287-296, 2011.

LOVELOCK, C. E.; et al. Testing the growth rate vs. geochemical hypothesis for latitudinal variation in plant nutrients. **Ecology Letters**, v. 10, n. 12, p. 1154-1163, 2007.

MÅREN, I. E.; BHATTARAI, K. R.; CHAUDHARY, R. P. Forest ecosystem services and biodiversity in contrasting Himalayan forest management systems. **Environmental Conservation**, v. 41, n. 1, p. 73-83, 2013.

MARICONI, F. A. M. As saúvas. (In: F. A. M. Mariconi) **Inseticidas e seu emprego no combate as pragas**. Nobel, 1981.

MARTORELL, C.; PETERS, E. M. The measurement of chronic disturbance and its effects on the threatened cactus *Mammillaria pectinifera*. **Biological Conservation**, v. 124, n. 2, p. 199-207, 2005.

MARTORELL, C.; PETERS, E. M. Disturbance-response analysis: A method for rapid assessment of the threat to species in disturbed areas. **Conservation Biology**, v. 23, n. 2, p. 377-387, 2009.

MAYER, V. E.; VOGLMAYR, H. Mycelial carton galleries of *Azteca brevis* (Formicidae) as a multi-species network. **Proceedings. Biological sciences**, v. 276, n. 1671, p. 3265-3273, 2009.

MEDEIROS, S. DE S.; et al. **Sinopse do censo demográfico para o Semiárido Brasileiro**. Instituto Brasileiro de Informação em Ciência e Tecnologia, 2012.

MELLARS, P. Why did modern human populations disperse from Africa ca. 60,000 years ago? A new model. **Proceedings of the National Academy of Sciences**, v. 103, n. 25, p. 9381-9387, 2006.

MEYER, S. T.; et al. Ecosystem engineering by leaf-cutting ants: Nests of *Atta cephalotes* drastically alter forest structure and microclimate. **Ecological Entomology**, v. 36, n. 1, p. 14-24, 2011.

MEYER, S. T.; et al. Leaf-cutting ants as ecosystem engineers: Topsoil and litter perturbations around *Atta cephalotes* nests reduce nutrient availability. **Ecological Entomology**, v. 38, n. 5, p. 497-504, 2013.

MEYER, S. T.; BÜDEL, B.; WIRTH, R. Ecosystem engineering in fragmented forests - Edge-mediated hyper-abundance of leaf-cutting ants and resulting impacts on forest structure, microclimate and regeneration. **Fachbereich Biologie**, p. 172, 2008.

MEYER, S. T.; LEAL, I. R.; WIRTH, R. Persisting hyper-abundance of leaf-cutting ants (*Atta* spp.) at the edge of an old Atlantic forest fragment. **Biotropica**, v. 41, n. 6, p.

711-716, 2009.

MEYER, S. T.; ROCES, F.; WIRTH, R. Selecting the drought stressed: Effects of plant stress on intraspecific and within-plant herbivory patterns of the leaf-cutting ant *Atta colombica*. **Functional Ecology**, v. 20, n. 6, p. 973-981, 2006.

MIKHEYEV, A. S.; MUELLER, U. G.; BOOMSMA, J. J. Population genetic signatures of diffuse co-evolution between leaf-cutting ants and their cultivar fungi. **Molecular Ecology**, v. 16, n. 1, p. 209-216, 2007.

MIKHEYEV, A. S.; VO, T.; MUELLER, U. G. Phylogeography of post-Pleistocene population expansion in a fungus-gardening ant and its microbial mutualists. **Molecular Ecology**, v. 17, n. 20, p. 4480-4488, 2008.

MILES, L.; et al. A global overview of the conservation status of tropical dry forests. **Journal of Biogeography**, v. 33, n. 3, p. 491-505, 2006.

MOONEY, H. A.; BULLOCK, S. H.; MEDINA, E. **Seasonally dry tropical forests**. Cambridge University Press, 1995.

MOREIRA, A.; et al. External and internal structure of *Atta bisphaerica* Forel (Hymenoptera: Formicidae) nests. **Journal of Applied Entomology**, v. 128, n. 3, p. 204-211, 2004a.

MOREIRA, A.; et al. Nest Architecture of *Atta laevigata* (F. Smith, 1858) (Hymenoptera: Formicidae). **Studies on Neotropical Fauna and Environment**, v. 39, n. 2, p. 109-116, 2004b.

MOUTINHO, A. P.; et al. Influence of leaf-cutting ant nests on secondary forest growth and soil properties in Amazonia. **Ecology**. v. 84, n. 5, p. 1265-1276, 2003.

MUELLER, U. G.; et al. the Evolution of Agriculture in insects. **Annual Review of Ecology, Evolution, and Systematics**, v. 36, n. 1, p. 563-595, 2005.

MUNDIM, F. M.; COSTA, A. N.; VASCONCELOS, H. L. Leaf nutrient content and host plant selection by leaf-cutter ants, *Atta laevigata*, in a Neotropical savanna. **Entomologia Experimentalis et Applicata**, v. 130, n. 1, p. 47-54, 2009.

MURPHY, P. G.; LUGO, A. E. Ecology of tropical dry forest. **Annual Review of Ecology and Systematics**, v. 17, n. 1, p. 67-88, 1986.

NASCIMENTO, C. E.; et al. The introduced tree *Prosopis juliflora* is a serious threat to native species of the Brazilian Caatinga vegetation. **Science of the Total Environment**, v. 481, n. 1, p. 108-113, 2014.

NICHOLS-ORIANS, C. M.; SCHULTZ, J. C. Leaf toughness affects leaf harvesting by the leaf cutter ant, *Atta cephalotes* (L.) (Hymenoptera: Formicidae)**. Biotropica**, v. 21, n. 1, p. 80-83, 1989.

NORTH, R. D.; JACKSON, C. W.; HOWSE, P. E. Evolutionary aspects of ant-fungus interactions in leaf-cutting ants.**Trends in Ecology and Evolution**, v. 12, n. 10, p. 386-389, 1997.

OLIVEIRA, F. M. P.; et al. Chronic anthropogenic disturbance as a secondary driver of ant community structure: interactions with soil type in Brazilian Caatinga. **Environmental Conservation**, v. 44, n. 2, p.115-123, 2016.

OLIVEIRA, M. A.; GRILLO, A. S.; TABARELLI, M. Forest edge in the Brazilian Atlantic forest: drastic changes in tree species assemblages. **Oryx**, v. 38, n. 4, p. 389-394, 2004.

OLIVEIRA, P. D. M.; et al. Caracterização de ninhos de *Acromyrmex landolti balzani* (Hymenoptera: Formicidae). **Revista Brasileira de Entomologia**, v. 50, n. 1, p.128-130, 2006

PARRY, L.; BARLOW, J.; PERES, C. A. Hunting for sustainability in tropical secondary forests. **Conservation Biology**, v. 23, n. 5, p. 1270-1280, 2009.

PEETERS, C. Fertility signaling as a general mechanism of regulating reproductive division of labor in ants. Pp.220-242. (In: J. Gadau & J. Fewell, eds) **Organization of Insects**.Havard University Press, 1995.

PENNINGTON, R. T.; PRADO, D. E.; PENDRY, C. A. Neotropical seasonally dry forests and Quaternary vegetation changes. **Journal of Biogeography**, v. 27, n. 2, p. 261-273, 2000.

PENNINGTON, R. T.; LAVIN, M.; OLIVEIRA-FILHO, A. Woody plant diversity, evolution, and ecology in the tropics: perspectives from seasonally dry tropical forests. **Annual Review of Ecology, Evolution, and Systematics**, v. 40, n. 1, p. 437-457, 2009.

PERES, C. A.; PALACIOS, E. Basin-wide effects of game harvest on vertebrate population densities in Amazonian forests: implications for animal-mediated seed dispersal. **Biotropica**, v. 39, n. 3, p. 304-315, 2007.

PILATI, A.; QUIRAN, E. M.; ESTELRICH, H. D. Actividad forrajera de *Acromyrmex lobicornis* Emery (Hymenoptera: Formicidae) en un pastizal natural semiarido de la provincia de la Pampa (Argentina). **Ecologia Austral**, v. 7, n. 2, p. 49-56, 1997.

PIZO, M. A.; OLIVEIRA, P. S. Interaction between ants and seeds of a nonmyrmecochorous neotropical tree, *Cabralea canjerana* (Meliaceae), in the Atlantic forest of southeast Brazil. **American Journal of Botany**, v. 85, n. 5, p. 669-674, 1998.

QUESADA, M.; et al. Succession and management of tropical dry forests in the Americas: review and new perspectives. **Forest Ecology and Management**, v. 258, n. 6, p. 1014-1024, 2009.

RAO, M.; TERBORGH, J.; NUÑEZ, P. Increased herbivory in forest isolates: Implications for plant community structure and composition. **Conservation Biology**, v. 15, n. 3, p. 624-633, 2001.

RAUDSEPP-HEARNE, C.; PETERSON, G. D.; BENNETT, E. M. Ecosystem service bundles for analyzing tradeoffs in diverse landscapes. **Proceedings of the National**

Academy of Sciences of the United States of America, v. 107, n. 11, p. 5242-7, 2010.

REID, R. S.; GALVIN, K. A.; KRUSKA, R. S. Global significance of extensive grazing lands and pastoral societies: An introduction. pp. 1-24. (In: K. A. Galvin, R. S. Reid, R. H. Behnke, & N. T. Hobbs, eds) **Fragmentation in Semi-Arid and Arid Landscapes: Consequences for Human and Natural Systems**. Springer, 2008.

RIBEIRO, E. M. S. Dissertação. Influencia de perturbacoes antropicas sobre populações de cactáceas em áreas de Caatinga. Universidade Federal de Pernambuco, p. 55, 2011.

RIBEIRO, E. M. S.; et al. Chronic anthropogenic disturbance drives the biological impoverishment of the Brazilian Caatinga vegetation. **Journal of Applied Ecology**, v. 52, n. 3, p. 611-620, 2015.

RIBEIRO-NETO, J. D.; et al. Drought stress drives intraspecific choice of food plants by *Atta* leaf-cutting ants. **Entomologia Experimentalis et Applicata**, v. 144, n. 2, p. 209-215, 2012.

RIBEIRO-NETO, J. D.; et al. Chronic anthropogenic disturbance causes homogenization of plant and ant communities in the Brazilian Caatinga. **Biodiversity and Conservation**, v. 25, n. 5, p. 943-956, 2016.

RICHARD, T.; FORMAN, T.; DEBLINGER, R. D. The ecological road-effect zone of a Massachusetts (U.S.A.) suburban highway. **Conservation Biology**, v. 14, n. 1, p. 36-46, 2000.

RITO, K. F.; et al. Precipitation mediates the effect of human disturbance on the Brazilian Caatinga vegetation. **Journal of Ecology**, v. 1005, n. 3, p. 828-838, 2016.

RODAL, M. J. N.; SAMPAIO, E. V. S. B. A vegetação do bioma caatinga. pp. 11-24. (In:E. V. S. B., SAMPAIO, A. M.; GIULIETTI, J. VIRGÍNIO & C. F. L. GAMARRA-ROJAS, eds.) **Vegetação e flora das Caatingas**. APNE / CNIP, Recife, PE.

SAGAR, R.; RAGHUBANSHI, A. S.; SINGH, J. S. Tree species composition, dispersion and diversity along a disturbance gradient in a dry tropical forest region of India. **Forest Ecology and Management**, v. 186, n. 1-3, p. 61-71, 2003.

SANTOS, B. A.; et al. Drastic erosion in functional attributes of tree assemblages in Atlantic forest fragments of northeastern Brazil. **Biological Conservation**, v. 141, n. 1, p. 249-260, 2008.

SANTOS, B. A.; et al. Edge-related loss of tree phylogenetic diversity in the severely fragmented brazilian atlantic forest. **PLoS one**, v. 5, n. 9, p. 1-7, 2010.

SAVERSCHEK, N.; et al. Avoiding plants unsuitable for the symbiotic fungus: learning and long-term memory in leaf-cutting ants. **Animal Behaviour**, v. 79, n. 3, p. 689-698, 2010.

SCHOEREDER, J. H.; COUTINHO, L. M. Fauna e estudo zoossociológico das espécies de saúvas (Formicidae, Attini) de duas regiões de cerrado do estado de São Paulo. **Revista Brasileira de Entomologia**, v. 34, n. 3, p. 561-568, 1990.

SCHULTZ, T. R.; BRADY, S. G. Major evolutionary transitions in ant agriculture. **Proceedings of the National Academy of Sciences of the United States of America**, v. 105, n. 14, p. 5435-5440, 2008.

SCHULZ, K.; et al. Grazing deteriorates the soil carbon stocks of Caatinga forest ecosystems in Brazil. **Forest Ecology and Management**, v. 367, n. 1, p. 62-70, 2016.

SHAHABUDDIN, G.; KUMAR, R. Influence of anthropogenic disturbance on bird communities in a tropical dry forest: role of vegetation structure. **Animal Conservation**, v. 9, n. 4, p. 404-413, 2006.

SHANKAR, U.; et al. Extraction of non-timber forest products in the forests of Biligiri Rangan Hills, India. 4. impact on floristic diversity and population structure in a thorn scrub forest. **Economic Botany**, v. 52, n. 3, p. 302-315, 1998.

SILVA, P. D.; et al. Harvesting of *Protium heptaphyllum* (Aubl.) March. seeds

(Burseraceae) by the leaf-cutting ant *Atta sexdens* L. promotes seed aggregation and seedling mortality. **Revista Brasileira de Botânica**, v. 30, n. 3, p. 553-560, 2007.

SILVA, P. S. D.; et al. Decreasing abundance of leaf-cutting ants across a chronosequence of advancing Atlantic forest regeneration. **Journal of Tropical Ecology**, v. 25, n. 2, p. 223, 2009.

SINGH, S. P. Chronic disturbance, a principal cause of environmental degradation in developing countries. **Environmental Conservation**, v. 25, n. 1, p. 1-2, 1998.

SOARES, I. M. F.; et al. Caracterização de ninhos e tamanho de colônia de *Acromyrmex rugosus* (F. Smith) (Hymenoptera, Formicidae, Attini) em restingas de Ilhéus, BA, Brasil. **Revista Brasileira de Entomologia**, v. 50, n. 1, p. 128-130, 2006.

SOUSA-SOUTO, L.; et al. Increased CO_2 emission and organic matter decomposition by leaf-cutting ant nests in a coastal environment. **Soil Biology and Biochemistry**, v. 44, n. 1, p. 21-25, 2012.

SOUZA, A. F.; CORTEZ, L. S. R.; LONGHI, S. J. Native forest management in subtropical South America: Long-term effects of logging and multiple-use on forest structure and diversity. **Biodiversity and Conservation**, v. 21, n. 8, p. 1953-1969, 2012.

STONER, K. E.; et al. Hunting and plant community dynamics in tropical forests: A synthesis and future directionsBiotropica. **Biotropica**, v. 39, n. 3, p. 385-392, 2007.

TABARELLI, M. I.; et al. Secondary forests as biodiversity repositories in human-modified landscapes: insights from the Neotropics Florestas secundárias como repositórios de biodiversidade em paisagens antrópicas: evidências dos neotrópicos. **Boletim do Museu Paranaense Emílio Goeldi. Ciências Naturais**, v. 7, n. 3, p. 319-328, 2012.

TABUTI, J. R. S. The uses, local perceptions and ecological status of 16 woody species of Gadumire Sub-county, Uganda. **Biodiversity and Conservation**, v. 16, n. 6, p. 1901-

1915, 2007.

TADEY, M.; FARJI-BRENER, A. G. Indirect effects of exotic grazers: Livestock decreases the nutrient content of refuse dumps of leaf-cutting ants through vegetation impoverishment. **Journal of Applied Ecology**, v. 44, n. 6, p. 1209-1218, 2007.

TAVARES, V. V. ALVES-JUNIOR, G. A. M. Does *Atta laevigata* (Smith, 1858) act as *Solanum lycocarpum* seed dispersers? **Sociobiology**, v. 63, n. 1, p. 682-687, 2016.

TERBORGH, J.; et al. Ecological meltdown in predator-free forest fragments. **Science**, v. 294, n. 5548, p. 1923-1926, 2001.

TROMBULAK, S. C.; FRISSELL, C. A. Review of ecological effects of roads on terrestrial and aquatic communities. **Conservation Biology**, v. 14, n. 1, p. 18-30, 2000.

ULYSSÉA, M. A.; BRANDÃO, C. R. F. 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**, v. 57, n. 2, p. 217-224, 2013.

URBAS, P.; et al. Cutting more from cut forests: Edge effects on foraging and herbivory of leaf-cutting ants in Brazil. **Biotropica**, v. 39, n. 4, p. 489-495, 2007.

URETA, C.; MARTORELL, C. Identifying the impacts of chronic anthropogenic disturbance on two threatened cacti to provide guidelines for population-dynamics restoration. **Biological Conservation**, v. 142, n. 10, p. 1992-2001, 2009.

VAN KLEUNEN, M.; WEBER, E.; FISCHER, M. A meta-analysis of trait differences between invasive and non-invasive plant species**. Ecology Letters**, v. 13, n. 2, p. 235-245, 2010.

VAN LENT, J.; et al. Defoliation effects on seed dispersal and seedling recruitment in a tropical rain forest understorey palm. **Journal of Ecology**, v. 102, n. 3, p. 709-720, 2014.

VASCONCELOS, H. L. Foraging activity of two species of leaf-cutting ants (*Atta*) in a primary forest of the Central Amazon. **Insectes Sociaux**, v. 37, n. 2, p. 131-145, 1990.

VASCONCELOS, H. L.; et al. Roads alter the colonization dynamics of a keystone herbivore in neotropical savannas. **Biotropica**, v. 38, n. 5, p. 661-665, 2006.

VASCONCELOS, H. L.; CHERRETT, J. M. The effect of wilting on the selection of leaves by the leafcutting ant *Atta laevigata*. **Entomologia Experimentalis Applicata**, v. 78, n. 2, p. 215-220, 1996.

VASCONCELOS, H. L.; CHERRETT, J. M. Leaf-cutting ants and early forest regeneration in central Amazonia: effects of herbivory on tree seedling establishment. **Journal of Tropical Ecology**, v. 13, n. 3, p. 357-370, 1997.

VERGLES, H. D.; et al. Dry forests, livelihoods and poverty alleviation: Understanding current trends. **International Forestry Review**, v. 17, n. S2, p. 54-69, 2015.

VIEIRA-NETO, E. H. M.; et al. Roads increase population growth rates of a native leaf-cutter ant in Neotropical savannahs. **Journal of Applied Ecology**, v. 53, n. 4, p. 983-992, 2016.

VIRA, B.; FORESTS, S.; et al. Trees and Landscapes for Food Security and Nutrition. (In: B. Vira, S. Mansourian & C. Wildburger, eds). **A Global Assessment Report.** IUFRO World Series, 2015

WARD, P. S.; et al. The evolution of myrmicine ants: Phylogeny and biogeography of a hyperdiverse ant clade (Hymenoptera: Formicidae). **Systematic Entomology**, v. 40, n. 1, p. 61-81, 2015.

WINSTON, M. E.; HERZ, H. Unpaved roads alter foraging patterns of the leafcutter ant *Atta colombica*. **Studies on Neotropical Fauna and Environment**, v. 521, n. May 2015, p. 1-8, 2015.

WIRTH, R.; LEAL, I. R. Cutting more from cut forests: Drastic edge effects on colony density and herbivory pressure of leaf-cutting ants. **Biotropica**, v. 39, n. 4, p. 489-495, 2007.

WIRTH, R.; et al. Herbivory of leaf-cutting ants: a case study on *Atta colombica* in the tropical rainforest of Panama. **Progress in Botany**, v. 69, p. 23-448, 2008

WITTE, V.; MASCHWITZ, U. Mushroom harvesting ants in the tropical rain forest. **Naturwissenschaften**, v. 95, n. 11, p. 1049-1054, 2008.

WONG, J. W. Y.; MEUNIER, J.; KÖLLIKER, M. The evolution of parental care in insects: The roles of ecology, life history and the social environment. **Ecological Entomology**, v. 38, n. 2, p, 123-137, 2013.

WYATT, T. D. **Pheromones and animal behavior: Chemical signals and signatures**. Crambridge University Press, 2014.

ZAVALA-HURTADO, J. Influence of leaf-cutting ants (*Atta mexicana*) on performance and dispersion patterns of perennial desert shrubs in an inter-tropical region of Central Mexico. **Journal of Arid Environments**, v. 46, n. 1, p. 93-102, 2000.

ANEXO 1 - Normas para publicação nos periódicos

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