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CLARISSA MENDES KNOECHELMANN

EFEITO DAS FORMIGAS CORTADEIRAS SOBRE A REGENERAÇÃO DA CAATINGA

Recife, 2019

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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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Orientadora: Dra. Inara Roberta Leal

Co-orientador: Dr. Rainer Wirth

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BANCA EXAMINADORA

Profa. Dra. Inara Roberta Leal – UFPE (Orientadora)

Prof. Dr. Marcelo Tabarelli – UFPE (Avaliador Interno)

Prof. Dr. Paulo S. Oliveira – UNICAMP (Avaliador Externo)

Dra. Fernanda Maria Pereira de Oliveira – UFPE (Avaliadora Externa)

Dr. Oswaldo Cruz Neto – UFPE (Avaliador Externo)

Profa. Dra. Emília Cristina Pereira de Arruda – UFPE (Suplente)

Dr. Bruno Karol Cordeiro Filgueiras – UFPE (Suplente)

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“Se não agirmos, certamente seremos arrastados pelos corredores longos, escuros e vergonhosos do tempo reservado para quem possui poder SEM COMPAIXÃO, potência SEM MORALIDADE e força SEM VISÃO”

Martin Luter King

“Só a vida sem obstáculos, efervescente, leva a milhares de novas formas e improvisações, traz à luz a força criadora, corrige os caminhos equivocados. A vida pública em países com liberdade limitada está sempre tão golpeada pela pobreza, é tão miserável, tão rígida, tão estéril, precisamente porque, ao excluir-se a democracia, fecham-se as fontes vivas de toda riqueza e progresso espirituais.”

Rosa de Luxemburgo

RESUMO

As perturbações antrópicas rearranjam comunidades biológicas através da substituição de espécies especialistas sensíveis à perturbação por espécies generalistas adaptadas à perturbação. As formigas cortadeiras (FC) são organismos que aumentam sua densidade em áreas perturbadas devido ao relaxamento dos controles populacionais ascendentes (recursos alimentares) e descendentes (pressão de inimigos naturais). Como são herbívoros vorazes, coletando toneladas de vegetação para a cultura do fungo simbionte, podem modificar a dinâmica de regeneração de áreas perturbadas. Neste estudo examinei como FC influenciam a regeneração de paisagens antrópicas na Caatinga, a maior e mais diversa floresta seca dos neotrópicos, mas também bastante perturbada por atividades antrópicas. A hipótese geral é que as FC têm influência negativa sobre a regeneração devido à coleta de grandes quantidades de sementes, plântulas e indivíduos jovens para o cultivo do fungo simbionte, e que este efeito será acentuado pelo aumento da cobertura florestal ao redor dos ninhos. O estudo foi conduzido no Parque Nacional do Catimbau, PE, com 15 ninhos de *Atta opaciceps* localizados em micro paisagens com diferentes coberturas florestais (8.7% – 87.8%). No Capítulo I identifiquei como FC podem influenciar no destino das sementes (local de deposição e predação) através do monitoramento bimensal de sementes presentes no banco de sementes do solo nas áreas dos ninhos, nas respectivas áreas de forrageamento e em áreas controle. Observei que as formigas diminuem a deposição e aumentam a predação de sementes na área de ninho, mas a cobertura florestal exerce um efeito pequeno sobre o papel das formigas no destino das sementes. No Capítulo II avaliei como as FC influenciam os regenerantes através do monitoramento bimensal de plântulas e indivíduos jovens recrutando nos ninhos, áreas de forrageamento e em áreas controle. A riqueza de espécies regenerantes aumentou ao longo do gradiente de cobertura florestal para as áreas de ninho, forrageamento e controle sem diferença entre estas áreas. Já a abundância de regenerantes foi menor nos ninhos seguido das áreas de forrageamento e controle, mas não foi afetada pela cobertura florestal ao redor da colônia. Esses resultados indicam que as FC têm efeito negativo sobre sementes e regenerantes em áreas com diferentes níveis de perturbação, uma vez que a cobertura florestal ao redor da colônia teve um efeito fraco sobre a influência das FC na regeneração da Caatinga.

Palavras-chaves: Sementes. Plântulas. Florestas Secas. *Atta opaciceps*.

ABSTRACT

Anthropogenic disturbances rearrange biological communities through the replacement of specialist, disturbance-sensitive species by generalist, disturbance adapted species. Leaf-cutting ants (LCA) are organisms that increase their colony density in disturbed areas due to the relaxation of bottom-up (food resource) and top-down (natural enemy pressure) population controls. As LCA are voracious herbivores, harvesting tons of plant material for the fungus-culturing, they may modify regeneration dynamics of disturbed areas. In this study I examined how LCA affect plant regeneration of human-modified landscapes in Caatinga, the largest and more diverse dry forest in the neotropics, but also very disturbed by human activities. The general hypothesis is that LCA negatively affect plant regeneration because harvest large amount of seeds, seedlings and young individuals for the fungus-culturing, and that this effect is potentialized by the increasing of forest cover around nests. The study was conducted in the Catimbau National Park, PE, with *Atta opaciceps* nests located in micro-landscapes with different forest cover (8.7% - 87.8%). I evaluated in the Chapter I how LCA influences the seed fate (deposition site and predation) through bimensal monitoring of seed soil bank in nest areas, the respective foraging areas and control areas. LCA decreased seed deposition and increased seed predation on nest areas, but forest cover around colonies had a weak effect on the seed fate. Chapter II was focused on the effects of LCA on plant regenerating assemblages via bimensal monitoring of seedlings and young individuals recruiting in nest sites, foraging areas and control areas. Species richness of regenerating plant assemblages increased along the forest cover gradient for nest sites, foraging and control areas, but there was no difference between these areas. The total abundance of regenerating plants was lower in nest areas, followed by foraging and control areas, but was not affected by forest cover. These results indicate that LCA negatively affect seeds and regenerants in areas with different levels of disturbance, as forest cover around colonies had a weak effect on the role LCA play in Caatinga regeneration.

Keywords: Seed. Seedlings. Dry Forests. *Atta opaciceps*.

LISTA DE FIGURAS

EFFECT OF LEAF-CUTTING ANTS ON SEED FATE IN CAATINGA REGENERATION AREAS

INFLUENCE OF THE LEAF-CUTTING ANTS *ATTA OPACICEPS* ON CAATINGA REGENERATION DYNAMICS

LISTA DE TABELAS

EFFECT OF LEAF-CUTTING ANTS ON SEED FATE IN CAATINGA REGENERATION AREAS

INFLUENCE OF THE LEAF-CUTTING ANTS *ATTA OPACICEPS* ON CAATINGA REGENERATION DYNAMICS

SUMÁRIO

1 INTRODUÇÃO

Nas últimas décadas tem crescido a atenção para o efeito das perturbações antrópicas sobre degradação dos ecossistemas naturais. Um pequeno número de espécies e/ou grupos que são adaptadas às perturbações se tornam cada vez mais dominantes nas paisagens antrópicas em detrimento de um grande número de espécies ou grupos sensíveis à perturbação (OLIVEIRA; GRILLO; TABARELLI, 2004; SANTOS et al., 2008; TABARELLI; PERES; MELO, 2012). 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 (LÔBO et al., 2011; RIBEIRO et al., 2015; RIBEIRO-NETO et al., 2016; SANTOS et al., 2010).

Neste contexto ecológico de paisagens fragmentadas dominadas por organismos vencedores, um grupo de organismo se destaca: as formigas cortadeiras especialmente as espécies do gênero *Atta* (LEAL; WIRTH; TABARELLI, 2014; TABARELLI et al., 2017 a; TERBORGH et al., 2001; WIRTH et al., 2007). Essas formigas são limitadas ao Novo Mundo, e são caracterizadas pelo cultivo de um fungo simbionte dentro dos seus ninhos à base de material vegetal. Coletam toneladas de vegetação, incluindo uma grande gama de espécies vegetais, e por isso são consideradas os herbívoros mais vorazes e polífagos do Novo Mundo, cortando anualmente mais de 15% da produção de folhas (URBAS et al., 2007; WIRTH et al., 2003) e mais de 50% das espécies da flora (WIRTH et al., 2003) dentro das áreas de forrageamento das colônias. E também podem ser consideradas engenheiras de ecossistemas devido a sua ampla atuação como modificadora do ambiente, alterando recursos e consequentemente a distribuição de espécies nas áreas sob sua influência (LEAL; WIRTH; TABARELLI, 2014; WIRTH et al., 2003).

Vários estudos já reportaram aumentos na densidade de colônias de várias espécies de formigas cortadeiras em áreas perturbadas, tais como: plantações (OLIVEIRA; DELLA LUCIA; ANJOS, 1998), pastagens (FOWLER, 1983), florestas em estádios iniciais de sucessão (FARJI-BRENER, 2001; FOWLER, 1983; HAINES, 1978; JAFFE; VILELA, 1989; VASCONCELOS, 1990; VASCONCELOS, CHERRETT, 1995), pequenos fragmentos florestais (RAO; TERBORGH; NUÑEZ, 2001; TERBORGH et al.; 2001), e nas bordas de pequenos e grandes fragmentos (DOHM et al., 2011; MEYER et al., 2009; WIRTH et al., 2007). Um recente estudo mostrou que as formigas cortadeiras também proliferam com o aumento das perturbações antrópicas na Caatinga (SIQUEIRA et al., 2017); porém, ainda não há nenhuma informação sobre o efeito das formigas cortadeiras sobre a regeneração de áreas perturbadas para este ecossistema.

Diante deste cenário, o objetivo desta tese foi verificar como as formigas cortadeiras *Atta opaciceps* afetam a regeneração de áreas degradadas de Caatinga. Esta tese é constituída por quatro seções, uma fundamentação teórica sobre o tema da pesquisa, dois capítulos já formatados de acordo com os jornais para os quais serão submetidos e as considerações finais. O Capítulo I é intitulado *"Effect of leaf-cutting ants on seed fate in Caatinga regeneration areas"* e será submetido para o jornal *Oecologia*, enquanto Capítulo 2, com título *"Influence of the leaf-cutting ants Atta opaciceps on Caatinga regeneration dynamics"*, será submetido para o jornal *Biotropica*.

2 FUNDAMENTAÇÃO TEÓRICA

2.1 PERTURBAÇÕES ANTRÓPICA

As perturbações antrópicas são a principal causa do declínio na biodiversidade em todo o Globo (SALA et al., 2000). As perturbações causadas por mudanças no uso do solo, ou seja, pela conversão da vegetação natural por sistemas agrícolas, pastagens, estradas ou outros tipos de uso do solo decorrentes de atividades humanas, são conhecidas como perturbações agudas porque envolvem a remoção total da vegetação e por isso causam perda e fragmentação de habitats (SINGH, 1998). Esse tipo de perturbação é mais comum em florestas úmidas e foi foco de estudos nas últimas quatro décadas (LAURENCE et al., 2001, 2014). A perda e a fragmentação de habitats têm efeitos sobre a diversidade biológica em diferentes níveis de organização, e podemos citar, por exemplo: (1) redução no número e no tamanho de populações de especialistas (eventualmente, até extinções locais), paralelo ao aumento daquelas adaptadas às perturbações em diferentes escalas espaciais (LEAL; WIRTH; TABARELLI, 2014; TABARELLI; PERES; MELO, 2012; WIRTH et al. 2007); (2) mudanças na composição taxonômica, funcional e filogenética das assembleias nas escalas local e de paisagem (FILGUEIRAS; IANUZZI; LEAL, 2011; HELMUS ET AL., 2010;; LEAL et al.,2012; SANTOS et al., 2010); (3) redução na riqueza de espécies e na diversidade funcional e filogenética das assembleias nas escalas local e de paisagem (ARROYO-RODRIGUEZ et al., 2017; LOPES et al., 2009; SANTOS et al., 2010; TABARELLI et al., 2010); (4) aumento de similaridade taxonômica entre assembleias nas escalas de paisagem e regional (LÔBO et al., 2011); (5) alteração, inclusive colapso, de interações entre espécies na escala local (GIRÃO et al., 2007; LEAL; ANDERSEN; LEAL, 2014; LEAL; WIRTH; TABARELLI, 2014; THOMPSON, 2002); e (6) mudanças nos padrões de fluxo e armazenamento de nutrientes (PAULA; COSTA; TABARELLI, 2011).

No entanto, as áreas remanescentes de vegetação natural sofrem outro tipo de perturbação, mais sútil, pois não envolve mudança no uso do solo, ou seja, a vegetação natural continua existindo, mas pequenas porções de biomassa são retiradas por populações humanas em um tipo de perturbação que foi conhecido como crônica (SINGH, 1998). Podemos citar a coleta de lenha, o corte seletivo de madeira, a exploração de produtos florestais não madeireiros, sobrepastoreio por animais domésticos, introdução de espécies exóticas usadas como forragem adicional para os animais domésticos, caça, entre outros, operando de forma crônica na escala de paisagem (HOBBS; HUENNEKE, 1992; SINGH, 1998; MARTORELL; PETERS, 2005, 2009; RIBEIRO et al., 2015). As perturbações crônicas são mais comuns em florestas secas e outros ecossistemas semiáridos e áridos onde a conversão da vegetação nativa por culturas e pastos não é viável (SING, 1998). De fato, as áreas de clima seco são as mais populosas e a menor estatura da vegetação, o clima mais adequado e a disponibilidade de forragem facilitam a agricultura e a criação de animais, com rebanhos muito grandes e animais criados de forma extensiva (MURPHY; LUGO, 1986; SAMPAIO, 1995; REID; GALVIN; KRUSKA, 2008). Assim, a população, normalmente de baixa renda, depende da vegetação natural para a sua subsistência (DJOUDI et al., 2015). As perturbações crônicas começaram a ser estudadas mais recentemente, mas já se tem um conjunto de evidências do seu papel negativo sobre a biodiversidade, o qual pode ter efeitos em cascata para outros processos ecossistêmicos. Por exemplo, já foi demonstrado que perturbações crônicas podem causar redução nas populações de especialistas paralelo ao aumento daquelas adaptadas às perturbações (OLIVEIRA et al.,2017; RITO; TABARELLI; LEAL, 2017, SIQUEIRA et al., 2017) levando a homogeneização biológica de comunidades de plantas e animais (RIBEIRO-NETO et al., 2016); redução na diversidade taxonômica, funcional e filogenética das comunidades de plantas e animais (ARNAN et al. 2018; RIBEIRO et al., 2015, 2016; RIBEIRO-NETO et al., 2016; RITO et al., 2017;); alteração, inclusive colapso, de interações entre plantas e animais como dispersão de sementes por formigas (LEAL; ANDERSEN; LEAL, 2014) e proteção de plantas contra herbívoros (LEAL; ANDERSEN; LEAL, 2015); e mudanças nos padrões de estoque e ciclagem de nutrientes (SCHULZ et al., 2016; SOUZA et al., 2019). Esses estudos demonstram que perturbações crônicas podem alterar de populações a ecossistemas, atuando de forma tão deletéria quanto às perturbações agudas para a integridade dos ecossistemas onde são comuns.

Dessa forma, tanto perturbações agudas como crônicas causam substituição de espécies sensíveis à perturbação por espécies adaptadas à perturbação, reorganizando comunidades e influenciando funções e serviços ecossistêmicos (CHAZAL; ROUNSEVELL, 2009; GARDNER et al., 2009; LEWIS; EDWARDS; GALBRAITH, 2015; SUPP; ERNEST, 2014). A diferença é que apenas as perturbações agudas, por removerem toda a vegetação original para implementação de outro uso do solo, darão início ao processo de sucessão após esse uso ser abandonado. Por exemplo, quando áreas agrícolas são abandonadas, por redução nos níveis de produtividade, por exemplo, inicia-se o processo de regeneração natural ao longo do tempo (CHAZDON, 2012). Todavia, o processo de regeneração pode ser alterado se a floresta em regeneração for submetida a perturbações crônicas. Caso a perturbação crônica ocorra de forma frequente ou intensa, pode haver um freio no processo de regeneração (i.e., sucessão travada ou *arrested succession*, PUTZ; CANHAM, 1992; SARMIENTO, 1997). Independente da papel das perturbações agudas e crônicas na reorganização das comunidades biológicas e na regeneração das florestas, os seres humanos moldaram e continuarão a moldar os ecossistemas em todo o Globo através de atividades de curto e longo prazo e entender se e como a vegetação é capaz de retornar sua estrutura anterior a perturbação é essencial para a compreensão contemporânea das interações que existe entre a nossa espécie e os ecossistemas (ALBUQUERQUE et al., 2017).

2.2 REGENERAÇÃO NATURAL

A regeneração natural ou sucessão secundária é a reorganização da comunidade biológica em termos de riqueza, biomassa e composição de espécies após uma área ter sua vegetação removida por perturbação (CHAZDON, 2012). Essa substituição de espécies segue uma mudança das condições físicas (e.g. temperatura, umidade, fertilidade do solo) que possibilitam a progressão de estágios sucessionais da vegetação, incluindo um enriquecimento gradual de espécies e um aumento em complexidade estrutural e funcional da comunidade com o tempo (LEBRIJA-TREJOS et al., 2010 a; CHAZDON, 2012). De acordo com os primeiros modelos de sucessão secundária, essa reorganização da comunidade se daria de forma direcional ao longo do tempo, onde espécies de plantas boas colonizadoras (i.e. pioneiras) ocupariam a área abandonada, melhorariam as condições abióticas da área (e.g. aumentando o sombreamento, a umidade do ar e do solo, a quantidade nutrientes no solo), favorecendo a ocorrência de espécies boas competidoras (tardias ou clímax) (CLEMENTS, 1916). Mas existem outros modelos de sucessão que não necessariamente implicam em uma substituição direcional das espécies. Por exemplo, Egler (1954) propôs o modelo de composição florística inicial, em que todas as espécies que ocorrem durante a sucessão secundária se estabelecem no processo inicial de sucessão, por já estarem no banco de sementes do solo à época do abandono da área. Posteriormente, Connel e Slayter (1977) propuseram três modelos de sucessão: facilitação, inibição e tolerância e apenas o primeiro modelo segue a ideia de substituição direcional no tempo. No modelo de inibição, as espécies colonizadoras são invasoras exóticas e retardam o processo de sucessão por inibirem a colonização de espécies tardias e clímax, e no de tolerância, as espécies colonizadoras iniciais causam transformações no ambiente, mas, com pouco ou nenhum efeito sobre o recrutamento e crescimento das espécies colonizadoras posteriores. Por fim, Lawton (1987) propôs um modelo de colonização ao acaso, em que todas as espécies são igualmente tolerantes às condições abióticas e podem estabelecer-se em qualquer estágio da sucessão, impedindo o estabelecimento de outras espécies durante seu tempo de vida. Essas comunidades são descritas como controladas pelos colonizadores (e.g. peixes na grande barreira de corais da Austrália, TOWNSEND et al., 2009).

Pelo número grande de modelos de sucessão desenvolvidos no último século, é possível perceber o quanto este tema tem recebido atenção dos ecólogos. Um outro tema de interesse dos pesquisadores é o que afeta o tempo de sucessão. De fato, alguns fatores podem acelerar ou retardar o processo de regeneração florestal ou sucessão secundária. Primeiramente, a severidade da perturbação afeta diretamente o tempo de sucessão (RICKLEFS, 2010). Por exemplo, uma clareira criada pela queda de uma árvore pode ser fechada através do crescimento de jovens do sub-bosque, já uma grande área queimada necessita que novas sementes, vindas da vegetação circundante intacta, atinjam a área e iniciem a sucessão. O histórico de uso da área, disponibilidade de água e nutrientes no solo, regime de precipitação, proximidade da área com florestas maduras (e.g. fonte de propágulos e fluxo de fauna dispersora), banco e chuva de sementes, também são fatores que atuam na recuperação da comunidade biológica e informam sobre a direção e taxas de mudanças no sistema (COLÓN; LUGO, 2006). Ou seja, esses processos/fatores podem afetar tanto a trajetória sucessional (i.e., padrão das mudanças) quando a resiliência (i.e., velocidade das mudanças) do ecossistema. Resiliência pode ser definido como a capacidade ou a taxa de recuperação do ecossistema, considerando qualquer um dos seus componentes (NEWTON; CANTARELLO, 2015).

Também desperta muito interesse a questão se florestas secas são mais ou menos resilientes após perturbação que as florestas úmidas, muito mais estudadas. Existem sugestões de que a menor complexidade estrutural e taxonômica da comunidade vegetal das florestas secas, além da elevada capacidade de rebrota de espécies de árvores e arbustos tornariam as florestas secas mais resilientes que as úmidas (QUESADA et al., 2009; VIEIRA; SCARIOT, 2006). No entanto, essas interpretações são baseadas em especulações e poucos estudos empíricos existem (ver revisão em QUESADA et al., 2009). A sazonalidade marcada, a alta imprevisibilidade das chuvas, a baixa produtividade e o curto período da estação de crescimento (i.e., estação chuvosa), além da dependência de animais para a polinização (COE; SOUSA, 2014; LEAL et al., 2017 b), desafiam a ideia de que florestas secas são mais resilientes que as úmidas. Além disso, a criação de animais de forma extensiva e a extração de recursos naturais, mais comuns em florestas secas, podem produzir uma paisagem com vegetação secundária permanente e ter um impacto significativo sobre a dinâmica da regeneração e conservação (CECCON; HUANTE; RINCÓN, 2006). O problema é que existem poucos estudos de sucessão em florestas secas e seus resultados são contraditórios, alguns mostram recuperação quase total da riqueza, biomassa e composição de espécies das florestas secundárias em relação às florestas maduras (LEBRIJA-TREJOS et al., 2010 b), o que indicaria uma forte resiliência, e outros mostram que essa recuperação não é tão frequentemente observada (QUESADA et al., 2009).

De fato, os mecanismos de regeneração de florestas secas são diferentes daqueles das florestas úmidas (ver revisões em MCDONALD; MC LAREN; NEWTON, 2010 e em VIEIRA; SCARIOT, 2006). Nas florestas úmidas, a regeneração é ligada à dinâmica de clareiras, mas a regeneração de florestas secas depende muito da disponibilidade de água para o estabelecimento das plântulas (MCDONALD; MC LAREN; NEWTON, 2010). O tempo e duração das chuvas é crucial, uma vez que existe alta probabilidade de as plântulas ficarem expostas às condições ambientais dessecantes (quente e seco), e, assim, a regeneração via sementes é mais rara em florestas secas que em florestas úmidas (ANDERSON-TEIXEIRA et al., 2013). Além desses fatores ambientais, a regeneração em florestas secas depende fortemente da proximidade de fontes de regenerantes. A dispersão abiótica é predominante e as distâncias de dispersão são menores (DERROIRE et al., 2016). O banco de sementes do solo tem baixa densidade de sementes e essas sementes tendem a germinar no ano seguinte a sua produção e dispersão (DERROIRE et al., 2016). No entanto, as sementes podem ser perdidas ao longo desse tempo por pouca quantidade de água disponível no solo, predação, patógenos e competição com espécies de gramíneas exóticas (quando estas estão presentes) (DERROIRE et al., 2016; VIEIRA et al., 2006). E mais importante, a reprodução vegetativa através de rebrotas é um mecanismo de regeneração muito frequente em florestas secas (VIEIRA; SCARIOT, 2006). As razões pelas quais a rebrota é um mecanismo de regeneração particularmente relevante em florestas secas ainda são incertas, mas a habilidade das plantas rebrotarem depende do regime de precipitação, frequência intensidade e duração da perturbação (CHAZDON, 2017; LUOGA; WITKOWSKI; BALKWIL, 2004; MC DONALD; MC LAREN; NEWTON, 2010; VIERA; PROCTOR, 2007). Em uma revisão sobre o papel da precipitação e do tempo de regeneração sobre os mecanismos de regeneração, Mc Donald et al (2010) verificaram que a proporção de indivíduos jovens provenientes de rebrota é maior que a de indivíduos provenientes de sementes em áreas de florestas com baixa precipitação, e essa proporção vai diminuindo à medida que a precipitação anual da área aumenta. Da mesma forma, a proporção de rebrotas é maior em áreas com pouco tempo de regeneração e vai diminuindo à medida que o tempo de regeneração aumenta (MC DONALD; MC LAREN; NEWTON, 2010).

A capacidade e taxa de recuperação da vegetação em termos de estrutura, composição de espécies e funcionamento depois de perturbações são um assunto de ampla audiência hoje em dia (ARROYO-RODRIGUEZ et al., 2017; DERROIRE et al., 2016). Nas florestas secas e em outros ambientes áridos e semiáridos, a capacidade de rebrota da vegetação pode indicar um alto grau de resiliência depois da implementação de pastos (VIEIRA et al., 2006) e de corte da vegetação ou de ciclones (CHAZDON, 2017). De outra forma, perturbações antrópicas podem reduzir a regeneração através de novos indivíduos provenientes de sementes, e, consequentemente, a resiliência do ecossistema (TYLIANAKYS et al., 2007), bem como as intrincadas interações entre fatores intrínsecos e extrínsecos que influenciam essa resiliência (LEBRIJA-TREJOS et al., 2010 b). Esses processos ecológicos estão só começando a ser descritos, apesar de sua importância para a manutenção da biodiversidade de áreas sob pressão antrópica.

2.3 CAATINGA

A Caatinga é um mosaico de florestas tropicais sazonalmente secas e vegetação arbustiva cobre 912,529 km^2 do nordeste brasileiro (SILVA ET AL., 2017a). O clima da Caatinga é severo; a temperatura é uniforme, embora sempre muito elevada, a umidade relativa do ar é baixíssima e as precipitações anuais estão entre 250-900 mm (NIMER, 1972). Há uma estação chuvosa de 3-5 meses durante o inverno, alternada por períodos de estiagem de 7-9 meses no verão (NIMER, 1972). A baixa pluviosidade, acompanhada de uma pronunciada irregularidade em sua distribuição no tempo e no espaço, por vezes culmina em secas catastróficas (NIMER, 1972). Tais características climatológicas levaram à evolução de uma vegetação tipicamente xerófila, com uma série de adaptações morfológicas, fisiológicas e anatômicas, que a torna capaz de driblar as condições severas a que estão sujeitas as espécies (QUEIROZ et al., 2017). A Caatinga tem cerca de 70% da sua área sobre o embasamento cristalino (Proterozoico) e 30% sobre as bacias sedimentares (Paleozoico e Mesozoico) formando superfícies achatadas entre 300-500 m acima do nível do mar (COLE, 1986; SAMPAIO, 1995). A região tem muitos tipos diferentes de solos, variando de rasos, rochosos e relativamente férteis sobre o cristalino a profundos, arenosos e pouco férteis sobre o sedimentar (SAMPAIO, 1995). A vegetação também varia muito, e é fortemente relacionada com o clima e os solos, variando de vegetação arbustiva aberta com muitas cactáceas, principalmente em afloramentos rochosos e em áreas mais secas do cristalino, às florestas altas em áreas com solos mais ricos e com clima mais úmido (QUEIROZ et al., 2017). Nessas diferentes comunidades de plantas da Caatinga, foram registradas 3,150 espécies de plantas, distribuídas em 950 gêneros e 152 famílias; um terço destas espécies são endêmicas da Caatinga (QUEIROZ et al., 2017).

A fauna da Caatinga também apresenta alta riqueza e nível de endemismo, sendo esta considerada uma das regiões semiáridas mais diversas do mundo (GARDA et al., 2017). Existem hoje 1.400 espécies de vertebrados ocorrendo na Caatinga, e 23% destas espécies são endêmicas (GARDA et al., 2017). Em relação a ictiofauna, muitas espécies são amplamente distribuídas nas bacias das ecorregiões da Caatinga e estão sob a influência do Cerrado e da Mata Atlântica, mas há espécies totalmente inserida na Caatinga, sendo considerada endêmicas (LIMA et al., 2017). O mesmo ocorre com os grupos dos anfíbios, dos lagartos e das aves, com espécies endêmicas da Caatinga e as que também ocorrem no Cerrado e na Mata Atlântica (ARAÚJO; SILVA, 2017; GARDA et al., 2017; MESQUITA et al., 2017). Para formigas, são registradas 276 espécies, mas as altas taxas de substituição de espécies entre diferentes localidades indicam que o número real de espécies nesse bioma deve ser muito maior caso mais áreas sejam amostradas (LEAL et al., 2017 a). São registradas apenas duas espécies endêmicas, *Atta opaciceps* e *Dinopnera quadriceps* (LEAL et al., 2017 a). Apesar da subamostragem da comunidade de formigas acima mencionada, podendo mudar os padrões de distribuição de espécies e porcentagens de endemismos à medida que mais áreas sejam estudadas, a fauna da formiga Caatinga parece ser um subconjunto da fauna do Cerrado (LEAL et al., 2017 a).

Apesar da elevada diversidade biológica para os padrões de clima semiárido (LEAL, TABARELLI; SILVA, 2003, 2005; SIQUEIRA-FILHO, 2012), a Caatinga vem sendo modificada drasticamente por atividades humanas desde o início da colonização europeia no século XVI (TABARELLI et al., 2017 b). Grandes áreas com solos mais produtivos foram convertidas em pastagem e agricultura nos últimos 500 anos; os rios permitiram que o gado fosse transportado e a madeira removida (SILVA; LEAL; TABARELLI, 2017). Como resultado, uma importante parcela da Caatinga já foi bastante modificada pelas atividades antrópicas e a porcentagem da vegetação original perdida é de aproximadamente 63%, colocando a região como o terceiro bioma brasileiro mais modificado pelo homem (SILVA; BARBOSA, 2017). Na porção leste, mais próxima da costa, a perda de habitat é severa e os fragmentos são pequenos e isolados; ao sul quase não há remanescentes e a oeste a cobertura vegetal é mais preservada com maiores fragmentos (ANTONGIOVANNI; VENTICINQUE; FONSECA, 2018). Além da perda de habitat, as áreas remanescentes com vegetação nativa também são alteradas por atividades humanas. A Caatinga é a região semiárida mais populosa do Globo com 26 habitantes/km2 (INSA, 2012), e por causa da sua baixa renda, depende dos recursos naturais da Caatinga para sua subsistência (ALBUQUERQUE et al., 2017), em um cenário típico de perturbação crônica (RIBEIRO et al., 2015). Atividades como coleta de lenha, extração de produtos florestais madeireiros e não madeiros, criação extensiva de animais domésticos, introdução de espécies exóticas forrageiras para suprir a carência da vegetação nativa durante a estação seca, agricultura de corte e queima são comuns na Caatinga desde o século XVI (ALBUQUERQUE et al., 2017; RAMOS et al., 2008), diminuindo sua produtividade e aumentando a chance de desertificação na região (TABARELLI et al., 2017 b). Em diferentes escalas espaciais, a Caatinga (ou o semiárido nordestino) pode ser descrita como um sistema socioecológico (sensu FU et al., 2013) dependente do extrativismo, incluindo os nutrientes do solo e da vegetação, os quais são continuamente perdidos/exportados através da produção agrícola e animal (KAUFFMAN et al., 1993), mas quase nunca reintroduzidos no sistema por técnicas de manejo agrícola.

A regeneração das áreas degradadas de Caatinga ainda é muito pouco estudada. Existem informações anedóticas que muitas plantas da Caatinga são capazes de rebrotar após o corte, mas se este é seguido de queima, a rebrota diminui de forma progressiva com o aumento na intensidade de combustão (SAMPAIO et al., 1998). E quando o corte interage com o uso da área como pastagem, é este último que afeta mais fortemente e negativamente a vegetação, tanto a comunidade em regeneração quanto a estabelecida (MARINHO et al., 2016). Em áreas abandonadas após apenas o corte, a sucessão se dá pela presença de sementes no banco do solo, principalmente de espécies autocóricas, mas, sobretudo, pela presença de árvores que podem rebrotar (LOPES et al., 2012). Esse é o caso de *Pityrocarpa moniliformes* (Fabaceae), uma árvore pioneira comum de caatingas de sedimentar (RITO; TABARELLI; LEAL, 2017). Essa espécie domina áreas de agricultura de corte e queima durante e depois do abandono (WANDERLEI et al., dados não publicados). No entanto, o que pareciam plântulas recrutando foram escavadas e foi observado um conjunto enorme de rebrotas de raízes (i.e. *root-sprouters* ou *root suckers* sensu JENIK,1994) ou rametes (WANDERLEI et al., dados não publicados). Essas rebrotas estava fisicamente conectadas às raízes de indivíduos adultos a cerca de 30 cm abaixo do nível do solo (WANDERLEI et al. dados não publicados). Em uma área de 200 m^2, estes autores encontraram 96 rebrotas conectadas através de uma rede de raízes horizontais somando quase 100 m de extensão. Isso demonstra que rebrotas podem ser um importante mecanismo de regeneração na Caatinga como já registrado para outros ecossistemas semiáridos do Globo (CHAZDON, 2017; LUOGA; WITKOWSKI; BALKWILL, 2004; MC DONALD; MC LAREN; NEWTON, 2010; VIERA; PROCTOR, 2007).

2.4 FORMIGAS CORTADEIRAS

As formigas cortadeiras compreendem os gêneros *Atta* e *Acromyrmex* da tribo Attini (Myrmicinae, Formicidae, Hymenoptera), a qual foi 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. São chamadas assim porque cortam folhas que servem de substrato para o fungo criado dentro dos seus ninhos e do qual se alimentam (DELLA LUCIA; SOUZA, 2011). A tribo Attini teve uma única origem há aproximadamente 50 milhões de anos (CHOMICKI; RENNER, 2017; SCHULTZ; BRADY, 2008), provavelmente nas florestas da América do Sul (SCHULTZ; BRADY, 2008; WARD et al., 2015). A agricultura é um produto de uma relação simbiótica entre três organismos, 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).

As espécies do gênero *Atta* são endêmicas do Novo Mundo, estando presentes no sul da América Central, na Bacia Amazônica e entorno, na Mata Atlântica, Cerrado, nos Pampas e na Caatinga (DELABIE et al., 2011). Algumas espécies são endêmicas (e.g. *A..robusta* na restinga e *A. opacicpes* na Caatinga) (FOWLER 1993;; TEIXEIRA et al., 2003; ULYSSÉIA; BRANDÃO, 2013), enquanto outras apresentam ampla distribuição (e.g. *A. sexdens* e *A. laevigata*) (FOWLER et al., 1989). As espécies de *Atta* constroem ninhos subterrâneos compostos por vários murundus grandes que cobrem uma superfície de mais de 250 m^2 (HÖLLDOBLER; WILSON, 1990; RAO, 2000; WIRTH et al., 2003) e podem suportar populações contendo cerca de um milhão de indivíduos (MOREIRA et al., 2004).

Essas formigas são consideradas espécie-chave ou engenheiras de ecossistemas devido a sua ampla atuação como modificadora do ambiente, influenciando um grande número de organismos em diferentes escalas, desde populações de plantas até todo o ecossistema (LEAL; WIRTH; TABARELLI, 2014; WIRTH et al., 2003). 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 podem levar a mudanças na composição e estrutura da comunidade (FARJI-BRENER, 2001; GARRETTSON et al., 1998) 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 (CORRÊA et al. 2010; RAO; TERBORGH; NUÑEZ, 2001). 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 (CORRÊA et al., 2010; GARRETTSON et al., 1998; 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).

Mas o aspecto mais importante relacionado às formigas cortadeiras do gênero *Atta* é a sua posição como herbívoro dominante em ecossistemas neotropicais (MIKHEYEV et al., 2008), uma vez que uma única colônia pode consumir, anualmente, centenas de quilogramas de material vegetal incluindo 50% da flora presente nas suas áreas de forrageamento (BEYSCHLAG; HÖLLDOBLER, 2007; COSTA; BRUNA; VASCONCELOS, et al., 2018; HERZ; WIRTH et al., 2003). 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 mortalidade (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 (CORRÊA et al., 2016; LEAL; WIRTH; TABARELLI, 2014; WIRTH et al., 2003).

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 removam da produção de folhas, a taxa de herbivoria varia entre 12 e 17% em áreas de floresta (URBAS et al., 2007; WIRTH et al., 2003), 17% em Cerrado

(COSTA; BRUNA; VASCONCELOS, 2018) e uma estimativa de 6% para pastagens (CALDATO et al., 2016).

As formigas cortadeiras também podem coletar uma grande quantidade de sementes como substrato para o fungo simbionte e, assim, têm um papel importante na regeneração dos ambientes onde ocorrem (LEAL; WIRTH; TABARELLI, 2014). Estudos em florestas tropicais têm demonstrado benefícios das formigas cortadeiras sobre a biologia de sementes de plantas (LEAL; OLIVEIRA, 1998; LIMA; OLIVEIRA; SILVEIRA, 2013; ZAVALA-HURTADO, 2000;). Elas atuam como agentes dispersores secundários de plantas dispersas primariamente por vertebrados (LEAL; OLIVEIRA, 1998; LEAL; WIRTH; TABARELLI, 2014), em alguns casos raros 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 o sucesso reprodutivo das plantas e a estrutura espacial das populações (KASPARI, 1993; LEAL; OLIVEIRA, 1998; ZAVALA-HURTADO, 2000). Em algumas ocasiões, as formigas cortadeiras apenas limpam as sementes (i.e., retiram a polpa do fruto), comportamento que pode evitar a infecção das sementes por fungos e patógenos, aumentando a taxa de germinação (FARJI-BRENER; SILVA, 1996; LEAL E OLIVEIRA, 1998; LIMA; OLIVEIRA; SILVEIRA, 2013; TAVARES et al., 2016). No entanto, existem evidências também destas formigas atuarem como predadoras de sementes (COSTA; VASCONCELOS; BRUNA, 2017; FERREIRA et al, 2011). Nesses casos, as formigas podem limitar estabelecimento de plântulas por reduzir a disponibilidade de sementes, afetando negativamente a regeneração (COSTA, BRUNA, VASCONCELOS, 2018; COSTA; VASCONCELOS; BRUNA, 2017; SILVA et al., 2012). Também já foi observado efeitos de *Atta* nas densidades e composição de espécies de plântulas, principalmente nos primeiros anos de regeneração florestal, já que com o passar do tempo há uma menor proporção de ataque a esses estágios ontogenéticos (VASCONCELOS; CHERRET, 1997).

Por outro lado, as formigas cortadeiras podem facilitar a regeneração da floresta através do descarte de suas lixeiras nas adjacências dos ninhos. As lixeiras são ricas em nutrientes e aumentam a fertilidade do solo, favorecendo o crescimento e desempenho de plantas ao redor do ninho (FARJI-BRENER; TADEY, 2009). As plântulas associadas às lixeiras frequentemente mostram crescimento mais rápido e maior biomassa de raízes e folhas, enquanto os adultos apresentam maior número de flores e produção de sementes (FARJI-BRENER; GHERMANDI 2008; FARJI-BRENER; TADEY, 2009; FARJI-BRENER; WERENKRAUT, 2017; ZAVAL HURTADO et al., 2000). Além disso, há mudanças na composição de espécies de plântulas recrutando próximas às lixeiras, mostrando que estas podem operar como filtro biológico favorecendo um determinado conjunto de espécies em detrimento de outro (FARJI-BRENER; GHERMANDI, 2004; FARJI-BRENER; ILLES 2000; FARJI-BRENER; TADEY 2009). Vale ressaltar que a localização da lixeira (se interna ou externa) depende do ambiente e da espécie de formiga cortadeira estudada (FARJI-BRENER; ILLES, 2000; FARJI-BRENER; TADEY, 2009).

Por fim, outro fator que pode interferir na regeneração de floresta devido às formigas cortadeiras é o abandono dos seus ninhos por migração ou morte da colônia. Estes ninhos agora sem as formigas podem servir como locais preferenciais para o recrutamento de plântulas porque apresentam altos níveis de luz, além da falta de vegetação que é cortada ou soterrada pelas formigas repetidamente, diminuindo a competição das plântulas (FARJI-BRENER; MEDINA, 2000). Em contraste, ninhos abandonados podem ter menor quantidade de matéria orgânica, serem mais compactos do que solos de floresta livres de ninhos apresentando um conjunto menor de plantas regeneradoras (BIEBER et al., 2011).

Estudos recentes na Caatinga indicam que as formigas podem ter um papel sobre a vegetação/regeneração ainda mais impressionante do que o registrado anteriormente para outros ecossistemas (TABARELLI et al., 2017 a). Siqueira et al. (2018) estimou que a taxa de herbivoria média das colônias de *Atta opaciceps* chega a 30% da vegetação presente nas áreas de forrageamento. Além disso, Siqueira et al. (2017) verificou que as formigas cortadeiras das três espécies que ocorrem na Caatinga, *Atta laevigata*, *A. opaciceps* e *A. sexdens*, aumentam a densidade de colônias em áreas mais perturbadas. Essa elevada taxa de herbivoria por colônia, associada à alta densidade de colônias das áreas perturbadas, indicam que as formigas podem ter um papel negativo sobre a regeneração da Caatinga como demonstrado para áreas de Floresta Atlântica (CORRÊA et al., 2010) e para o Cerrado (COSTA; BRUNA; VASCONCELOS, 2018). Contudo, as colônias das três espécies de formigas cortadeiras que ocorrem na Caatinga colocam as lixeiras para fora do ninho (SIQUEIRA et al. 2017, 2018), o que pode aumentar a fertilidade dos solos adjacentes aos ninhos e facilitar o recrutamento de plântulas e a regeneração da vegetação (TABARELLI et al. 2017 a). Portanto é importante verificar o resultado líquido dos efeitos das formigas cortadeiras sobre a regeneração da Caatinga, pesando os aspectos negativos (predação de sementes, herbivoria de plântulas e adultos) e os aspectos positivos (fertilização dos solos pela localização externa das lixeiras) para termos um melhor entendimento de como áreas perturbadas e com alta densidade de formigas cortadeiras podem ter sua vegetação recuperada (TABARELLI et al., 2017 a). Essas questões ainda precisam ser investigadas e esse é o tema desta tese.

3 EFFECT OF LEAF-CUTTING ANTS ON SEED FATE IN CAATINGA REGENERATION AREAS

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Effect of leaf-cutting ants on seed fate in Caatinga regeneration areas

Clarissa M. Knoechelmann[1,2], Rainer Wirth[3], Inara R. Leal[4,*]

1Programa de Pós-Graduação em Biologia Vegetal, Universidade Federal de Pernambuco, Av. Prof. Moraes Rego s/n, Cidade Universitária, 50670-901, Recife, PE, Brazil

2Faculdade de Ciências Biológicas, Universidade Federal do Sul e Sudeste do Pará - Folha 31, Quadra 07, Lote Especial, s/n. Bairro: Nova Marabá - Marabá/PA Brasil - CEP 68507-590

3Plant Ecology and Systematics, University of Kaiserslautern, PO Box 3049, 67663, Kaiserslautern, Germany

4Departamento de Botânica, Universidade Federal de Pernambuco, Av. Prof. Moraes Rego s/nº, Cidade Universitária, 50670-901, Recife, PE, Brazil

*Author for correspondence: irleal@ufpe.br

Abstract

Regeneration mechanisms (e.g. seed rain and seed bank) may influence the success or dominance of a species in successional communities. Leaf-cutting ants (LCA) proliferate in disturbed areas and may influence regeneration dynamics because their harvesting of seeds for fungus-culturing. Here we investigate how LCA influence seed fate in human-modified areas of Caatinga dry forest. We evaluate the seed deposition site and predation on *Atta opaciceps* nests, foraging areas and control areas of 15 colonies located in areas with different forest cover. For each treatment, four plots of 50 cm^2 were randomly stablished and all seeds on soil surface were collected bimonthly along one year. We recorded 13,628 seeds distributed among 47 species. From this total, 4,984 (36.57% of the total observed) did not present any trace of predation. We found no effects of treatment and forest cover on total seed richness. However, the richness of undamaged seeds was lower in nest sites, followed by foraging and control areas; forest cover did not alter the richness of undamaged seeds. Total seed abundance in nest mounds was lower than in foraging and control areas and forest cover influenced only the seed abundance in nest sites during the rainy. There were no effects of explanatory variables on the abundance of undamaged seeds. Treatment did not influence seed species composition, but forest cover did. These results indicate that LCA decrease seed deposition and increase seed predation in areas under their influence, but forest cover has only a weak effect on seed fate. As LCA profit from human disturbance in Caatinga, its role as seed 'sink' should be higher on disturbed patches of Caatinga making vegetation regeneration difficult.

Key words: forest cover, foraging activity, seed dispersal, regeneration mechanism, seasonally dry tropical forest

Introduction

The expansion of agricultural lands has reduced the cover of tropical forests worldwide recognizing habitat loss and fragmentation as the major threat to biodiversity persistence (Clark and Covey 2012). The major process subjacent to these disturbance-driven changes is the replacement of a diverse group of disturbance-sensitive species by a less diverse group of disturbance-adapted species, i.e. biotic homogenization (Olden and Rooney 2006, Tabarelli et al. 2012). Rainforest fragments for instance experience a collapse of populations of old-growth trees from the emergent stratum (Oliveira et al. 2004), which has important functional implications because such trees have particular special life-history traits such as shade-tolerant recruitment (Santos et al. 2008), pollination by specialized vectors (Girão et al. 2007; Lopes et al. 2009), large seeds, and mast-fruiting (Melo et al. 2006; Tabarelli et al. 2010). Conversely, a small (about 20%) set of disturbance-adapted species with very different life-history traits tend to proliferate in fragmented habitats (Santos et al. 2008; Tabarelli et al. 2012). All these changes in plant community in fragmented forests are related to problems with regeneration mechanisms, but few studies evaluate how reduction in forest cover influence those mechanism such as seed rain and seed bank (Joly et al. 2014).

Regeneration mechanisms (e.g. seed rain and seed bank) may influence the success or dominance of a species in successional communities (Kennard et al. 2002). Persistence of plant species in fragmented landscapes is influenced by how seed characteristics interact with disperser attributes, because it is important to define whether the species is more resilient to fragmentation (Cramer et al. 2007; McConkey et al. 2012). The availability of propagules and dispersal agents influence seed rain and seed bank, which ensure the structural re-establishment of the vegetation following disturbance (Grombone-Guaratini and Rodrigues 2002). However, forest loss and fragmentation may negatively affect one or more of these processes, and some plant species are not able to disperse their seed and consequently recruit new individuals in landscapes with reduced forest cover (Honnay et al. 2002). For example, Silva and Tabarelli (2000) proposed that the extirpation of frugivorous vertebrates can cause a decline or even extinction of a third percent of tree species of the very fragmented Atlantic Forest. But in the lack of frugivorous vertebrate, seeds became available for the most common insect in the forest floor, ants (Leal and Oliveira 1998, Bieber et al. 2014).

Several studies have documented that ground-dwelling ants can play a key role in the dispersal, germination and, to a lesser degree, establishment of myrmecochores (i.e. plants with elaiosome-bearing seeds dispersed by ants) and non-myrmecochores (plants with flesh fruits dispersed primarily by vertebrate and secondarily by ants) (e.g. Leal and Oliveira 1998, Pizo and Oliveira 2000, Christianini and Oliveira 2009, Leal et al. 2007). Leaf-cutting ants (LCA, genera *Atta* and *Acromyrmex*) are a common group of species that interact with fruits and seed in the forest floor (Leal and Oliveira 1998, 2000; Pizo and Oliveira 2000), as they collect large amount of plant material (leaves, flowers, fruits and seeds) for the cultivation of the symbiotic fungus inside their nests (Leal and Oliveira 1998). Despite their relatively large body size and ability to transport seeds for long distances, LCA are classified as low-quality dispersers because they usually cut or bury all seedlings growing on or near their nests (Leal et al. 2017; Tabarelli et al. 2017). LCA proliferate in fragmented areas in the Atlantic (Wirth et al. 2007, Meyer et al. 2009) and Amazon (Dohm et al. 2011) forests, as well as in the Cerrado savannas (Vasconcelos et al. 2006) and Caatinga (Siqueira et al. 2017, 2018) because of increased palatable plant resource (Urbas et al. 2007; Falcão et al. 2011; Siqueira et al. 2018) and decreased natural enemies (Almeida et al. 2008, Wirth et al. 2008). Thus, any effect they have on seed dispersal and seedling recruitment can be potentialized in human-modified areas (Leal et al. 2014 a).

Our study aims to investigate how LCA affect the seed fate (i.e. seed deposition site and seed predation) in the Caatinga dry forest. Caatinga is considered one of the most endangered ecosystems in Brazil due to extensive conversion to agriculture; 63% of its original cover has been modified by human activities (Silva et al. 2017), and remaining area is distributed in 47,100 forest fragments (Antogiovanni et al. 2018). We examine how *Atta opaciceps* colonies located along a gradient of forest cover influence the seed fate. Our general hypothesis is that LCA have a negative effect on the seed fate because they discard seeds in unsuitable sites and increase seed predation, and that this effect increases as the cover of arboreal Caatinga increases. We thus expect that areas affected by LCA (ant nests and the respective foraging areas) will present (1) lower abundance and (2) species richness of seeds, (3) lower proportion of undamaged seeds (in terms of abundance and richness), and (4) different species composition of seeds as compared to control areas, and (5) that these differences will increase across the gradient of arboreal Caatinga cover.

Materials and Methods

Study area

This study was conducted in Catimbau National Park (Catimbau NP), which covers an area of nearly 640 km^2, located in Pernambuco, north-eastern Brazil (8º 24 '00 "and 8º 36 '35

"- S and 37º 09 '30" and 37º 14'40 "W) (Figure 1). The climate is semi-arid with the annual temperature averaging 23ºC. Annual rainfall varies markedly in Catimbau NP because of topographic influences, from 480 to 1100 mm, concentrated between March and July. Quartzite soils are predominant (approximately 70%) in the Park (Sociedade Nordestina de Ecologia 2002), supporting a relatively open and low-stature (ca. 6 m tall) vegetation in which Fabaceae, Euphorbiaceae and Myrtaceeae are the dominant families (Rito et al. 2017).

Study species

Atta opaciceps (Borgemeier, 1930) is the most common LCA species that occur in Catimbau NP (Figure 2a). It is an ant species endemic to Caatinga, occurring in Piauí, Ceará, Rio Grande do Norte, Pernambuco, Sergipe and Bahia states (Fowler 1993; Ulysséia and Brandão 2013). Although it has been recorded from open habitats (e.g. abandoned field crops) to forest patches (Siqueira et al. 2017), its abundance is positively related to increasing anthropogenic disturbances such as areas with lower forest cover and near to roads (Delabie et al. 1997; Siqueira et al. 2017).

Experimental design

We first selected 15 nests of *Atta opaciceps,* which were separated by a minimum of 400 m and occurred within an area of 70,000 m^2 (Figure 2b). We included only nests with foraging activity during the sampling effort. We used a randomized block design and each block included three treatments: nest mound, foraging area of the respective nest (i.e. areas affected by LCA) and control area. Control areas were considered areas 20 m away from the foraging area, and then there were no effects of ants, while foraging areas were established at the terminal segment of the main trunk trails during the time of higher foraging activity (Corrêa et al. 2010). Trunk trails are relatively cleared paths that direct foragers through the littered forest floor to their host plants (Kost et al. 2005).

Measurement of forest cover

Using a buffer of 200 m from the center of the nest, we delimited a micro-landscape around each nest (Figure 2b and c). We adopt 200 m as buffer, based on foraging area to *A. opaciceps* (Siqueira et al. 2018) to avoided overlapping trails from the neighboring nests. The forest cover in each micro-landscape was calculated using ArcGis 10.1, following a supervised classification of a mosaic of two high resolution RapdyEye scenes (2435123_2012-03-21T133949_RE4_3A-NAC_10955665_148448 and 2435223_2012-03-21T133945_RE4_3A-

NAC_10960352_148469) acquired in March 2012 and provided by Brazilian Government (GeoCatálogo - MMA). We conducted image interpretation using the Maximum Likelihood method based on clearly distinguishable land cover classes. Our own experience supported by a sum of 121 reference points distributed along the 14 classes of land cover allowed us to define training samples base on easily distinguishable land cover aspects for land cover validation. Considering different landscape structure in each Rapdeye scene, the classes represented (1) exposed soil; (2) high clay content in exposed soil; (3) open fields irregularly covered by pasture/herbaceous plants; (4) open fields evenly covered by pasture/herbaceous plants; (5) fields with sparse trees (tree plantations like and croplands); (6) rocky soil covered by herbaceous; (7) rocky soil densely covered by shrubs and herbaceous plants; (8) medium density shrub-tree vegetation (low structured continuous forest); (9) high density shrub-tree vegetation (high structured continuous forest); and (10) groups of riparian or non-deciduous species. Besides that, (11) urban areas and pavement, (12) clouds, (13) cloud and topographic shading and (14) water were also considered in classification. To calculate the forest cover, we considered as forest only physiognomy composed by shrubs and tree species (i.e. woody plants) in a medium to high density of individuals. The forest cover inside each micro-landscape around focal nests ranged from 8.73% in areas of low cover to 87.84% in areas with high density of vegetation.

Seeds sampling in nests, foraging areas and control areas

We first established randomly in each treatment four plots of 50 cm^2 in which we collected all the seeds on soil surface. In the laboratory, seeds were identified to species, or to morphospecies when species identification was not possible. We registered also the quantity of seeds for each morphospecies and if the seed was intact or predated based on physical characteristics (i.e. signal of predation). We surveyed seeds from November 2016 to November 2017, in bimonthly intervals. As Caatinga is very seasonal and we collected seeds along the whole year, we included season in our models, although we are not particularly interested in the effect of seasonally on LCA seed deposition site and predation.

Structure of seeds richness

We calculated sample coverage to evaluate if our survey was satisfactory for sampling units (i.e. all replicates of the three treatments and for each season) using the coverage estimator recommended by Chao and Shen (2010). Species richness is very sensitive to variations in the number of singletons and doubletons (Jost 2006) and because of this we estimated the species richness for all sampling units using coverage-based extrapolations with the iNEXT software (Hsieh et al. 2013). We estimated species richness (or ^0D) (Jost 2006) with the same unit to satisfy the replication principle, the formula of ^0D is detailed elsewhere (Jost 2006). The same procedure was applied for the species richness of undamaged seeds.

Data analyses

We used general linear mixed models (GLMMs) to evaluate the effects of forest cover, treatment, season, and the interactions between forest cover and season, and forest cover and treatment on the overall seed richness (i.e. sum of richness per plot) and abundance (i.e. sum of abundance per plot), and on the proportion of undamaged seed richness and abundance. Block was included in the models as random factors to control for spatial clustering. To species richness date and the proportion of undamaged seed richness, we used the estimated species richness (^0D) (described above). Data that did not obey homoscedastic criteria were log (x +1) transformed. We used lme4 version 1.1-7 package (Bates et al., 2014) to build general and generalized mixed models in R software (version 3.4.3, 2017).

The effects of forest cover and treatment on the composition of seed species were evaluated using canonical correspondence analyses (CCA). For this analysis, we considered the abundance of each morphospecies. We performed a randomization test (10000 aleatorizations) to obtain the statistical significance of forest cover and treatment as explanatory variables (Legendre et al. 2011). We used vegan version 2.3 package (Oksanen et al. 2015) to perform a CCA in R (version 3.4.3, 2017).

Results

We recorded 13,628 seeds, distributed among 47 species, of which 31 were identified to species level. The total richness of seeds varied from 0 - 12 (mean ± SD = 4.55 ± 2.84) in nests, 1-11 (5.34 ± 2.27) in foraging areas and 2-11 (5.71 ± 2.01) in control areas. We found no effects of treatment, forest cover, season and their interactions on seed richness (Table 1, Figure 3a). The total abundance of seeds varied from 0-729 (mean ± SD= 75.77 ± 123.74) in nests, 6-328 (73.37 ± 70.22) in foraging areas and 6-515 (81.83 ± 100.97) in control areas. We found effects of treatment, with more seeds in the control areas followed by foraging areas and nests, although the difference between these two last treatments was not significant. Forest cover affected seed abundance only in nest sites and during rainy season, as showed by the interactions between treatment and forest cover and season and forest cover (Table 1, Figure 3b). We found no effect of forest cover and season on seed abundance (Table 1, Figure 3b).

We found 4984 (36.57% of the total observed) undamaged seeds and 8644 (63.42%) damaged seeds. Undamaged seeds varied from 0-413 (30.96 ± 64.00) in nests, 0-223 (26.35 ±

45.94) in foraging areas and 0-429 (27.15 ± 64.34) in control areas. In relation to the proportion of undamaged seed richness, we found effects of the treatment and season, with lower proportion in nest mounds compared control areas (Tabela 1, Figure 3c). We found no effects of forest cover and interactions between forest cover and treatment and forest cover and season on the proportion undamaged seed richness (Table 1, Figure 3c). For the proportion of undamaged seed abundance, we found no effects of any explanatory variables (Table 1, Figure 3d).

In relation to seed species composition, the first axis of the CCA explained 5.7% of the variation (Figure 4). The seed species composition varied significantly with forest cover, but not with treatment (Table 2, Figure 4). *Cnidoscolus quercifolius* and *Jatropha molissima* were associated with higher forest cover, whereas *Croton nepetifolius* were associated with low forest cover (Figure 4).

Discussion

In this study we investigated the effect of the LCA *Atta opaciceps* on seed fate (seed deposition site and seed predation) in colonies located along a forest cover gradient. Our results indicate that (1) total seed abundance and proportion of undamaged seeds (in terms of species richness) were higher in control areas compared to areas affected by LCA, (2) forest cover play a weak role on seed fate, influencing only the seed abundance in nest sites during the rainy, season and (3) forest cover around nests affected seed composition, but it was not affected by LCA.

Fruit and seed harvesting by LCAs have been reported for dozens of tree and shrub species in neotropical forests (Dalling and Wirth 1998; Farji-Brener and Medina 2000; Pizo and Oliveira 1998), Cerrado savannas (Leal and Oliveira 1998), and dry lands as Chaco (Varela and Perera 2003) and Caatinga (Leal et al. 2007; Siqueira et al. 2018). However, the outcome of this interaction is less studied and is highly context dependent. Leal et al. (2014 a) included in their review at least four potential factors affecting the result of the LCA-seed interactions: (1) the ant’s behavior towards diaspores, (2) the final deposition site, (3) the soil quality and (4) seedling defoliation when seeds are deposited on ant nests. The ant’s behavior toward diaspores and deposition site are important factor for the context of our study. Seed cleaning without seed removal from parental plants or seed removal associated to deposition of high amount of seeds in ant nest adjacencies are both expected to impose higher seed/seedling predation (Silva et al. 2007). Seed removal and loss along foraging trails reduces seed aggregation and enhances the probability of seed deposition in a suitable habitat for germination (Dalling and Wirth 1998;

Leal and Oliveira 1998). Amongst the seeds carried towards ant nests, those discarded inside nests do not germinate (Moutinho et al. 1993), whereas those deposited outside nests allow the recruitment of new plants (Farji-Brener and Medina 2000) but are frequently buried by LCA after a while (Corrêa et al. 2010). Thus, in most cases, the outcome of this interaction is negative in terms of recruitment of new individuals (Silva et al. 2007, Corrêa et al. 2010, Leal et al. 2014 a).

One could expect that our results of reduced seed abundance around *A. opaciceps* nests compared to foraging and control areas can be due to the location of the nest refuse dumps deposition (Leal et al. 2014 a). In fact, Farji Brener and Medina (2000) demonstrated that nests of *A. colombica*, with external refuse dumps, present more seeds than control areas, while nests of *A. cephalotes*, with internal refuse dumps, did not differ in seed abundance and richness from control areas. *Atta opaciceps* deposit their refuse dumps externally, at least once in the year in the beginning of the rainy season (Siqueira et al. 2018). However, as our focal colonies rarely deposited refuse dumps externally along the studied year, nest plots were located at mounds rather than refuse dumps. Thus, we believe that a potential increment in seed abundance should occur only very close to refuse dumps not in the entire nest area. Additionally, LCA nest areas, with their large size and high light incidence at ground level, are frequently low-density and impoverished in sapling and large plant assemblages (Garretson et al 1998; Farji-Brener and Illes 2000; Corrêa et al 2010). Consequently, seed production in nest mound and surrounding areas may be smaller than areas not affected by LCA, as we found for nests of *Atta opaciceps* in our study.

In addition to reduced amount of seeds, *A. opaciceps* nests also presented reduced proportion of undamaged seeds in terms of richness, not in terms of abundance. According to the Janzen-Connell predators pressure hypothesis, areas below parental plants present higher seed/seedling predation because host-specific predators, herbivores, pathogens, or other natural enemies (referred to as predators) are attracted to higher densities of seeds/seedlings (Connell 1970; Janzen 1970). Thus, if nest areas present less seeds than control areas, the proportion of damaged seeds should be smaller in these areas affected by LCA not higher as we observed. Our results indicate that workers of LCA were the predators of the collected seeds, acting as seed predators rather than as seed dispersers. Most of studies on seed dispersal by LCA report a positive effect of ant manipulation on seed germination (Leal and Oliveira 1998; Pizo and Oliveira 1998). However, a recent study of Fernandes et al. (2018) demonstrated that seed scarification of *Mabea fistulifera* (Euphobiaceae) by *Acromyrmex subterraneus* was the most detrimental behavior to seed germination. Potential effects of LCA-seed interactions on plant recruitment and establishment is also still poorly understood, as most studies on seed fate have been monitored only for germination, not for seedling establishment or survival. Two studies in the Atlantic forest have documented elevated mortality following the defoliation of seedlings from seeds previously aggregated by LCA around their nests (Silva *et al.* 2007, Corrêa *et al.* 2010).

Forest cover in micro-landscapes around LCA nests had a weak effect on seed fate, influencing general species composition and total abundance only in nest sites and during rainy season. This could be due to the large proportion of Caatinga flora presenting abiotic dispersal syndromes (Leal et al. 2017), which would be less affected by habitat loss because the general short distance dispersal. Several studies documented a reduced seed shadow/seedling recruitment in fragmented landscapes because lack of long-distance dispersal agents, particularly in rainforests (i.e. dispersal limitation, sensu Dalling et al. 2002) (e.g. Silva and Tabarelli 2000; Cramer et al. 2007; Santos et al. 2006; Cordeiro et al. 2009). Caatinga is one of the most endangered ecosystems in Brazil due to changes in land use, and 63% of its area has been deforested or severely altered by human activities (Silva and Barbosa, 2017). Additionally, remaining areas of Caatinga are chronically exploited by a dense and low-incoming human population highly dependent on forest resources for their livelihoods, such as firewood collection, fodder, exploitation of timber and non-timber forest products, extensive creation of domestic animals and hunting (Ribeiro et al. 2015; Ribeiro-Neto et al. 2016) in a typical chronic disturbance regime (sensu Singh 1998). All these unsustainable uses have threatened populations, communities, plant-animal interactions, and ecosystem functions and services in Caatinga (Leal et al. 2014b; Ribeiro et al. 2015; Schultz et al. 2016; Ribeiro-Neto et al. 2016; Rito et al. 2017). This negative effect of habitat loss and fragmentation (i.e. acute disturbance) and chronic disturbances in Caatinga can be potentialized by climate change, as predictions converge for a reduction in rainfall around 30% and an increasing in temperature up to 6°C (i.e. increasing aridity) until the end of this century (Magrin et al. 2014). Reduced seed shadow in a semi-arid climate ecosystem as Caatinga can intensify problems with plant recruitment because high temperature in the soil level (Paz et al 2015), but increasing aridity will turn plant recruitment even more difficult or even impossible. The good news in that a recent study by Paula (2017) has observed that regeneration of areas in Caatinga that were previously used as agriculture (i.e. increased successional age) positively affects seed rain, which could facilitate Caatinga vegetation regeneration.

In synthesis, we demonstrated here that LCA decrease seed deposition and increase seed predation in Caatinga vegetation and that differences in seed fate between nest sites and control areas increase as forest cover increases only during rainy season. These results indicate (1) that LCA especially in nest areas act as seed 'sink' and (2) that small patches of arboreal or less disturbed Caatinga are already impoverished in seed rain/shadow indicating dispersal limitation. As LCA profit from human disturbance in Caatinga (Siqueira et al. 2017), its role as seed 'sink' should be potentialized in disturbed patches of Caatinga making vegetation regeneration difficult.

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Table 1. Results from general linear mixed models (GLMM) to compare seed richness and proportion of undamaged seed richness, seed abundance and proportion of undamaged seed abundance. These response variables were compared between the treatments (nest mound, foraging areas and control areas) of 15 *Atta opaciceps* nests located along a gradient of forest cover during dry and wet seasons at the Catimbau National Park, northeastern Brazil. R^2 represents the coefficient of determination of the whole statistical model. Significant values are in bold.

Response Variable	Explanatory variables	d.f.	F	P	R2
Total richness	Treatment	2	5.2543	0.07228	0.22
	Forest Cover	1	0.5215	0.47021	
	Forest Cover * Treatment	2	1.1740	0.55599	
	Season	1	0.0519	0.81977	
	Season * Forest Cover	1	0.2149	0.64296	
% Undamaged seeds richness	Treatment	2	7.8739	**0.019507**	0.10
	Forest Cover	1	0.5008	0.479146	
	Forest Cover * Treatment	2	2.6457	0.266375	
	Season	1	8.2153	**0.004154**	
	Season * Forest Cover	1	0.8087	0.368495	
Total abundance	Treatment	2	13.98	**0.0009178**	0.99
	Forest Cover	1	0.3163	0.5738328	
	Forest Cover * Treatment	2	7.8426	**0.0198157**	

	Season	1	0.0155	0.9009457	
	Season * Forest Cover		4.3117	**0.0378509**	
% Undamaged seeds abundance	Treatment	2	1.4230	0.4909	0.48
	Forest Cover	1	0.9011	0.3425	
	Forest Cover * Treatment	2	2.3763	0.3048	
	Season	1	1.1719	0.2790	
	Season * Forest Cover	1	1.7907	0.1808	

Table 2. Results of the canonical correspondence analysis (CCA) used to verify the influence of forest cover and treatment (nest mound, foraging areas and control areas) on the composition of seed species collected in 15 Atta opaciceps nests located along a gradient of forest cover at the Catimbau National Park, northeastern Brazil. Significant values are in bold.

Source of variation	DF	χ^2	F	P
Axis				
CCA 1	1	0.2979	2.38	**0.036**
CCA 2	1	0.16	1.34	0.351
Variables				
Forest Cover	1	0.2840	2.27	**0.01**
Treatment	1	0.1817	1.45	0.255
Residual	38	4.74		

Legend for figures

Figure 1. Location of the Catimbau National Park, Pernambuco state, northeastern Brazil.

Figure 2. Colonies of *Atta opaciceps* located at the Catimbau National Park, northeastern Brazil. (a) Aerial view of a colony at the Fazenda Brejo, Catimbau National Park, northeastern Brazil. (b) Fifteen focal colonies separated by a minimum of 400 m and occurring within an area of 70,000 m^2 (gray area = forest cover, white area = non-forest habitats). (c) Three focal colonies showing in detail the micro-landscape around nest (buffer zone of 200 m); from the left to right: less forest cover (8.7%), middle forest cover (53%) and high forest cover (87%) (c).

Figure 3. Seeds assemblages in areas affect by leaf-cutting ants (i.e. nest mound and foraging areas) and control areas of 15 *Atta opcaciceps* colonies located in different forest cover in the Catimbau National Park, northeast Brazil. Total richness of seeds (a), total abundance of seeds (b), proportion of undamaged seeds richness (c) and proportion of undamaged seed abundance (d).

Figure 4. Effects of forest cover and treatment (nest mound, foraging areas and control areas) on the composition of seed species collected in 15 Atta opaciceps nests located along a gradient of forest cover at the Catimbau National Park, northeastern Brazil. (Treat= Treatment, F.C. = Forest Cover). Sp.2= *Acanthosperma ispido*, Sp.8= *Croton argyrophilloides*, Sp.9= *Croton heliotropii*folius, Sp.10= *Croton nepetaefolius*, Sp.11= *Canavalia brasiliensis*, Sp.12= *Cardiospermum corindum*, Sp.13= *Cenostigma pyramidale*, Sp.14= *Cnidosculus pubescens*, Sp.15= *Cnidosculus quercifolius*, Sp.16= *Commiphora leptophloeos*, Sp.21= *gramínea sp. 1*, Sp.22= gramínea sp. 2, Sp.23= Herissantia sp., Sp.24= Indigofera sufruticosa, Sp.25= *Ipomea* sp.1, Sp.26= *Ipomea* sp.2, Sp.27= *Jatropha ribifolia*, Sp.28= *Jatropha molissima*, Sp.29= *Jatropha mutabilis*, Sp.31= *Manihot cartiginensis*, Sp.32= *Marrenia aegyptea*, Sp.34= *Physostemon* sp., Sp.37= *Portulaca mucronata*, Sp.38= *Pytirocarpa moniliformis*, Sp.39= *Senna obtusifolia*, Sp.40= *Sida* sp., Sp.41= *Solanum* sp., Sp.42= *Syagrus coronate*, Sp.43= *Tragus* sp., Sp.44= *Vigna* sp., Sp.47= *Ziziphus joazeiro*.

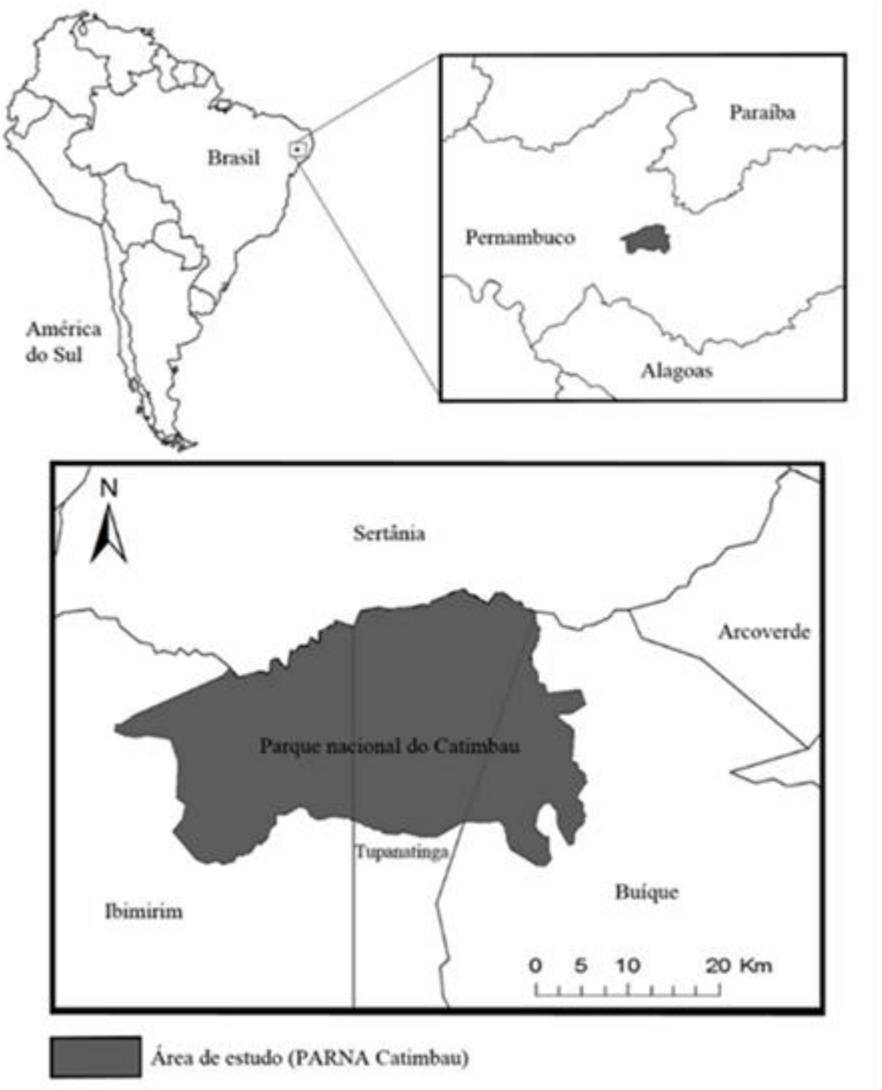

Brasil
América do Sul
Paraíba
Pernambuco
Alagoas
N
Sertânia
Arcoverde
Parque nacional do Catimbau
Tupanatinga
Buíque
Ibimirim
0 5 10 20 Km
Área de estudo (PARNA Catimbau)

Figure 1

Figure 2

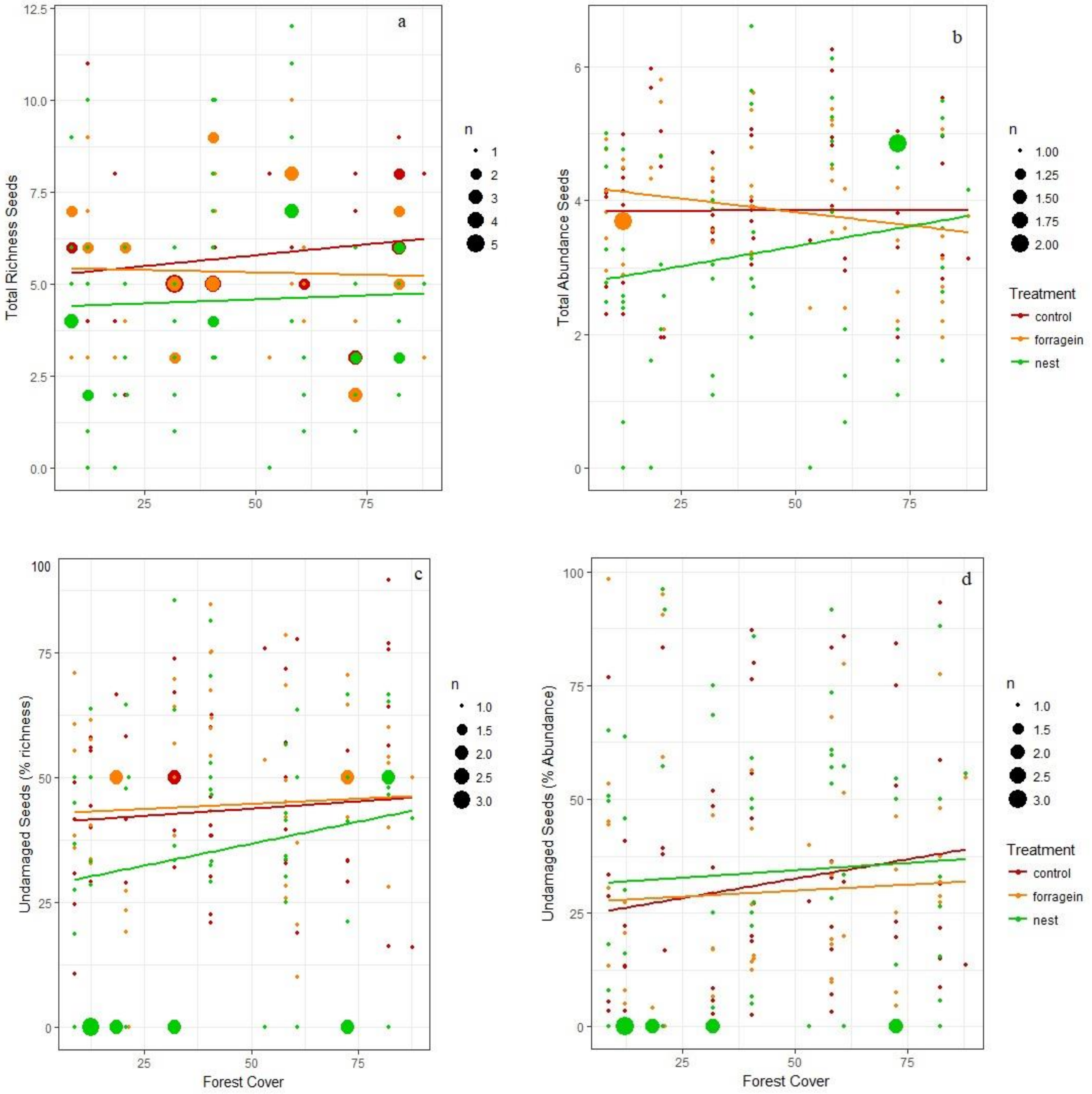
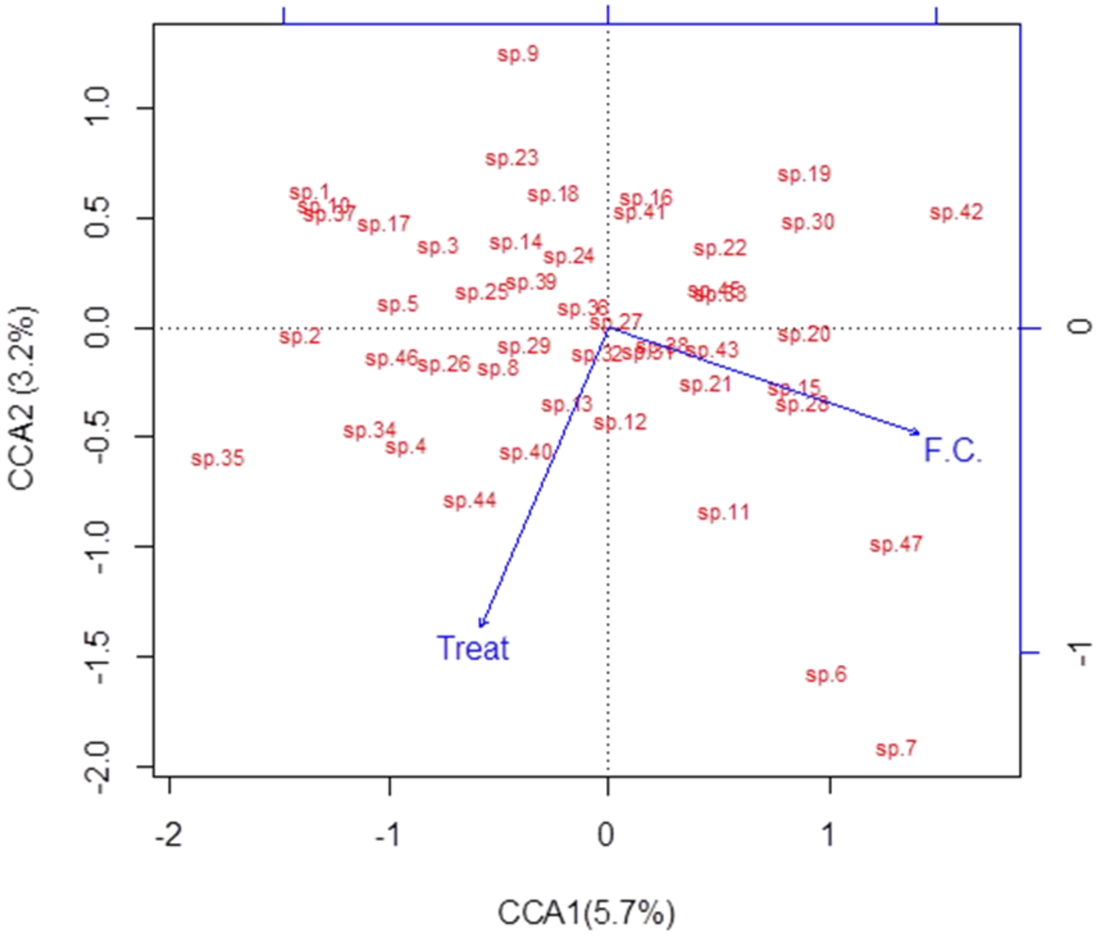

a
b
c
d
Total Richness Seeds
12.5
10.0
7.5
5.0
2.5
0.0
Total Abundance Seeds
6
4
2
0
Undamaged Seeds (% richness)
Undamaged Seeds (% Abundance)
100
75
50
25
0
Forest Cover
Forest Cover
n
1
2
3
4
5
1.00
1.25
1.50
1.75
2.00
1.0
1.5
2.0
2.5
3.0
Treatment
control
forragein
nest

Figure 3


sp.9
sp.23
sp.19
sp.1
sp.10
sp.37
sp.17
sp.18
sp.16
sp.41
sp.30
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sp.5
sp.36
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sp.2
sp.20
sp.29
sp.46
sp.26
sp.8
sp.32
sp.38
sp.31
sp.43
sp.21
sp.15
sp.28
sp.13
sp.12
sp.34
sp.4
sp.40
sp.35
F.C.
sp.44
sp.11
sp.47
Treat
sp.6
sp.7
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
CCA2 (3.2%)
-2
-1
0
1
CCA1(5.7%)
0
-1

Figure 4

4 INFLUENCE OF THE LEAF-CUTTING ANTS *ATTA OPACICEPS* ON CAATINGA REGENERATION DYNAMICS

Manuscrito a ser submetido para o jornal *BIOTROPICA*

Influence of the leaf-cutting ants *Atta opaciceps* on Caatinga regeneration dynamics

Clarissa M. Knoechelmann[1,2], Felipe F. S. Siqueira[1,2], Rainer Wirth[3], Inara R. Leal[4,*]

[1]Programa de Pós-Graduação em Biologia Vegetal, Universidade Federal de Pernambuco, Av. Prof. Moraes Rego s/n, Cidade Universitária, 50670-901, Recife, PE, Brazil

[2]Faculdade de Ciências Biológicas, Universidade Federal do Sul e Sudeste do Pará - Folha 31, Quadra 07, Lote Especial, s/n. Bairro: Nova Marabá - Marabá/PA Brasil - CEP 68507-590

[3]Plant Ecology and Systematics, University of Kaiserslautern, PO Box 3049, 67663, Kaiserslautern, Germany

[4]Departamento de Botânica, Universidade Federal de Pernambuco, Av. Prof. Moraes Rego s/nº, Cidade Universitária, 50670-901, Recife, PE, Brazil

*Author for correspondence: irleal@ufpe.

Abstract

Leaf cutting ants (LCA) of the genus *Atta* are a prime example of a disturbance adapted organism. In addition to the hyper-abundance, individual colonies increase herbivory rate in disturbed areas and thus may affect early-regenerating stands in human-modified landscapes. Here we investigate the effect of the LCA *Atta opaciceps* on regenerating plant assemblage in Caatinga dry forest. Our study encompassed 15 *Atta opaciceps* colonies located in micro-landscapes with a gradient of forest cover from 8.7% to 87.8%, where we monitored regenerating individuals (seedling and saplings of woody plants and herbs) bimonthly along a year in nest mounds, foraging areas and control areas. We recorded 3,024 regenerating plant individuals, distributed among 58 species from 23 families. Herbs represented 82.2% of the total of individuals and woody plant 17.8%. Species richness of the whole regenerating plant assemblage and of herb assemblages increased along forest cover gradient for nests, foraging areas and control areas, but without difference between these treatments. The total abundance of regenerating assemblage was higher in control areas followed by foraging areas and nests and this pattern occurred for both woody plants and herbs. Forest cover did not affect total abundance of regenerating assemblages as well as abundance of woody plants and herbs. Species composition of regenerating assemblages was different between treatment and forest cover. These results together indicate that LCA is able to negatively affect regenerating plant assemblages in areas of Caatinga and increasing forest cover does not influence the interaction between LCA and seedlings and saplings. As LCA proliferate in human modified landscapes, they may prevent plant regeneration of disturbed areas.

Key words: forest cover, foraging activity, plant recruitment, seasonally dry tropical forest.

INTRODUCTION

HABITAT LOSS ARE THE PRIMARY DRIVERS OF BIODIVERSITY DECLINE GLOBALLY (Pereira et al. 2010). In the last decades, a myriad of changes triggered by habitat loss has been reported, particularly in tropical forests, ranging from population (e.g. decreasing in the population number and size of specialist groups parallel to increasing in generalists groups, Tabarelli *et al.* 2012) to community (e.g. loss of taxonomic, phylogenetic and functional diversity, Santos *et* *al.* 2008, 2010) and ecosystem-level (e.g. changes in nutrient stocks and cycling, Paula *et al.* 2011). This is especially true in seasonally dry tropical forests (hereafter dry forest), one of the most endangered ecosystems in the world due to massive deforestation (Miles *et al*. 2006, Stoner and Sánchez-Azofeifa 2009). But in addition to habitat loss, dry forests are home of dense and low-incoming human populations that use natural resources for their livelihood and increase the degradation of remaining habitat (Murphy and Lugo 1986, Martorell & Peters 2005). This, associated with the marked seasonality, high intra and interannual variability of rainfalls and the weak capacity of recolonization of many tree species (Maass & Burgos 2011) can produce a landscape with permanent secondary vegetation (Ceccon *et al*. 2015) or even lead dry forest to new stable states, such as shrublands or grasslands (Anderson-Teixeira *et al*. 2013).

The Brazilian Caatinga is the largest and most diverse dry forest globally (Silva *et al*. 2017) and is a good example of ecosystem where human activities are a source of forest degradation (Tabarelli *et al.* 2017a). Caatinga is considered one of the most endangered ecosystems in Brazil due to extensive conversion of native vegetation to agriculture fields, and nowadays only 37% of the original habitat remains (Silva and Barbosa, 2017). Moreover, Caatinga is the most populated semi-arid region worldwide and sustains over 28 million people (Silva *et al*. 2017). As a result, remaining vegetation can be described as the combination of old-growth and regenerating forest patches of varying ages and permanently exposed to human chronic disturbances such as firewood collection, exploitation of non-timber forest products, and livestock grazing (Silva *et al*. 2017). Caatinga is also threatened by climate change as the forecast for the region is a reduction in rainfall of 22% and an increase in temperature up to 6°C by 2100 (Magrin *et al*. 2014). Recent studies have reported negative impacts of habitat loss, chronic disturbance and climate change on Caatinga communities of both plants (Ribeiro *et al*. 2015; Rito *et al*. 2017a) and animals (Ribeiro-Neto *et al*. 2016, Oliveira *et al*. 2016; Arnan *et al*. 2018), as well as disruption of plant-animal interaction as seed dispersal and plant protection against herbivores (Leal *et al*. 2014a, 2015; Câmara *et al.* 2018, Oliveira *et al*. 2019). The major process subjacent to these disturbance-driven changes is the replacement of a diverse group of disturbance-sensitive species by a less diverse group of disturbance-adapted (Ribeiro-Neto *et al*. 2016) or 'winner' species (sensu Tabarelli *et al*. 2012).

Leaf cutting ants (LCA) of the genus *Atta* are a prime example of a disturbance-adapted group in the Caatinga (Siqueira *et al*. 2017). LCA species such as *A. laevigata*, *A. opaciceps* and *A. sexdens* benefit from the proliferation of woody pioneers (e.g. Euphorbiaceae species, Rito *et al*. 2017b) and herbaceous plant species, which dominate regenerating forest stands following the abandonment of agricultural fields (i.e. slash-and-burn agriculture), pasture lands and roadside vegetation (Siqueira *et al*. 2017). In fact, colony density along Caatinga vegetation paralleling roads is five-fold higher than sites distant to roads (Siqueira *et al*. 2017), a trend in line with previous findings from tropical rain forests (Dohm *et al*. 2011), Cerrado savannas (Vasconcelos *et al*. 2006) and arid steppe of Patagonia (Farji-Brener1996). Among the factors driving LCA nest density in Caatinga we identified (1) road proximity, (2) vegetation cover, (3) chronic disturbance, and (4) rainfall (Backé 2015, Siqueira *et al*. 2017).

In addition to the hyper-abundance of colonies in human-modified sites, edaphic engineering and intense herbivory in early-regenerating stands reinforce the chance that LCA can affect Caatinga regeneration. LCA may affect seedling recruitment and survival directly through foliage removal, and indirectly via decreasing topsoil fertility and increasing light levels in nest and foraging areas (see reviews in Leal *et al*. 2014b; Farji-Brener & Werenkraut 2015; Tabarelli *et al*. 2017b). The net outcomes of these effects negatively affect plant regeneration, reduce seedling/sapling recruitment of shade-tolerant and disturbance-sensitive species, and alter the dynamics and structure of tree assemblages, especially in edge-affected rainforest patches (Corrêa *et al*. 2010, 2016). For the Caatinga, a recent study indicates that leaf consumption and herbivory rate of *Atta opaciceps* colonies are higher in more disturbed areas and reach levels as high as in rainforest and savanna habitats (Siqueira *et al*. 2018). While both nest density and harvesting rates provide indirect evidence, we still entirely lack empirical information on whether and how this important herbivore/ecosystem engineer drives alterations on Caatinga plant assemblages equivalent to those described for other neotropical environments (Leal *et al*. 2014b).

The general objective of this study was therefore to identify how leaf-cutting ants influence the regenerating plant assemblage of Caatinga vegetation. To assess this, we evaluate the recruitment of seedlings and saplings on *Atta opaciceps* nests, in the respective foraging areas and in areas not affect by ants (i.e. control areas) with colonies located in areas with different cover of arboreal Caatinga. Our working hypothesis is that LCA have a negative effect on regenerating plant assemblage and that this effect increases as the forest cover in Caatinga increases. We thus expect that areas affected by LCA will present (1) lower abundance, (2) lower species richness and (3) different species composition of seedlings and saplings as compared to control areas and (4) these differences will increase across the gradient of forest cover Caatinga.

METHODS

Study area

Our study was conducted in Catimbau National Park (Catimbau NP) (8º 24 '00 "and 8º 36 '35 "- S and 37º 09 '30" and 37º 14'40 "W) located in Pernambuco State, northeastern Brazil (Figure 1). The climate is semi-arid, with annual temperature averaging 23ºC, and mean annual rainfall varying from 480 to 1100 mm per year, concentrated between March and July, but with marked inter-annual variation (Sociedade Nordestina de Ecologia 2002). The predominant soil is quartzite sand occupying about 72.30% of the total area and supporting a relatively open, low-stature vegetation in which Fabaceae, Euphorbiaceae and Myrtaceeae are the dominant families (Sociedade Nordestina de Ecologia 2002; Rito *et al*. 2017a).

Studied species

Atta opaciceps (Borgemeier, 1930) is the most abundant LCA species that occur in Catimbau NP (Figure 2a), achieving a population density of 2.45 colonies/ha (Siqueira *et al.* 2017). It has been recorded from open habitats (e.g. abandoned field crops) to forest patches, but its abundance is positively related to areas with lower forest cover and near roads (Delabie *et a*l. 1997; Siqueira *et al.* 2017). It is endemic to Caatinga, occurring in Piauí, Ceará, Rio Grande do Norte, Pernambuco, Sergipe and Bahia states (Fowler 1993; Ulysséia & Brandão 2013).

Sampling design

Our study encompassed 15 nests of *Atta opaciceps* with micro-landscapes limited by a 200 m-buffer around each nest in an area of approximately 70,000 m² (Figure 2 b). We adopt 200 m buffer size based on *A. opaciceps* foraging area (Siqueira *et al.*, 2018). We choose nests following two main criteria: the existence of foraging activity during the sampling effort and a relative spatial independence, considering non-overlapping of micro-landscapes (at least, 400 m of distance between nests). As explanatory variables for changes on ant behaviour and nest activity, we used percentage of forest cover, associated to acute disturbance, inside each buffer, considering as forest only physiognomy composed by shrubs and tree species in a relative medium-to-high density of individuals (see classes of land cover) (Figure 2c).

Landcover classification

The forest cover in each micro-landscape was calculated using ArcGis 10.1, following a supervised classification of a mosaic of two high resolution RapdyEye scenes (2435123_2012-03-21T133949_RE4_3A-NAC_10955665_148448 and 2435223_2012-03-21T133945_RE4_3A-NAC_10960352_148469) acquired in March 2012 and provided by

Brazilian government (GeoCatálogo - MMA). We conducted image interpretation using the Maximum Likelihood method based on clearly distinguishable land cover classes. Our own experience supported by a sum of 121 reference points distributed along the 14 classes of land cover allowed us to define training samples base on easily distinguishable land cover aspects for land cover validation. Considering different landscape structure in each Rapdeye scene, the classes represented (1) exposed soil; (2) high clay content in exposed soil; (3) open fields irregularly covered by pasture/herbaceous; (4) open fields evenly covered by pasture/herbaceous; (5) fields with sparse trees (tree plantations like and croplands); (6) rocky soil covered by herbaceous; (7) rocky soil densely covered by shrubs and herbaceous; (8) medium density shrub-tree vegetation (low structured continuous forest); (9) high density shrub-tree vegetation (high structured continuous forest); and (10) groups of riparian or non-deciduous species. Besides that, (11) urban areas and pavement, (12) clouds, (13) cloud and topographic shading and (14) water were also considered in classification. The forest cover inside each micro-landscape around focal nests ranged from 8.73% in areas of low cover to 87.84% in areas with high density of vegetation.

Regenerating plant assemblages

For each nest, three sampling areas (i.e. treatments) were established (1) nest mound, (2) foraging area of the respective nest and (3) control area (i.e. 20 m away from the foraging area and then not affect by ants). Foraging areas were established during nocturnal surveys (the time of foraging activity) at the terminal segment of the main trunk trails (Corrêa *et al*. 2010). Trunk trails are relatively cleared paths direct foragers through the littered forest floor to their host plants (Kost *et al*. 2005). Four plots of 1m^2 were randomly included in each of the three treatments, where we verified all regenerating individuals up to 1m high including both woody and herb plant species. We considered woody plants and herbs separately because they have different growth rates and life expectancy, thus LCA effects on their recruitment and survival could be different. Finally, we registered the quantity of individuals for each species for each focal nest. We surveyed regenerating plant assemblage from November 2016 to November 2017, in bimonthly intervals. As Caatinga is very seasonal and we collected regenerating plant along the whole year, we included season in our models, although we are not particularly interested in the effect of seasonally on LCA seed deposition site and predation.

Structure of regenerating plant assemblages

We first calculated sample coverage to evaluate if our survey was satisfactory for all sampling units (i.e. all replicates of the three treatments nests, foraging area and control area) using the coverage estimator recommended by Chao & Shen (2010). Because species richness is very sensitive to variations in the number of singletons and doubletons (Jost 2006), we estimated the species richness for all sampling units using coverage-based extrapolations with the iNEXT software (Hsieh *et al*. 2013). Latter inventoried regenerating plant assemblages were separated in woody and herbs. The species richness was estimated for the whole regenerating plant assemblages, as well as for woody plants and herbs separately in each sampling unit and was calculated using coverage-based extrapolations based on completeness inventory described above.

Data analyses

To compare the total species richness and abundance of regenerating plant assemblages (woody plants + herbs) between treatments, different forest cover and seasons we used generalized linear mixed models (GLMM) with nests as random variable. Additionally, we also used GLMM to compare richness and abundance of woody plants and herbs separately between treatments, different forest cover and seasons with nests as a random variable. We estimated species richness (^{0}D) with coverage-based extrapolations for total species richness, as well as for richness of wood plants and herbs separately. We transformed data which did not obey homoscedastic criteria with log(x+1). Season was included in the models due the potential effects on the response variables. All the GLMMs were performed using the package lme4 version 1.1-7 (Bates *et al*., 2014) in R software (version 3.4.3, 2017).

The effects of forest cover and treatment on the species composition of regenerating plant assemblage were evaluated using canonical correspondence analyses (CCA). For these analyses, we considered the abundance of each species. We performed a randomization test (10000 aleatorizations) to obtain the statistical significance of forest cover and treatment as explanatory variables (Legendre *et al*. 2011). We used vegan version 2.3 package (Oksanen *et al*. 2015) to perform a CCA in R (version 3.4.3, 2017).

RESULTS

We recorded 3024 regenerating plant individuals, distributed among 58 species from 23 families. The most species rich families were Euphorbiaceae (10 species), Rubiaceae (6 species) and Fabaceae (5 species). Herbs represented 82.2% of the total of individuals and woody plants 17.8%. The total richness of plant individuals varied from 1-14 (3.20 ± 2.57, mean ± SD) in nests, 0-10 (3.62 ± 2.45) in foraging areas and 1-14 (4.10 ± 3.35) in control areas. The total abundance of plant individual varied from 0-61 (10.86 ± 12.52) in nests, 0-73 (14.49 ± 15.45) in foraging areas and 1-263 (25.89 ± 40.84) in control areas.

Species richness of the whole regenerating plant assemblage increased along the forest cover gradient for nests, foraging areas and control areas, but without difference between these treatments (Figure 3a, Table 1). Total species richness was not affected by either interactions between forest cover and season or between forest cover and treatment (Figure 3a, Table 1). Richness of woody plants was higher during rainy season and richness of herbs decreased with increasing forest cover (Table 1), but they were not affected by either treatment or the interaction between forest cover and treatment and forest cover and season (Figure 3c and e, Table 1).

Total abundance of regenerating assemblage varied according to the treatment, with more plant individuals in the control areas followed by foraging areas and nests, although without significant differences between these last two treatments (Figure 3b, Table 1). The same pattern was registered for woody and herb assemblages separately (Figure 3d and f, Table 1). Moreover, total abundance and abundance of woody plants and herbs were higher during rainy season (Figure 3b, d and f, Table 1). Forest cover and the interactions between forest cover and season and between forest cover and treatment were not significant for the total abundance and for the abundance of woody plants and herbs (Figure 3b, d and f, Table 1).

In relation to species composition of regenerating plant assemblages, the first axis of the CCA explained 7.1% of the variation (Figure 4). Species composition varied significantly with forest cover and treatment (Table 2, Figure 4). *Melocactus bahiensis* was associated with higher forest cover, whereas *Zornia grandiflora* were associated with low forest cover (Figure 4). *Mytracarpus* sp. was associated with nest, *Medusantha martiusdi* with foraging area and *Diodella grandiflora* with control area (Figure 4).

DISCUSSION

In this study we investigated the effect of the LCA *Atta opaciceps* on regenerating plant assemblages (seedlings + saplings) on nests, their respective foraging areas and in areas not affect by ants (i.e. control areas) along a gradient of forest cover in Caatinga. Our results indicate that LCA is able to negatively affect recruitment of plants in terms of abundance, but this effect is not translated to species richness. More specifically, nest mounds were cover by less seedlings and saplings than foraging and control areas, and this patter occur for both woody and herbaceous plants. In addition, areas affected by ants present a different species composition than control areas, reinforcing the idea that LCA can change plant recruitment in nest and foraging areas. The increasing in forest cover lead to an increasing in species richness of regenerating assemblages but without influence on the interaction between LCA and regenerating assemblages.

Our results on reduced abundance of regenerating plant assemblage in areas affected by LCA in Caatinga dry forest are in line with previous studies from rainforest (Garrettson *et al*. 1998; Hull-Sanders & Howard 2003; Corrêa *et al*. 2010, 2016; Meyer *et al*. 2011) and savanna ecosystems (Costa *et al*. 2018). LCA nests and close adjacencies are low-density and strongly contrast with the surrounding forest (Correa *et al*. 2010; Meyer *et al*. 2011). However, previous studies in rainforests and savannas demonstrated that LCA nests area also impoverished in species richness (Corrêa *et al*. 2010, Costa *et al*. 2018), while in Patagonian steps nest areas showed similar plant richness than adjacent non-nest soils (Farji- Brener & Werenkraut, 2017) as we demonstrated here. Finally, most of studies addressing species composition of regenerating plant assemblage in nest affected areas compared to control areas have demonstrated a strong reorganization of assemblages mediated by LCA (Corrêa *et al.* 2010, 2016; Bieber *et al.* 2011; Silva *et al.* 2012, Costa *et al.* 2018), while we observed a slightly difference in species composition between areas affected by LCA and control areas.

The reduced abundance of seedlings and saplings in LCA nest mounds observed here is probably due to the disturbance caused by nest construction and maintenance. The colossal nests of *Atta* colonies are composed of several hundred up to 8000 subterraneous interconnected chambers reaching to eight meters underground and large mounds of soil above their surface reaching up to 250 m^2 in area (Leal *et al.* 2014b). For the construction and maintenance of these structures LCA move large quantities of soil to the nest surface (more than 20 m^3 or 40 tons of soil; see Farji-Brener & Illes 2000 for a revision). LCA also reduce the litter cover (bare-soiled nest clearings), thus depressing nutrient availability on the nest areas and in the surrounding forest as documented for *Atta cephalotes* in Atlantic forest (Meyer *et al.* 2013). All this bioturbation can reduce seed germination rate on nest area and its vicinity (Corrêa *et al*. 2010). In addition, recruited seedlings may be buried or experience defoliation while leaf litter is removed during nest cleaning activities, as documented for *Atta cephalotes* by Corrêa et al. (2010) and Meyer et al. (2011a, b, 2013).

The reduced abundance of seedlings and saplings in foraging areas compared to areas not affected by LCA is related to LCA foraging activity. It is not novelty that LCA are able to alter forest structure and light availability in rainforests, since foliage removal reduces light interception allowing increased light penetration through the vegetation (Wirth et al. 2003; Corrêa et al. 2016). However, Caatinga vegetation present a lower stature and reduced canopy cover compared to rainforest (Oliveira *et al*. 2013) and the effect of LCA might be related solely to their herbivory. LCA are among the most polyphagous and voracious herbivorous insects, cutting up to 15 percent of the standing leaf crop (Wirth *et al*. 2003; Urbas *et al*. 2007) and up to 50% of the species of a given forest flora (Vasconcelos & Fowler 1990; Wirth *et al*. 2003) in their colony's territory each year. In the case of Caatinga, we recorded even higher herbivory rate, around 30% (Siqueira *et al*. 2018). However, our results indicate that LCA seems to collect plant species according to their availability, do not concentrating their foraging effort in some specific species/group of species and do not causing a reduction in species richness as observed in rainforest (e.g. Corrêa *et al*. 2010, 2016).

As in rainforests and savannas, LCA profit of human disturbance in Caatinga vegetation increasing colony density near to roads, in areas with low forest cover and with higher chronic anthropogenic disturbance (Siqueira *et al*. 2017; Tabarelli *et al.* 2017 b). Herbivory rate of colonies also increases in more disturbed areas due to the proliferation of palatable plants which dominate regenerating forest stands following the abandonment of agricultural fields (Siqueira *et al*. 2017; Leal *et al.* 2017; Tabarelli *et al.* 2017 b). That is the reason why we expected that the negative effect of LCA on plant recruitment would increase in areas with higher forest cover, where there would exist higher density and species richness than in nest affected areas. However, we did not observe any influence of increasing forest cover on the effects of LCA over plant recruitment. This could occur because plant recruitment in Caatinga depends more strongly on resprout than on true seedlings, as observed for other regenerating area of dry forests (Mostacedo *et al.*, 2009). In fact, it was recently recorded a high proportion of resprout among recruit individuals from different species in areas of Caatinga (Vanderlei *et al.*, unpublished data). Resprouting has been reported to be triggered by extensive biomass loss at the individual level (i.e. disturbance) such as those promoted by fire, windstorms, forest clearance or herbivory (Kammesheidt, 1999, Franklin *et al.* 2010, McDonald *et al*. 2010). Thus, the effect of LCA herbivory on young individuals in Caatinga vegetation seems to be less important than we think before, at least for a considerable part of the regenerating assemblage, which is able to resprouts. Future studies addressing the effects of LCA on regenerating plant assemblages should identify if young individuals come from seeds or are resprouts in order to verify if and how these herbivores can influence regeneration dynamic as observed for other less dry/seasonal ecosystems.

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Table 1. Results from general linear mixed model (GLMM) to compare regenerating plant assemblages in terms of total richness and abundance and richness and abundance of woody plants and herbs between treatments (nests, foraging areas and control areas) of 15 *Atta opaciceps* colonies located along a gradient of forest cover e during both seasons (dry and wet) in Caatinga areas at the Catimbau National Park, northeastern Brazil. R^2 represents the coefficient of determination of the whole statistical model. Significant values are in bold.

Response Variable	Explanatory variables	d.f.	F	P	R2
Total richness	Treatment	2	1.7925	0.408106	0.22
	Forest Cover	1	7.9398	**0.004836**	
	Forest Cover * Treatment	2	0.9187	0.631700	
	Season	1	15.5630	**7.98 e^{-}05**	
	Season * Forest Cover	1	2.3773	0.123107	
Richness of wood plant	Treatment	2	3.0417	0.2185	0.10
	Forest Cover	1	1.4179	0.2337	
	Forest Cover * Treatment	2	0.6300	0.7298	
	Season	1	5.9762	**0.0145**	
	Season * Forest Cover	1	0.0010	0.9752	
Richness of herbs	Treatment	2	1.6202	0.44482	0.99
	Forest Cover	1	4.0068	**0.04532**	

	Forest Cover * Treatment	2	3.5020	0.17630	
	Season	1	3.6013	0.06	
	Season * Forest Cover		0.8103	0.36802	
Total abundance	Treatment	2	23.3504	**8.502 e $^{-}$ 06**	0.48
	Forest Cover	1	0.1548	0.6940	
	Forest Cover * Treatment	2	3.5445	0.1700	
	Season	1	22.9059	**1.701 e^{-} 06**	
	Season * Forest Cover	1	0.0214	0.8838	
Abundance of wood plant	Treatment	2	9.4729	**0.008770**	
	Forest Cover	1	0.7560	0.384571	
	Forest Cover * Treatment	2	0.9966	0.607563	
	Season	1	10.7106	**0.001065**	
	Season * Forest Cover	1	0.0475	0.827530	
Abundance of herbs	Treatment	2	12.2597	**0.002177**	
	Forest Cover	1	0.0930	0.760375	
	Forest Cover * Treatment	2	5.3760	0.068016	
	Season	1	10.2882	**0.001339**	

	Season * Forest Cover	1	0.0016	0.967808

Table 2. Results of the canonical correspondence analysis (CCA) to compare the species composition of regenerating plant assemblages between treatment (nests, foraging areas and control areas) of 15 *Atta opaciceps* colonies located along a gradient of forest cover e during both seasons (dry and wet) in Caatinga areas at the Catimbau National Park, northeastern Brazil. Significant values are in bold.

Source of variation	DF	χ^2	F	P
Axis				
CCA 1	1	0.3314	3.1173	**0.009**
CCA 2	1	0.1633	1.5361	0.285
Variables				
Forest Cover	1	0.2639	2.4825	**0.025**
Treatment	1	0.2308	2.1709	**0.049**
Residual	39	4.1461		

Legend for figures

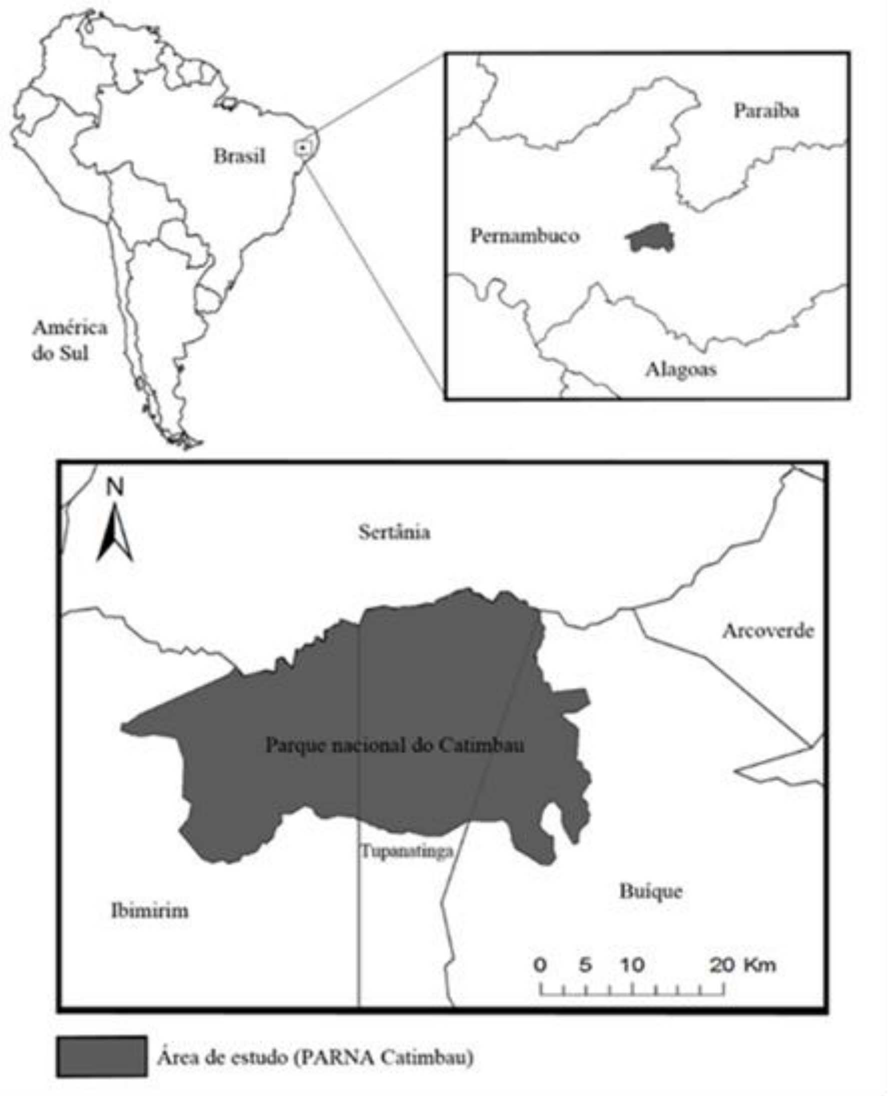
Figure 1. Location of the Catimbau National Park, Pernambuco state, northeastern Brazil.

Figure 2. Colonies of *Atta opaciceps* located at the Catimbau National Park, northeastern Brazil. (a) Aerial view of a colony at the Fazenda Brejo, Catimbau National Park, northeastern Brazil. (b) Fifteen focal colonies separated by a minimum of 400 m and occurring within an area of 70,000 m^2 (gray area = forest cover, white area = non-forest habitats). (c) Three focal colonies showing in detail the micro-landscape around nest (buffer zone of 200 m); from the left to right: less forest cover (8.7%), middle forest cover (53%) and high forest cover (87%) (c).

Figure 3. Regenerating plant assemblages in areas affect by leaf-cutting ants (i.e. nest mound and foraging areas) and control areas of 15 *Atta opcaciceps* colonies located in different forest cover at the Catimbau National Park, northeastern Brazil. Total species richness of regenerating plant assemblage (a), total abundance of regenerating plant assemblage (b), richness of woody plants (c) abundance of woody plants (d), richness of herb plants (e) and abundance of herb plants (f).

Figure 4. Effects of forest cover and treatment (nest mound, foraging areas and control areas) on the species composition of regenerating plant assemblages collected in 15 *Atta opaciceps* nests located along a gradient of forest cover at the Catimbau National Park, northeastern Brazil. (Treat= Treatment, F.C.= Forest Cover) Sp.1= *Acanthospermum* sp., Sp.2= *Aeschinomne viscidula*, Sp.3=*Allophylus quercifolius*, Sp.4= *Athenantera tenella*, Sp.5= *Amaranthus viridis*, Sp.6= *Ayenia eresta*, Sp.7= *Blainvillea* sp. , Sp.8=*Boerhavia diffusa*, Sp.9= *Borreria* sp., Sp.10= *Cenchrus ciliaris*, Sp.11= *Camecrista* sp., Sp.12= *Clhoris* sp. , Sp.13= *Cnidosculus pubescens*, Sp.14= *Cnidosculus quercifolius*, Sp.15= *Commelina obliqua*, Sp.16= *Croton argirofilus*, Sp.17= *Croton blanchetianus*, Sp.18= *Croton* sp., Sp.19= *Croton heliotropiifolius*, Sp.20= *Croton nepeteafolius*, Sp.21= *Croton tricolor*, Sp.22= *Diodella gardineri*, Sp.23= *Diodella grandiflora*, Sp.24= *Diodella teres*, Sp.25= *Evolvulus* sp., Sp.26 *Froelichia* sp., Sp.27= gramínea, Sp.28= *Herissantia crispa*, Sp.29= *Heliotropium angiospermum*, Sp.30= *Indigofera sufruticosa*, Sp.31= *Jatropha molissima*, Sp.32= *Jatropha mutabilis*, Sp.33= *Jatropha ribifolia*, Sp.34= *Lepidoploa chalypaea*, Sp.35= *Lippia gracilis*, Sp.36= *Medusantha martiusdi*, Sp.37= *Melocactus bahiensis*, Sp.38= *Merrenia aegyptea*, Sp.39= *Microtia panicullata*, Sp.40= *Mollugo* sp., Sp.41= *Mytracarpus* sp., Sp.42= *Neoglaziovia variegata*, Sp.43= *Pavonia blanchetiana*, Sp.44= *Physostemon rotundifolium*, Sp.45= *Piriqueta* sp.

Sp.46= *Portullaca* sp., Sp.47= *Richardia* sp., Sp.48= *Senegalia* sp., Sp.49 *Sida* sp., Sp.50= *Solanum rhytidoandrum*, Sp.51= *Tacinga inamoena*, Sp.52= *Tacinga palmadora*, Sp.53= *Talinum* sp., Sp.54= *Tarenaya* sp., Sp.55= *Tragus berterunianus*, Sp.56= *Turnera* sp., Sp.57= *Uroclhoa* sp., Sp.58= *Zornia grandiflora.*


Brasil
América do Sul
Paraíba
Pernambuco
Alagoas
N
Sertânia
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Parque nacional do Catimbau
Tupanatinga
Buíque
Ibimirim
0 5 10 20 Km
Área de estudo (PARNA Catimbau)

Figure 1

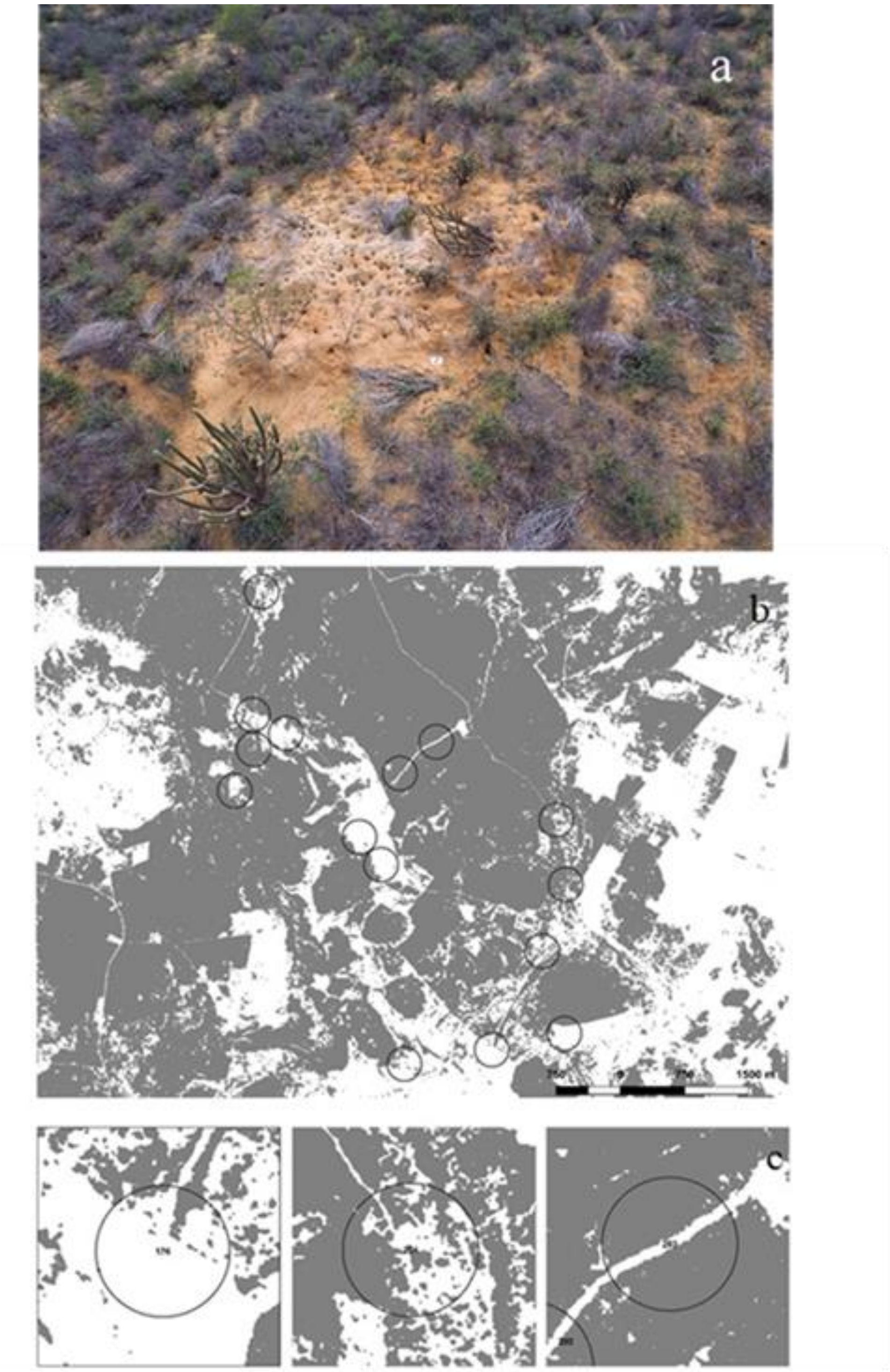


Figure 2

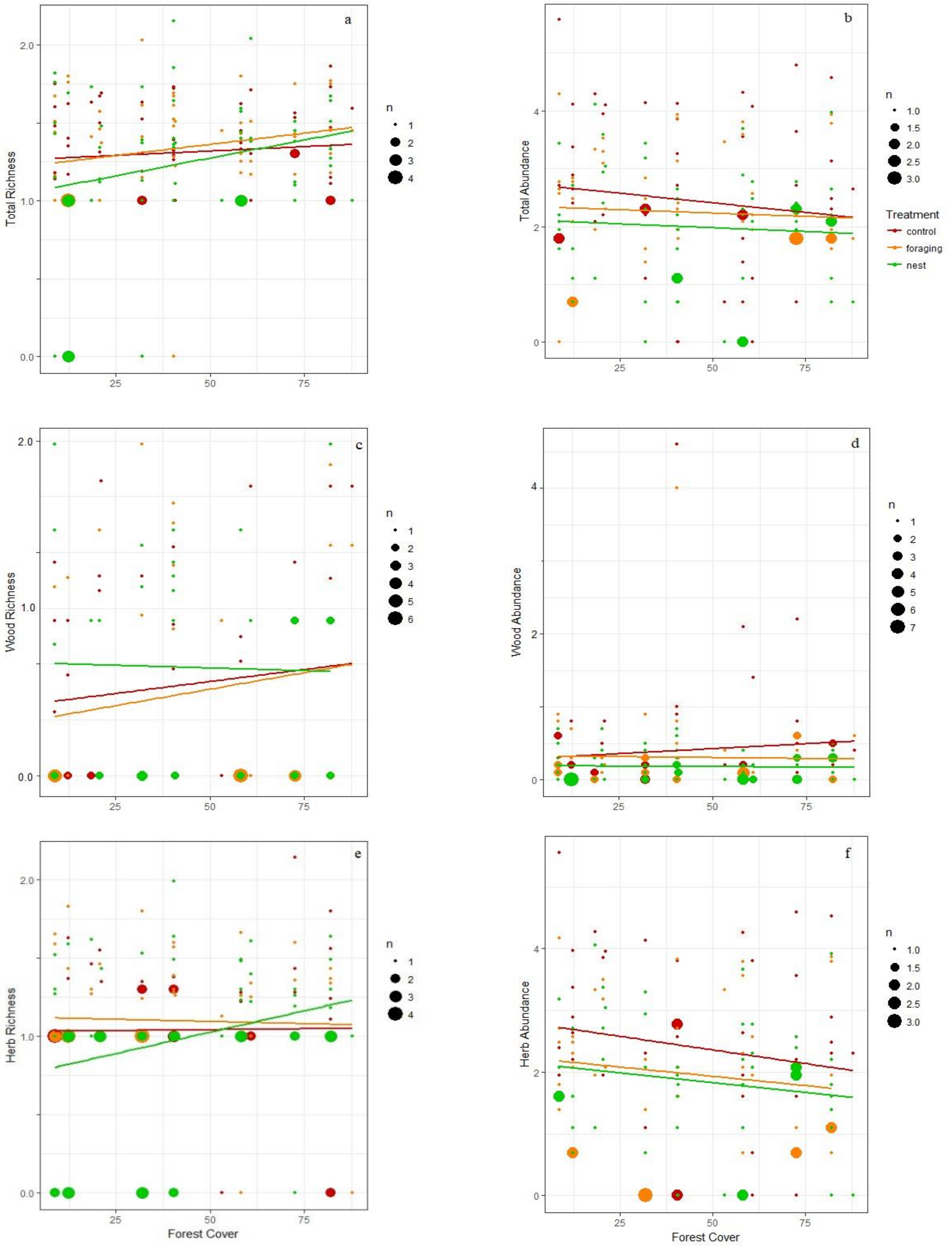
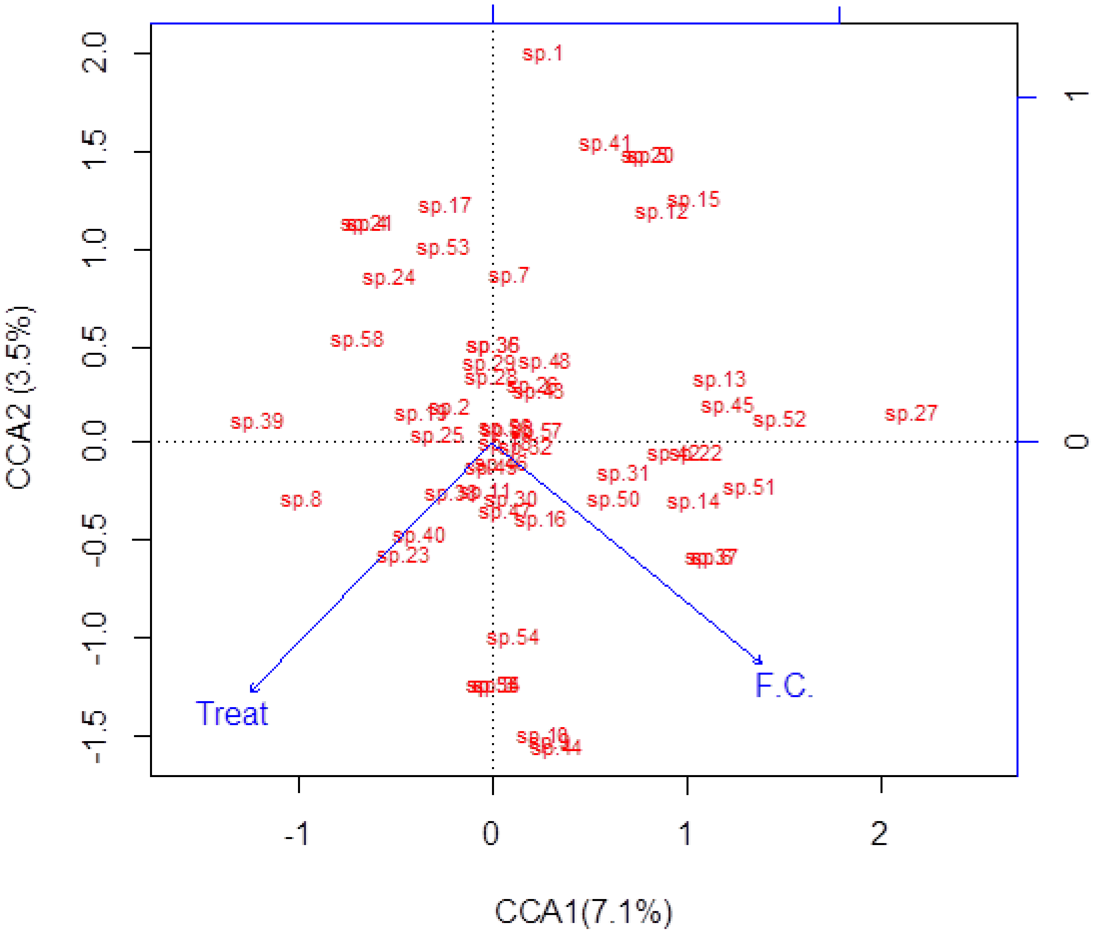

a
b
c
d
e
f
Total Richness
Total Abundance
Wood Richness
Wood Abundance
Herb Richness
Herb Abundance
Forest Cover
Forest Cover
0.0
1.0
2.0
0
2
4
25
50
75
n
1
2
3
4
5
6
7
1.0
1.5
2.0
2.5
3.0
Treatment
control
foraging
nest

Figure 3


sp.1
sp.41
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sp.53
sp.24
sp.7
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sp.36
sp.29
sp.48
sp.28
sp.13
sp.45
sp.52
sp.27
sp.39
sp.2
sp.25
sp.57
sp.31
sp.8
sp.50
sp.14
sp.51
sp.30
sp.16
sp.40
sp.23
sp.54
Treat
F.C.
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
1
0
-1
0
1
2
CCA2 (3.5%)
CCA1(7.1%)

Figure 4

5 CONCLUSÕES

Este estudo traz contribuições sobre o papel da formiga cortadeira *Atta opaciceps* sobre a dinâmica de regeneração de áreas de Caatinga com diferentes coberturas florestal. Como essas formigas coletam uma grande quantidade de material vegetal para o cultivo do fungo simbionte, incluindo sementes, plântulas e indivíduos jovens, era razoável esperar um efeito negativo sobre a regeneração, mas esse tipo de informação era completamente desconhecido até este estudo. Com o aumento da cobertura florestal ao redor dos ninhos deve aumentar a densidade de indivíduos e a riqueza de espécies da comunidade de plantas, também seria razoável esperar que a diferença entre as áreas afetadas pelas formigas e as áreas controle aumentassem. Depois do monitoramento do banco de sementes e do recrutamento de plântulas e indivíduos jovens em ninhos, áreas de forrageamento e áreas não afetadas pelas formigas cortadeiras podemos confirmar esse efeito negativo sobre sementes e regenerantes, mas não verificamos um papel importante da cobertura florestal mediando a interação das formigas cortadeiras com os regenerantes. Entre os resultados obtidos, destaco:

- As formigas cortadeiras diminuem a deposição e aumentam a predação de sementes nas áreas afetadas pelas colônias (i.e. ninhos e áreas de forrageamento), dificultando o processo de regeneração.
- Apesar de menor número de sementes nos ninhos, estas áreas também apresentam menor riqueza de sementes sem danos de herbívoros, o que evidencia que são as próprias formigas cortadeiras as predadoras de sementes.
- As formigas cortadeiras também influenciam negativamente o recrutamento de plântulas e indivíduos jovens, pois ninhos e áreas de forrageamento apresentam menor densidade de indivíduos que áreas não afetadas pelas formigas.
- O papel das formigas cortadeiras como 'sumidouro' de sementes e herbívoros de regenerantes deve ser potencializado em manchas perturbadas da Caatinga, devido a maior densidade de colônias, dificultando a regeneração da vegetação.
- O incremento da cobertura florestal ao redor das colônias não aumentou a diferença entre o número de sementes e de regenerantes presentes nas áreas afetadas pelas formigas cortadeiras e em áreas controle. Pelo menos para o recrutamento de plântulas, isso pode ser devido à alta proporção da flora da Caatinga que é capaz de rebrotar, uma vez que rebrotas são mais resistentes à herbivoria.

- Futuros estudos sobre os efeitos das formigas cortadeiras na regeneração de assembleias de plantas devem identificar se os indivíduos jovens vêm de sementes ou são rebrotas para verificar como esse herbívoro pode influenciar a dinâmica de regeneração da Caatinga.

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