UNIVERSIDADE FEDERAL DE PERNAMBUCO
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HAYMÉE NASCIMENTO DE ALENCAR

INFLUÊNCIA DAS FORMIGAS CORTADEIRAS NO PROCESSO DE REGENERAÇÃO VEGETAL NA CAATINGA

Recife, 2023

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RESUMO

Mudanças no uso da terra devido a atividades antrópicas são as principais causas de perda de biodiversidade, funções e serviços ecossistêmicos, levando a degradação dos ecossistemas naturais. Neste cenário de perturbação antrópica, o processo de regeneração pode recuperar não apenas a biodiversidade, mas funções serviços ecossistêmicos associados, o que desperta o interesse em estudar processos que a influenciem, como as interações entre solo, plantas e animais como as formigas cortadeiras. As formigas cortadeiras são um dos organismos que proliferam em áreas degradadas e seus efeitos na regeneração podem ser causados tanto pela coleta da vegetação como pelas alterações nas propriedades do solo. Diante disso, o objetivo geral deste estudo foi verificar a influência das formigas cortadeiras no processo de regeneração na Caatinga, levando em conta seus efeitos sobre os atributos químicos e físicos do solo e sobre a produtividade vegetal acima do solo e sobrevivência de plantas, três importantes drivers da regeneração. O estudo foi desenvolvido no Parque Nacional do Catimbau, Buíque, PE, em áreas com históricos de uso do solo para agricultura e pecuária, e áreas sem histórico de perturbação antrópica aguda. Em cada área foram coletadas amostras de solo de três ninhos das formigas cortadeiras *Atta opaciceps* e três amostras de solo em locais sem efeito do ninho de formigas cortadeiras (i.e., controle) para analisar os atributos químicos e físicos dos solos. Para quantificar o crescimento vegetal acima do solo estabelecemos 10 parcelas de 3m x 3m em cada um dos tipos de uso da terra, totalizando 30 parcelas. Nestas parcelas, transplantamos 10 plantas jovens produzidas em casa de vegetação de três espécies arbóreas nativas da família Fabaceae (i.e., *Cenostigma pyramidale, Cenostigma microphyllum e Pityrocapra moliniformis*), totalizando 30 indivíduos por parcelas. Posteriormente, realizamos o monitoramos dos indivíduos vegetais durante um ano, utilizando atributos de crescimento vegetal acima do solo como comprimento e espessura do caule e número de folhas e ramos como medidas de produtividade e contabilizamos a sobrevivência das plantas. Nossos resultados demonstram que os solos de ninhos de *A. opaciceps* apresentou menor compactação do solo e maior capacidade de retenção de água e ponto de murcha permanente, tornando o solo sob efeito do ninho mais úmido e heterogêneo. Quanto aos atributos químicos, vimos que o solo do ninho aumentou a concentração de nutrientes como magnésio e sódio e apresentam um pH pouco ácido. Em relação a sobrevivência das plantas e os atributos de crescimento vegetal acima do solo, nós não vimos nenhuma diferença nos tratamentos do solo e nas áreas em regeneração e na área de floresta madura (i.e., controle). Esses resultados em conjunto indicam que os solos sob influência das formigas cortadeira têm melhor qualidade, sobretudo dos atributos físicos, todavia não contribuem com crescimento vegetal acima do solo e não promovem maior sobrevivência de plantas.

Palavras-chave: Degradações ambientais; Formigas cortadeiras; Florestas tropicais sazonalmente secas; Produtividade; Perturbações antrópicas; Qualidade do solo.

ABSTRACT

Changes in land use due to human activities are the main causes of loss of biodiversity, ecosystem functions and services, leading to the degradation of natural ecosystems. In this scenario of anthropogenic disturbance, the regeneration process can recover not only biodiversity, but associated ecosystem service functions, which arouses interest in studying processes that influence it, such as interactions between soil, plants and animals such as leaf-cutting ants. Leaf-cutting ants are one of the organisms that proliferate in degraded areas and their effects on regeneration can be caused both by the collection of vegetation and by changes in soil properties. Therefore, the general objective of this study was to verify the influence of leaf-cutting ants on the regeneration process in the Caatinga, taking into account their effects on the chemical and physical attributes of the soil and on above-ground plant productivity and plant survival, three important drivers of regeneration. The study was carried out in the Catimbau National Park, Buíque, PE, in areas with a history of land use for agriculture and livestock, and areas without a history of acute anthropogenic disturbance. In each area, soil samples were collected from three nests of the leaf-cutting ants *Atta opaciceps* and three soil samples from sites with no effect on the leaf-cutting ant nest (i.e., control) to analyze the chemical and physical attributes of the soils. To quantify above-ground plant growth, we established 10 plots of 3m x 3m in each of the land use types, totaling 30 plots. In these plots, we transplanted 10 young plants produced in a greenhouse of three native tree species from the Fabaceae family (i.e., *Cenostigma pyramidale*, *Cenostigma microphyllum* and *Pityrocapra moliniformis*), totaling 30 individuals per plot. Subsequently, we monitored plant individuals for a year, using above-ground plant growth attributes such as stem length and thickness and number of leaves and branches as productivity measures and counted plant survival. Our results demonstrate that the soils of *A. opaciceps* nests showed less soil compaction and greater water retention capacity and permanent wilting point, making the soil under the effect of the nest more humid and heterogeneous. As for chemical attributes, we saw that the nest soil had an increased concentration of nutrients such as magnesium and sodium and had a slightly acidic pH. Regarding plant survival and above-ground plant growth attributes, we did not see any differences in soil treatments and in the regenerating areas and in the mature forest area (i.e., control). These results together indicate that soils under the influence of leafcutter ants have better quality, especially in terms of physical attributes, however they do not contribute to plant growth above the ground and do not promote greater plant survival.

Keywords: Environmental degradations; Leaf-cutting ants; Seasonally dry tropical forests; Productivity; Anthropogenic disturbances; Soil quality.

LISTA DE FIGURAS

CAPÍTULO 1 - EFEITOS DAS FORMIGAS CORTADORES NA QUALIDADE DO SOLO DE ÁREAS EM REGENERAÇÃO NA FLORESTA SECA DA CAATINGA

LISTA DE FIGURAS

CAPÍTULO II - INFLUÊNCIA DE FORMIGAS CORTADORAS NA PRODUTIVIDADE DE MUDAS EM ÁREAS COM DIFERENTES HISTÓRICOS DE USO DO SOLO NA CAATINGA

LISTA DE TABELAS

CAPÍTULO 1 - EFEITOS DAS FORMIGAS CORTADORES NA QUALIDADE DO SOLO DE ÁREAS EM REGENERAÇÃO NA FLORESTA SECA DA CAATINGA

LISTA DE TABELAS

CAPÍTULO II - INFLUÊNCIA DE FORMIGAS CORTADORAS NA PRODUTIVIDADE DE MUDAS EM ÁREAS COM DIFERENTES HISTÓRICOS DE USO DO SOLO NA CAATINGA

SUMÁRIO

1 INTRODUÇÃO

As florestas tropicais são responsáveis por fornecer uma ampla gama de funções e serviços ecossistêmicos, no entanto estão sendo convertidas em campos de agricultura e pastagens para criação de animais domésticos (BATTISTI; POETA; FANELLI, 2016; FAO, 2019; TABARELLI, 2010). Um dos ecossistemas mais degradado em função dessas perturbações antrópicas são as florestas secas, que são mais alteradas por atividades antrópicas dada seu clima favorável e vegetação de baixo porte adequada para a pastagem por animais domésticos (ANTONGIOVANNI; VENTICINQUE; FONSECA, 2018; D'ODORICO et al., 2013; FAO, 2019, 2020; TABARELLI et al., 2017). Como resultado, grande parte de suas áreas encontram-se atualmente em processo de regeneração (CHAZDON, 2012; LEBRIJA-TREJOS et al., 2010). E alguns dos remanescentes florestais ainda experimentam perturbações antrópicas crônicas como a coleta de lenha e de produtos florestais não madeireiros (i.e., sementes, óleos), a criação de animais domésticos de forma extensiva e a caça (RIBEIRO et al., 2015). Estas perturbações antrópicas acabam prejudicando ou até mesmo impedindo a dinâmica de regeneração da vegetação desse ecossistema (RIBEIRO et al., 2015), incluindo das interações ecológicas (LEAL; WIRTH; TABARELLI, 2014b; LEAL; ANDERSEN; LEAL, 2015). A continuidade de perturbações antrópicas em áreas em regeneração pode levar a estados alternativos estáveis, tais como a sucessão interrompida, assembleias distorcidas, como aquelas dominadas por arbustos ou por espécies de plantas exóticas, e por último e mais preocupante, a desertificação, que é o estado alternativos mais deletério encontrado em florestas secas (TABARELLI et al., 2022).

Um dos organismos que proliferam em áreas de florestas secas são as formigas cortadeiras (SIQUEIRA et al., 2017). As formigas cortadeiras desempenham grande influência na modificação do ambiente ao seu redor, removendo aproximadamente 17% produção foliar nas suas áreas de forrageamento (URBAS et al., 2007). Além disso, também removem, flores, frutos, sementes e galhos (FALCÃO et al., 2011), podendo influenciar diretamente o destino de sementes (OLIVEIRA et al., 2023a), o recrutamento de plântulas

(KNOECHELMANN et al., 2020) e a reprodução de indivíduos adultos (CÂMARA et al., 2018; OLIVEIRA et al., 2023b), com impactos negativos na regeneração. Por outro lado, há estudos que mostram um efeito positivo e compensatório da herbivoria no fitness da planta gerando um aumento na produção de flores e frutos (COZZOLINO et al., 2015; HASS & LORTIE, 2020; OLIVEIRA et al., 2023). Adicionalmente, as formigas cortadeiras também apresentam efeitos variados na qualidade do solo devido a construção e manutenção dos seus ninhos (Farji-Brener & Werenkraut, 2015;2017; Meyer et al., 2013). Neste processo de formação do ninho, bastante material mineral é colocado na superfície do ninho (FARJI-BRENER; WERENKRAUT, 2015; LEAL, 2014). Esta nova camada de solo, acaba aumentando os teores de minerais e reduzindo a concentração de nutrientes (LEAL, 2014). Por outro lado, algumas espécies de formigas cortadeiras depositam as lixeiras dos seus ninhos externamente, criando ilhas de fertilidade de solo (SIQUEIRA et al; 2018 OLIVEIRA et al., 2023b). Assim, a alteração no solo devido a construção e manutenção do ninho pode gerar impactos positivos e negativos no desempenho das plantas (OLIVEIRA et al., 2023b).Embora já existam alguns padrões descritos para as mudanças observadas na flora devido a ação das formigas cortadeira durante a sucessão secundária (KNOECHELMANN et al., 2020; Oliveira et al. 2023a; SIQUEIRA et al., 2018), ainda não sabemos como interações ecológicas entre os atributos químicos e físicos do solo, manutenção dos ninhos de formiga cortadeira e sobrevivência e crescimento de plântulas estão sendo afetadas pela regeneração vegetal na Caatinga.

Dessa forma, o objetivo deste estudo foi avaliar como as formigas cortadeiras estão alterando a qualidade do solo, produtividade vegetal e sobrevivência de plantas em áreas com diferentes usos do solo na Caatinga. Mais precisamente, nós avaliamos os atributos químicos e físicos dos solos de formigas cortadeira (capítulo 1) e a taxa de crescimento de três espécies arbóreas nativas da família Fabaceae (*Cenostigma pyramidale, Cenostigma microphyllum e Pityrocapra moliniformis*) como proxy de produtividade (capítulo 2) em áreas com diferentes usos do solo. Esta tese está dividida em quatro partes, a primeira é fundamentação teórica que aborda o tema da pesquisa, seguida por dois artigos científicos independentes, e, por fim, são apresentadas as considerações finais.

2 FUNDAMENTAÇÃO TEÓRICA

2.1 PERTURBAÇÕES NATURAIS E ANTRÓPICAS AGUDA E CRÔNICA

Historicamente, todos os sistemas naturais provavelmente experimentaram ou experimentam perturbações em alguma escala espacial e temporal que podem influenciar a natureza de organismos, populações e comunidades inteiras, além de também seus padrões de funcionamento (BATTISTI; POETA; FANELLI, 2016; DREW, 2010; PULSFORD; LINDENMAYER; DRISCOLL, 2014; WHITE; PICKETT, 1985). Neste sentido, existe um amplo interesse em compreender como as perturbações interferem na dinâmica dos ecossistemas já que as perturbações exercem forte papel na seleção natural dos organismos ao modificar o ambiente em que vivem (HOBBS; HUENNEKE, 1992; KREBS, 1989).

As perturbações podem ser definidas como qualquer evento que leve a retirada de biomassa ao longo do tempo e espaço de forma contínua ou discreta gerando mudanças nas estruturas das populações, comunidades e ecossistemas, e como consequência, alteram a disponibilidade de recursos e modificam as condições físicas do ambiente (PICKET E WHITE 1985). As perturbações são consideradas naturais quando os eventos que as causam não apresentam em sua gênese a ação humana, como por exemplo: terremotos, tsunamis, inundações, fogos, geadas, tempestades de ventos, herbivoria, morte de uma árvore devido à doença ou à idade avançada (CHATURVEDI et al., 2017; CHAZDON et al., 2003; HOBBS; HUENNEKE, 1992; PULSFORD; LINDENMAYER; DRISCOLL, 2014). Diferente das perturbações naturais, existem perturbações que são resultado das atividades humanas, ou seja, perturbações antrópicas. As perturbações antrópicas, por sua vez, são em sua maioria danosas aos ecossistemas e sua biota (BATTISTI; 2016), e cada vez mais os ecossistemas enfrentam as perturbações antrópicas com mais frequência e intensidade em curto tempo e em diferentes escalas de paisagem (WHITE; PICKETT, 1985). Além disso, as perturbações antrópicas são capazes de impor nos ecossistemas alterações nos regimes de perturbações naturais, podendo interromper ou catalisar os impactos dos mesmos (BATTISTI; POETA; FANELLI, 2016; CHATURVEDI et al., 2017; HOBBS; HUENNEKE, 1992). Diante disso, mesmo que as perturbações naturais e antrópicas tenham semelhança em sua origem, por ambas constituírem ações que removem biomassa, há diferenças entre os regimes dessas perturbações (BATTISTI; POETA; FANELLI ,2016).

Uma das perturbações antrópicas mais intensas e que gera modificações imediatas nos ecossistemas são as perturbações agudas (BATTISTI et al., 2016). As perturbações agudas estão representadas por mudanças no uso do solo como o corte raso da vegetação para estabelecimentos de culturas agrícolas e pastagens (LAURANCE; SAYER; CASSMAN, 2014a, 2014b; PERES; BARLOW; LAURANCE, 2006; SINGH, 1998), causando perda e fragmentação de habitat e diminuindo a fertilidade do solo como também, gerando processos de desertificação em ecossistemas naturalmente mais vulneráveis (DENT; JOSEPH WRIGHT, 2009; LAURANCE; SAYER; CASSMAN, 2014b; PERES; BARLOW; LAURANCE, 2006; WRIGHT, 2010), tais como os ecossistemas de floresta tropicais secas e sazonalmente secas, que são caracterizados por apresentar baixa produtividade, precipitação escassa e/ou sazonal, possuem baixa umidade do ar e radiação solar abundante resultando em alta evapotranspiração (D'ODORICO et al., 2013; PENNINGTON; LAVIN; OLIVEIRA-FILHO, 2009; REYNOLDS et al., 2007), e onde o processo de regeneração vegetal ocorre somente em estações favoráveis (QUESADA et al., 2009; TABARELLI et al., 2017). As perturbações principalmente nas florestas secas e sazonalmente secas representam uma forte ameaça para sustentação da biodiversidade e para regeneração da vegetação por gerar efeitos mais intensos e em cascata nas funções e serviços ecossistêmicos em múltiplas escalas espaciais (TSCHARNTKE et al., 2012).

2.2 REGENERAÇÃO DA VEGETAÇÃO

A regeneração pode ser entendida como um processo em que florestas após perturbadas de forma natural ou antrópica podem assumir características da floresta madura (FAO, 2020; LAURANCE; SAYER; CASSMAN, 2014a). Apesar da regeneração da vegetação não ser capaz de substituir florestas primárias, elas podem manter importantes serviços ecossistêmicos como o sequestro de carbono (COOK-PATTON et al., 2020; POORTER et al., 2016), a ciclagem de nutrientes (POWERS; MARÍN-SPIOTTA, 2017), regulação no sistema hidrológico (POWERS;MARÍN-SPIOTTA, 2017), restabelecimento da biodiversidade (ROZENDAAL et al., 2019), conectividade entre fragmentos florestais (ARROYO-RODRÍGUEZ et al., 2017) e oferecer habitats adequados a várias espécies florestais (CHAZDON, 2014a; CHAZDON et al., 2009), com alterações direcionais na composição de espécies (CHAZDON, 2012a, 2008a, 2008b; LETCHER; CHAZDON, 2009). Essas alterações de espécies são resultado de mudanças nas condições físicas e químicas dos ambientes (e.g. temperatura, umidade do ar e do solo, precipitação e fertilidade do solo), as quais permitem o avanço gradativo dos estágios de regeneração da vegetação, incluindo um aumento gradual na riqueza de espécies, alteração nas estratégias de vida das espécies e um aumento complexidade estrutural e funcional da comunidade ao longo do tempo (BARROS et al., 2021a; CHAZDON, 2012b; LEBRIJA-TREJOS et al., 2010b; LOHBECK et al., 2014).

A velocidade dessas mudanças durante todo o processo da regeneração depende de vários fatores, como por exemplo, a qualidade química e física do solo, o tipo de perturbação, intensidade e frequência da perturbação, histórico de uso da terra, quantidade de habitat ao redor da área perturbada, conectividade da paisagem, entre outros fatores (BARROS et al., 2021; CHAZDON, 2008a; DENT; JOSEPH WRIGHT, 2009; GUARIGUATA; OSTERTAG, 2001; QUESADA et al., 2009). Avaliar, por exemplo, fatores como a intensidade do uso da terra afeta a regeneração pode fornecer informações para selecionar práticas de manejo com menor efeito negativo para a biodiversidade, assim como localizar áreas que precisam de maior intervenção para sua recuperação (BALVANERA et al., 2021; JAKOVAC et al., 2021; MARTÍNEZ-RAMOS et al., 2016), como também podem ser uma promessa para aliar a conservação das florestas tropicais e os benefícios humanos por elas ofertados (CHAZDON, 2014).

As florestas secundárias que representam boa parte de toda cobertura vegetal na maioria das paisagens tropicais (WRIGHT, 2010), cobrindo cerca de 600 milhões de hectares em todo o globo (PAN et al., 2011), contribuem com o fornecimento de serviços ecossistêmicos para o homem, como forragem para o gado, lenha e produtos não madeireiros (BONGERS et al., 2015; PÉREZ-CÁRDENAS et al., 2021; STRASSBURG et al., 2016). Também são importantes para mitigar as alterações climáticas devido a sua enorme capacidade de capturar carbono (COOK-PATTON et al., 2020; PAN et al., 2011; PÉREZ-CÁRDENAS et al., 2021; POORTER et al., 2016, 2021). Além disso, geram efeitos diretos sobre a diversidade e a composição de espécies das comunidades vegetais e animais, e auxiliam na recuperação da qualidade do solo, o que permite ser uma aceleração na regeneração natural e no desenvolvimento de estratégias de restauração ecológica (CHAZDON; GUARIGUATA, 2016; POORTER et al., 2016; ROZENDAAL et al., 2019), podendo evitar estágios menos deletérios nos ecossistemas tropicais.

Sendo assim, esses fatores que controlam a velocidade e eficiências da regeneração podem resultar numa aceleração do processo de regeneração ou mudar a trajetória sucessional levando a estados alternativos estáveis, tais como a sucessão interrompida, assembleias distorcidas, com assembleias de plantas dominadas por arbustos ou por espécies de plantas exóticas, ou, em um cenário mais deletério, a desertificação (TABARELLI et al., 2017). Para mitigar ou até mesmo evitar estados alternativos estáveis mais deletérios como a desertificação (JAKOVAC ET AL., 2016; MESQUITA ET AL., 2015; TABARELLI et al., 2021), é necessário combater os agentes perturbadores, identificar áreas onde são necessárias intervenções através da restauração ecológica, para assim permitir que a regeneração alcance um estado mais próximo das condições de florestas madura (ARROYO-RODRÍGUEZ et al., 2015; CHAZDON, 2008a).

2.3 FORMIGAS CORTADEIRAS

As formigas cortadeiras pertencem aos gêneros *Atta* (FABRICIUS, 1804) e *Acromyrmex* (MAYR, 1865) da tribo Attini, subfamília Myrmicinae. Essas formigas são chamadas de cortadeiras pois removem folhas frescas que servem de substrato para o fungo criado dentro dos seus ninhos e do qual se alimentam (DELLA LUCIA; SOUZA, 2011). Os fungos, na maioria dos casos dos gêneros *Leucoagaricus* e *Leucocoprinos*, ambos da família Lepiotaceae (Agaricales: Basidiomycota), ocorrem exclusivamente dentro dos ninhos. Por outro lado, as formigas cortadeiras alimentam-se exclusivamente dos fungos, formando então uma simbiose (FARJI-BRENER; WERENKRAUT, 2015b; MAYHE-NUNES; JAFFE K, 1998). As formigas cortadeiras são encontradas desde o sul da América Central até o sul da Argentina (HÖLLDOBLER; WILSON E. O., 1990). No Brasil, ocorrem na Mata Atlântica, floresta Amazônica, Pampas, Pantanal, Cerrado e na Caatinga (COSTA; BRUNA; VASCONCELOS, 2018; DELABIE et al., 2011).

As formigas cortadeiras são reconhecidas como os principais herbívoros da região neotropical, pois são capazes de remover de 12 e 17% da produção de folhas dentro das suas áreas de forrageamento (URBAS et al., 2007) representando mais de uma tonelada de material vegetal por ano (FOLGARATI, 1998). Além das altas taxas de herbivoria foliar, esses organismos também removem outras estruturas vegetais como: sementes, botões, flores, frutos, galhos, e material vegetal em processo de decomposição na serrapilheira (COSTA et al., 2008; FALCÃO et al., 2011). Todo esse material provém de uma grande diversidade de espécies vegetais, correspondendo mais de 50% das espécies da flora local dentro de suas áreas de forrageamento (WIRTH et al., 2003). O uso de indivíduos adultos pode reduzir o crescimento e sucesso reprodutivo das espécies preferidas (WIRTH et al. 2003; OLIVEIRA et al. 2023). Adicionalmente, o uso de sementes (OLIVEIRA et al. 2023) e plântulas (KNOECHELMANN et al. 2020), pode dificultar o estabelecimento de novos indivíduos.

Além da herbivoria, as formigas cortadeiras também são consideradas importantes engenheiras de ecossistemas, pois alteram as propriedades físico-químicas dos solos e o regime de luz ao redor dos seus ninhos gigantescos, influenciando a disponibilidade destes recursos para outras espécies (LEAL; WIRTH; TABARELLI, 2014b; WIRTH et al., 2003). As alterações no solo são devidas à construção de seus ninhos subterrâneos que são formados por numerosas câmaras e galerias, podendo alcançar até 8 m abaixo do solo (MOREIRA et al., 2004). Adicionalmente, o solo removido para a construção do ninho é depositado em montes na superfície do solo conhecidos como murundus (FARJI-BRENER; TADEY, 2009; FARJI-BRENER; WERENKRAUT, 2015a, 2017; RAO, 2000). Os murundus podem cobrir uma superfície que varia de 50 m² até mais de 250 m², e pode até mesmo chegar a se mover, expandir e contrair devido as chuvas fortes, quedas de árvores e outros distúrbios (VAN GILS; VANDERWOUDE, 2012). Como resultados, as formigas cortadeiras invertem as camadas do solo, depositando solos minerais e pouco férteis na superfície e uma grande quantidade de material orgânico relacionado ao cultivo do fungo simbionte, em grandes profundidades, aumentando o teor de nutrientes (FARJI-BRENER; WERENKRAUT, 2015). Além disso, as inúmeras e extensas galerias e câmaras existentes dentro do ninho alteram a estrutura do solo tornando-o mais poroso, aerado, permeável e drenado (FARJI-BRENER; TADEY, 2017; FARJI-BRENER; WERENKRAUT, 2015b; LEAL; WIRTH; TABARELLI, 2014b). Como resultado da limpeza e manutenção dos ninhos, as formigas cortadeiras, acabam descartando resíduos de fungos e material vegetal (i,g., folhas, galhos, flores, frutos e sementes) em decomposição, rico em nutrientes (FARJI-BRENER; TADEY, 2017; FARJI-BRENER; WERENKRAUT, 2015b). Todo este material, por sua vez, é alocado em câmaras subterrâneas (i.e., lixeiras internas) que possuem níveis mais baixos de nutrientes, afetando negativamente a germinação das sementes, a sobrevivência e o crescimento das plântulas (CORRÊA et al., 2010; MEYER et al., 2011c). Já as lixeiras externas que se encontram em ilhas na superfície das margens dos ninhos (este último comportamento ocorrendo conforme a espécie de Atta) (FARJI-BRENER; MEDINA, 2000), apresentam efeito contrário as lixeiras internas, contendo mais nutrientes, podendo favorecer o desenvolvimento de plantas (FARJI-BRENER; WERENKRAUT, 2015).

Acima dos ninhos também são criadas clareiras no dossel da floresta que geram uma série de modificações tanto no regime de luz, quanto nas condições microclimáticas em torno dos seus ninhos (MEYER et al., 2011a, 2013b), que geram alterações nas espécies vegetais sub-bosque e nas áreas de forrageamento (FARJI-BRENER; TADEY, 2017; MEYER et al., 2011b)

Adicionalmente, os efeitos das clareiras criadas pelas formigas cortadeiras também alteram o recrutamento e a estruturação das assembleias vegetais no ninho (CORRÊA et al., 2010; LEAL; WIRTH; TABARELLI, 2014; MEYER et al., 2011a, 2013). Neste sentido, os ninhos ativos de formiga cortadeiras podem sustentar um número limitado e por tempo limitado, reduzindo dessa forma a riqueza de espécies (CORRÊA et al., 2010; MEYER et al., 2011a). A influência das formigas cortadeiras no microclima, demostra clara evidência da existência de filtros ambientais para o estabelecimento de plantas como parte de suas atividades de engenharia de ecossistema (CORRÊA et al., 2010; LEAL; WIRTH; TABARELLI, 2014b; MEYER et al., 2011b, 2011a). Por consequências dessas modificações dos atributos microclimáticos e físico-químicos do solo, as formigas cortadeiras estão entre os animais que mais provocam modificações no ambiente (FARJI-BRENER; MEDINA, 2000; FARJI-BRENER; TADEY, 2009; FARJI-BRENER; WERENKRAUT, 2017), fortalecendo a ideia de engenheiras de ecossistemas.

Devido ao seu papel como herbívoro e engenheiro do ecossistema, as formigas cortadeiras podem alterar a regeneração da floresta. Ao coletar sementes e plântulas para cultivar o fungo simbionte a regeneração é fortemente comprometida na região sob influência dos ninhos e áreas de forrageamento das formigas cortadeiras (LEAL; WIRTH; TABARELLI, 2014; ZAVALA-HURTADO et al., 2000; KNOECHELMANN et al., 2020). No caso das sementes, apesar de formigas cortadeiras poderem atuar como dispersoras de sementes, seus efeitos sobre as sementes são normalmente negativos, uma vez que podem atuar como predadoras de sementes ou como sumidouros de sementes, quando estas são depositadas em câmaras internas que não permitem a germinação (COSTA; BRUNA; VASCONCELOS, 2018; VAZ FERREIRA; BRUNA; VASCONCELOS, 2011; KNOECHELMANN et al., 2020). Nessa situação, as formigas cortadeiras reduzem a disponibilidade de sementes e consequentemente restringem o estabelecimento de plântulas, afetando negativamente a regeneração vegetal (COSTA; BRUNA; VASCONCELOS, 2018; SILVA et al., 2011). A regeneração também pode ser alterada pela redução da abundância de plântulas de espécies herbáceas e lenhosas nos ninhos (KNOECHELMANN et al., 2020). Os efeitos das formigas cortadeiras sobre o recrutamento, desenvolvimento e estabelecimento de plântulas, resultam numa redução na densidade e riqueza

(SILVA et al., 2012, KNOECHELMANN et al., 2020), bem como na alteração da composição de espécies (KNOECHELMANN et al., 2020; SILVA et al., 2011), em especial, nos primeiros estágios de regeneração florestal. Com o avanço da regeneração, a frequência de ataque vai mudando em decorrência dos estágios ontogenéticos das plantas (COSTA; BRUNA; VASCONCELOS, 2018; SILVA et al., 2012).

A regeneração da floresta também pode ser influenciada pelos ninhos vivos de Atta que cobrem o solo da floresta com grandes quantidades de solo mineral escavado e acumulam uma enorme quantidade de resíduos orgânicos rico em nutriente (CORRÊA et al., 2010; FARJI-BRENER; WERENKRAUT, 2015b; MEYER et al., 2013a; MOUTINHO; NEPSTAD; DAVIDSON, 2003). Estudos passados viram que os ninhos ativos de Atta possuem melhores teores de nutrientes ao redor dos locais de nidificação e que as plantas podem se beneficiar investindo em maior crescimento, abundância e/ou desempenho (FARJI-BRENER; TADEY, 2009; FARJI-BRENER; WERENKRAUT, 2015b). Todavia, estudos recentes encontraram tendencia oposta a esses achados, demostrando que os ninhos ativos além de soterrarem as plântulas, levam a redução de nutrientes do solo (BIEBER et al., 2011; MEYER et al., 2013) como efeitos diretos e indiretos no crescimento e sobrevivência das plantas, e afetando também as plantas a nível de espécie, população e comunidade (CORREA et al., 2016; FARJI-BRENER; WERENKRAUT, 2015; MEYER et al., 2011b). Em contraste aos ninhos ativos, os ninhos abandonados devido à migração ou morte da colônia (BIEBER et al., 2011; GARRETTSON et al., 1998), podem servir como uma “fonte” para o recrutamento de plântulas, por possuir altos níveis de luz que favorecem o desenvolvimento das plântulas (MEYER et al., 2011a; SWANSON et al., 2019), além de possuírem poucos indivíduos o que implica em menor competição interespecíficas ou intraespecífica de plântulas (FARJI-BRENER; MEDINA, 2000). Por outro lado, também há evidências que os ninhos abandonados podem constituir locais desfavoráveis para o recrutamento, por possuírem pouco teor de matéria orgânica e serem mais compactos do que os solos que não tiveram influência das formigas, afetando negativamente o recrutamento de plântulas e a regeneração da floresta (BIEBER et al., 2011) De fato, foi observado que até 15 anos depois da morte da colônia ou abandono no ninho, a comunidades de plantas regenerantes possuía diferente composição de espécies e ainda não havia atingido a densidade e riqueza de áreas não afetadas pelas formigas (BIEBER et al., 2011). Diante dessas evidências contrastantes, fica em aberto se as plantas são ou não beneficiadas pelos ninhos de formigas cortadeiras (FARJI-BRENER; WERENKRAUT, 2015; OLIVEIRA et al 2023).

Diversos estudos já verificaram aumentos na densidade de colônias de várias espécies de formigas cortadeiras em áreas perturbadas, tais como: (1) plantações (OLIVEIRA et al., 1998), (2) pastagens (FOWLER, 1983), (3) florestas em estádios iniciais de sucessão (DE VASCONCELOS, 1990; FARJI-BRENER, 2001; FOWLER, 1983; HAINES, 1978; JAFFE; VILELA, 1989; VASCONCELOS; CHERRETT, 1995), (4) pequenos fragmentos florestais (RAO, 2000; TERBORGH et al., 2001), (5) bordas de pequenos e grandes fragmentos (WIRTH et al., 2007), e (6) em área sob perturbações crônicas como criação extensiva de animais domésticos e exploração de produtos florestais (SIQUEIRA et al., 2017). As causas para este aumento incluem proliferação de habitats abertos preferidos pelas rainhas na hora do estabelecimento inicial das colônias (DE VASCONCELOS, 1990; SIQUEIRA et al., 2017), a proliferação de plantas pioneiras ou herbáceas (OLIVEIRA; SANTOS; TABARELLI, 2008; SIQUEIRA et al., 2018), as quais são mais palatáveis (FARJI-BRENER, 2001b) e mais utilizadas pelas formigas cortadeiras (FALCÃO et al., 2011; URBAS et al., 2007; SIQUEIRA et al., 2018) e a redução de inimigos naturais, como predadores (WIRTH et al., 2008) e moscas parasitoides (DE ALMEIDA; WIRTH; LEAL, 2008). Nessas áreas mais perturbadas, os efeitos das formigas cortadeiras em termos de herbivoria ou de engenharia de solo devem ser mais intensos, devido ao grande número de colônias, com potencial para influenciar a regeneração da comunidade vegetal.

2.4 QUALIDADE DOS SOLOS

Por muito tempo o conhecimento sobre o funcionamento do solo foi deixado de lado até compreender que é um recurso vital para o funcionamento do ecossistema terrestre e apresenta intima relação com fatores químicos, físicos e biológicos (BÜNEMANN et al., 2018; DREW, 2010; HEWITT et al., 2015; MUÑOZ-ROJAS, 2018). Apesar de sua importância, a maioria dos estudos são focados na formação e distribuição do solo (BÜNEMANN et al., 2018; MEA, 2005; SWINTON et al., 2006). Todavia, os conhecimentos sobre a qualidade do solo são incompletos (BÜNEMANN et al., 2018). Segundo (DORAN; PARKIN, 1994) a qualidade do solo pode ser definida como a capacidade de um solo funcionar de acordo com o limite de cada ecossistema e do uso da terra, sendo possível sustentar a regeneração da vegetação, produtividade biológica, manter a qualidade ambiental e promover a saúde vegetal e animal (ARAÚJO et al., 2012; DELGADO; GÓMEZ, 2016; MUÑOZ-ROJAS, 2018). No entanto, atualmente entende-se qualidade do solo como a capacidade intrínseca de um solo para contribuir com os serviços ecossistêmicos, como por exemplo produção de biomassa, regulação da água e do clima (BOUMA et al., 2017). Logo, a ideia de qualidade do solo não é difícil de entender uma vez que boa parte do que produzimos para nossa sobrevivência e conservação da biodiversidade tem o solo como ambiente (BREVIK, 2010), embora seja um dos ecossistemas mais ameaçados no mundo devido ao mau manejo pelas atividades humanas (FAO, 2018).

A maioria das mudanças que causam degradação dos solos tem como causa as atividades antrópicas que se comportam de acordo com o ecossistema em que se encontram associados (BREVIK, 2010), gerando alterações lentas nos solos, o que torna difícil identificar as condições de qualidade de solo (NORTCLIFF, 2002). Os principais agentes de degradações do solo no globo são: a acidificação e salinização devido a irrigação realizada de forma inadequada, desmatamento e queimadas para o estabelecimento de atividades agropecuárias, compactação e erosão devido à sobrepastoreio por animais domésticos, entre outros (ADHIKARI; HARTEMINK, 2016; FAO, 2019; MEA, 2005). Nas florestas secas, as degradações do solo são em decorrência da agricultura de corte-e-queima, criação extensiva de animais domésticos e exploração de produtos florestais não madeireiros que podem reduzir a fertilidade dos solos e reduzir a produtividade dos sistemas (SCHULZ et al., 2018, 2019; TABARELLI et al., 2017), prejudicando a regeneração nas florestas secas a um ponto tão crítico que pode levar a desertificação (TABARELLI et al., 2017). Para recuperar, minimizar ou evitar as reduções na qualidade do solo e a perda de produtividade, é necessário realizar avaliações para considerar se as mudanças no solo estão permitindo um declínio ou perda de função e serviços ecossistêmicos (ADHIKARI; HARTEMINK, 2016).

A qualidade do solo pode ser avaliada tanto no ponto de vista dos agroecossistemas, em que o principal objetivo é a produtividade, como também nos ecossistemas naturais, em que se têm como principais objetivos a regeneração da vegetação, manutenção da qualidade ambiental a conservação da biodiversidade (TABARELLI et al., 2017; BÜNEMANN et al., 2018). Sendo assim, é importante identificar os atributos do solo que descrevem a capacidade de um solo funcionar, os quais podem ser usados como indicadores da qualidade do solo (BÜNEMANN et al., 2018; VASU et al., 2019). As propriedades do solo se enquadram em três categorias: atributos químicos, físicos e biológicos do solo (KHAN et al., 2013; NORTCLIFF, 2002). Os atributos químicos estão diretamente relacionados com a atividade biológica, crescimento vegetal e disponibilidade de nutrientes para as plantas e outros organismos (MUÑOZ-ROJAS, 2018). Os principais atributos químicos utilizados frequentemente para compreender os processos do solo e suas relações são: matéria orgânica total, Carbono, pH, fósforo disponível, textura, potássio disponível, nitrogênio total (BREVIK, 2010; BÜNEMANN et al., 2018). Já os atributos físicos do solo são crucias para compreender os processos que ocorrem no solo, já que auxiliam no suporte e crescimento radicular; armazenamento e suprimento de água e nutrientes, trocas gasosas e atividade biológica (REYNOLDS et al., 2007). Os principais indicadores físicos geralmente utilizados são: a espessura; densidade do solo; densidade aparente, capacidade de troca catiônica, resistência à penetração, porosidade, capacidade de retenção d'água condutividade hidráulica e estabilidade de agregados (ARAÚJO et al., 2012; DELGADO; GÓMEZ, 2016; MUÑOZ-ROJAS, 2018). Por último, os atributos biológicos do solo são representados principalmente pelas bactérias, fungos, algas, nematoides, insetos como cupins e formigas, além de vertebrados como cutias, porcos selvagens e tatus (FARJI-BRENER; TADEY, 2009; MUÑOZ-ROJAS, 2018; PEY et al., 2014). Todos esses organismos são considerados indicadores de alguns processos que ocorrem no solo em resposta às degradações antrópicas, constituindo-se importantes variáveis para predizer a qualidade dos solos nos ecossistemas (EISENBEIS, 2006; MUÑOZ-ROJAS, 2018; PEY et al., 2014).

Diante disto, os atributos acima mencionados são geralmente selecionados por serem os mais viáveis do ponto de vista prático, financeiro, na maioria das circunstâncias, e também porque conseguem representar de forma adequada as condições do solo (BÜNEMANN et al., 2018), ao ponto de quantificarem a produtividade de um ecossistema (BREVIK, 2010). Além disso, servem para auxiliar os agricultores, políticos e tomadores de decisões a estarem prontos ao ponto de serem capazes de reconhecer quaisquer mudanças no solo que levem a estados alternativos estáveis críticos, os quais podem levar à perda de funções e serviços ecossistêmicos (BÜNEMANN et al., 2018; FAO, 2020; NORTCLIFF, 2002).

CAPÍTULO I: EFEITOS DE FORMIGAS CORTADORAS NA QUALIDADE DO SOLO EM ÁREAS DE REGENERAÇÃO NA FLORESTA SECA DA CAATINGA

MANUSCRITO A SER ENVIADO AO JORNAL *BIOTROPICA*

3 EFFECTS OF LEAF-CUTTING ANTS ON SOIL QUALITY IN REGENERATION AREAS IN THE CAATINGA DRY FOREST

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ABSTRACT

In tropical forests, environmental degradation threatens biodiversity, which can compromise ecosystem functions and services. However, some organisms proliferate with increasing disturbances and their effects on ecosystem functions become severe in disturbed areas. This is the case of leaf-cutting ants, voracious herbivores and ecosystem engineers, which alter the physical-chemical attributes of the soil. Here we evaluate the contribution of the nest of the leafcutter ant, *Atta opaciceps,* in soil quality in the Caatinga dry forest. The study was carried out in three areas with different land use types: an area undergoing regeneration after agriculture, an area undergoing regeneration after pasture, and an area of mature forest. In these areas, physical and chemical attributes of the soil were evaluated in the nest soil of three leaf-cutting ants colonies and three non-nest soil sites (i.e., control soil 10 m from the edge of the nest). In general, nest soil presented superior physical-chemical quality than non-nest soil and this difference was greater in areas regenerating after pasture than in forests regenerating after agriculture and mature forest areas. We observed that for physical attributes, the apparent density, field capacity and permanent wilting point of the soil were higher in nest soil than in non-nest soil. We also saw that for apparent density and permanent wilting point, this difference in nest soil and non-nest soil was greater in areas regenerating after pasture than in other land use types. However, we did not see a difference in field capacity in nest soil and non-nest soil in different land use types. For chemical attributes, we saw that magnesium and sodium presented a higher concentration in nest soil than in non-nest soil, with a greater difference in magnesium concentration in nest soil than in non-nest soil in areas undergoing regeneration after pasture than in other land use types. For sodium, however, we saw no difference in nest soil and non-nest soil across different land use types. In relation to pH, it was slightly more acidic in nest soil than in non-nest soil, but without differences between soil treatments and land use types. Finally, the cation exchange capacity (CEC) did not change in the soil treatments, but there was a greater difference in nest soil and non-nest soil in areas undergoing regeneration after pasture than in other land use types. Given this, this study indicated that leaf-cutting ants can improve the quality of the soil in their nests, especially in areas undergoing regeneration. These findings indicate a positive role for leafcutter ants in the recovery of degraded areas, providing conditions to improve soil quality and assist in forest regeneration.

Keywords: Atta opaciceps, anthropogenic disturbance, ecosystem engineering, forest recovery, soil attributes.

INTRODUCTION

Tropical forests are critically important for maintaining biodiversity, as these ecosystems are responsible for providing a wide range of ecosystem functions and services (i.e. climate regulation, carbon storage, water and soil provision, pollination and production of economic goods) important for the development of the human population at regional and global level (Beer *et al.* 2010, Laurance *et al.* 2014, Arroyo-Rodríguez *et al.* 2015, Liang *et al.* 2016, Brockerhoff *et al.* 2017). Although the relevance of tropical forests is undeniable, they are continually transformed into areas devoted to agriculture, logging, livestock raising and encroachment of dense urban centers (Tabarelli 2010, Wright 2010, Chazdon *et al.* 2011, Chazdon 2014, Battisti *et al.* 2016). As a result of these transformations, large areas of tropical forests are currently secondary forests or regenerating stands (Chazdon *et al.* 2003, 2011, Poorter *et al.* 2019). According to FAO (2018), in certain parts of the globe, there are already more secondary forests than mature forests. Thus, secondary forests present themselves as an essential repository for biodiversity conservation and provision of ecosystem services that directly influence the way of life of populations (Dent & Joseph Wright 2009, Letcher & Chazdon 2009, Lennox *et al.* 2018, Rozendaal *et al.* 2019).

Understanding the capacity of secondary forests to maintain biodiversity, ecosystem function and services is crucial to create policy measures that help to restore these areas (Arroyo-Rodríguez *et al.* 2017, FAO 2018, Poorter *et al.* 2019). This scenario is common in tropical regions where part of the people depend on the forest for their livelihood, such as seasonally dry tropical forests (hereafter dry forests) (Pennington *et al.* 2009). In this ecosystem, the low-income and very dense population dependent on the extraction of firewood, exploitation of timber and non-timber products, extensive livestock raising in a typical chronic anthropogenic disturbance regime (Singh 1998, Ribeiro *et al.* 2015). Additionally, slash and burn agriculture annually converts remnants of vegetation into short-cycle crops (D'Odorico et al. 2013, FAO 2019, Souza, et al. 2019). In dry forests, recovery rate (i.e. the speed at which forest attributes such as biomass and species richness reach the scores exhibited by old-growth forests) and successional trajectories (patterns of species replacements as regeneration proceeds) may vary more than in rainforests (Lebrija-Trejos *et al.* 2008, 2011, Chazdon 2012, Lohbeck *et al.* 2013). Abiotic and biotic factors such as water availability, soil quality, plant-animal interaction, resprouting ability and stochastic events are examples of how variable recovery rates and successional trajectories of dry forests can be (Lohbeck *et al.* 2013, Arroyo-Rodríguez *et al.* 2017, Barros *et al.* 2021a). These factors make the succession in dry forests ends up being equal, faster or even slower than that of rainforests (Lebrija-Trejos *et al.* 2008, 2011, Quesada *et al.* 2009, Lebrija-Trejos, Meave, *et al.* 2010, Lebrija-Trejos, Perez-Garcia, *et al.* 2010, Mora *et al.* 2014).

The Caatinga is one of the largest and most diverse dry forest worldwide and it is characterized by a mix of old-growth and secondary forest stands (Silva *et al.* 2017). Historically, the Caatinga has been converted into agricultural fields and pastures, leading to loss of habitats and degradation (Souza, et al. 2019). It is already known that the Caatinga has already lost about 63% of its area due to human activities (Silva & Barbosa 2017). However, the remaining forests and regenerating forest stands continue to suffer from chronic disturbances, such as the extensive livestock raising, collection of firewood, extraction of timber and non-timber forest products (Leal et al. 2005, Rocha-Ortega et al. 2018). In addition to anthropogenic disturbances, the climatic characteristics of this ecosystem and biological aspects can drive or even act as synergistic agents, which can lead to loss of biological productivity and soil quality in arresting forest regeneration (Rito et al. 2017, Souza, Sfair, de Paula, et al. 2019, Barros et al. 2021). However, secondary forests and other human-modified areas in Caatinga present a high density of an important herbivore and ecosystem engineer, the leaf-cutting ants (Siqueira *et al*. 2017).

Leaf-cutting ants belong to the genera *Atta* (Fabricius, 1804) e *Acromyrmex* (Mayr, 1865) (Attini, Myrmicinae), and comprise the main herbivores of the neotropical region, collecting between 12 and 17% of the annual leaf production in their foraging area and up to 50% of the species of the local flora (Wirth *et al.* 2003, Corrêa *et al.* 2010) and being able to influence the succession trajectory of the plant community (Corrêa *et al.* 2010, Silva *et al.* 2012). In addition to voracious herbivore (Wirth *et al*. 2003), these ants are seed dispersers/predators and influence the spatial distribution and structure of plant communities (Leal & Oliveira 1998, Wirth *et al.* 2003). Recent studies reported a lower seed deposition (Oliveira *et al.* 2023) and seedling recruitment in leaf-cutting ant nest-related habitat (Knoechelmann *et al.* 2020), indicating a negative effect of this ants to Caatinga regeneration.

Leaf-cutting ants alter soil attributes due to the construction and maintenance of nests, and are considered important ecosystem engineers (Meyer *et al.* 2013, Farji-Brener & Werenkraut 2015, 2017). Due to all this maintenance on the nests soil, it is possible that the mineral soil, which is not very rich in nutrients, and which was previously located inside the nest, ends up being transported and deposited on the surface of the nest. On the other hand, the organic soil richer in nutrients is deposited at great depths in the nest, which generates changes in the soil structure, making it more porous, aerated, permeable and drained (Leal *et al.* 2014a, Farji-Brener & Werenkraut 2015), with greater variability of carbon and other soil nutrients within the nest area (Moutinho *et al.* 2003, Meyer *et al.* 2013, Swanson *et al.* 2019). In addition to these effects, the maintenance and cleaning carried out by workers leads to the disposal of waste from the fungus and decomposing plant material, rich in nutrients ((Farji-Brener & Werenkraut 2015, Farji-Brener & Tadey 2017a). All this material, in turn, is allocated to underground chambers (i.e., waste dumps internal) that have lower levels of nutrients, negatively affecting seed germination, survival and seedling growth (Corrêa *et al.* 2010, Meyer *et al.* 2011), which leads to a reduction in soil fertility, also affecting the recruitment of seedlings and altering the structure of the plant community (Meyer *et al.* 2013, Farji-Brener & Werenkraut 2015). The waste dumps external, which are found on islands on the surface of the nest margins (the latter behavior occurring according to the Atta species) (Farji-Brener & Ghermandi 2000), have the opposite effect to internal refuse dumps, containing more nutrients available in the soil, which can favor the establishment and development of plants (Farji-Brener & Werenkraut 2015, Farji-Brener & Tadey 2017, Baena et al. 2023). It was already demonstrated that leaf-cutting ants not only proliferate in human-modified landscapes of Caatinga, but also increase their herbivory rates per colony (Siqueira *et al.* 2017, 2018). Thus, leaf-cutting ants are key-organisms in regenerating forest stands, with potential to mediate soil physic-chemical proprieties and affect Caatinga regeneration (Knoechelmann *et al.* 2020; Siqueira *et al*. 2017, 2018)

The main objective of this study is to evaluate the effects of the leaf-cutting ants, *Atta opaciceps*, on soil attributes in areas undergoing regeneration after agriculture and pasture and in areas of mature forest in the Caatinga dry forest. More precisely, we verified physical-chemical attributes of the soil (e.g., apparent and real density, field capacity, permanent wilting point, water available for plants and nutrients) in leaf-cutting ants nest soil and in non-nest soil (i.e., control) in areas undergoing regeneration after agriculture, pasture and in mature forest areas. We have two general hypotheses (1) leaf-cutting ants contribute to improving the soil through the construction and maintenance of nests, favoring soil aeration, humidity soil and the concentration of nutrients in the external refusing dumps of nest and (2) the differences in soil attributes between nest soil and non-nest soil of leaf-cutting ants will be more pronounced in regenerating areas than in mature forests. This expectation initially arises from the high soil degradation in regenerating areas, making any improvements resulting from the presence of nests more visible compared to the relatively lower soil degradation in mature forests. We predict that nest soils will have higher water content, reduced compaction and elevated nutrient concentrations compared to non-nest soils. Additionally, we anticipate that these differences will be particularly pronounced in areas undergoing regeneration.

2. METHODOLOGY

2.1 Study area

The study was carried out in the Catimbau National Park (8°24'00" and 8°36'35" South and 37°09'30" and 37°14'40" West), a 607 km² protected area located in the state of Pernambuco, northeast Brazil. The characteristic climate for the region is of the Bsh type (semi-arid) with transition to the tropical rainy type As’, according to the climatic classification established by Köppen. Annual rainfall varies between 480 and 1100 mm and the average annual temperature fluctuates around 23°C (Rito *et al.* 2017). The predominant soils are quartzitic sands (Siqueira et al. 2017) and the vegetation is a mosaic of low stature dry forest and shrub vegetation (Rito et al. 2017). The Park was created in 2002, but the owners have not yet been compensated and continue to use natural vegetation resources for their livelihood.

2.1 Study species

More than 300 colonies of leaf-cutting ants of the species *Atta laevigata, A. opaciceps* and *A. sexdens* have already been marked in the park area (Siqueira et al. 2017). We focus this study on the species endemic to Caatinga, *Atta opaciceps* (Borgmeier, 1939), which is the most abundant leaf-cutting ants in the Park (Siqueira *et al.* 2017). Colonies of *A. opaciceps* are usually found in human-modified areas and regenerating forest stands, such those previously used as cattle pasture and agriculture fields (Siqueira *et al.* 2017) (Figure 8.a). Their nests can cover an area of approximately 38 m² on average (Siqueira *et al.* 2018) and can reach a density of up to 35.5 colonies ha-1 in the Catimbau National Park (Siqueira *et al.* 2017) and to remove of 244 kg of dry weight/colony/yr (Siqueira *et al.* 2018) (Figure 8.a).

2.3 Methodological procedures

To estimate the effect of leaf-cutting ants on soil attributes, we used areas with three with different land use types (1) areas that suffered clear-cutting, had been used for corn and bean plantations for 3-4 years and then were abandoned and are regenerating for 12 years (i.e. regenerating forest stands after agriculture use) (Figure 8.c), (2) areas that suffered clear-cutting, had been used for at least 30 years as pasture (Digitaria bicornis) for cattle and goat and now are regenerating for 8-10 years (i.e. areas regeneration forest after pasture use) (Figure 8.d), and (3) areas of mature forest with no historical of land use for at least 80 years (Figure 8.e). The information about the historical use of the areas were first collected from locals and from two housekeepers of the Brejo farm, a region that is part of the Catimbau National Park, with subsequent field recognition and validation through satellite images with time series. The annual precipitation level at the Brejo farm is 640 mm and the soils consist of sandy quartzite soils (SNE 2002).

The physical and chemical properties of the soil were evaluated in nine colonies (i.e. three colonies of *Atta oppaciceps* in each types of habitat). For each, colony we collected soil samples in the nest mound with a depth of 0-5 cm. As a control, we used non-nest soil collected 10 meters from the edge of the nest in a randomly selected direction, with the same procedure described for the nest soil. Soil samples were taken to the Instituto Agronômico de Pernambuco (IPA) to obtain the following soil physical attributes bulk density, field density, permanent wilting point, field capacity, available water plant. For chemical attributes, we included pH, P, exchangeable cations (Ca, Mg, Na, K, Al) and potential acidity (H+Al). We also calculate CEC (cation exchange capacity) and base saturation. For the nutrients Carbon and Nitrogen, we also quantified the total soil concentration using a EuroVector elemental analyzer (EA3000) coupled to a Denta V Advantage isotope ratio mass spectrometer (Thermo Scientific). The elemental analyzer configured with a CHN reactor filled with chromium oxide, reduced copper wires and silver cobalt oxide, a water adsorption trap (cobalt magnesium) and a chromatographic separation column were used. Then, we quantified the masses of soil organic carbon (SOC) and total nitrogen in the soil samples by fitting an analytical curve ($R \geq 0.995$), using the sediment B2151 as a reference (elemental microanalysis N = 0.52% ; C = 7.45%; δ 13C = -28.85 ‰; δ15N = + 4.32 ‰). Nutrient concentrations analyzed by IPA are in the unit of ($cmolc/dm^3$) with the exception of the phosphorus nutrient which is in mg/dm^3 and the nutrients C and N are in the unit of g / kg. For the physical attributes, only the apparent and real density are in (g/cm^3), the other attributes are in percentage (%).

2.4 Data analysis

To verify our hypothesis that leaf-cutting ants contribute to soil improvement through the construction and maintenance of nests, favoring soil aeration, soil moisture and nutrient concentration in the nests external refuse dumps and differences in soil attributes between nest ground and non-nest ground will be more pronounced in regenerating areas than in mature forest , we used Generalized Linear Mixed Models (GLMM) with soil treatment (nest soils and non-nest soils) and land use types (areas regenerating after agriculture, area regenerating after pasture and mature forest) as explanatory variables. As a response variable, we used the physical attributes (i.e., apparent density, permanent wilting point, field capacity, real density and water available for plants) and chemical attributes of the soil (concentration of nutrients in the soil), and nest as a factor random. We tested the effects of the explanatory variable and the interactions between them on the physical and chemical attributes of the soil. All of these analyzes were performed with the Lme4 and lmerTest packages in R (Bates *et al.* 2015, Kuznetsova *et al.* 2017).

3. RESULTS

Our results indicate that for physical attributes, the apparent density was higher in the nest soil than in the non-nest soil (χ^2 = 8.56, df = 1, P = 0.003; Table 1; Figure 1), presenting 1.48 ± 0.06 g/cm^3 (mean ± standard deviation), ranging from 1.38 to 1.57 g/cm^3. Regarding the land use types, we saw that the apparent density was higher in areas undergoing regeneration after pasture than in areas of regeneration after agriculture and mature forest areas (χ^2 = 39.96, df = 2, P = 0.00002; Table 1; Figure 1). Furthermore, there was no difference in apparent density between soil treatments and land use types (χ^2 = 0.11, df = 2, P = 0.94; Table 1; Figure 1). This shows that there is greater compaction in non-nest soil and in areas regenerating after pasture. For field capacity, we found that the nest soils had a greater water retention capacity than the non-nest soil (χ^2 = 11.51, df = 1, P = 0.0006 Table 1; Figure 2), with 8. 54±3.21% (mean ± standard deviation), ranging from 2.84 to 14.12%. Additionally, field capacity did not show a significant difference between land use types (χ^2 = 1.95, df = 2, P = 0.37; Table 1; Figure 2), nor did it differ between soil treatments and land use types (χ^2 = 1.55 df = 2, P = 0.45; Table 1; Figure 2). Regarding the permanent wilting point, we saw greater moisture retention conditions for plants in nests soil than in non-nest soil (χ^2 = 16.05, df = 1, P = 0.00006; Table 1; Figure 3), with 3.47±1.76% (mean ± standard deviation), ranging from 1.27 to 6.28%. We also saw that the permanent wilting point was higher in areas regenerating after pasture than in areas regenerating after agriculture and areas of mature forest (χ^2 = 8.17, df = 2, P = 0.01; Table 1; Figure 3), however, we saw no difference between soil treatment and land use types (χ^2 = 1.70, df = 2, P = 0.42; Table 1; Figure 3). Finally, we saw no difference between nest soil and non-nest soil in actual density and water available to plants (χ^2 = 1.33, df = 1, P = 0.24 and χ^2 = 2.62, df = 1, P = 0.10, respectively; Table 1) as well as, it was also not significant for the real density and water available for plants in the land use types (χ^2 = 1.83, df = 2, P = 0.40 and χ^2 = 0.04 gl = 2, P = 0.97, respectively; Table 1) and there was also no difference between soil treatments and land use types (χ^2 = 0, df = 2, P = 1 and χ^2 = 0.82 gl = 2, P = 0.66, respectively; Table 1).

Regarding chemical attributes, we found that magnesium had a higher concentration in the nest soil than in the non-nest soil (χ^2 = 13.84 gl = 1, P = 0.0001; Table 2; Figure 4), with 1.21 ± 0 .48 cmolc/dm^3 (mean ± standard deviation), ranging from 0.6 to 2.5 cmolc/dm^3. Regarding the land use types, we saw that the area undergoing regeneration after pasture had a higher concentration of magnesium than the areas undergoing regeneration after agriculture and mature forest areas χ^2 = 13.84 gl = 1, P = 0.0001; Table 2; Figure 4). Furthermore, we saw that there was an interaction in the increase in magnesium concentration between soil treatments and land use types (χ^2 = 22.78, gl = 2, P = 0.0007), demonstrating that the nest soil and areas in regeneration after pasture, they influence the magnesium concentration in the soil. As for sodium, we saw a higher concentration in the nest soil than in non-nest soil (χ^2 = 11.18, df = 1, P = 0.0008; Table 2; Figure 5). It had an average of 0.06 ± 0.08, ranging from 0.01 to 0.25 cmolc/dm³, but there was no difference in sodium concentration across land use types (χ^2 = 4.99, df = 2, P = 0.08; Table 2; Figure 5) as well as did not differ for the interaction between soil treatments and land use types (χ^2 = 4.99, df = 2, P = 0.08; Table 2; Figure 5). Regarding pH, we saw that it was better in the nest soil than non-nest soil (χ^2 = 5.34, df = 1, P = 0.02; Table 2; Figure 6) with a slightly acidic pH. In general, pH had a mean of 6.27±0.51 (mean ± standard deviation), ranging from 5.4 to 7.1. For land use treatments, there was no difference in pH (χ^2 = 2.91, df = 2, P = 0.23; Table 2; Figure 6) and there was also no difference between soil treatments and land use types (χ^2 = 1.01, df = 2, P = 0.60; Table 2; Figure 6). For cation exchange capacity (CEC), we saw no difference between soil treatments (χ^2 = 0.15, df = 1, P = 0.69; Table 2; Figure 7), the average value of cation exchange capacity (CEC) was 5.13 ± 2.90 cmolc/dm³ (mean ± standard deviation), ranging from 1.67 to 11.75 cmolc/dm³. For land use types, the cation exchange capacity (CEC) showed higher values in areas regenerating after pasture than in areas regenerating after agriculture and mature forest areas (χ^2 =8.10, df = 2, P =0.01; Table 2; Figure 7). However, we saw no difference in the interaction between soil treatments and land use types (χ^2 =0.43, df = 2, P =0.80; Table 2; Figure 7). For the other chemical attributes (i.e., C, N, P, K, Al, H and Saturation per base) we did not find significant differences for both the nest soil and non-nest soil and for the areas regenerating after agriculture, pasture, and mature forest area and for interaction between soil treatments and land use types (Table 2).

4. DISCUSSION

In this study, we evaluated how leaf-cutting ants influence the physico-chemical attributes of the soil in three different land use types (i.e., area undergoing regeneration after agriculture, livestock farming and mature forest). Our hypothesis that leaf-cutting ants contribute to soil improvement through the construction and maintenance of nests, favoring soil aeration, soil humidity and nutrient concentration in external refuse dumps and the differences in soil attributes between the nest soil and non-nest soil from leaf-cutting ants will being more pronounced in regenerating areas than in mature forests was partially corroborated. Our results indicate that leaf-cutting ants nest soil has better soil attributes when compared to non-nest soil (i.e., control), promoting lower apparent density, greater field capacity and higher permanent wilting point. Additionally, we saw that the difference in apparent density and permanent wilting point in nest soil and non-nest soil were greater in the areas regenerating after pasture than in the area regenerating after agriculture and mature forest. We also observed better pH and higher concentrations of some nutrients, such as magnesium and sodium, in the nest soil than in the non-nest soil. Furthermore, we saw that the magnesium concentration was influenced by the nest soil and the area regenerating after pasture. For the other nutrients, there was no difference between soil treatments and land use type. Finally, for the cation exchange capacity (CEC) we saw that it was better in the area undergoing regeneration after pasture. Given these findings, we verified the importance of leaf-cutter ants in mediating soil quality, with possible positive effects on the regeneration of the Caatinga dry forest.

The better soil quality of A. opaciceps nests is in line with studies carried out with other *Atta species* that observed an increase in nutrients in nest soils when compared to non-nest soil (Moutinho et al 2003, Farji-Brener & Tadey 2017). However, these studies used soil samples close to residues (degraded plant materials and fungal remains) deposited in underground chambers (i.e., internal refuse dumps, Moutinho et al 2003) or soil samples from external refuse dumps (Farji- Brener & Tadey 2017). The soil under the influence of external refuse dumps is richer in nutrients when compared to the nest mound soil, which has more mineral soil accumulation (Leal *et al.* 2014b, Farji-Brener & Werenkraut 2015). Unlike internal refuse dumps, where nutrients are difficult for plants to access, external refuse dumps have nutrients that are easily accessible to plants in the most superficial strata of the soil (Leal *et al.* 2014, Farji-Brener & Werenkraut 2015). However, the presence of external refuse dumps occurs in few Atta species and in specific ecosystems (Farji-Brener & Medina 2000, Farji-Brener & Tadey 2017). In fact, a recent review demonstrated that in arid and semi-arid ecosystems, leaf-cutter ants tend to deposit their waste externally, while in humid tropical forests internal refuse dumps are more common. According to this study, our focal species, Atta opaciceps, deposits its external refuse dumps at least once a year, at the beginning of the rainy season (Siqueira *et al.* 2018, Knoechelmann *et al.* 2020, Oliveira *et al.* 2023). Therefore, and as observed in the pattern of most studies that evaluate the soil of anthills of the Atta species, better physical and chemical quality is expected in the nest soil due to the construction and frequent maintenance by worker ants that promote greater soil aeration, remove plants and litter on the surface of the nests, which contributes to an increase in the concentration of organic matter and nutrients in the soil (seeFarji-Brener & Ghermandi 2000, Moutinho et al. 2003, Farji-Brener & Ghermandi 2008, Hudson et al. 2009, Farji-Brener & Werenkraut 2015), deposited in internal refuse dumps (Moutinho et al. 2003; Farji-Brener & Tadey 2017) and in external refuse dumps (Farji-Brener & Tadey 2009, 2017b, Farji-Brener & Werenkraut 2015) which, in addition to receiving organic waste collected by Leaf-cutter ants also receive an extra supply of litter that falls from the surrounding vegetation (Farji-Brener & Werenkraut 2015).

The lower apparent density of nest soils in areas undergoing regeneration after pasture indicates that leaf-cutting ants can improve historically degraded environments, as it reduces soil compaction, generating greater macroporosity and lower microporosity (Moutinho et al. 2003). The same pattern can be observed for field capacity and permanent wilting point, which was higher in nest soils, demonstrating a greater possibility of having water readily available for absorption by plant roots for longer, favoring the establishment and development of plant roots (Moutinho et al. 2011, Farji-Brener & Werenkraut 2015). Although we did not see a difference in field capacity in land use treatments and in the interaction between soil treatments and types of land use, we saw that another soil moisture parameter, which is the permanent wilting point, presented greater capacity of the plant to retain soil moisture without losing its turgidity in an area undergoing regeneration after pasture. These changes in soil structure have a positive effect on the activity of soil biota, favoring soil quality around the nest area (Moutinho *et al.* 2003; Farji-Brener & Tadey 2009; Farji-Brener & Werenkraut 2015, 2017). As for the pH found in the nest soils, we can consider that the pH presented slightly low acidity and should allow good absorption of nutrients by the plants. This is because the average pH found is above the limit of 6.0, which is the minimum value for a crop to present good productivity and not present an accumulation of toxic elements in the soil (i.e., aluminum) (EMBRAPA 2010, Prezotti & Guarçoni 2013). In general, the soils of Catimbau National Park are very acidic and impoverished, with little difference between areas with different regeneration ages (Barros *et al.* 2021b). It is possible that the better pH in the nest soil than in the non-nest soil occurs due to the large amount of organic material deposition in the nests by leafcutter ants. The deposition of this organic material in the nest's soil is decomposed and therefore acidifies the soil, allowing the occurrence of pH with an intermediate capacity to promote the increase of micronutrients and nutrients such as magnesium and sodium (EMBRAPA 2010, Prezotti & Guarçoni 2013). Regarding nutrients, we saw that sodium was higher in the nest soil than in the non-nest soil; however, it does not pose a risk to the absorption of water and nutrients by plants as it has a low concentration (Prezotti & Guarçoni 2013). Sodium also did not differ between types of land use and showed no interaction with soil treatment and type of land use, demonstrating that the highest concentration of sodium is directly due to the activity of building and maintaining the nest by leafcutter ants. As for magnesium, we saw that the nest presented a higher concentration in the nest soil (see Moutinho *et al* 2003 and Farji-Brener & Werenkraut 2015) and in the area undergoing regeneration after pasture, as was also seen in another study (Moutinho *et al* 2003). Furthermore, we saw that magnesium showed an interaction between soil treatment and types of land use, demonstrating that the nest soil and the area undergoing regeneration after pasture promote an increase in magnesium concentration. Finally, for cation exchange capacity, we saw no difference between soil treatments and in the interaction with soil treatment and type of land use, but we saw a difference in areas regenerating after pasture. However, although we have seen a higher CEC value found in areas undergoing regeneration after pasture, this increase is not sufficient to retain cations in exchangeable form in the soil (EMBRAPA, 2010).

This study indicated that leaf-cutting ant nests have a positive effect on the quality of the soil near their nests, mainly related to physical attributes, and this difference between soils with and without nests is even greater in regenerating forest stands. This finding may indicate that leafcutter ants *Atta opaciceps* could help improve soils in degraded areas, such as those previously used for agriculture and pastures. As leaf-cutting ants also benefit from disturbance in dry Caatinga forest (Siqueira *et al.* 2017), these results may indicate even more important effects on regeneration in human-modified Caatinga landscapes (Moutinho *et al.* 2003, Farji-Brener & Tadey 2017b, Silva & Barbosa 2017, Tabarelli *et al.* 2017).

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Tabela 1. Results of physical attributes in relation to soil treatment of nest soil and non-nest soil (i.e., control) and land use types (i.e., areas undergoing regeneration after agriculture, pasture, and maturity forest), and the interaction between these two variables explanatory for soils with and without Atta opaciceps nests in Catimbau National Park, Pernambuco, Brazil. For each variable we indicate the chi-square (χ^2), the degree of freedom (gl) and 95% confidence intervals. Significant variables (according to 95% confidence intervals).

Predictors	Bulk density			Field capacity			Permanent wilting point			Actual density			Available water for planting		
	χ^2	*df*	$p<0.05$	χ^2	*df*	$p<0.05$	χ^2	*df*	$p<0.05$	χ^2	*df*	$p<0.05$	χ^2	*df*	$p<0.05$
Soil treatments	8.56	1	0.003*	11.51	1	0.0006 *	16.05	1	0.0006*	1.33	1	0.24	2.62	1	0.10
Land use types	39.96	2	0.00002*	1.95	2	0.37	8.17	2	0.01*	1.83	2	0.40	0.04	2	0.97
Soil treatments: Land use types	0.11	2	0.94	0.67	2	0.71	1.70	2	0.42	0	2	1	0.82	2	0.66

Tabela 2. Results of chemical attributes in relation to soil treatment of nest soil and non-nest soil (i.e., control) and land use types (i.e., areas undergoing regeneration after agriculture, pasture, and maturity forest), and the interaction between these two variables explanatory for soils with and without Atta opaciceps nests in Catimbau National Park, Pernambuco, Brazil. For each variable we indicate the chi-square (χ^2), the degree of freedom (gl) and 95% confidence intervals. Significant variables (according to 95% confidence intervals).

Predictors	C			N			P			K			Ca			Na		
	χ^2	*df*	p<0.05	χ^2	*df*	p<0.05	χ^2	*df*	p<0.05	χ^2	*df*	p<0.05	χ^2	*df*	p<0.05	χ^2	*df*	p<0.05
Soil treatments	0.05	1	0.81	0.69	1	0.40	0.01	1	0.89	1.33	1	0.24	0.25	1	0.61	11.18	1	0.0008*
Land use types	2.61	2	0.27	2.43	2	0.29	0.10	2	0.95	5.59	2	0.06	2.66	2	0.26	4.99	2	0.08
Soil treatment: Land use types	01.89	2	0.38	1.89	2	0.38	3.84	2	0.14	0.12	2	0.94	2.40	2	0.30	4.17	2	0.12

Predictors	Mg			Al			H			pH			CEC			V		
	χ^2	*df*	p<0.05	χ^2	*df*	p<0.05	χ^2	*df*	p<0.05	χ^2	*df*	p<0.05	χ^2	*df*	p<0.05	χ^2	*df*	p<0.05
Soil treatments	13.17	1	0.0002*	2.77	1	0.09	0.49	1	0.48	5.34	1	0.02*	0.15	1	0.69	0.42	1	0.51
Land use types	22.33	2	0.0005*	0.22	2	0.89	3.00	2	0.22	2.91	2	0.23	8.10	2	0.01*	3.14	2	0.20
Soil treatment: Land use types	10.34	2	0.005*	0.22	2	0.89	0.99	2	0.60	1.01	2	0.60	0.43	2	0.80	0.85	2	0.65

LEGEND OF THE FIGURES

Figure 1. Effects of nest soil and non-nest soil treatments and land use types (i.e., area in undergoing regeneration after agriculture, pasture, and mature forest), as well as the interaction between these two factors, on bulk density in soils of *Atta opaciceps* colonies in Catimbau National Park, Buíque, PE, Brazil.

Figure 2. Effects of nest soil and non-nest soil treatments and land use types (i.e., area in undergoing regeneration after agriculture, pasture, and mature forest), as well as the interaction between these two factors on field capacity in soils from *Atta opaciceps* colonies in the Catimbau National Park, Buíque, PE, Brazil.

Figure 3. Effects of nest soil and non-nest soil treatments and land use types (i.e., area in undergoing regeneration after agriculture, pasture, and mature forest), as well as the interaction between these two factors, on permanent wilting point in soils from *Atta opaciceps* colonies in the Catimbau National Park, Buíque, PE, Brazil.

Figure 4. Effects of nest soil and non-nest soil treatments and land use types (i.e., area in undergoing regeneration after agriculture, pasture, and mature forest), as well as the interaction between these two factors, on magnesium (Mg) concentration in soils from *Atta opaciceps* colonies in Catimbau National Park, Buíque, PE, Brazil.

Figure 5. Effects of nest soil and non-nest soil treatments and land use types (i.e., area in undergoing regeneration after agriculture, pasture, and mature forest), as well as the interaction between these two factors on sodium (Na) concentration in soils from *Atta opaciceps* colonies in Catimbau National Park, Buíque, PE, Brazil.

Figure 6. Effects of nest soil and non-nest soil treatments and land use types (i.e., area in undergoing regeneration after agriculture, pasture, and mature forest), as well as the

interaction between these two factors on pH soils from *Atta opaciceps* colonies on Catimbau National Park, Buíque, PE, Brazil.

Figure 7. Effects of nest soil and non-nest soil treatments and land use types (i.e., area in undergoing regeneration after agriculture, pasture, and mature forest), as well as the interaction between these two factors on CEC (cation exchange capacity) in the soils of *Atta opaciceps* colonies in the Catimbau National Park, Buíque, PE, Brazil.

Figure 8. *Atta opaciceps* nest soil where the soil was collected for physical-chemical analyzes (a); external refuse dumps litter of the *A. opaciceps* nest with organic matter residues (b). area undergoing regeneration after agriculture (c); area regenerating after pasture (d) and area of mature forest (e).

Figure 1.

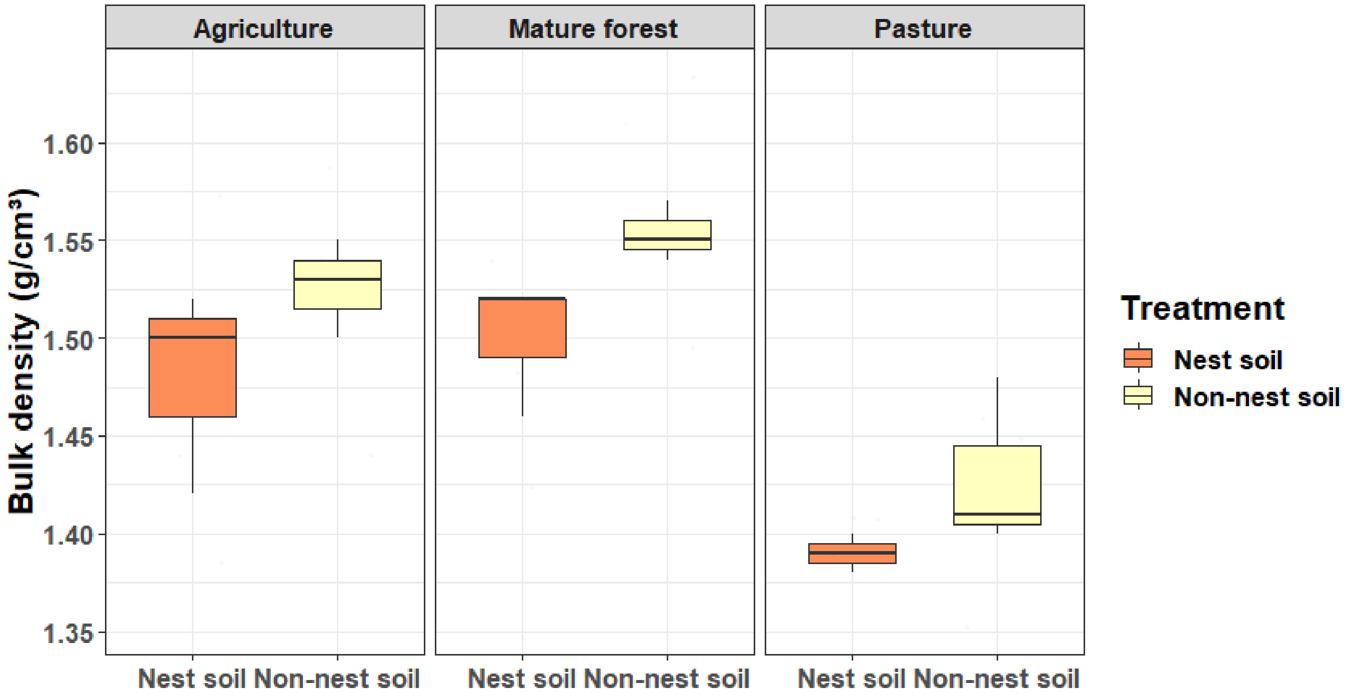
Agriculture
Mature forest
Pasture
Bulk density (g/cm³)
1.60
1.55
1.50
1.45
1.40
1.35
Nest soil
Non-nest soil
Nest soil
Non-nest soil
Nest soil
Non-nest soil
Treatment
Nest soil
Non-nest soil

Figure 2.

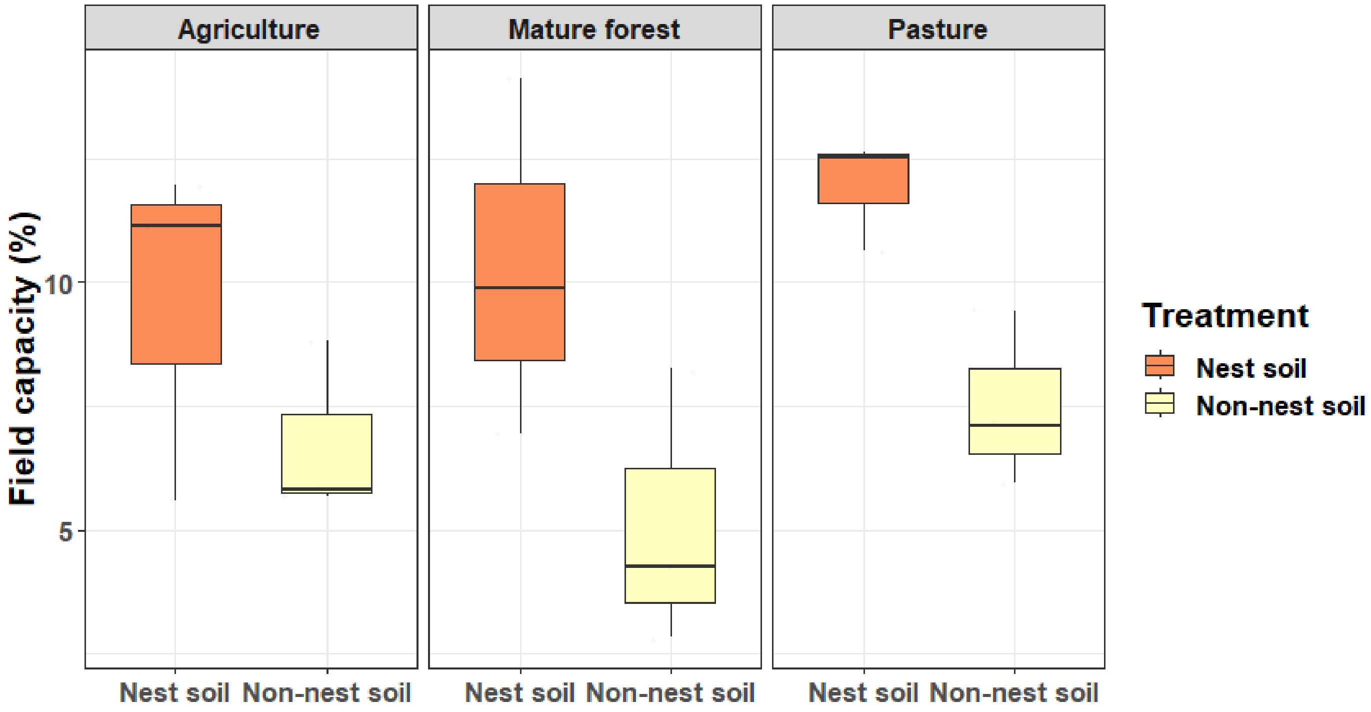
Agriculture
Mature forest
Pasture
Field capacity (%)
10
5
Nest soil
Non-nest soil
Nest soil
Non-nest soil
Nest soil
Non-nest soil
Treatment
Nest soil
Non-nest soil

Figure 3.

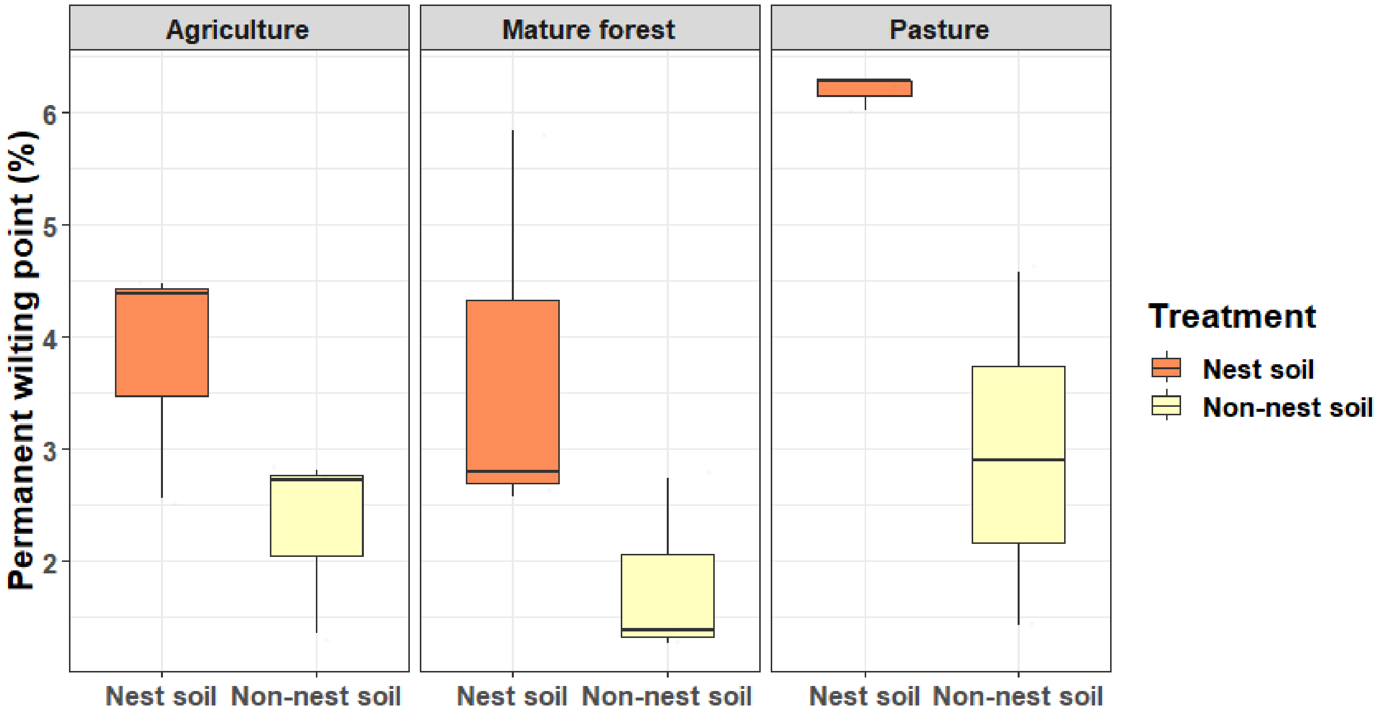
Agriculture
Mature forest
Pasture
Permanent wilting point (%)
2
3
4
5
6
Nest soil
Non-nest soil
Nest soil
Non-nest soil
Nest soil
Non-nest soil
Treatment
Nest soil
Non-nest soil

Figure 4.

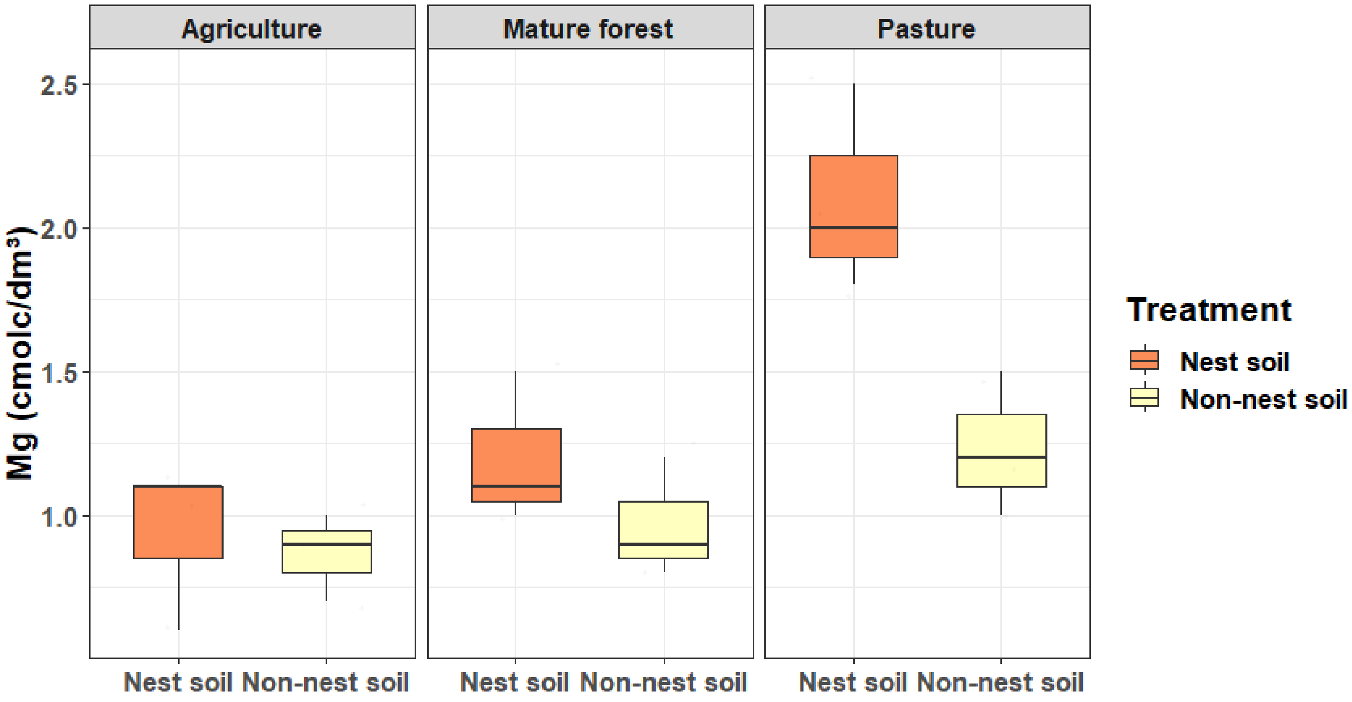
Agriculture
Mature forest
Pasture
Mg (cmolc/dm³)
2.5
2.0
1.5
1.0
Nest soil
Non-nest soil
Nest soil
Non-nest soil
Nest soil
Non-nest soil
Treatment
Nest soil
Non-nest soil

Figure 5.

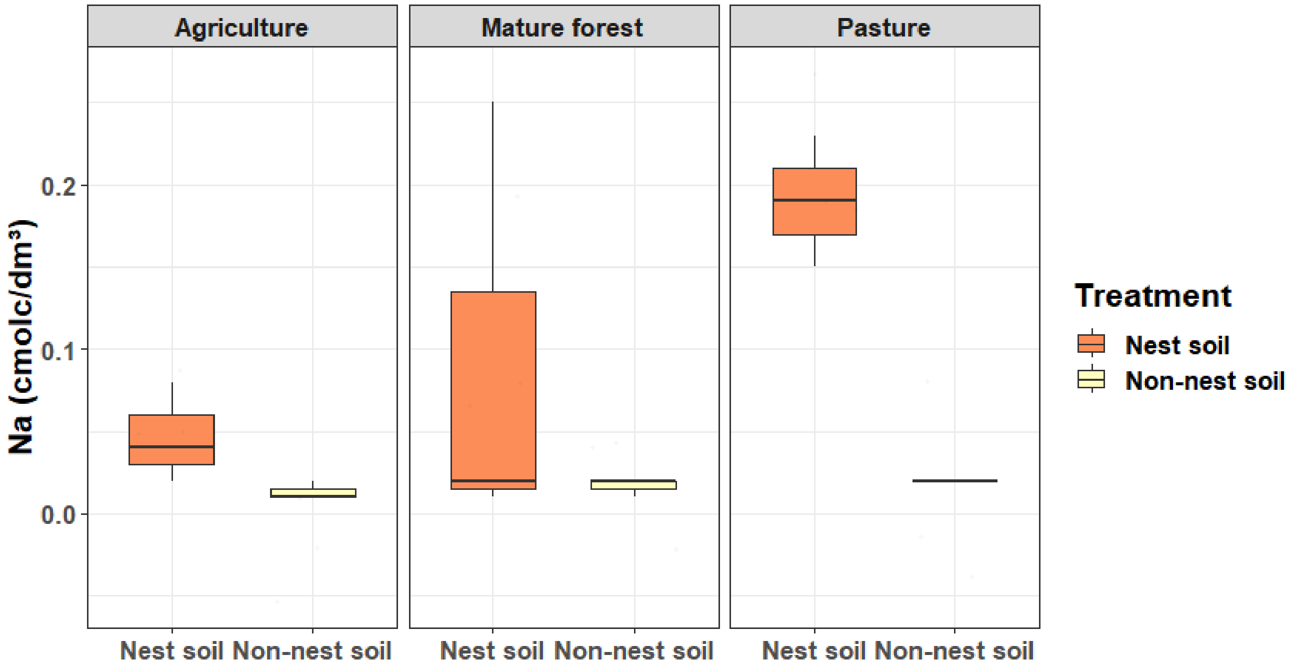
Agriculture
Mature forest
Pasture
Na (cmolc/dm³)
0.2
0.1
0.0
Nest soil
Non-nest soil
Nest soil
Non-nest soil
Nest soil
Non-nest soil
Treatment
Nest soil
Non-nest soil

Figure 6.

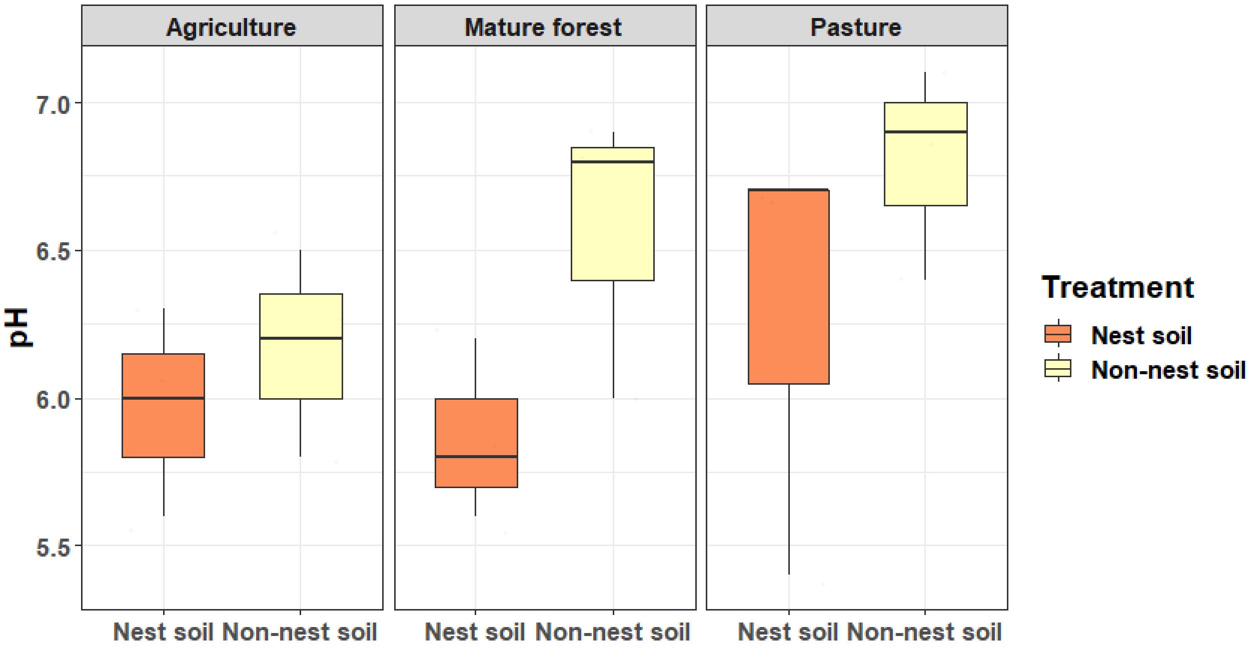
Agriculture
Mature forest
Pasture
pH
7.0
6.5
6.0
5.5
Nest soil
Non-nest soil
Nest soil
Non-nest soil
Nest soil
Non-nest soil
Treatment
Nest soil
Non-nest soil

Figure 7.

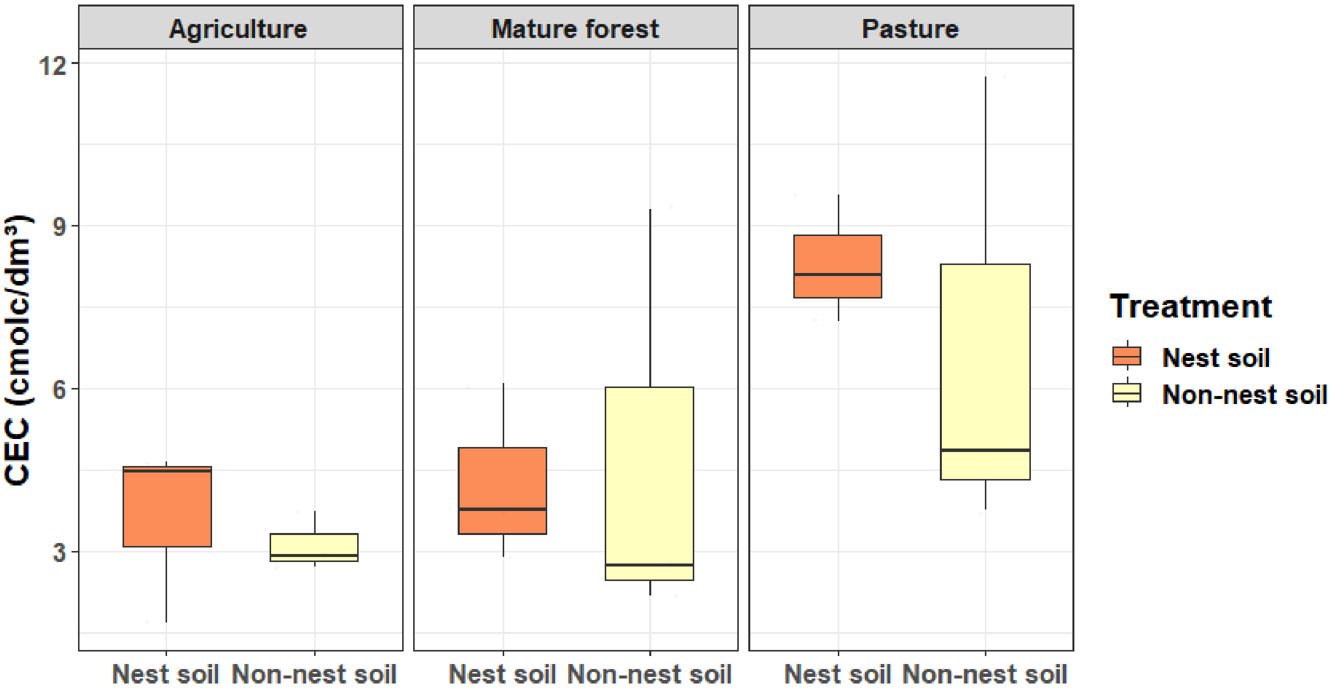
Agriculture
Mature forest
Pasture
12
9
6
3
CEC (cmolc/dm³)
Nest soil
Non-nest soil
Nest soil
Non-nest soil
Nest soil
Non-nest soil
Treatment
Nest soil
Non-nest soil

Figure 8.

CAPÍTULO II: INFLUÊNCIA DO SOLOS DE FORMIGAS CORTADORAS NA PRODUTIVIDADE DE PLANTAS EM ÁREAS COM DIFERENTES HISTÓRICOS DE USO DA TERRA NA CAATINGA

MANUSCRITO A SER SUBMETIDO NO PERIODICO

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4 INFLUENCE OF LEAF-CUTTING ANTS SOILS ON PLANT PRODUCTIVITY IN AREAS WITH DIFFERENT HISTORY OF LAND USE IN CAATINGA

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ABSTRACT

Tropical forests are important for maintaining biodiversity. However, these forests were transformed into agriculture and pasture, abandoned and are currently in the process of regeneration. Leaf-cutting ants proliferate in these secondary forests and can influence the successional trajectory of the forest. In this study we evaluated the effect of the construction and maintenance of leaf-cutting ant nests on the survival and growth rate of above-ground plants in areas regenerating after agriculture, pasture and in areas of mature forest in the Caatinga dry forest. The study was carried out in three areas with different land use types (areas regenerating after agriculture, areas regenerating after pasture and mature forest). In the three different land use types, we established ten plots, five in *Atta opaciceps* nest soils and five with no nest soil effect. In each plot, 30 individuals were transplanted, ten individuals from each of the three plant species of the Fabaceae family (i.e., Cenostigma pyramide, *Cenostigma microphyllum* and *Pityrocapra moliniformis*). Subsequently, we monitored for one year the survival of plants and the growth rate of plants above ground (stem diameter, stem length and emission of leaves and branches) of all individuals of the three plant species selected for this study. Thus, our results indicate that plant survival after one year did not differ between soil treatments, land use types and there was also no interaction between soil treatments and land use types. Stem diameter did not differ between soil treatments and did not differ between land use types, nor was there any interaction between soil treatments and land use types. For stem length, we also did not observe differences between soil treatments, as well as for land use types and for the interaction between soil treatment and land use types. Finally, for the emission of leaves and branches we did not observe differences between soil treatments, for areas with different land use types and for the interaction between soil treatment and land use types. Our results indicate that *Atta opaciceps* nests have a neutral effect on plant survival and aboveground plant growth. Therefore, more studies are needed to verify whether in fact the soils of leaf-cutting ant nests have a neutral and/or positive or negative effect on the regeneration process of Caatinga vegetation, just as the negative effect via herbivory on plant regeneration has already been found.

Keywords: environmental degradation, plant productivity, leaf-cutting ants, tropical dry forests.

1. INTRODUCTION

Tropical forests are important repositories of biodiversity and ecosystem functions that directly and indirectly offer essential goods and services for the survival of human populations at all geographic scales (Liang *et al.* 2016, Arroyo-Rodríguez *et al.* 2017, Brockerhoff *et al.* 2017, IPCC 2019, Poorter *et al.* 2021). But changes in land cover and land use threaten tropical forests, among which we can mention agriculture, logging, livestock, mining, energy generation and other infrastructures (Tabarelli 2010, Chazdon *et al.* 2011, Battisti *et al.* 2016, Melito *et al.* 2021). As a consequence, tropical forest areas present high rates of deforestation, habitat loss and land degradation that convert the landscapes of these forests into landscapes dominated by secondary forests (i.e., forests in regeneration process) (Chazdon 2014, Liang *et al.* 2016, Rito *et al.* 2017, Poorter *et al.* 2021). Globally, more than half of old-growth forests have been converted to secondary forests (Poorter *et al.* 2016, FAO 2018). In the Neotropical region, secondary or regenerating forests represent up to a third of forest areas (Chazdon & Guariguata 2016, Poorter *et al.* 2021). In this way, secondary forests are essential for conserving biodiversity and maintaining the way and quality of life of human populations (Letcher & Chazdon 2009, Lennox *et al.* 2018, Poorter *et al.* 2019). Given this scenario, there is great scientific interest in understanding the processes that are influencing regeneration in secondary forests (Arroyo-Rodríguez *et al.* 2015, Poorter *et al.* 2021). This knowledge is crucial to understanding the capacity of secondary forests to maintain biodiversity, ecosystem function and services, advance succession theory, design forest restoration strategies, and capitalize on climate change mitigation potential (Chazdon 2008, Chazdon & Guariguata 2016, Arroyo-Rodríguez *et al.* 2017, Rozendaal *et al.* 2019, Poorter *et al.* 2021). Within tropical forests, these concerns and goals are also projected for seasonally dry tropical forests (Pennington *et al.* 2009).

Seasonally dry tropical forests (hereafter dry forests) experience various types of human disturbance, including slash-and-burn agriculture, which annually converts vegetation remnants into short-cycle crops (Souza, Sfair, de Paula, *et al.* 2019). Additionally, both, old-growth forests remnants and regenerating forest stands are also subject to livestock farming and the exploitation of timber and non-timber forest products that provide livelihoods for low-income human populations (Chazdon *et al.* 2011, D’Odorico *et al.* 2013, Ribeiro *et al.* 2015, FAO 2019, Souza, Sfair, Souza, Alexandre Paula, *et al.* 2019), known as chronic disturbance (Singh 1998). Studies on regeneration in dry forests have investigated whether the recovery rate and the successional trajectory present similar patters to the much more studied tropical rain forests (Lebrija-Trejos *et al.* 2008, Lohbeck *et al.* 2013). Some studies report an increase in forest biomass, species richness and deterministic successional trajectories as reported for rain forests (Lebrija-Trejos *et al.* 2008, Mora *et al.* 2014). However, other studies also report the possibility that alternative successional trajectories may exist depending on different biotic and abiotic filtering, such as high spatio-temporal water availability, low productivity, seed viability, seedling recruitment and survival, resprouting ability, specialized plant-animal interactions and chronic disturbance pressure (Lohbeck *et al.* 2013, Arroyo-Rodríguez *et al.* 2017, Barros *et al.* 2021). These abiotic and biotic agents can drive succession and act as a synergistic agent to accelerate, reduce or equate recovery rates and successional trajectories to those of the tropical rain forest (Vieira & Scariot 2006, Lebrija-Trejos *et al.* 2010, D'Odorico *et al.* 2013, Lohbeck *et al.* 2013, Mora *et al.* 2014, Barros *et al.* 2021).

The Caatinga dry forest is the largest and most diverse dry forests in the world (Silva & Barbosa 2017). Since the XVI century with the European colonization Caatinga vegetation have been explored by human activities, and nowadays around 63% of its the original cover have been lost to the establishment of agricultural fields and pasturelands, leading to habitat loss and environmental degradation (Souza *et al.* 2019). The remaining vegetation is currently subdivided into 47,100 fragments of varying sizes and three-quarters of this remaining vegetation (32 million ha) lies within one kilometer of the edge, exposing the majority of this forest for human use (Antongiovanni *et al.* 2018, 2020). These remnants are also exposed to human activities such as extensive livestock farming, firewood collection, extraction of timber and non-timber forest products, in addition to slash-and-burn agriculture, which annually converts vegetation remnants into cash crops (Leal *et al.* 2015, Ribeiro *et al.* 2015, Silva & Barbosa 2017, Arnan *et al.* 2018) addition to these degradation agents, the 30% increasing in aridity predicted for the Caatinga dry forest (Magrin *et al.* 2014) may act synergistically to human disturbance leading to loss of plant productivity and soil quality (Rito et al. 2017, Souza et al. 2019). These conditions contribute to the high density of leaf-cutting ants in human-modified landscapes and regenerating stands of the Caatinga dry forest (Siqueira *et al.* 2017, 2018).

Leaf-cutting ants of the genera *Atta* (Fabricius, 1804) and *Acromyrmex* (Mayr, 1865) are considered the most voracious herbivores in the neotropics, being able to collect up to half a ton of leaves per colony and per year, comprising up to 50% of the local flora species (Wirth *et al.* 2003). In addition to removing leaves, these ants collect flower, fruits, seeds and seedlings, influencing the spatial distribution and structure of plant communities and altering the successional trajectory of plant assemblages (Wirth *et al.* 2003, Corrêa *et al.* 2010, Silva *et al.* 2012, Swanson *et al.* 2019). In addition to seed predation and herbivory, leaf-cutting ants can also interfere with plant development via changes in soil resulting from the construction and maintenance of nests (Farji-Brener & Medina 2000, Meyer *et al.* 2013, Farji-Brener & Werenkraut 2015a). During nest construction and maintenance, leaf-cutting ants end up inverting the soil horizon, depositing more mineral soil on the surface of the nest and more nutrient-rich soil is deposited within underground chambers (Moutinho *et al.* 2003, Meyer *et al.* 2013, Swanson *et al.* 2019) or on the soil surface depending on the Atta species (Farji-Brener & Ghermandi 2000, Farji-Brener & Werenkraut 2015b, Farji-Brener & Tadey 2017, Oliveira, Centeno-Alvarado, *et al.* 2023). As a result of these activities in the nest, leaf-cutting ants promote increased porosity, aeration, temperature, and greater variability of soil nutrients in the nest area (Moutinho *et al.* 2003, Meyer *et al.* 2013, Swanson *et al.* 2019). Previous studies demonstrate an improvement in the concentration of soil nutrients within the nest area, favoring greater growth, development, abundance, and fitness of plants (Farji-Brener & Tadey 2009, 2017, Farji-Brener & Werenkraut 2015, Oliveira et al. 2023). However, several studies have reported that in Atta species with internal refuse dumps, there was a reduction in the availability of nutrients in the nest soil when compared to areas without influence of the nest soil, negatively affecting seedling recruitment, seed germination, survival, seedling growth and plant community structure (Corrêa et al. 2010, Meyer et al. 2011b, a, 2013, Madureira et al. 2013, Knoechelmann et al. 2020, Oliveira, et al. 2023). Therefore, the disturbances generated by the construction and maintenance of nests can generate positive and negative impacts on the development of plants Farji-Brener & Werenkraut 2015, Oliveira, et al. 2023).

In the dry forest of the Caatinga, the occurrence of three species of leaf-cutting ants has already been observed (i.e., *Atta laevigata* (Smith, 1858); *Atta sexdens*; (Linnaues, 1758; Siqueira et al., 2017) and *Atta opaciceps* (Borgmeier, 1939), with the species *A. opaciceps* being endemic to the Caatinga (Siqueira, *et al.* 2018). The three species of leaf-cutting ants already mentioned, in addition to having internal refuse dumps, can also deposit waste from their nests in external refuse dumps, resulting in fertility mosaics along the entire length of the nest (Siqueira et al. 2017, 2018, Knoechelmann et al. 2020, Oliveira, et al. 2023). For the species A. opaciceps, the proliferation of its colonies has already been seen in the dry forests of the Caatinga in areas modified by man (Siqueira *et al.* 2017), as well as the anthropogenic landscapes of the Caatinga also showing higher rates of herbivory (Siqueira *et al*. 2017, 2018), which results in greater herbivory pressure on vegetation in general. Furthermore, a recent study reported lower seed deposition in the soil (Oliveira, et al. 2023) and lower seedling recruitment (Knoechelmann *et al.* 2020) in areas affected by ant nests and foraging areas in the Caatinga dry forest, indicating a negative effect of these ants on the regeneration of the Caatinga. However, another recent study in the Caatinga area showed a neutral effect of herbivory and changes in the soil of A. opaciceps on the fitness of the plant species *Cenostigma pyramidale* and a positive effect of herbivory on the plant species *Indigofera suffruticosa,* which boosted greater fruit production in the nests and twice as much production of flowers and fruits in the external refuse dumps as in the nest soil (Oliveira, et al. 2023). Thus, we can consider that leaf-cutting ants are key organisms in forest regeneration both due to their effects as herbivores and via soil change, presenting a high potential to directly and indirectly influence plant survival and plant growth above ground (Siqueira et al. 2017, 2018, Knoechelmann et al. 2020, Oliveira, et al. 2023, Oliveira, et al. 2023).

The general objective of this study was to evaluate the effect of the construction and maintenance of leaf-cutting ant nests on the survival and growth rate of above-ground plants in areas regenerating after agriculture, pasture and in areas of mature forest in the dry forest of the Caatinga. We hypothesize that (1) leaf-cutting ants contribute to improved seedling survival and growth and (2) differences in plant survival and growth between nest soils and non-nest soils will be more pronounced in areas in regenerating forests than in mature forests. This expectation arises due to soil degradation in regenerating areas, making any improvements resulting from the presence of nests more visible compared to the relatively less soil degradation in mature forests. We expect nest soils to have greater plant survival, greater stem length, greater stem diameter, and greater leaf and branch emission compared to non-nest soils.

2. METHODOLOGY

2.1 Study area

This study was carried out in the Catimbau National Park (8°24'00" and 8°36'35" South and 37°09'30" and 37°14'40" West), located in the state of Pernambuco, northeast of Brazil. The park covers 607 km² in area and has a characteristic climate of the Bsh type (semi-arid) with transition to the rainy tropical type As', according to the Köppen classification. Annual precipitation varies between 480 and 1100 mm and the average annual temperature fluctuates around 23°C (Rito *et al.* 2017). The soils found in the park are predominantly quartz sands (Siqueira *et al.* 2017) and the vegetation is low-sized dry forest (Rito *et al.* 2017). The Park was created in 2002, but few people were compensated, which leads the population to exploit natural resources for their subsistence, generating significant pressure on the vegetation (Lins *et al.* 2022, Noutcheu *et al.* 2023, Oliveira, *et al.* 2023).

2.2 Study species

In the area that covers the entire park, more than 300 colonies of leaf-cutting ants of the species *Atta laevigata, A. opaciceps* and *A. sexdens* have been recorded (Siqueira *et al.* 2017). In this study we focus on the endemic species *Atta opaciceps* (Borgmeier, 1939), which is the leaf-cutting ant with the highest colony density in the park (Siqueira *et al.* 2017). Colonies are generally more abundant in regenerating forest stands and other human-modified landscapes (Siqueira *et al.* 2017). Their nests expand to an area of approximately 38 m² (Siqueira *et al.* 2018), reaching an average density of up to 35.5 ha-1 in the Catimbau National Park (Siqueira *et al.* 2017) and removing 244 kg of dry weight/ colony/year (Siqueira *et al.* 2018).

2.3 Methodological procedures

To verify the influence of leaf-cutting ant nest construction on plant growth in regenerating forest stands after agriculture and pasture and in old-growth forest areas, we initially selected three species of plants that are abundant in the park and also harvested by leaf-cutting ants (Siqueira *et al.* 2017). The three selected species belong to the Fabaceae family: *Cenostigma microphyllum* (Mart. ex G. Don) E. Gagnon & G. P. Lewis. *Cenostigma pyramidale* (Tul.) Gagnon & GPLewis and *Ptyrocarpa moniliformis* (Benth.) Luckow & RW Jobson. Seeds from these three species were donated by NEMA (Núcleo de Ecologia e Monitoramento Ambiental) and were sown in the park's greenhouse using the OmniVerdi Riza technique (see Pereira et al. 2021). Briefly, this technique involves the entire root of the seedlings as well as their roots in a permeable tissue that is later inserted into a PVC tube 75 cm long and 6 cm wide. With this technique it is possible to reduce mechanical pressure at the time of planting, protecting the root system (Pereira *et al.*2021). Seed dormancy was broken by immersing the seeds of *Cenostigma pyramidale* and *Cenostigma microphyllum* in water for 24 hours and of *Ptyrocarpa moniliformis* in sulfuric acid (H_2SO_4) for 20 minutes. All seeds of the three plant species were sown in October 2020. After germination, the seedlings remained in a greenhouse for 6 months until they reached 5 cm in height to be transplanted into the field.

In parallel with the germination phase, we selected three areas that represent the main land use types within the park: (1) areas that were used for at least 30 years as pasture for cattle and goats and are now undergoing regeneration for 8-10 years (i.e. regenerating forest stands after pasture use) (2) areas that were deforested and used to grow corn and beans for 3-4 years and then abandoned and are in the process of regeneration for 12 years (i.e., regenerating forest stands after agriculture) and (3) areas covered by old-growth forest, i.e., with no history of land use for at least 80 years (i.e., old-growth forest stands) (see Santos-Neto 2021 for more detail on the areas). As there are goats and cattle in the park and we wanted to avoid their trampling and herbivory on the seedlings, we installed a pair of 3m x 3m (9 m^2) plots, one above the nest (i.e. nest plot) and the other one 10 meters from the nest edge (i.e. control plot non-nest soil) (Figure 1). In total, 30 paired plots were established, 10 for each treatment (regenerating forest stands after agriculture, regenerating forest stands after pasture and mature forest stands) being five plots above the nest and five plots 10 m from the edge of the nest. After establishing the plots, 100 seedlings of each species were transplanted to the field according to the following methods: 10 seedlings were transplanted to each land use types (regenerating forest stands after agriculture, regenerating forest stands after pasture and and mature forest stands), of which five seedlings were transplanted to each soil treatments (nest and control soils), totaling 900 seedlings. These seedlings also received Tanglefoot® entomological glue (Tanglefoot Company, Grand Rapids, Michigan USA) around the stem to prevent herbivory by leaf-cutting ants (Oliveira *et al.* 2019) (Figure. 2.b); we thus nullified the herbivory effect and evaluated only the leaf-cutting ant effect related to nest construction and maintenance on seedling performance. We monitored seedling survival and aboveground plant attributes (i.e., stem diameter, stem length, number of leaves and branches). We did not measure plant attributes below ground because these seedlings were transplanted for long-term monitoring. To measure aboveground plant growth, a digital caliper and a 50 cm ruler were used in the field. Survival, stem diameter and length, number of leaves and branches produced were measured every two months from December 2021 to December 2022. We obtained six readings for the aboveground plant growth attributes. To account for seedling survival by species, soil treatment and land use types, we quantified the number of individuals during the study period. Subsequently, we calculated the survival of the seedlings using the formula:

$$Sobreviv\hat{e}ncia\ (i, f) = \frac{n^{\underline{o}}\ mudas\ (f)}{n^{\underline{o}}\ mudas\ (i\ )} x100$$

Where number of seedlings *(f)* is the final number of seedlings in the plots at the end of the experiment and number of seedlings *(i)* is the number of seedlings at the beginning of the experiment.

To measure the relative growth rate in plant attributes above ground, we use the following formula:

$$TCR = \frac{ln\ Mf - ln\ Mi}{Tf - Ti}$$

Where (Mf) can be the length, diameter, average final number of leaves and branches and (Mi) can be the initial average diameter, length, number of leaves and branches. (Tf) and (Ti) are the final and initial time intervals and (ln) is the Neperian or natural logarithm, according to the methodology of BENICASA (2004).

2.4 Data analysis

To verify our hypothesis that leaf-cutting ants contribute to improved seedling survival and growth, differences in plant survival and growth between nest soils and non-nest soils will be more pronounced in regenerating areas than in in mature forests, we used Generalized Linear Mixed Models (GLMM) with soil treatment (nest soils and non-nest soil) and land use types (areas regenerating after agriculture, areas regenerating after pasture and mature forest) as explanatory variables. As a response variable, we used survival and plant growth attributes above ground (i.e., stem diameter, stem length, number of leaves and branches) and nest as a random factor. We tested the effects of the explanatory variable and the interactions between them on survival and above-ground plant growth attributes. All of these analyzes were performed with the Lme4 and lmerTest packages in R (Bates *et al.* 2015, Kuznetsova *et al.* 2017).

3. RESULTS

Overall, we found low seedling survival for the three focal plant species, slightly higher for Cenostigma microphyllum (28%), followed by Cenostigma piramidale (23%) and Ptyrocarpa moniliformis (6%). Regarding soil treatments, nest soils had a plant survival percentage of 52% and non-nest soil 63%, with no significant difference (χ^2 = 3.16, df = 1, P = 0.07; Table 1). Regarding the types of land use, we observed that the survival of seedlings in the area regenerating after agriculture was 28%, followed by the area regenerating after pasture with 16% and the mature forest area with 13%, without significant difference (χ^2 =2.43, df =2, P = 0.29; Table 1) and that the difference between nest soil and non-nest soil across land use types was also not significant (χ^2 =1.66, df =2 , P = 0.43; Table 1).

Regarding plant growth attributes above ground, the average stem diameter was 2.68±0.84 mm, ranging from 0.64 to 5.98 mm. We found that stem diameter did not differ between soil treatments (χ^2 = 0.48; df = 1; P = 0.48; Table 1) and was not significant across land use types (χ^2 = 0.88 df = 2, P = 0.64; Table 1). Furthermore, stem diameter did not differ between soil treatments and land use types (χ^2 = 1.55 df = 2, P = 0.45; Table 1). The same pattern was observed for stem length, which averaged 8.35±4.44 cm, varying from 0.28 to 30 cm. We saw that stem length did not present significant differences between soil treatments (χ^2 = 0.84; df = 1; P = 0.35; Table 1) and land use treatments (χ^2 = 0.09 df = 2; P = 0.95; Table 1), as well as did not differ between soil treatment and type of land use (χ^2 = 1.96, df = 1; P = 0.37; Table 1). Leaf production had an average of 4.16±3.58, ranging from 1 to 35. We found that leaf production was not significant in the soil treatments (χ^2 =0.95; df = 1; P = 0.32 ; Table 1), in the types of land use (χ^2 =3.05; df = 2; P = 0.21; Table 1) and showed no difference between soil treatments and types of land use (χ^2 =2 .33; df = 2; P = 0.31; Table 1). Regarding the number of branches, there was no difference between soil treatments (χ^2 =0.09; df = 1; P = 0.76; Table 1), as well as between types of land use (χ^2 =3, 06; df = 2; P = 0.21; Table 1) and there was no difference between soil treatments and types of land use (χ^2 =2.79; df = 2; P = 0.24; Table 1) . Finally, the production of branches reached an average of 1.26±0.56, ranging from 1 to 7.

4. DISCUSSION

In this study we evaluated how leaf-cutting ants influence plant survival and plant growth attributes through soil changes due to nest construction and maintenance in areas regenerating after agriculture, pasture and mature forest. We hypothesize that (1) leaf-cutting ants contribute to improved survival and growth of above-ground plants and (2) differences in plant survival and growth between nest soils and non-nest soils will be greater. pronounced in regenerating areas than in mature forests. Our hypotheses were not corroborated, as our results did not demonstrate any variation in seedling survival or plant growth between soils treatments and land use types. Although we have observed (1) higher quality of soil physic-chemical attributes under leaf-cutting ant nest influence, and (2) higher differences between nest and control soils in regenerating forest stands in the first chapter of this thesis, it seems that this soil improvement related to leaf-cutting ant nests did not result in better plant performance.

Our results remain unchanged from the general pattern of studies that observed plants growing in soil under the influence of anthills showing greater growth rate, abundance and/or performance (Farji-Brener & Tadey 2009, 2017, Farji-Brener & Werenkraut 2015, 2017). In these studies, they showed an increase in the availability of nutrients in the nest soil for plants, being up to 80 times higher in nutrients than soils without the effect of the nest (Farji-Brener & Werenkraut 2015). Furthermore, studies also found an improvement in the physical conditions of the soil in the nest, promoting lower resistance to penetration, lower apparent density, higher humidity, and greater nutrients available to plants such as Ca, Mg, K and nitrate (Mouitnho *et al.* 2023; Farji-Brener & Werenkraut 2015). , as it has also been seen that plants assimilate nitrogen in nesting sites (Farji-Brener & Ghermandi 2008), promoting - an increase in biomass and fitness (Farji-Brener & Ghermandi 2000, Moutinho *et al.* 2003, Farji-Brener & Ghermandi 2008, Farji-Brener *et al.* 2010), with this increase in biomass and fitness being even greater, especially in places with the effect of external trash (Farji-Brener & Werenkraut 2015, Oliveira, et al. 2023). Additionally, it has been found that the external litter is richer in nutrients through which leaf-cutter ants improve soil fertility when compared to the internal litter (Farji-Brener & Ghermandi 2004, Hudson *et al.* 2009). Typically, it is more common to find organic residues above the nest floor than below the nest floor (Farji-Brener *et al.* 2010, Sousa-Souto *et al.* 2012). Furthermore, only the external refuse dumps can receive additional input of organic matter from the surrounding forest, thus reflecting the general idea that the soils on the surface and/or soils in the external dumps contribute to the plants responding with greater growth, abundance and/or performance (Farji-Brener & Werenkraut 2015).

The lack of change to plant survival and above-ground plant growth attributes related to soil treatments and land use type may be related to construction and maintenance done by worker ants that move large amounts of nutrient-poor mineral soil to the surface of the nest (Meyer et al. 2011a,2011b, 2013). Furthermore, workers also frequently clean the nest surface by removing or burying plants on the nest surface (Bieber *et al.* 2011; Corrêa *et al.* 2010; Meyer *et al.,* 2011a, 2011b, 2013; Stephan *et al.* 2015). However, in the first chapter of this thesis, we observed that the nest soils had lower apparent density, greater field capacity and higher permanent wilting point. We also saw that the pH and concentration of nutrients such as magnesium and sodium were better in soils related to nests. Therefore, it is possible that the plants evaluated in our study have other limitations in addition to the nutrients available in the nest soil. Therefore, even considering that soils under the influence of nests have higher quality attributes, which should be related to greater plant performance, their effect may be small or even secondary when compared to potentially limiting resources for plants (Moutinho *et al.* 2003; Farji-Brener & Werenkraut 2015; Farji-Brener & Tadey 2017), such as the availability of water, which is scarce, seasonal and very unpredictable in the dry Caatinga forest (Ribeiro *et al.* 2021), being more limiting than soil nutrients in dry regions (Farji-Brener *et al.* 2017). Additionally, another factor such as anthropogenic disturbance can also limit the ability of plants to allocate nutrients for their development (Ribeiro *et al.* 2015, Ribeiro-Neto *et al.* 2016). Therefore, even drought-tolerant plants, as is the case of the three plant species used in this study, can suffer from water scarcity when associated with anthropogenic disturbance events (Ribeiro *et al.* 2015; Ribeiro-Neto *et al.* 2016). This may explain the lack of variation in our findings in this study.

Therefore, our results from chapter one show that although leaf-cutting ant nests alter some soil attributes, there is no detectable effect on plant survival and growth, proving to be of little relevance in the recovery processes of degraded areas (Moutinho *et al.* 2003, Farji-Brener *et al.* 2010, Leal *et al.* 2014). It has been seen for other ecosystems, negative effects on the survival and growth of plants above ground, acting as voracious herbivores removing plant structures (i.e. leaves, flowers, twigs, fruits, seeds) (Wirth et *al.* 2003, Leal *et al.* 2014). However, for the Caatinga, our findings indicate that leaf-cutting ants have a neutral effect on plant survival and growth. However, they can also have a positive and/or neutral effect on plant reproduction both via herbivory and by altering soil properties (Oliveira *et al.* 2023). However, it has also been observed in the Caatinga dry forest that leaf-cutting ants benefit from human disturbance and not only proliferate but increase herbivory rates per colony (Siqueira *et al.* 2017, 2018). As well, previous studies in the Caatinga reported lower, less dense and impoverished seed assemblages and decreased seedling recruitment in areas affected by colonies such as nesting and foraging areas (Knoechelmann *et al.* 2020, Oliveira *et al.* 2023), which could negatively impact forest regeneration. Finally, the reproduction of adult individuals is affected in a neutral or even positive way by the herbivory of leaf-cutter ants and by changes in soil attributes related to the construction and maintenance of nests (Oliveira et al. 2023). Thus, the influence of leaf-cutting ants on forest regeneration is indisputable, a positive, negative, and neutral influence on the survival, growth, and reproduction of plants (Siqueira *et al.* 2017, 2018, Knoechelmann *et al.* 2020, Oliveira *et al.* 2023a; 2023b).

Although the role of leaf-cutting ants in the Caatinga vegetation regeneration process is still unclear, as positive, negative, and neutral effects have been reported, their importance is undoubted. The amount of vegetation harvested by each colony (30% of the stand leaf-crop in their foraging area, Siqueira *et al.* 2018), associated to the higher colony density (up to 16 colonies per hectare, Siqueira *et al.* 2017) in disturbed areas may indicate a very strong effect on the regeneration of Caatinga. This effect may include a delay in the regeneration (i.e. arrested succession) or promote new critical and stable alternative states, such as desertification (Silva & Barbosa 2017, Siqueira *et al.* 2017, Tabarelli *et al.* 2017).

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Table 1. Results of the growth attributes of plants above ground in relation to soil treatments (nest soils and non- nest soil) of *Atta opaciceps*, in land use types (areas regenerating after agriculture, pasture and mature forest) and the interaction between these explanatory variables in Catimbau National Park, Pernambuco, Brazil. For each variable we indicate the chi-square (χ^2), the degree of freedom (gl) and 95% confidence intervals. Significant variables (according to 95% confidence intervals).

	Stem Diameter (mm)			Stem Length (cm)			Leaf (N◦)			Branches (N◦)			Survival (%)		
Predictors	X^2	*df*	$p<0.05$	X^2	*df*	$p<0.05$	X^2	*df*	$p<0.05$	X^2	*df*	$p<0.05$	X^2	*df*	$p<0.05$
Soil treatments	0.48	1	0.48	0.84	1	0.35	0.95	1	0.32	0.09	1	0.76	3.16	1	0.07
Land use types	0.88	2	0.64	0.09	2	0.95	3.05	2	0.21	3.06	2	0.21	2.43	2	0.29
Soil treatments: Land use types	1.55	2	0.45	1.96	2	0.37	2.33	2	0.31	2.79	2	0.24	1.66	2	0.43

LEGEND OF THE FIGURES

Figure 1. Plot in the Atta opaciceps nest in the area undergoing regeneration after agriculture (a); non-nest soil plot in the area in the an area undergoing regeneration after agriculture (b); nest soil plot in the area regenerating after pasture (c); non-nest soil plot in the area regenerating after pasture (d); nest soil plot in mature forest area (e); non-nest soil plot in the area in mature forest area (control) (f) in Catimbau National Park, Buíque, Pernambuco, Brazil.

Figure 2. Production of seedlings in the nursery of the three Fabaceae species: *Cenostigma microphyllum*, *Cenostigma pyramidale* and *Ptyrocarpa moniliformis* (a); addition of tanglefoot to the stem of seedlings to prevent herbivory by leaf-cutting ants (b); young individual of the species *Cenostigma pyramidale* (c); young individual of the species *Ptyrocarpa moniliformis* (d); young individual of the species *Cenostigma microphyllum* (e), in Catimbau National Park, Buíque, Pernambuco, Brazil.

Figure 1.

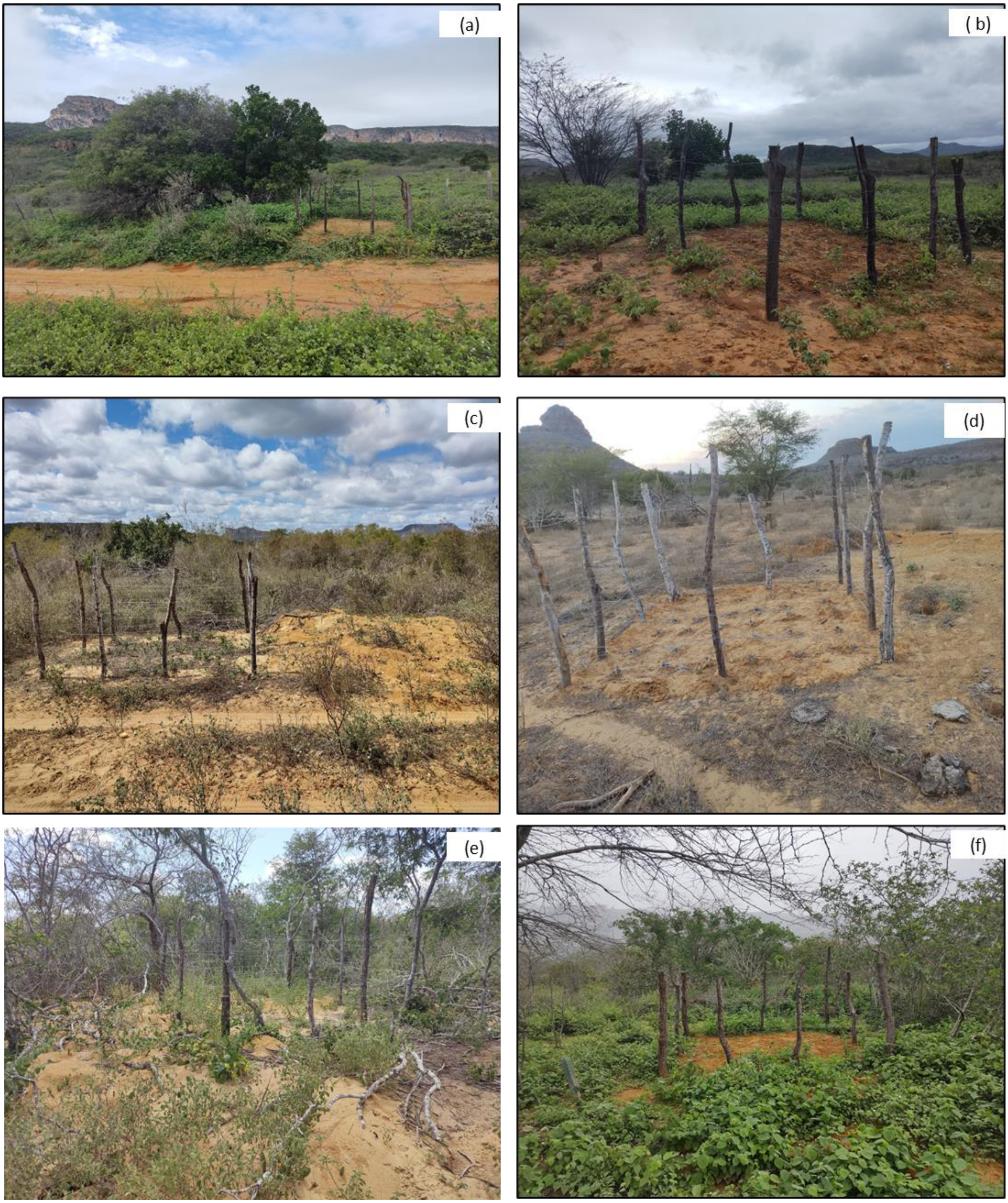

Figure 2.

5 CONCLUSÕES

Neste estudo invetigamos o efeito da construção e manutenção de ninhos de formigas cortadeiras na sobrevivência e taxa de crescimento de plantas acima do solo em áreas em regeneração após agricultura, pastagem e em áreas de floresta madura na floresta seca da Caatinga. Os resultados do capítulo 1 indicam que os solos dos ninhos de fromigas cortadeiras melhoram os atributos físico-químicos do solo principalmente em áreas em regeneração após o uso de pastagem. Mais especificamente, observamos que o solo dos ninhos das formigas cortadeiras possui melhores atributos do solo quando comparado ao solo sem ninhos (isto é, controle), promovendo menor densidade aparente, maior capacidade de campo e maior ponto de murcha permanente. Além disso, vimos que a diferença na densidade aparente e no ponto de murcha permanente no solo de ninho e no solo sem ninho foi maior nas áreas em regeneração após pastagem do que na área em regeneração após agricultura e floresta madura. Também observámos concentrações mais elevadas de alguns nutrientes, como o magnésio e o sódio, além do valor de pH com acidez adequada para desenvolvimento de culturas no solo dos ninhos do que no solo sem ninhos, enquanto para outros nutrientes não houve diferença entre os tratamentos do solo e os tipos de uso da terra. Dessa forma, solos sob influência de formigas cortadeiras podem ajudar na recuperação de áreas degradadas por perturbações antropicas que aceleram o processo de degradação. Todavia, esta melhoria nos atributos do solo nos ninhos de formigas cortadeiras não repercutiu na sobrevivência e desempenho da planta como sugerem os resultados do capítulo 2. Especificamente, a sobrevivência e crescimento de planta acima do solo (i.e., diamentro do caule, comprimento do caule, emissão de folhas e ramos) permaneceu inaltarável em relação os tratamento do solo e tipo de uso da terra.

É bem conhecido que as formigas cortadeiras se beneficiam com perturbações antrópicas em todos os ecossistemas neotropicais, incluindo a Caatinga. Há um aumento no número de colônias em áreas perturbadas e em regeneração (SIQUEIRA et al. 2017), bem como nos danos causados à vegetação destas áreas (SIQUEIRA et al. 2018, KNOECHELMANN et al. 2020, OLIVEIRA et al. 2022). Os benefícios na qualidade dos solos observados neste estudo, sobretudo em áreas em estágios iniciais de sucessão, podem indicar um efeito positivo destas formigas à vegetação, mesmo que não tenhamos observado tal efeito no nosso estudo. Neste sentido, o efeito das formigas cortadeiras nos atributos físico-químicos dos solos talvez consiga ajudar a recuperar a qualidade do solo de áreas degradadas. Esses achados se somam ao estudo recentemente publicado que demonstra efeito neutro ou até mesmo positivo das formigas cortadeiras no sucesso reprodutivo de plantas da Caatinga, tanto via alterações nos solos devido a contsrução dos ninhos como devido ao seu papel como herbivoros dominantes (OLIVEIRA et al. 2023).

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Divida seu artigo em seções claramente definidas e numeradas. As subseções devem ser numeradas 1.1 (depois 1.1.1, 1.1.2, ...), 1.2, etc. (o resumo não está incluído na numeração das seções). Use esta numeração também para referências cruzadas internas: não se refira apenas ao 'texto'. Qualquer subseção pode receber um breve título. Cada título deve aparecer em sua própria linha separada.

Introdução

Declare os objetivos do trabalho e forneça uma base adequada, evitando um levantamento detalhado da literatura ou um resumo dos resultados.

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Fornecer detalhes suficientes para permitir que o trabalho seja reproduzido por um pesquisador independente. Os métodos já publicados devem ser resumidos e indicados por uma referência. Se citar diretamente de um método publicado anteriormente, use aspas e também cite a fonte. Quaisquer modificações nos métodos existentes também devem ser descritas.

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Palavras-chave Imediatamente após o resumo, forneça no máximo 6 palavras-chave, usando a ortografia americana e evitando termos gerais e plurais e conceitos múltiplos (evite, por exemplo, 'e', 'de'). Seja poupado com abreviaturas: apenas as abreviaturas firmemente estabelecidas no campo podem ser elegíveis. Essas palavras-chave serão usadas para fins de indexação.

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