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FERNANDA MARIA PEREIRA DE OLIVEIRA

PERTURBAÇÕES ANTRÓPICAS E MUDANÇAS CLIMÁTICAS NA CAATINGA: EFEITOS SOBRE OS SERVIÇOS PROVIDOS POR FORMIGAS ÀS PLANTAS

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Tese apresentada ao Programa de Pós-Graduação em Biologia Vegetal da Universidade Federal de Pernambuco, Área de concentração Ecologia e Conservação, da Universidade Federal de Pernambuco, como requisito parcial para obtenção do título de doutor em Biologia Vegetal.

Orientadora: Profa. Dra. Inara Roberta Leal

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Aprovada em 27/02/2018

COMISSÃO EXAMINADORA:

_____

Profa. Dra. Inara Roberta Leal (Orientadora)
Departamento de Botânica – UFPE

_____

Prof. Dr. Rainer Wirth (Titular externo)
Plant Ecology and Systematics – University of Kaiserslautern

_____

Prof. Dr. Paulo Sérgio Moreira Carvalho de Oliveira (Titular externo)
Departamento de Biologia Animal – UNICAMP

_____

Profa. Dra. Ariadna Valentina de Freitas Lopes (Titular interna)
Departamento de Botânica – UFPE

_____

Prof. Dr. Marcelo Tabarelli (Titular interno)
Departamento de Botânica – UFPE

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RESUMO

A maioria dos ecossistemas terrestres do mundo é composta por um mosaico de remanescentes florestais em diferentes estágios de sucessão e expostos a mudanças climáticas. Tanto perturbações antrópicas quanto mudanças climáticas ao modificarem a composição de espécies que ocorrem em um determinado local, tem o potencial de desencadear efeitos em cascata que se propagam nas interações bióticas e nos serviços resultantes dessas interações. Nesta tese, investigamos como perturbações antrópicas e precipitação afetam a eficiência dos serviços providos por formigas às plantas na Caatinga. O estudo foi conduzido em parcelas estabelecidas dentro do Parque Nacional do Catimbau distribuídas ao longo de gradientes de perturbação antrópica e precipitação. Apesar do local de estudo ser uma unidade de conservação, ele ainda está sujeito a diferentes pressões de perturbações antrópicas crônicas (PAC) desenvolvidas pelas pessoas residentes cujas atividades principais são criação de caprinos e bovinos, extração de lenha e coletas de produtos não madeireiros. Além disso, o local de estudo cobre uma área com diferentes regimes de precipitação variando de 510 a 940 (mm), proporcionando uma grande oportunidade para analisar os efeitos das mudanças climáticas. No primeiro capítulo, nós investigamos como PAC, precipitação e a interação entre esses fatores afetam o serviço de dispersão de sementes por formigas. Para isso, conduzimos experimentos oferecendo diásporos de seis espécies de plantas dispersas por formigas e observamos as taxas de remoção e distância de dispersão desses diásporos. Nós encontramos pouca evidência de efeitos interativos e nenhum efeito de PAC sobre o serviço de dispersão de sementes, mas encontramos um forte efeito da redução da precipitação, a qual reduziu tanto as taxas de remoção quanto as distâncias de dispersão. No segundo capítulo, nós investigamos os efeitos de PAC e precipitação sobre as interações entre formigas e plantas com nectários extraflorais (NEFs). Nós utilizamos *Pityrocarpa moniliformis* como espécie focal devido a sua abundância e distribuição no nosso local de estudo. Nós estimamos a produção de néctar extrafloral, amostramos as formigas que visitam os NEFs e documentamos a eficiência da proteção provida por formigas com a utilização de cupins como herbívoros simulados. Nós encontramos que PAC afetou negativamente o volume de néctar extrafloral. No entanto, essas mudanças não se refletiram na composição de formigas que atendem NEFs nem na eficiência de proteção contra herbívoros. Já a redução da precipitação não afetou a produção de néctar extrafloral, mas mudou a composição de espécies de formigas que visitam NEFs levando à substituição de espécies mais eficiente por menos eficientes. Essas mudanças na composição de espécies, por sua vez,

levaram à redução da eficiência do serviço de proteção. Nossos resultados indicam que PAC e precipitação tem efeitos independentes sobre os serviços providos por formigas às plantas na Caatinga. Além disso, mostramos que o mecanismo responsável pela alteração dos serviços é a mudança na composição de espécies de formigas. Estes resultados podem resultar em efeitos negativos na aptidão de plantas da Caatinga, levando à redução da resiliência desse ecossistema frente ao cenário de redução de precipitação previsto para o final deste século.

Palavras-chave: Mutualismos. Perturbações antrópicas. Mudanças climáticas.

ABSTRACT

Most of the world's terrestrial ecosystems are composed by a mosaic of forest remnants in different successional stages and exposed to climate change. Both anthropic disturbances and climatic changes by modifying the species composition that occur in a given location have the potential to trigger cascade effects on the biotic interactions and the services resulting from these interactions. In this thesis, we investigated how anthropic disturbances and rainfall affect the effectiveness of the services provided by ants to plants in the Caatinga. The study was conducted in plots established within the Catimbau National Park and distributed along gradients of anthropic disturbance and precipitation. Although the study site is a conservation unit, it is still subject to different pressures of chronic anthropic disturbances (CAD) by low-income rural populations that depend on natural resources for their livelihoods. The main activities are livestock pressure (herbivory by goats and cattle), wood extraction (live and dead wood). In addition, the study site covers an area with different rainfall regimes, ranging from 510 to 940 (mm), and providing a great opportunity to analyze the effects of climate change. In the first chapter, we investigated how CAD, precipitation and their interactions affect the seed dispersal services by ants. We conducted experiments offering diaspores of six species of plants dispersed by ants and observed the removal rates and dispersal distances. We found little evidence of interactive effects and no effects of CAD on the seed dispersal services, but we found a strong effect of the reduction of precipitation, which reduced both removal rates and dispersal distances. In the second chapter, we investigated the effects of CAD and precipitation on extrafloral nectary- mediated plant protection services by ants. We used *Pityrocarpa moniliformis* as a focal species, the most common and widely distributed EFN-bearing plant species occurring in our study area. We estimated the extrafloral nectar production, sampled attending ants and documented the effectiveness of EFN-mediated plant protection services by ants by measuring attack on termites as simulated insect herbivore. We found that CAD affected negatively the volume of extrafloral nectar. However, these changes were not translated to the composition of attendant ant species and to the protection effectiveness. On the other hand, the reduction of precipitation did not affect extrafloral nectar production, but it changed the composition of attendant ant species, leading to replacement of more effective by less effective ant protectors. These changes in species composition, in turn, led to a reduction of the protection effectiveness. In general, our results indicate that CAD and precipitation have independent effects on the services provided by ants to plants in the Caatinga. In addition, we showed that

the mechanism responsible for the alteration of the services is the change in ant species composition. These results can lead to negative effects on the fitness of a wide variety of plant species in the Caatinga, reducing the resilience of this ecosystem to the predicted decreasing rainfall scenario forecast to the end of this century.

Key-words: Mutualisms. Anthropogenic disturbances. Climatic change.

LISTA DE FIGURAS

LISTA DE TABELAS

SUMÁRIO

1 INTRODUÇÃO

Mutualismos são responsáveis por diversos serviços ecossistêmicos importantes como polinização, dispersão de sementes e ciclagem de nutrientes (TERBORGH et al., 2008; WILSON et al. 2009; POTTS et al., 2010). Embora interações mutualistas sejam frequentemente consideradas como interações benéficas, mutualismos são muito variáveis no espaço e no tempo (BRONSTEIN, 1994a; NESS; MORRIS, BRONSTEIN, 2006). Em função disso, essas interações podem variar de mutualmente benéfica a prejudicial para pelo menos uma das espécies envolvidas na interação (BRONSTEIN, 1994a). Contudo, essas variações podem aumentar ainda mais com as modificações nas paisagens naturais geradas pelas perturbações antrópicas e mudanças climáticas, comprometendo a eficiência dos serviços ecossistêmicos providos por mutualismos.

Florestas tropicais estão sendo constantemente submetidas a intensos regimes de perturbações de origem antrópica (GARDNER et al., 2009; SUPP; ERNEST, 2014). Estudos recentes vêm chamando a atenção para um tipo de perturbação antrópica caracterizada pela contínua retirada de pequenas quantidades de biomassa florestal: a perturbação antrópica crônica (PAC, sensu SINGH, 1998). Atividades caracterizadas como PAC, como a criação de animais e a extração de lenha e produtos não-madeireiros, são capazes de promover o empobrecimento da comunidade de plantas (RIBEIRO et al., 2015; RIBEIRO-NETO et al., 2016), animais (RIBEIRO-NETO et al., 2016; OLIVEIRA et al., 2017) e interações mutualísticas (LEAL; ANDESEN, LEAL et al., 2014; 2015). Essa situação gerada por PAC, por si só, pode ser considerada um quadro alarmante para a conservação da biodiversidade e manutenção de serviços ecossistêmicos. Contudo, a situação pode se tornar ainda mais grave se considerarmos o cenário de mudanças climáticas globais a que estas florestas estarão submetidas. Para florestas tropicais secas, por exemplo, é esperado que haja um aumento da temperatura e uma redução da precipitação (MAGRIN et al., 2004). Mudanças nas condições ambientais geradas por mudanças climáticas podem alterar ainda mais o padrão de riqueza e composição de espécies nessas paisagens sob intensa perturbação antrópica (GIBB et al., 2015). Ao alterar o conjunto de espécies que ocorrem no habitat, tanto perturbações antrópicas quanto mudanças climáticas também alteram a quantidade e qualidade dos parceiros disponíveis para interações ecológicas, comprometendo a qualidade dos serviços ecossistêmicos resultantes destas interações (REY-BENAYAS et al. 2009).

Uma das interações mais comuns e diversas em ecossistemas tropicais são as interações mutualistas entre plantas e formigas. De forma geral, as formigas interagem com a vegetação

influenciando positivamente a sobrevivência e o sucesso reprodutivo das plantas (RICO-GRAY; OLIVEIRA, 2007). Contudo, as formigas compõem um grupo que apresenta espécies com distintas sensibilidades às perturbações antrópicas e às variações na precipitação (PHILPORT et al. 2010, DUNN et al. 2010). Dessa forma, algumas espécies podem ser especialmente afetadas com o aumento das perturbações antrópicas e as mudanças nos padrões de precipitação previstas nos cenários de mudança climática global, o que pode afetar diretamente as interações das quais essas espécies fazem parte e os benefícios resultantes dessas interações para as plantas. Nesse contexto, o objetivo da tese é investigar como os serviços providos por formigas às plantas são modificados pelos efeitos de PAC e precipitação na Caatinga. Assim, serão avaliados a eficiência dos serviços de dispersão de sementes (Capítulo 1) e proteção contra herbívoros (Capítulo 2).

2 FUNDAMENTAÇÃO TEÓRICA

2.1 EFEITOS DE PERTURBAÇÕES ANTRÓPICAS E MUDANÇAS CLIMÁTICAS SOBRE OS SERVIÇOS PROVIDOS POR INTERAÇÕES MUTUALÍSTICAS

Mutualismos são interações interespecíficas de cooperação onde espécies parceiras se beneficiam da interação através do incremento recíproco da sua aptidão (JANZEN, 1975; BRONSTEIN, 2009). Essas interações são essenciais para a manutenção da biodiversidade ao redor do globo (BASCOMPTE; JORDANO, 2007) uma vez que todas as espécies estão envolvidas direta ou indiretamente em uma ou mais interações desse tipo (BRONSTEIN et al., 1994b). Além disso, uma série de serviços ecossistêmicos essenciais para a sobrevivência e reprodução de diversos organismos, como a polinização, a dispersão de sementes e a ciclagem de nutrientes, são resultado de interações mutualísticas (TERBORGH *et al*., 2008, WILSON, 2009, POTTS *et al*., 2010).

Apesar de mutualismos serem frequentemente vistos como interações sempre "positivas", a produção de recursos que servem como recompensa para os parceiros da interação ou a prestação de serviços oferecida pelo parceiro pode ser custosa energeticamente e deve ser compensada pelo incremento da aptidão dos organismos quando envolvidos na interação (BRONSTEIN, 1994b). A manutenção de mutualismos é determinada por essa demanda conflitante entre custos e benefícios (BRONSTEIN, 1994a, 2015). Em função disso, variações temporais ou espaciais na composição de parceiros da interação ou nas condições ambientais que desloquem o saldo benéfico das interações mutualísticas irão afetar o resultado dessa interação (BERTNESS; CALLAWAY, 1994; BILLICK; TONKEL, 2003; JORGE; HOWE, 2009; CHAMBERLAIN et al., 2014). Isso faz com que essas interações possam ocupar um contínuo de possíveis resultados para os parceiros que vão desde interações de cooperação a interações antagonistas ou até mesmo que haja quebra total da interação com os parceiros não interagindo mais (BRONSTEIN, 1994a; IZZO; VASCONCELOS, 2001; KERSCH; FONSECA, 2005). Nesse contexto, modificações nas paisagens naturais causadas por perturbações antrópicas e mudanças climáticas, ao mudarem o cenário ecológico no qual essas interações ocorrem, têm potencias efeitos sobre a manutenção de interações mutualísticas e, consequentemente, sobre a qualidade dos serviços providos por essas interações.

De fato, nas últimas décadas, estudos vêm mostrando que perturbações antrópicas e mudanças climáticas são capazes de alterar interações mutualísticas (TYLIANAKIS et al., 2008; KIERS et al., 2010). Ao promoverem extinções de espécies e/ou o rearranjo das

assembleias de espécies, tanto perturbações antrópicas quanto mudanças climáticas podem alterar a composição de parceiros disponíveis para as interações mutualísticas e até mesmo promover a ruptura dessas interações, com consequências na qualidade dos serviços providos por essas interações (KEARNS et al., 1998; STADDON et al., 2004; CHACOFF; AIZEN, 2006; AGUILAR et al., 2006; OPIK et al., 2006). Um exemplo disso é a defaunação em florestas tropicais. Nessas paisagens, grande parte das plantas tem sua dispersão por vertebrados, e muitos desses animais tiveram suas populações fortemente reduzidas ou já foram considerados localmente extintos devido a pressões antrópicas (PERES; PALACIOS, 2007; DIRZO et al, 2014). Esse rearranjo nas comunidades de dispersores de sementes pode ocasionar redução nas taxas de remoção e distâncias de dispersão, ou até mesmo a perda do serviço de dispersão de sementes (EMER et al. 2018; PIRES et al., 2018) com consequências negativas para o recrutamento e a distribuição espacial de diversas espécies de plantas (SILVA; TABARELLI, 2000; GALETTI et al., 2006; JORDANO et al., 2007; PERES; PALACIOS, 2007).

Além das mudanças relacionadas à composição de espécies dos parceiros de interação, perturbações antrópicas e mudanças climáticas podem também alterar características comportamentais e fisiológicas desses parceiros sem necessariamente alterar a composição deles no ambiente (JORDANO, 2000; TYLIANAKIS; TSCHARNTKE; LEWIS et al., 2007; CÂMARA, 2017). Alterações na fenologia reprodutiva de plantas, na reprodução e atividade de forrageamento de animais, são algumas dessas mudanças que podem levar à diminuição na frequência de encontros ou até mesmo a total assincronia entre os parceiros, com consequências para o resultado final da interação e para a qualidade dos serviços providos por essas interações (CHEPTOU; AVENDANO, 2006; MEMMOT et al., 2007, TYLIANAKIS; TSCHARNTKE; LEWIS et al., 2007; RAFFERTY et al., 2015). Como exemplo temos que mudanças na fenologia reprodutiva de plantas induzidas pelo aquecimento global podem gerar uma assincronia temporal entre aves polinizadoras e os recursos florais dos quais elas se alimentam, e o resultado previsto da interrupção dessas interações pode ser a extinção tanto dos polinizadores quanto das plantas (MEMMOT et al., 2007).

Além do quadro alarmante resultante dos efeitos individuais que tanto perturbações antrópicas quanto mudanças climáticas podem causar em relação à perda de biodiversidade e de interações bióticas (SALA et al., 2000; TYLIANAKIS et al., 2008; KIERS et al., 2010), atualmente existe uma crescente preocupação com os efeitos interativos de perturbações antrópicas e mudanças climáticas (SIRAMI et al., 2017). Alguns desses estudos têm mostrado que mudanças climáticas podem exacerbar os efeitos de perturbações antrópicas (TRAVIS,

2003; PONCE-REYES et al., 2013; FRISHKOFF et al., 2016; RITO et al., 2017). Tem sido sugerido que tanto perturbações antrópicas quanto mudanças climáticas podem agir como filtros ambientais similares favorecendo o mesmo conjunto de espécies, desencadeando um processo de homogeneização biótica (FRISHKOFF et al., 2016) que pode tornar os ambientes mais áridos semelhantes a ambientes mais perturbados. Essa homogeneização, por sua vez, pode levar à redução na resiliência do ecossistema (HIROTA et al., 2011; IVES; CARPENTER, 2007) através da perda de serviços ecológicos essenciais providos por interações mutualísticas. No entanto, esses efeitos interativos são pouco entendidos e estudados e atualmente parecem se limitar às respostas na biodiversidade de espécies (SIRAMI et al., 2017).

Embora interações mutualísticas venham se mostrando sensíveis às perturbações antrópicas e mudanças climáticas, essas interações variam quanto à obrigatoriedade entre os parceiros, podendo os impactos de perturbações antrópicas e mudanças climáticas variarem em sua magnitude nos diferentes tipos de mutualismos (KIERS et al., 2010). Mutualismos obrigatórios são tidos como mais sensíveis a mudanças ambientais, uma vez que existe uma interdependência constante dos serviços e/ou recursos compartilhados entre os parceiros (BRONSTEIN et al., 2006). Nesse tipo de mutualismo, a perda de um dos parceiros ou do serviço fornecido por este parceiro geralmente leva à coextinção do outro parceiro (DUNN et al., 2009). Por outro lado, os mutualismos facultativos (não obrigatórios) permitem uma maior flexibilidade de respostas a mudanças ambientais (BRONSTEIN et al., 2004), uma vez que a perda de espécies que interagem, a alteração do meio ambiente abiótico ou outra mudança drástica pode levar à combinações de novos parceiros (BRONSTEIN et al, 2004; SACHS; SIMMS, 2006; WORNIK; GRUBE, 2010), aumentando as chances de existir pelo menos alguns parceiros que sejam resistentes às mudanças e que consiga manter o serviço (BASCOMPTE; STOUFER, 2009).

Mudanças na combinação de parceiros frequentemente ocorrem naturalmente dentro dos mutualismos, mas as mudanças ambientais parecem aumentar a sua frequência (BRONSTEIN et al., 2004; JONES et al, 2008; HEGLAND et al, 2009). Entretanto, essa flexibilidade e variedade de parceiros não impede que mutualismos facultativos sejam sensíveis a perturbações antrópicas e mudanças climáticas (KIERS et al., 2010). Uma vez que diferentes parceiros diferem quanto à qualidade do serviço prestado, os mutualismos podem acabar substituindo parceiros que oferecem um serviço de alta qualidade por parceiros que oferecem um serviço de baixa qualidade como consequência de perturbações antrópicas e mudanças climáticas (AGUILAR et al., 2006; KIERS et al., 2010; LEAL; ANDERSEN; LEAL, 2014). Entretanto, a maioria dos estudos avaliando os efeitos de perturbações antrópicas e mudanças

climáticas sobre esses mutualismos focam frequentemente sobre determinados atributos funcionais ou na frequência de encontros dos parceiros (MEMMOT et al., 2009; SCHLEUNING et al., 2016; AINZEN et al., 2012; MENKE et al., 2012; ALBRECHT et al, 2013). Para um melhor entendimento das implicações de perturbações antrópicas e mudanças climáticas sobre os mutualismos e suas implicações para a estabilidade dos ecossistemas, é necessária uma abordagem sobre a eficiência desses mutualismos, ou seja, uma combinação da quantidade e qualidade dos serviços providos por essas interações (SCHUPP; JORDANO; GÓMEZ, 2017) e de seus mecanismos subjacentes.

2.2 INTERAÇÕES MUTUALÍSTICAS ENTRE PLANTAS E FORMIGAS E OS SERVIÇOS PROVIDOS POR FORMIGAS ÀS PLANTAS

As formigas consistem em um dos grupos dominantes no planeta (FITTKAU; KLINGE, 1973; WILSON; HOLDOBLER, 2005) e desempenham diversos serviços ecossistêmicos importantes na maioria dos ecossistemas terrestres (FOLGARAIT, 1998; DEL TORO et al., 2012; BEATTIE, 2017). Isso levou ao reconhecimento da importância das formigas nas interações com plantas, cujo crescimento e sucesso reprodutivo são muito influenciados pela qualidade desses serviços (RICO-GRAY; OLIVEIRA, 2007). Os efeitos dos serviços providos por formigas sobre as plantas podem ser diretos, como na dispersão de sementes e proteção contra herbívoros, ou indiretos, através de mudanças ambientais locais promovidas pelas formigas como a modificação nas características físicas e químicas do solo pela construção dos seus ninhos (BEATTIE, 2017).

Ao removerem sementes para os ninhos, as formigas podem diminuir a taxa de mortalidade dessas sementes devido a fatores dependentes da densidade, promover a colonização de novas áreas pelo transporte de sementes para áreas além dos limites da população e aumentar o recrutamento de novos indivíduos ao depositar as sementes em áreas próximas aos ninhos, onde as condições físicas e químicas do solo podem ser favoráveis para a germinação (BEATTIE, 1985; HUGHES; WESTOBY, 1992; GILADI, 2006; LEAL; LEAL; ANDERSEN, 2015). Considerando o serviço de proteção das plantas contra herbívoros, as formigas reduzem a taxa de ataque por herbívoros ao serem atraídas para estruturas presentes nas plantas, como domáceas ou nectários extraflorais, que servem como abrigos ou alimento para as formigas (RICO-GRAY; OLIVEIRA, 2007). Dessa forma, plantas visitadas por formigas podem apresentar incremento em suas taxas de crescimento, sobrevivência e sucesso

reprodutivo (LEAL et al., 2006; NASCIMENTO; DEL-CLARO, 2010; MARAZZI et al., 2013). As formigas também têm sido consideradas importantes engenheiras do ecossistema, principalmente devido às mudanças que causam no solo ao construírem e manterem os seus ninhos (FARJI-BRENER; ILLES, 2000; LEAL; WIRTH; TABARELLI, 2014). A atividade das formigas melhora a drenagem, aeração e reduz a compactação do solo, por exemplo. Por meio do armazenamento de alimentos e do acúmulo de fezes e restos de animais, as formigas também aumentam a disponibilidade de nutrientes no solo dos ninhos e nas suas proximidades, propiciando sítios mais favoráveis ao estabelecimento e desenvolvimento das plantas (FOLGARAIT, 1998; MOUTINHO et al., 2003; FARJI-BRENER; WRENKRAUT, 2015).

As interações entre plantas e formigas são normalmente difusas, envolvendo conjuntos de espécies distintas que diferem quanto à qualidade do serviço ecológico prestado. Na dispersão de sementes por formigas, por exemplo, existem grupos de formigas consideradas mutualistas-chave que promovem maiores taxas de remoção de sementes e maiores distâncias de dispersão, sendo consideradas mais eficientes na realização do serviço de dispersão de sementes (NESS et al., 2004; GOVE et al., 2007; LEAL et al., 2014). O mesmo também ocorre no serviço de proteção contra herbívoros, onde algumas espécies são mais eficientes do que outras em proteger as plantas contra herbívoros (LEAL et al., 2006; FAGUNDES et al., 2017). Dessa forma, a eficiência dessas interações e dos serviços providos por formigas às plantas dependerão fortemente das espécies de formigas presentes nos mais variados habitats (NESS et al., 2010).

Diversas espécies de formigas podem ser muito sensíveis à transformação e perturbação do habitat. Perturbações antrópicas, por exemplo, podem levar à redução da riqueza e alterar a composição taxonômica e funcional da comunidade de formigas (HOFFMAN; ANDERSEN 2003; PHILPOTT et al., 2010; LEAL et al., 2012). No entanto, perturbações antrópicas também podem levar à substituição de grupos mais especialistas por grupos mais generalistas, capazes de tolerar e recolonizar áreas que sofreram perturbações antrópicas (ANDERSEN, 2000; LEAL et al., 2012). Todos esses efeitos na comunidade formigas podem ser traduzidas em efeitos nas interações planta-formiga e nos serviços providos por formigas às plantas (OLIVEIRA; KOPTUR, 2017). Por exemplo, ao reduzir a abundância das mutualistas-chave, perturbações antrópicas podem levar à redução das taxas de remoção e distância de dispersão de sementes, reduzindo a qualidade do serviço de dispersão de sementes em áreas perturbadas (ALMEIDA et al., 2013, LEAL; ANDERSEN; LEAL, 2014; LEAL et al., 2017).

Além de perturbações antrópicas, variáveis climáticas como precipitação e temperatura são reconhecidas como fatores importantes estruturando a comunidade de formigas

(KASPARI; WEISER, 2000; KASPARI et al., 2000; DUNN et al., 2009; PÉREZ-SÁNCHEZ et al., 2013), o que também pode levar a mudanças nos serviços providos por formigas às plantas (OLIVEIRA; KOPTUR, 2017). Alguns estudos têm mostrado que a temperatura é um dos principais fatores determinantes tanto para a atividade de forrageamento de formigas quanto para a liberação das sementes pelas plantas, e variações de temperatura podem levar à uma assincronia fenológica entre os agentes dispersores e a produção e liberação de sementes (WARREN et al., 2011, 2017). Além disso, variáveis climáticas podem interagir com distúrbios de formas complexas, mediando ou intensificando os efeitos de perturbação nas comunidades de formigas (GIBB et al., 2015). Entretanto, as consequências desses efeitos interativos para os serviços providos por formigas às plantas ainda são desconhecidas.

2.3 O CENÁRIO DA CAATINGA E SUAS IMPLICAÇÕES PARA OS SERVIÇOS PROVIDOS POR FORMIGAS ÀS PLANTAS

As florestas tropicais sazonalmente secas, cujo principal representante no Brasil é a Caatinga, estão entre os ecossistemas terrestres mais ameaçados do Globo devido às atividades humanas (BANDA-R et al., 2016; MMA, 2017). A degradação ambiental da Caatinga é resultado de mais de três séculos de uso do solo e dos recursos naturais de forma inadequada (LEAL et al., 2005), o qual é apontado como uma das principais causas do aumento de áreas em processo de desertificação dentro do território nacional (MMA, 2010). Estudos recentes na Caatinga vêm chamando atenção para os efeitos deletérios de um tipo de perturbação antrópica caracterizada pela contínua retirada de pequenas quantidades de biomassa florestal: a perturbação antrópica crônica (PAC, sensu SINGH, 1998). Atividades caracterizadas como PAC, como a criação de caprinos e bovinos, e a extração de lenha e de produtos florestais não-madeireiros, são capazes de promover o empobrecimento taxonômico e filogenético de comunidades de plantas (RIBEIRO et al., 2015; RIBEIRO-NETO et al., 2016), animais (RIBEIRO-NETO et al., 2016; OLIVEIRA et al., 2017) e interações mutualísticas (LEAL; ANDERSEN; LEAL et al., 2014; 2015).

A Caatinga também é um ecossistema com condições abióticas severas, como alta temperatura, alta evapotranspiração e baixa precipitação (NIMER, 1972; SAMPAIO, 1995; LEAL et al., 2003), as quais possuem profunda influência na sua biota (SAMPAIO et al., 1981). Além disso, projeções de mudanças climáticas indicam que a região da Caatinga enfrentará uma diminuição na precipitação em torno de 22% até o fim do século 21 (MAGRIN et al., 2014), o que poderá intensificar as condições adversas da Caatinga, uma vez que a precipitação

é uma das variáveis climáticas que limita fortemente o crescimento e a reprodução de espécies, principalmente em ambientes mais xéricos (MURPHY; LUGO, 1986). Quando consideramos os efeitos das mudanças climáticas sobre a resiliência dos ecossistemas, por exemplo, espera-se que com a redução da umidade e precipitação, florestas sejam convertidas em ambientes mais abertos. Por exemplo, áreas de floresta (as quais possuem, tipicamente, mais de 80% de cobertura vegetal) que tenham sua cobertura florestal reduzida a menos de 60% tendem a uma mudança autopropagável e irreversível em savanas (20% de cobertura florestal) ou em vegetação arbustiva (HIROTA et al., 2011). Dessa forma, a intensificação de perturbações antrópicas crônicas, comum nas áreas de Caatinga, pode levar as áreas cobertas por este tipo de vegetação a se tornarem cada vez mais savânicas ou mesmo arbustivas. Assim, para compreender como a biota da Caatinga responde às perturbações antrópicas e às variações de precipitação é preciso investigar também como os serviços ecológicos como os providos por formigas às plantas mudam frente estas perturbações. Além disso, essa compreensão é importante para modelar e estabelecer potenciais cenários biológicos futuros em resposta a intensificação das perturbações e mudanças climáticas.

Apesar de estar submetida à forte pressão antrópicas e condições ambientais severas como descrito acima, a Caatinga suporta uma grande diversidade de espécies (LEAL; TABARELLI; SILVA, 2003; SILVA; LEAL; TABARELLI, 2018) e interações bióticas, inclusive interações mutualísticas entre plantas e formigas (CÂMARA, 2017, LEAL et al., 2018a). Nos últimos anos, por exemplo, a Caatinga vem sendo reconhecida como um *hotspot* de mirmecocoria (LEAL; LEAL; ANDERSEN, 2015; LEAL et al. 2017), principalmente pela prevalência dessa síndrome de dispersão em Euphorbiaceae, a segunda maior família de plantas da Caatinga (MORO et al., 2014). Além disso, formigas dispersam uma grande variedade de espécies de muitas famílias de plantas não mirmecocóricas (LEAL et al., 2007, 2017). As interações ente formigas e plantas com nectários também são muito abundantes na Caatinga (LEAL; ANDERSEN; LEAL, 2015; CÂMARA, 2017; LEAL et al., 2018a). Plantas com nectários extraflorais são muito diversificadas e abundantes local e regionalmente na Caatinga (MELO et al., 2010; REIS, 2016), principalmente pela contribuição de famílias como Fabaceae, Euphorbiaceae e Cactaceae que englobam 34% das espécies de todo mundo que apresentam estas glândulas (WEBER; PORTURAS; KEELER,. 2013).

Dado que perturbações antrópicas crônicas causam mudanças na assembleia de formigas (RIBEIRO-NETO et al., 2016; OLIVEIRA et al., 2017; LEAL et al. 2018b), os serviços providos por formigas às plantas também podem ser alterados (LEAL; ANDERSEN; LEAL, 2014, 2015). No entanto, existe uma grande variação espacial de precipitação na

Caatinga, e pouco se sabe se e como os efeitos de perturbação variam com a precipitação. Um estudo recente mostrou que o aumento da perturbação e da aridez têm efeitos interativos complexos sobre a diversidade das plantas de Caatinga, a qual é afetada negativamente por perturbações em áreas mais secas, mas positivamente afetadas em áreas mais quentes (RITO et al., 2017). A Caatinga é, portanto, um excelente sistema de estudo para investigar os efeitos isolados e interativos da aridez e de perturbações antrópicas crônicas na eficiência dos serviços ecossistêmicos providos por interações mutualistas.

Diante do exposto nessa fundamentação teórica, o objetivo geral desse estudo foi investigar os efeitos das perturbações antrópicas crônicas e mudanças climáticas, particularmente a redução da precipitação, sobre os serviços providos por formigas às plantas, com o intuito de fazer previsões de respostas acerca da resiliência desse ecossistema aos impactos de perturbações antrópicas e ao cenário de mudanças climáticas de aumento de aridez.

3 CLIMATE CHANGE AND ANTHROPOGENIC DISTURBANCE HAVE INDEPENDENT EFFECTS ON SEED DISPERSAL BY ANTS IN BRAZILIAN CAATINGA

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Running head: Seed dispersal by ants

Climate change and anthropogenic disturbance have independent effects on seed dispersal by ants in Brazilian Caatinga

Fernanda M. P. Oliveira[1], Alan N. Andersen[2,3], Xavier Arnan[1,4], José Domingos Ribeiro-Neto[1,5], Gabriela B. Arcoverde[2,3] and Inara R. Leal[6]

[1]Programa de Pós-Graduação em Biologia Vegetal, Universidade Federal de Pernambuco, Av. Prof. Moraes Rêgo s/n, Cidade Universitária, 50690-901, Recife, PE, Brazil

[2]Research School of Environment and Livelihoods, Charles Darwin University, Darwin, NT 0909, Australia

[3]CSIRO Land & Water, Tropical Ecosystems Research Centre, PMB 44 Winnellie, NT 0822, Australia

[4]CREAF, Cerdanyola del Vallès, Catalunya, Spain

[5]Departamento Fitotecnia e Ciências Ambientais, Universidade Federal da Paraíba, Rodovia Pb – 079 km 12, Areia, PB, Brazil

[6]Departamento de Botânica, Universidade Federal de Pernambuco, Av. Prof. Moraes Rêgo s/n, Cidade Universitária, 50690-901, Recife, PE, Brazil

Corresponding author: email: irleal@ufpe.br, phone: 55-81-21267814, fax: 55-81-21268348

ABSTRACT

Anthropogenic disturbance and climate change are the main drivers of loss of biodiversity and ecological services around the globe. There is concern that climate change will exacerbate the impacts of disturbance and thereby promote biotic homogenization. We investigated the individual and interactive effects of chronic anthropogenic disturbance (CAD) and aridity (i.e. rainfall reduction) on seed dispersal services provided by ants in Caatinga vegetation of northeastern Brazil. We considered both myrmecochorous diaspores and fleshy fruits that are secondarily dispersed by ants. The study was conducted in Catimbau National Park, Pernambuco, Brazil. Within an area of 214 km^2, we established nineteen 50 x 20 m plots that encompassed gradients of both CAD and aridity. We offered diaspores of six plant species representing the morphological range of seeds that are dispersed by ants in the region. We then quantified the number of interactions, seed removal rates and dispersal distances, and noted the identity of interacting ant species. Finally, we used pitfall trap data to quantify the abundance of ant disperser species in each plot. Our results show that overall composition of ant disperser species varied along the gradients of CAD and aridity, but the composition of high-quality dispersers varied only with aridity. The total number of interactions, rates of removal and mean distance of removal all declined with increasing aridity, but were not related to CAD. These same patterns were found when considering only high-quality disperser species, driven by the responses of the dominant disperser *Dinoponera quadriceps*. We found little evidence of interactive effects of CAD and aridity on seed dispersal services by ants. Our study indicates that CAD and aridity act independently on ant-mediated seed dispersal services in Caatinga, such that the impacts of anthropogenic disturbance are unlikely to change under the forecast climate of increased aridity. However, our findings highlight the vulnerability of seed dispersal services under an increasingly arid climate due to low functional redundancy in high-quality disperser species. Given the large number of plant species dependent

48 on ants for seed dispersal, this has important implications for future plant recruitment and,
49 consequently, for the composition of Caatinga plant communities.
50
51 KEY-WORDS: anthropogenic disturbances, climate change, biotic interactions, plant-animal
52 interactions, ant-dispersal mutualisms, functional redundancy, functional rarity, seasonally dry
53 tropical forest, semiarid ecosystem.
54
55

INTRODUCTION

Both anthropogenic disturbance and climate change are primary conservation threats in virtually all ecosystems (Sala et al. 2000), having the potential to rearrange species assemblages, with cascading effects on biotic interactions and the provision of ecological services (Tylianakis et al. 2008, Kiers *et al*. 2010). There is increasing concern that climate change might exacerbate the effects of anthropogenic disturbance (Travis 2003, Hirota et al. 2011, Ponce-Reyes et al. 2013). However, the combined and interactive effects on biodiversity of anthropogenic disturbance and climate change remain poorly understood (Sirami et al. 2017; but see Brook et al. 2008, Gibb et al. 2015, Frishkoff et al. 2016). It has been suggested that anthropogenic disturbance and climate change may favour the same set of species, triggering a process of biotic homogenization (Frishkoff et al. 2016) that could make drier ecosystems similar to highly disturbed ones. Such homogenization is likely to reduce ecosystem resilience (Hirota et al. 2011) following the loss of key ecological services such as pollination and seed dispersal (Memmott et al. 2007, Tylianakis et al. 2008, Hegland et al. 2009).

Ants are providers of key ecological services in most terrestrial ecosystems (Folgarait 1998, del Toro et al. 2012). One such service is myrmecochory, a globally important seed dispersal syndrome found among 11,000 angiosperm species from 77 plant families (Lengyel et al. 2009), whose diaspores possess a lipid-rich appendage (elaiosome) for attracting and aiding transport by ants (Berg 1975, Gorb and Gorb 2003). Ants typically transfer the diaspores to their nests, remove the elaiosome and discard the intact seed in nest galleries or outside refuse piles (Beattie 1985) where they can germinate and establish (Hughes and Westoby 1992a, Manzaneda and Rey 2012). Seed dispersal by ants is not restricted to myrmecochorous plants, as ants can opportunistically disperse a wide variety of fleshy fruits (the whole fruits or seeds from these fruits) after being attracted by the pulp (Pizo and Oliveira 2000, Passos and Oliveira 2003, Leal et

al. 2007). By secondarily dispersing fleshy fruits, ants can positively affect seed fate and germination of diaspores primarily adapted for vertebrate dispersal (Levey and Bryne 1993, Christianini et al. 2007, Christianini et al. 2014).

Myrmecochory can be strongly affected by human disturbance (Andersen and Morrison 1998, Parr et al. 2007, Philpott et al. 2010). Highest quality seed-dispersal services are typically provided by large-bodied ant species because they readily collect seeds and transport them over large distances (Andersen and Morrison 1998, Leal et al. 2014a). Large ant species are especially sensitive to disturbance (Leal et al. 2014b, Gibb et al. 2018), and this can result in severe reductions in the quality of seed-dispersal services in disturbed habitats (Gove et al. 2007, Ness et al. 2004, Leal et al. 2014b). It has also been suggested that seed-disperser ants and large-bodied ant species are particularly vulnerable to climate change (del Toro et al. 2015, Dunn et al. 2010). Temperature is a key driver for both the time plants release their seeds and ant foraging activity, and variation in activation temperatures among ant species may lead to phenological asynchrony between ant dispersers and seed availability (Warren et al. 2011, Tanaka and Tokuda 2017). Given that temperature and rainfall play major roles in shaping ant communities (Kaspari and Weiser 2000, Kaspari et al. 2000, Dunn et al. 2009, Pérez-Sánchez et al. 2013, Gibb et al. 2015), these climate variables might interact with disturbance in complex ways, including mediation or intensification of disturbance effects on ant communities, with hot and arid environments likely to be at greatest risk (Gibb et al. 2015).

Our study aims to investigate how anthropogenic disturbance and increasing aridity interact to influence ant-mediated seed dispersal (both myrmecochory and non-myrmecochory) in Caatinga, a mosaic of seasonally dry tropical forest and semi-arid scrubland in northeastern Brazil that is recognized as a global hotspot for myrmecochory (Leal et al. 2007, 2014a, 2014b). Anthropogenic disturbance has been previously shown to reduce ant-mediated seed dispersal

104 services for myrmecochorous diaspores at one Caatinga site (Leal et al. 2014b). However, there is
105 marked spatial variation in rainfall in Caatinga, and it is unknown if and how the effects of
106 disturbance vary with aridity. We specifically tested two hypotheses. Our first hypothesis is that
107 increasing anthropogenic disturbance has similar effects as increasing aridity on seed dispersal by
108 ants. We predict that both increasing anthropogenic disturbance and aridity reduce the number of
109 interactions between diaspores and ants, and reduce the quality of seed dispersal services (i.e.
110 seed removal rate and seed dispersal distance) by changing ant disperser species composition,
111 particularly reducing the abundance of high-quality seed dispersers. Our second hypothesis is that
112 there are also interactive effects of anthropogenic disturbance and aridity, such that the effects of
113 disturbance are contingent on the level of aridity. We predict that disturbance has a greater
114 impact in more arid sites, due to the lower primary productivity conferring lower resilience to ant
115 communities and, consequently, to seed dispersal services by ants.
116
117 MATERIALS AND METHODS
118 **Study area**
119 Caatinga is a mosaic of seasonally dry tropical forests and scrub vegetation (Pennington et al.
120 2009) that covers 826,411 km² of northeastern Brazil (MMA 2011) (Appendix S1). It is
121 considered one of the most endangered ecosystems in Brazil due to extensive conversion to
122 agriculture (45% of its area has been deforested; MMA 2011). In addition, remaining vegetation
123 is exploited by high densities of people (26 inhabitants / km^2) who are highly dependent on forest
124 resources for their livelihoods (Albuquerque et al. 2007, Nascimento et al. 2012, Ramos and
125 Albuquerque 2012), and therefore exert high levels of chronic anthropogenic disturbance (CAD,
126 Singh 1998, Ribeiro et al. 2015, Rito et al. 2017). Under future climate change, the Caatinga
127 region is projected to receive about 22% less rainfall than it currently does (Magrin et al. 2014).

Our study was conducted in Catimbau National Park, Pernambuco State (8º24'00" and 8º36'35" S; 37º0'30" and 37º1'40" W) (Appendix S1). Mean annual rainfall varies markedly in Catimbau, from 1100 mm in the southeast to 480 mm in the northwest, and the mean temperature is 23ºC (Rito et al. 2017). Approximately 70% of its 607 km^2 is covered by quartzite sandy soils supporting low stature (up to 6 m) caatinga vegetation. The Park was created in 2002, and low-income rural populations still live in the park, using it for grazing and browsing by livestock, collection of living and dead wood, harvesting of non-timber forest products, and hunting (Rito et al. 2017).

We selected nineteen 20 x 50 m plots to cover a wide range of disturbance and annual rainfall based on RapidEye satellite imagery and field observations (Appendix S1). All plots were on sandy soil, had similar slope, and supported old-growth vegetation that had not experienced slash-and-burn agriculture for at least 50 years. Plots were separated by a minimum of 2 km, and occurred within an area of 214.3 km^2 (Rito et al. 2017).

Measurement of CAD and aridity

To characterize the level of CAD in the 19 plots, we computed a global multi-metric index that integrates eight disturbance indicators related to the three main sources of CAD in Catimbau (Arnan et al., unpublished data): livestock pressure (herbivory by goats and cattle), wood extraction (live and dead wood) and extraction of non-timber forest products (medicinal plants, food items for humans, hunting and livestock fodder). These CAD indicators were measured using three approaches: 1) Geographic distances based on remote sensing techniques: proximity to the nearest house and proximity to the nearest road. These distances were measured from the center of each plot, using satellite imagery and ArcGIS 10.1 software. Since distance is inversely related to level of disturbance, we used the inverse of distance; 2) Interviews with local

inhabitants: number of people in the nearest village with influence weighted by distance. We identified the nearest village to each plot using GIS and then conducted informal and semi structured interviews to assess the number of people in each village; and, 3) Measures of disturbance in the field: goat trail length, goat dung, cattle dung, alive wood extraction (stem cuts) and coarse woody debris extraction (litter) (see Appendix S2 for more details). The global multi-metric index was then computed using the following formula:

$$I = \frac{\sum_{i=1}^{n}(y_i - y_{\min})/(y_{\max} - y_{\min})}{n} \times 100 \quad (158)$$

where I is the disturbance intensity index, y_i the observed value for one disturbance metric in plot *i*, y_{min} the minimum observed value for the disturbance metric considering all plots, y_{max} the maximum observed value for the disturbance metric considering all plots, and *n* the number of individual disturbance metrics considered in the index. The values of each disturbance metric were first standardized between 0 and 1 to make component metrics of equal importance. The index ranges from 2 to 58 (from the lowest to the highest disturbance intensity) among the plots (Arnan et al., unpublished data).

To characterize the aridity gradient, data on mean annual precipitation were acquired from the WorldClim database (Hijmans et al. 2005). We downloaded the dataset at 30 arc seconds resolution (http://www.worldclim.org), and the value of mean annual precipitation at each plot was extracted using package *maptolls* **(**Bivand and Lewin-Koh 2015) in the R software (R Core Team 2016). Mean annual precipitation in our plots ranged from 940 mm to 510 mm. Such a large range in mean annual rainfall within a small geographic area makes Catimbau an ideal study system for analysing ecological responses to variation in aridity. Aridity is usually considered as the ratio of mean annual precipitation to potential evapotranspiration (Armas et al. 2011); we also computed a global aridity index, but since it was very highly correlated with

precipitation (r = 0.98; see Appendix S3 for more details) we retain precipitation as our measure of aridity because it is more commonly used in diversity studies (Hawkins et al. 2003, Dunn et al. 2009, Rito et al. 2017).

Seed dispersal by ants

To quantify ant-mediated seed dispersal services, we used diaspores from six locally abundant plant species that represent the morphological range of diaspores dispersed by ants in the region: the myrmecochores *Jatropha mutabilis*, *Jatropha ribifolia* and *Croton nepetaefolius* (species with carunculate elaiosomes for attracting ants and facilitating seed transport), and the non-myrmecochores *Simaba ferruginea*, *Sideroxylon obtusifolium* and *Melocactus bahiensis* (Table 1). We observed ant-diaspore interactions at six stations separated by 10 m along each of two 50 m transects (separated by 20 m) established in each plot. At each station, five conspecific diaspores were placed on a white filter paper card (6 cm x 6 cm) as described in Leal et al. (2014b). During each observation period, all diaspores on a transect were from the same species, and the two transects within a plot had different species. There were three observation periods (between March and May 2015 and in April 2016), such that all six diaspore species were observed once in each plot. Stations were monitored at 15-min intervals from 06:00 h to 18:00 h over one day for each monitoring period, and removed diaspores were not replaced. Any ant contact with a diaspore for the apparent purpose of feeding was considered as an interaction (Leal et al. 2007), and different ant species could interact more than once with a diaspore (i.e. more than one interaction event for each diaspore). For each observed interaction, we recorded the identity of the ant species, whether or not the diaspore was removed (we considered a removal event when a diaspore was moved $\geq$ 5 cm), and the distance of any removal (defined as the displacement from the station to where the diaspore was either dropped or taken into an ant nest).

We classified interacting ant species as either high- or low-quality dispersers following Leal et al. (2014a) and confirmed with field observations. High-quality seed dispersers comprised medium to large (body length > 5.0 mm) ants that transport diaspores over relatively long (>2 m) distances and deposit them isolated or in small groups in nests or in nest refuse piles. Low-quality seed dispersers were small ants (<5.0 mm) that feed on the diaspores *in situ* without diaspore removal, or transport diaspores over short distances (<2 m) and deposit them in large groups in nest refuse piles (Leal et al. 2014a, 2017). Leaf-cutting ants were also classified as low-quality dispersers despite their relatively large body size and ability to transport seeds over long distances, because they usually cut or bury all seedlings growing on or near their nests (Leal et al. 2017).

Abundance of seed-disperser ants

We used results from a survey of ants using 20 pitfall traps operated for 48 hrs in each plot during March 2015 (Arcoverde et al., unpublished data) for data on the abundances of seed-dispersing ants. This survey recorded 17 of the 20 ant disperser species observed during our study; the other three species (*Pheidole fera*, *Pheidole pr. fracticeps* and *Pheidole* sp. A) were responsible for <1% of total removal events (see Table 2) and were not considered in analyses of the species composition of disperser ants.

Statistical analysis

Unless otherwise specified, our unit of analysis was observation station for analyses of seed dispersal, and plot for analysis of pitfall data. To evaluate the effects of CAD, precipitation and their interaction on the richness of ant disperser species (based on pitfall data), we used generalized linear models (GLMs) with a Poisson error distribution. To evaluate the effects of

CAD, precipitation and their interaction on the composition of ant seed disperser species at the plot level (also based on pitfall data), we conducted a Canonical Correspondence Analysis (CCA) using the frequency of occurrence of species as a measure of species abundance. We performed a randomization test (1000 aleatorizations) to obtain the statistical significance of explanatory variables. Further, we performed Spearman's correlations between the abundance of each ant disperser species and the CCA axes significantly associated with the CAD and aridity gradients considering the first two axes.

We used generalized linear mixed models (GLMMs) with Gaussian error distribution to analyse the effects of CAD, precipitation and their interaction on the total number of interactions between ants and diaspores, and on the number of interactions performed by low- and high-quality dispersers separately. We also used GLMMs to evaluate the effects of CAD, precipitation and their interaction on removal rates (proportion of observed diaspore removals out of five diaspores offered per station) and mean removal distances, considering all ant disperser species and high- and low-quality dispersers separately. For all these models, we used plot and diaspore species as random factors. Additionally, we built GLMMs to evaluate the effects of CAD, precipitation and their interaction on removal rates and mean removal distances for each diaspore species individually (using plot as a random factor), as well as for the four most common ant species removing the diaspores (using plot and diaspore species as random factors). For the removal rate-models we used a binomial error distribution, and for the removal distance models we used a Gaussian error distribution. Analyses were performed in R. We checked residuals for normality and homoscedasticity in all models. Data that did not meet homoscedastic criteria were log(x) +1 transformed. We used the packages *vegan* version 2.3 (Oksanen et al. 2015) for CCA analysis and *lme4* version 1.1-7 (Bates et al. 2004) to build the GLMM models.

248 RESULTS

249 **Seed-disperser ants**

250 We observed 1453 ant-diaspore interactions involving 33 ant species, with 66.1% of these
251 interactions involving myrmecochorous seeds. Diaspores were removed in 60.6% of the
252 interactions (68.5% for myrmecochorous seeds), involving 20 ant species (Table 2). Based on
253 pitfall catches, the number of these species ranged from six to 12 per plot, and did not vary with
254 precipitation (GLM: $\chi^2 = 2.06$, DF = 15, p = 0.23), CAD ($\chi^2 = 0.06$, DF = 15, p = 0.86) or their
255 interaction ($\chi^2 = 0.46$, DF = 15, p = 0.49). Two ant species were classified as high-quality
256 dispersers: *Dinoponera quadriceps* and *Ectatomma muticum*, and they were responsible for 49%
257 of all removals. Low-quality dispersers were species of *Dorymyrmex*, *Pheidole*, *Solenopsis* and
258 *Tetramorium* (Table 2). The abundance of high-quality dispersers (*D. quadriceps* and *E.*
259 *muticum*) based on pitfall catches was positively correlated to the number of removals from
260 observation stations (Spearman's $r = 0.53$, p = 0.02) and mean dispersal distance (Spearman's $r =$
261 0.52, p = 0.02).
262 According to our CCA, composition of ant disperser species varied significantly with
263 precipitation ($F_{1,15} = 1.96$, p = 0.03, Fig. 1) and CAD ($F_{1,15} = 1.91$, p = 0.04, Fig. 1), but not with
264 their interaction ($F_{1,15} = 1.44$, p = 0.19, see Appendix S4 for more details on CCA results).
265 Aridity was associated to axis 1 while CAD was associated to axis 2. The abundance of *D.*
266 *quadriceps* increased with increasing precipitation (Spearman's $r = 0.74$, $p < 0.01$), but that of *E.*
267 *muticum* decreased (Spearman's $r = -0.48$, p = 0.04). However, CAD had no effect on the
268 abundance of both ant species (Spearman's $r = -0.05$, p = 0.82; and Spearman's $r = 0.14$, p = 0.56
269 respectively to *D. quadriceps* and *E. muticum*). The responses of the abundance of low-quality
270 dispersers at species-level were highly variable. For example, CAD was negatively related to the
271 abundance of *Solenopsis* sp. 1 (Spearman's $r = -0.47$, p = 0.04), but positively to that of

Acromyrmex rugosus (Spearman's $r = 0.50$, $p = 0.03$). Similarly, increasing precipitation was negatively related to the abundance of *Solenopis virullens* (Spearman's $r = -0.51$, $p = 0.02$), but positively for *Dorymyrmex thoracicus* (Spearman's $r = 0.54$, $p = 0.01$) and *Pheidole* sp. C (Spearman's $r = 0.59$, $p < 0.01$, Appendix S5).

Seed dispersal

The number of interactions per plot ranged from 27 to 144. It increased with increasing precipitation (GLMM; $F_{1,678} = 5.84$, $p = 0.03$; Fig.2a), but did not vary with CAD ($F_{1,678} = 0.36$, $p = 0.79$) nor with the interaction between precipitation and CAD ($F_{1,678} = 0.48$, $p = 0.49$). The number of interactions by high-quality dispersers likewise increased with increasing precipitation (GLMM; $F_{1,678} = 5.42$, $p = 0.04$, Fig. 2b), and did not vary with CAD ($F_{1,678} = 0.23$, $p = 0.56$) nor with the interaction between precipitation and CAD ($F_{1,678} = 3.42$, $p = 0.06$). The number of interactions involving low-quality dispersers (52% of all interactions) did not vary with precipitation (GLMM; $F_{1,678} = 2.47$, $p = 0.07$), CAD ($F_{1,678} = 0.41$, $p = 0.87$), or their interaction ($F_{1,678} = 1.17$, $p = 0.27$).

Removal rates varied markedly among diaspore species: *S. obtusifolium,* 40.2%; *J. ribifolia,* 38.6%; *C. nepetaefolius,* 33.7%; *J. mutabilis,* 28.6%; *M. bahiensis*, 7%; and *S. ferruginea*, 0.53%. The most common ant species removing diaspores were *D. quadriceps* (41.2% of total removals), *Pheidole radoskowskii* (12.2%), *E. muticum* (8.1%) and *Solenopsis tridens* (6.3%). The largest ant species by far was the high-quality disperser *D. quadriceps* (Table 2), and it was a particularly dominant disperser of the largest diaspores, especially *S. ferruginea* (100% of removals), *S. obtusifolium* (94.3%) and *J. mutabilis* (92.2%). It removed very few smaller diaspores such as those of *C. nepetaefolius* (1.1%) and *J. ribifolia* (no removal). The overall removal rate ranged from 4.6% to 44% per plot; it was positively related to precipitation (Fig.

2c), but did not vary with CAD nor with the interaction between CAD and precipitation (Appendix S6). These patterns were also shown by high-quality dispersers (Fig. 2d), whereas removal rates by low-quality dispersers did not vary with precipitation, CAD or their interaction (Appendix S7).

Diaspores were removed up to 27.5 m, with a mean of 3.72 ± 2.05 m (± SD). *D. quadriceps* was responsible for the longest mean removal distance (7.67 ± 4.49 m), followed by *Atta sexdens* (1.55 ± 1.35 m) and *E. muticum* (0.90 ± 1.54 m). Mean removal distance per plot varied from 0.06 to 5.94 m, and was positively related to precipitation (Fig. 2e) but did not vary with CAD or the interaction between CAD and precipitation (Appendix S6). As was the case for removal rates, these patterns were also shown by high-quality dispersers (Fig. 2f), whereas dispersal distances obtained by low-quality dispersers did not vary with precipitation, CAD or their interaction (Appendix S7).

Relationships between removal rates and distances with precipitation and CAD varied markedly among diaspore species. Both removal rates and distances increased with increasing precipitation for *J. mutabilis* and *S. obtusifolium* (Appendix S6 and S8), and there was an interactive effect of precipitation and CAD on removal rate and distance for *J. mutabilis* (Appendix S6 and S9). Moreover, precipitation positively affected both removal rate and distance by *D. quadriceps*, the most common ant seed disperser species (Fig. 2g, h, Appendix S7).

DISCUSSION

Our study addressed the individual and interactive effects of CAD and aridity on seed dispersal by ants in Brazilian Caatinga in the context of predicting responses to disturbance under a future climate scenario. We first hypothesized that increasing CAD and aridity would have similar effects on seed dispersal services, but we did not find evidence of this. The abundance of high-

quality dispersers, number of interactions between ants and diaspores, rates of seed removal, and mean removal distance all varied significantly with aridity, but not with CAD.

We predicted that both increasing CAD and aridity will reduce the number of interactions between ants and diaspores, along with the quality of seed dispersal by ants by changing ant disperser species composition, and particularly by reducing the abundance of high-quality disperses. This was not the case for CAD, but was somewhat true for aridity, because the abundance of the dominant high-quality disperser, *Dinoponera quadriceps*, decreased with increasing aridity. Of all disperser species, *D. quadriceps* had most interactions with diaspores, highest removal rates and by far the longest removal distances, and, as was the case for *D. quadriceps* abundance, all these variables were negatively affected by aridity. Previous studies have shown that the reduction of abundance of one key disperser species can lead to drastic reductions in the quality of seed-dispersal services (Gove et al. 2007, Ness et al. 2004, Leal et al. 2014b). According to *D. quadriceps* patterns of occurrence (highly frequent and abundant over Caatinga sites, Arcoverde et al., unpublished data) and ecological role (most important and largest high-quality seed disperser, Leal L. et al. 2014a, Leal I. et al. 2017, this study), this species are regarded as possessing "dominant distinct traits", which is a way of being functionally rare (*sensu* Violle et al. 2017). It means that *D. quadriceps* traits that make it a high-quality seed disperser are geographically widespread but they are present in very few species, rendering important implications as we can see below.

The importance of *D. quadriceps* as a high-quality disperser species is further illustrated by considering individual plant species. The two diaspore species with the highest removal rates, *Sideroxylon obtusifolium* and *Jatropha mutabilis*, both showed the same pattern of reduction in dispersal with increasing aridity as that of all species combined, and both were dispersed almost exclusively by *D. quadriceps*. Apparently, these diaspores are the most beneficial resources for

D. quadriceps independently of diaspore type (myrmecochorous or non-myrmecochorous). High-quality disperser ants show a strong preference for diaspore species with high elaiosome/seed-size ratios (Hughes and Westoby 1992b, Peters et al. 2003, Reinferath et al. 2012), and this is the case for *D. quadriceps* and *J. mutabilis* (Leal et al. 2014a). However, *D. quadriceps* showed a similarly high preference for the non-myrmecochorous diaspores of *S. obtusifolium*, probably because it possesses a large volume of pulp in relation to seed. The potential dispersal benefits provided by *D. quadriceps* are not restricted to seed removal and transport, but also relate to seed fate. Compared with control areas, post-dispersal seed predation is lower in areas near the nest entrances of *D. quadriceps* where dispersed seeds are deposited, and seedling abundance is more than twice as high (Leal et al. 2017). Therefore, the high-quality dispersal services provided by *D. quadriceps* extend to a positive influence on plant reproductive success following seed transport.

Although CAD modified overall ant species composition, it did not affect the abundance of any of the high-quality dispersers, and this explains why it had no effects on seed dispersal services. Such results are contrary to those of Leal et al. (2014b), who found at another Caatinga location that CAD had negative effects on the abundance of high-quality dispersers and consequently on seed dispersal services by ants. However, our study was conducted on sandy soils while in the later study the authors considered sandy and clay soils, and Caatinga ant communities on sandy soils have been previously shown to be particularly resilient to CAD (Oliveira et al. 2017). In addition, mean annual rainfall in that study was only 550 mm, at the arid extreme of our study, and, in association with the different soil types, this might also be a factor explaining the higher sensitivity of seed-disperser ants to disturbance. If so, it would indicate an interaction between CAD and aridity at the low-rainfall extreme for Caatinga.

We found little evidence to support our second hypothesis that CAD and aridity will have interactive effects. We found interactive effects for only one diaspore species - removal rates and distances for diaspores of *J. mutabilis* declined with increasing aridity in less-disturbed areas, but increased slightly with increasing aridity in more disturbed areas. Most studies that have found interactive effects between climate change and anthropogenic disturbance were conducted at larger spatial scales than our study (Brook et al. 2008, Gibb et al. 2015, Frishkoff et al. 2016). For example, Gibb et al. 2015 found interactive effects of disturbance and precipitation on ant communities, but over a precipitation range from 500 mm to 3000 mm (more than five times the range in our study), and covered a broad range of ecosystem types. However, Rito et al. 2017 found interactive effects of CAD and aridity on plant communities at our study sites. They showed that CAD reduces plant diversity only in drier areas, suggesting high resilience in the wetter and more-productive end of the rainfall gradient. The higher sensitivity of plants compared with ants to disturbance at low-rainfall sites can be explained by the fact that resource extraction directly affects plants but not ants making ant community less prone to be affected by CAD (Ribeiro-Neto et al. 2016).

Although we found little evidence of interactive effects of CAD and aridity, our findings of the effects of aridity have important implications for the vulnerability of seed dispersal services to climate change. To a large extent, high-quality seed-dispersal services across the full rainfall gradient in Caatinga are provided by a single species, *Dinoponera quadriceps*, and its abundance and consequently the overall provision of dispersal services by ants declined markedly with increased aridity. The high sensitivity of ant dispersal services to increasing aridity can therefore be attributed to the functional rarity of *D. quadriceps* among seed disperser ants, and highlights the threat of low functional diversity to the maintenance of ecological services (Violle et al. 2017). Given that such a large proportion of species of the Caatinga flora are dispersed by ants

(e.g. one quarter of local woody flora in Leal et al. 2007), such low functional redundancy has important implications for plant recruitment and, consequently, for the composition of plant communities under a future climate.

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581

582 **Table 1.** Diaspores species used in the seed dispersal experiments at Catimbau National Park,
583 Pernambuco, Brazil. Fruit type, fruit and seed size are provided according to Lorenzi (1998) and
584 Barroso et al. (1999). Elaiosome type is provided *sensu* Gorb and Gorb (2003).

Diaspore species	Fruit type	Fruit size (mm)	Seed size (mm)	Elaiosome type
Simaroubaceae				
Simaba ferruginea A.St.-Hil.	Drupe	35*	30	-
Sapotaceae				
Sideroxylon obtusifolium (Roem. & Schult.) T.D.Penn.	Berry	13.5*	9	-
Cactaceae				
Melocactus bahiensis (Britton & Rose) Luetzelb.	Berry	15*	1.2	-
Euphorbiaceae				
Croton nepetaefolius Baill.	Capsule	10	5*	Caruncle
Jatropha mutabilis Pohl. (Baill.)	Capsule	24	12*	Caruncle
Jatropha ribifolia (Pohl) Baill.	Capsule	13	7*	Caruncle

585 ***** Diaspores used in seed dispersal experiments

586

587 **Table 2.** Total removed diaspores and mean removal distance for each ant species removing
588 diaspores along the rainfall and chronic anthropogenic disturbance gradients at Catimbau
589 National Park, Pernambuco, Brazil. Ant species were classified in low-quality dispersers (LQ)
590 and high-quality dispersers (HQ) following Leal *et al.* (2014a, 2017). Mean Weber's length
591 values are considered an indicative of worker body size (Parr et al. 2016) and were obtained from
592 another work conducted in the same study area (Arnan et al., unpublished data).

Ant species	Quality	Mean (±SD) Weber's length (mm)	Number of removed seeds	Mean (±SD) removal distance (cm)
Acromyrmex rugosus (Smith)	L	1.7 ± 0.31	1	5.0 ± 0.0
Atta sexdens (L.)	L	2.0 ± 0.35	10	155.1 ± 134.6
Dinoponera quadriceps (Kempf)	H	8.8 ± 0.28	349	767.1 ± 449.3
Dorymyrmex thoracicus (Gallardo)	L	1.3 ± 0.07	9	8.5 ± 3.2
Ectatomma muticum (Mayr)	H	3.6 ± 0.30	70	90.4 ± 154.0
Pheidole fera (Santschi)	L	0.9 ± 0.0	1	9.0 ± 0.0
Pheidole pr. Fracticeps	L	0.6 ± 0.09	1	5.0 ± 0.0
Pheidole radoskowskii (Mayr)	L	0.8 ± 0.04	102	15.5 ± 15.7
Pheidole triconstricta (Forel)	L	0.8 ± 0.12	1	7.0 ± 0.0
Pheidole sp. A	L	0.6 ± 0.09	3	6.5 ± 2.1
Pheidole sp. B	L	0.6 ± 0.03	14	9.1 ± 3.2
Pheidole sp. C	L	0.8 ± 0.06	20	31.5 ± 35.7
Pheidole sp. D	L	0.6 ± 0.06	16	10.7 ± 2.1
Pheidole sp. E	L	0.7 ± 0.03	28	21.5 ± 21.1

Pheidole sp. P	L	0.9 ± 0.03	4	13.0 ± 7.0
Solenopsis tridens (Forel)	L	0.8 ± 0.05	55	11.6 ± 5.7
Solenopsis virullens (Smith)	L	0.7 ± 0.07	22	18.5 ± 16.3
Solenopsis sp. B	L	0.4 ± 0.04	2	10.0 ± 5.6
Solenopsis sp. C	L	0.4 ± 0.07	3	7.0 ± 0.0
Tetramorium sp.	L	0.4 ± 0.05	1	40.0 ± 0.0

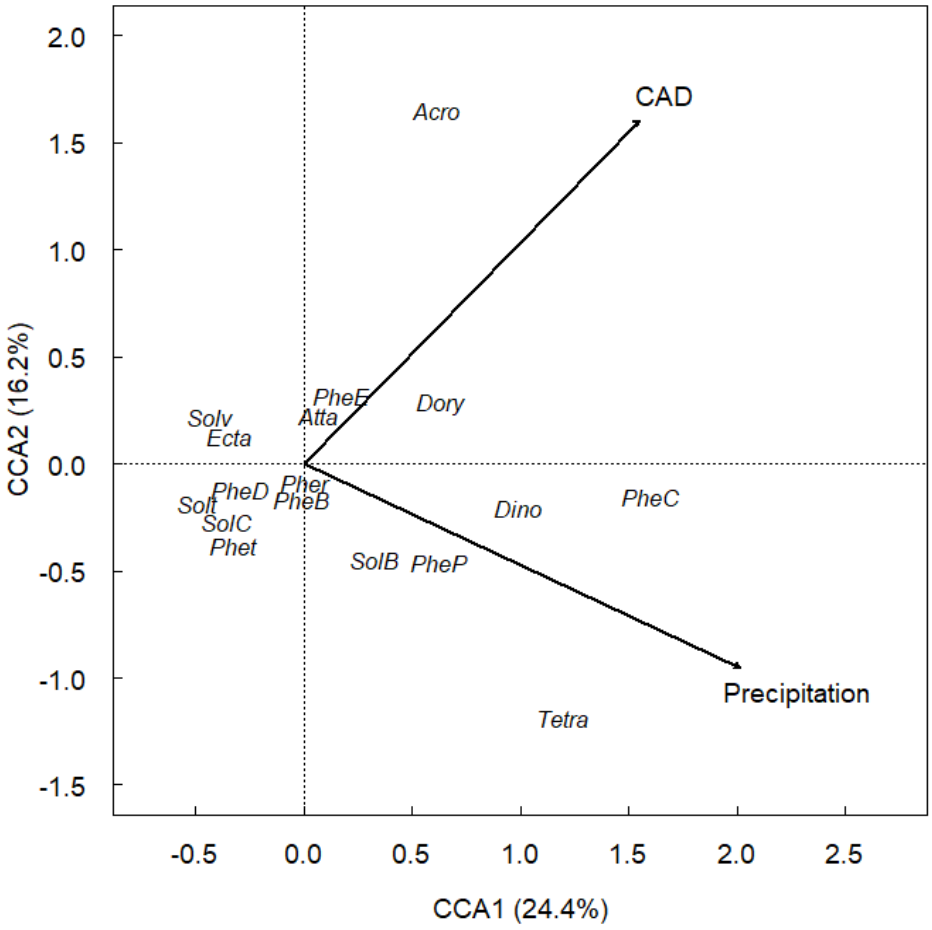
593

Figure legends

Figure 1 – Representation of ant species and environmental gradients (precipitation and chronic anthropogenic disturbance - CAD) affecting ant disperser community composition at Catimbau National Park, on the first two axes of the canonical correspondence analysis (CCA). Abbreviations: *Acro*, *Acromyrmex rugosus*; *Atta*, *Atta sexdens*; *Dino*, *Dinoponera quadriceps*; *Dory*, *Dorymyrmex thoracicus*; *Ecta*, *Ectatomma muticum*; *Pheir*, *Pheidole radoskowiskii*; *Pheit*, *Pheidole triconstricta*; *PheB*, *Pheidole* sp. B; *PheC*, *Pheidole* sp. C; *PheD*, *Pheidole* sp. D; *PheiE*, *Pheidole* sp. E; *PheiP*, *Pheidole* sp. P; *Solt*, *Solenopsis tridens*; *Solv*, *Solenopsis virulens*; *SolB*, *Solenopsis* sp. B; *SolC*, *Solenopsis* sp. C; *Tetra*, *Tetramorium* sp. 1.

Figure 2 – Number of interactions between diaspores and ants, removal rates, and mean removal distances considering all ant species (a, c, e) and only high-quality ant dispersers (HQ) (b, d, f), and removal rate (g) and mean removal distance (h) considering only *Dinoponera quadriceps* (*DQ*) over the precipitation gradient at Catimbau National Park, Pernambuco, Brazil. Black dots represent means and bars represent standard errors considering all stations per plot.

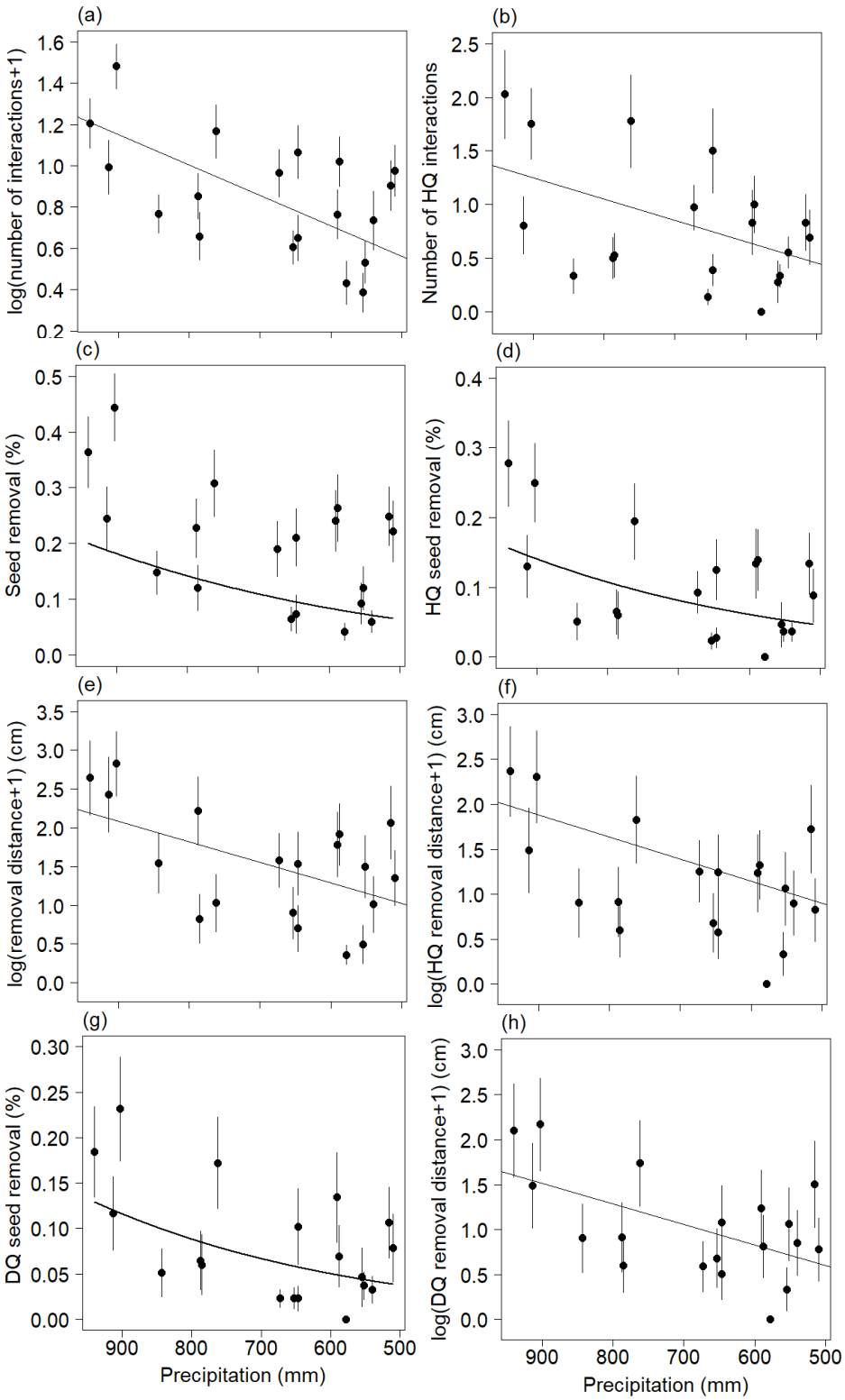
610 **Figure 1**



611

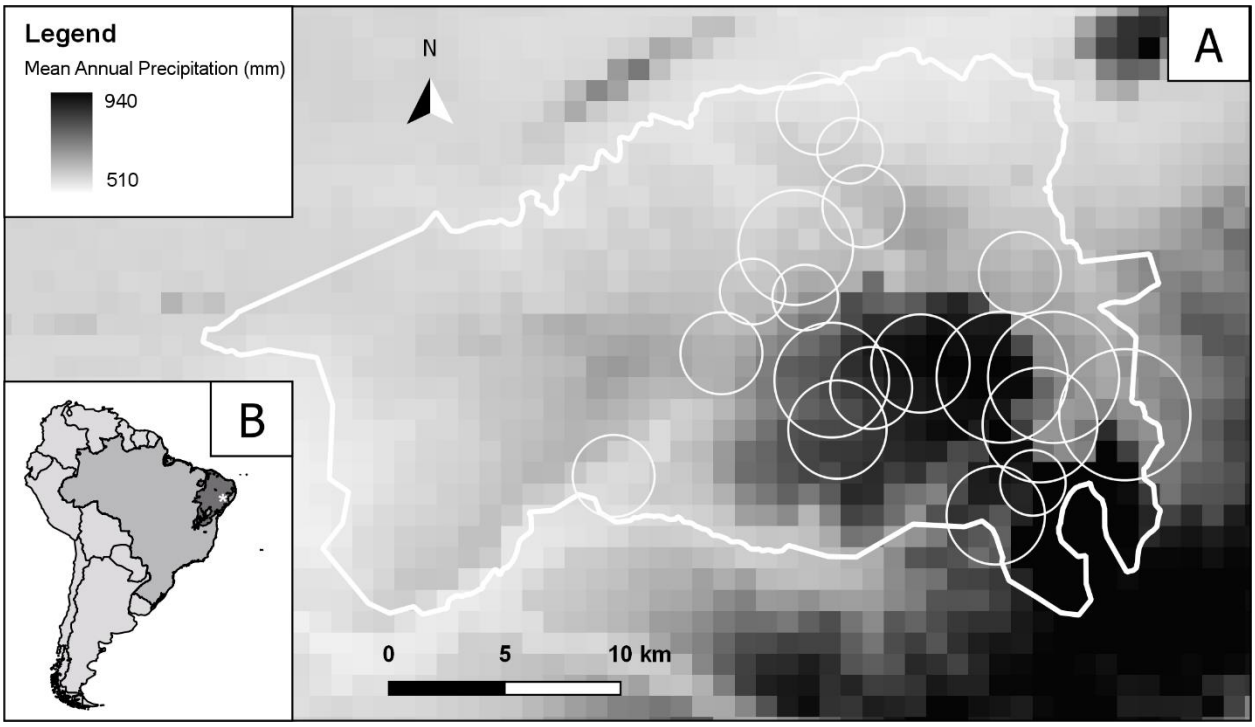
612

Figure 2


(a)
log(number of interactions+1)
(b)
Number of HQ interactions
(c)
Seed removal (%)
(d)
HQ seed removal (%)
(e)
log(removal distance+1) (cm)
(f)
log(HQ removal distance+1) (cm)
(g)
DQ seed removal (%)
(h)
log(DQ removal distance+1) (cm)
900 800 700 600 500
Precipitation (mm)
900 800 700 600 500
Precipitation (mm)

SUPPLEMENTARY MATERIAL

Appendix S1. Representation of the study area in different scales: distribution of the nineteen 50 m x 20 m plots (circles with white outline) over precipitation and chronic anthropogenic disturbance (CAD) gradients at Catimbau National Park (map with white outline) (A) and the localization of Catimabau National Park (white asterisk) in Caatinga vegetation (dark grey) and in Brazil (light grey) (B). The circles size represents the CAD gradient with largest circles representing more disturbed areas.



Appendix S2. Measures of human activity taken at field: goat trail length, goat drops, cattle drops, alive wood extraction (stem cuts) and coarse woody debris extraction (litter).

Goat trail length was measured by using an odometer in each 50 x 20 m plot. We counted the number of *goat drops* within four 5 x 5 m (100 m^2 per plot) and *cattle drops* (bovine and equine) within each entire plot. For the a*live wood extraction*, we quantified all the signs of stems cut and the diameter of each stem was measured. We then measured the overall basal area cut per plot. *Coarse woody debris extraction* was measured within four 4 m^2 subplots within each plot. In each subplot, we measured the two diameters and length of each dead log or stem laying on the ground, and dead biomass was computed following the equation of the volume of a conical frustum. Then we used a mean value of the wood density of the tree species present in the area to transform the volume values to biomass. Since the amount of available coarse woody litter is dependent on its production, we divided the total amount of wood litter by the total biomass of the plot. To transform the volume values of coarse wood debris extraction to biomass we used a mean value of the wood density of the tree species present in the area. Tree species wood density was measured in accordance with protocol of standardized measurements of Perez-Harguindeguy *et al*. (2013). Additionally, we obtained wood density in Global Wood Density Database (http://datadryad.org/handle/10255/dryad.235) for some species we did not get data at field. We assume that the lowest relative amount of coarse woody litter (in relation to overall biomass), the highest fuelwood extraction (i.e. the highest disturbance intensity). Then, we used the inverse of the relative amount of wood litter in order to put this metric in the same direction than the other disturbance metrics. Total biomass per plot was estimated through an allometric equation for Caatinga vegetation ($Biomass_{kg} = 0.173\ DAS_{cm}^{2.295}$, which is based on diameter at soil height (DBH) (Amorim *et al*. 2005, Rito et al. 2017).

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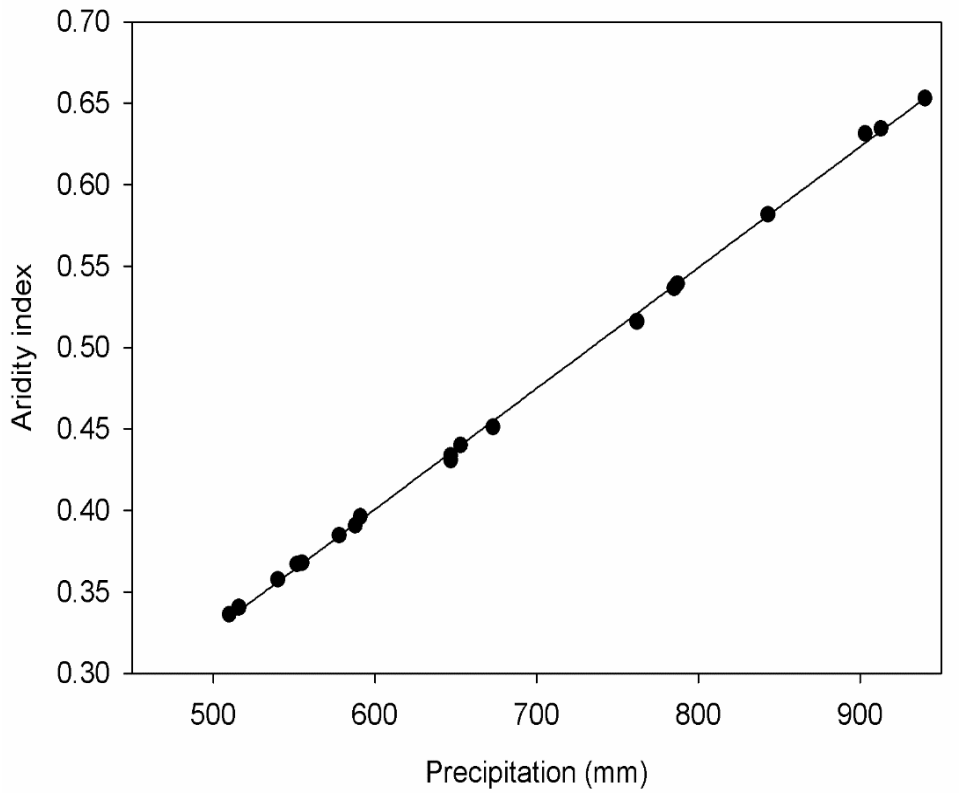
Appendix S3. Aridity measure and its correlation with precipitation

Global aridity index was obtained from CGIAR-CSI Global Aridity and PET Database (http://www.cgiar-csi.org, Zomer *et al*. 2007, 2008) where is calculated using the following formula: Aridity Index (AI) = MAP / MAE, where MAP is the Mean Annual Precipitation and MAE is the Mean Annual Potential Evapotranspiration. This index is modeled using the data available from WorldClim database (http://www.worldclim.org) and its values increase for more humid conditions, and decrease with more arid conditions (Global Aridity and Global PET Methodology available in http://www.cgiar-csi.org). Our index ranged from 0.33 to 0.65 per plot and was highly correlated with mean annual precipitation (Pearson's correlation; r = 0.98, p <0.001):



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682

683 **Appendix S4.** Results of the canonical correspondence analysis (CCA) used to test the influence
684 of precipitation, chronic anthropogenic disturbance and their interaction on the species
685 composition of ants disperser species at Catimbau National Park, Pernambuco, Brazil. Significant
686 values are in bold.

Source of variation	**DF**	χ^2	**F**	**P**
Axis				
CCA1	1	0.1	2.71	**0.02**
CCA2	1	0.07	0.07	**0.04**
Residual	1	0.53	0.53	
Variables				
Precipitation	1	0.07	2.00	**0.03**
CAD	1	0.07	1.96	**0.04**
Precipitation x CAD	1	0.05	1.44	0.19
Residual	15	0.53		

687

688

689 **Appendix S5.** Spearman's correlations between the abundance of each ant disperser species and
690 the CCA axes significantly associated with precipitation (CCA 1) and chronic anthropogenic
691 disturbance (CCA2) at Catimbau National Park, Pernambuco, Brazil. Significant values are in
692 bold.

Ant disperser species	CCA 1		CCA 2	
	R	p	R	p
Acromyrmex rugosus	0.20	0.40	0.50	**0.03**
Atta sexdens	0.13	0.5	0.23	0.33
Dinoponera quadriceps	0.74	**<0.01**	-0.05	0.82
Dorymyrmex thoracicus	0.54	**0.01**	0.32	0.17
Ectatomma muticum	-0.48	**0.04**	0.14	0.56
Pheidole radoskowskii	-0.02	0.93	-0.03	0.9
Pheidole sp. B	0.1	0.68	-0.09	0.71
Pheidole sp. C	0.59	**<0.01**	-0.08	0.73
Pheidole sp. D	-0.25	0.29	-0.17	0.48
Pheidole sp. E	0.24	0.31	0.24	0.31
Pheidole sp. P	0.18	0.45	-0.12	0.31
Pheidole triconstricta	-0.15	0.52	-0.07	0.77
Solenopsis sp. B	0.35	0.14	-0.47	**0.04**
Solenopsis sp. C	-0.26	0.27	-0.11	0.65
Solenopsis tridens	-0.27	0.26	0.01	0.97
Solenopsis virullens	-0.51	**0.02**	0.37	0.11
Tetramorium sp.	0.29	0.23	-0.25	0.29

693

694 **Appendix S6.** Effects of precipitation, chronic anthropogenic disturbance (CAD) and their
695 interaction on seed removal and distance considering the overall diaspores and each diaspore
696 species individually at Catimbau National Park, Pernambuco, Brazil. Abbreviations: *SF*, *Simaba*
697 *ferruginea*; *JM*, *Jatropha mutabilis*; *SO*, *Sideroxylum obtusifolium*; *CN*, *Croton nepetaefolius*;
698 *JR*, *Jatropha ribifolia*; *MB*, *Melocatus bahiensis*. R^2 represents the coefficient of determination of
699 the whole model. Significant values are in bold.

Diaspore Species	Variables	Removal rate				Removal distance			
		R^2	DF	F	P	R^2	DF	F	P
Overall	Precipitation	0.52	1,678	5.9	**0.03**	0.36	1,678	8.1	**<0.01**
	CAD		1,678	0.2	0.85		1,678	0.2	0.37
	Precipitation x CAD		1,678	0.6	0.41		1,678	0.1	0.71
SF	Precipitation	0.32	1, 109	0.7	0.30	0.02	1, 109	0.5	0.59
	CAD		1, 109	0.1	0.31		1, 109	1.3	0.26
	Precipitation x CAD		1, 109	0.6	0.41		1, 109	0.4	0.53
JM	Precipitation	0.40	1, 109	7.0	**0.04**	0.19	1, 109	8.5	**0.02**
	CAD		1, 109	0.1	0.97		1, 109	0.1	0.82
	Precipitation x CAD		1, 109	4.5	**0.03**		1, 109	4.1	**0.04**
SO	Precipitation	0.29	1, 109	7.5	**0.01**	0.28	1, 109	6.2	**0.01**
	CAD		1, 109	1.0	0.95		1, 109	0.2	0.15
	Precipitation x CAD		1, 109	0.6	0.43		1, 109	2.0	0.16
CN	Precipitation	0.12	1, 109	0.0	0.89	0.09	1, 109	0.7	0.49
	CAD		1, 109	0.7	0.45		1, 109	0.3	0.60

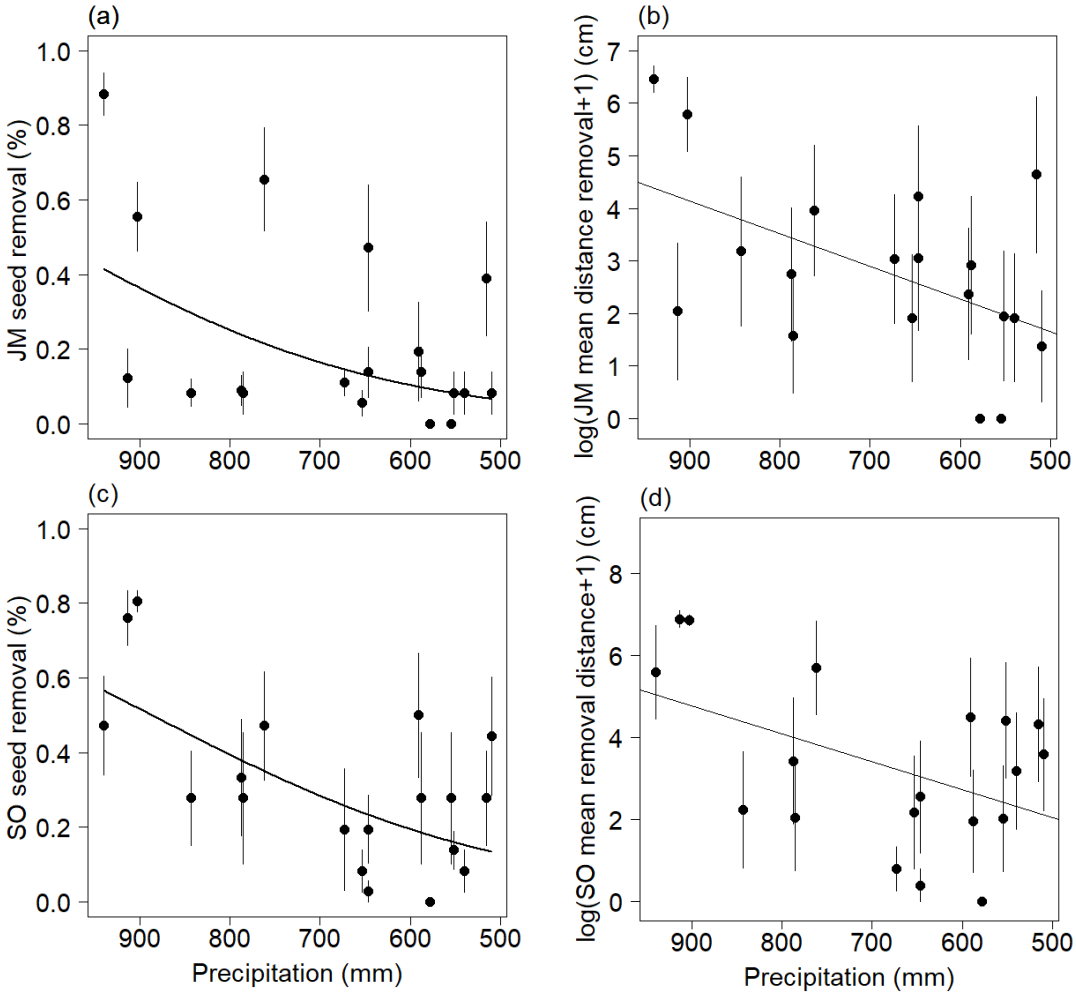
	Precipitation x CAD		1, 109	0.0	0.86		1, 109	0.3	0.60
JR	Precipitation	0.25	1, 109	3.4	0.08	0.21	1, 109	2.2	0.17
	CAD		1, 109	0.1	0.51		1, 109	0.7	0.31
	Precipitation x CAD		1, 109	0.0	0.85		1, 109	0.1	0.78
MB	Precipitation	0.36	1, 109	1.1	0.90	0.06	1, 109	0.0	0.95
	CAD		1, 109	0.5	0.95		1, 109	0.5	0.76
	Precipitation x CAD		1, 109	3.1	0.08		1, 109	1.2	0.26

Appendix S7. Effects of precipitation, chronic anthropogenic disturbance (CAD) and their interaction on seed removal rate and distance considering the high-quality (HQ) and low-quality (LQ) ant dispersers, and the most common ant disperser species removing diaspores at Catimbau National Park, Pernambuco, Brazil. *DQ = Dinoponera quadriceps, PR = Pheidole radoskowskii, EM = Ectatomma muticum, ST = Solenopsis tridens*. R^2 represents the coefficient of determination of the whole model. Significant values are in bold.

Ant disperser species	Variables	Removal rate				Removal distance			
		R^2	DF	F	P	R^2	DF	F	P
HQ	Precipitation	0.55	1,678	5.2	**0.04**	0.34	1,678	5.4	**0.02**
	CAD		1,678	0	0.45		1,678	0	0.44
	Precipitation x CAD		1,678	0	0.92		1,678	0	0.92
LQ	Precipitation	0.63	1,678	2.7	0.12	0.32	1, 678	2.6	0.08
	CAD		1,678	0.1	0.99		1, 678	0.1	0.76
	Precipitation x CAD		1,678	0	0.99		1, 678	0.6	0.32
DQ	Precipitation	0.74	1,678	5.7	**0.03**	0.43	1,678	9.1	**0.01**
	CAD		1,678	0.1	0.96		1,678	0.3	0.24
	Precipitation x CAD		1,678	0.3	0.58		1,678	0.0	0.93
PR	Precipitation	0.81	1,678	0.7	0.87	0.16	1,678	0.3	0.46
	CAD		1,678	0,2	0.74		1,678	0.3	0.36
	Precipitation x CAD		1,678	0.8	0.43		1,678	0.7	0.38
EM	Precipitation	0.77	1,678	0.0	0.87	0.08	1,678	0.1	0.89
	CAD		1,678	0.7	0.74		1,678	0.1	0.40
	Precipitation x CAD		1,678	0.0	0.43		1,678	3.3	0.07

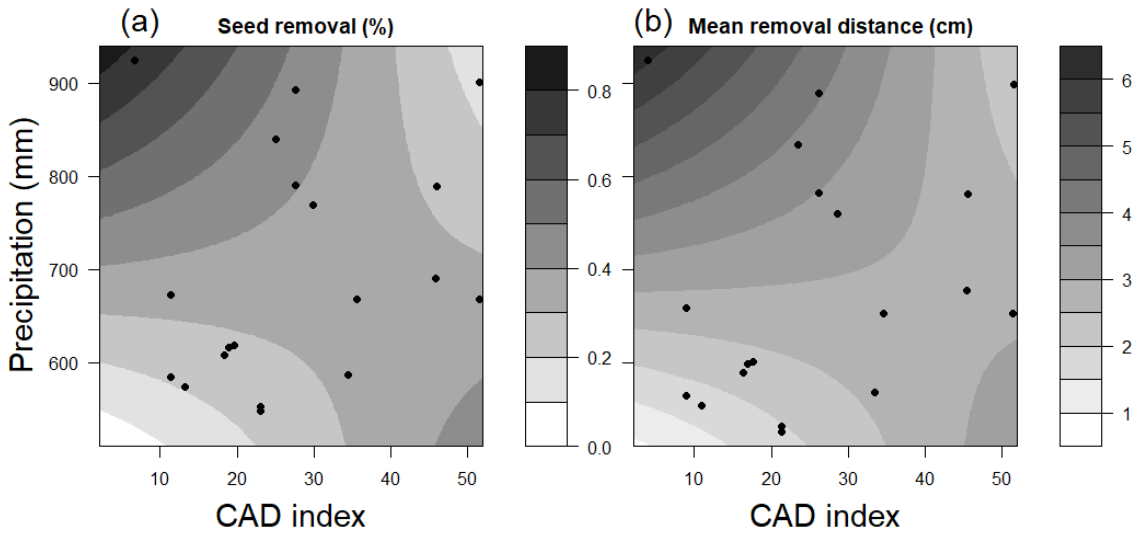
ST	Precipitation	0.29	1,678	0.0	0.92	0.27	1,678	0.5	0.57
	CAD		1, 109	0.0	0.81		1, 109	0.0	0.91
	Precipitation x CAD		1, 109	0.0	0.86		1, 109	0.0	0.92

712 **Appendix S8**. Removal rate (a,c) and mean removal distance (b, d) by ants of *J. mutabilis* (*JM*)
713 and *S. obtusifolium* (*SO*) diaspores per site over the precipitation gradient at Catimbau National
714 Park, Pernambuco, Brazil. Black dots represent means and bars represent standard errors
715 considering all stations per plot.



716

Appendix S9. Contour plots showing the interactive effect of precipitation and anthropogenic disturbance on seed removal rate (a) and mean removal distance (b) by ants of *Jatropha mutabilis* diaspores at Catimbau National Park, Pernambuco, Brazil.



4 EFFECTS OF CHRONIC ANTHROPOGENIC DISTURBANCE AND ARIDITY ON THE EFFECTIVENESS OF EXTRAFLORAL NECTARY-MEDIATED PLANT PROTECTION SERVICES PROVIDED BY ANTS IN BRAZILIAN CAATINGA

MANUSCRITO A SER SUBMETIDO

AO PERIÓDICO DIVERSITY AND DISTIRBUTIONS

Standard paper – Diversity and Distributions

Effects of chronic anthropogenic disturbance and aridity on the effectiveness of extrafloral nectary-mediated plant protection services provided by ants in Brazilian Caatinga

Fernanda M. P. Oliveira[1], Talita Câmara[1], José I. F. Durval[2], Caroline L. S. Oliveira[2], Xavier Arnan[1,3], Alan N. Andersen[4,5], Elâine M. S. Ribeiro[1,6] and Inara R. Leal[7,*]

[1]Programa de Pós-Graduação em Biologia Vegetal, Universidade Federal de Pernambuco, Av. Prof. Moraes Rêgo s/n, Cidade Universitária, 50690-901, Recife, PE, Brazil

[2]Labratório de Interações Planta-Animal , Universidade Federal de Pernambuco, Av. Prof. Moraes Rêgo s/n, Cidade Universitária, 50690-901, Recife, PE, Brazil

[3]CREAF, Cerdanyola del Vallès, Catalunya, Spain

[4]Research School of Environment and Livelihoods, Charles Darwin University, Darwin, NT 0909, Australia

[5]CSIRO Land & Water, Tropical Ecosystems Research Centre, PMB 44 Winnellie, NT 0822, Australia

[6]Universidade de Pernambuco – *Campus* Petrolina, BR 203, km 2, s/n, Vila Eduardo, CEP: 56328-903 - Petrolina, PE- Brazil

[7]Departamento de Botânica, Universidade Federal de Pernambuco, Av. Prof. Moraes Rêgo s/n, Cidade Universitária, 50690-901, Recife, PE, Brazil

*Corresponding author: email: ir.leal@ufpe.br, phone: 55-81-21267814, fax: 55-81-21268348

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ABSTRACT

Aim: Most terrestrial species occur in human-modified landscapes that are experiencing climate change. In addition to direct impacts on species, both CAD and climate change can have important indirect effects through changes in species interactions, including through the disruption of mutualisms. Here we investigated how CAD and aridity affect the mutualism between ants and plants bearing extrafloral nectaries (EFNs).

Location: Caatinga vegetation of Catimbau National Park in northeastern Brazil, wich is forecast to receive 22% less rainfall by 2100.

Methods: We focus on *Pityrocarpa moniliformis*, the most common and widely distributed EFN-bearing tree plant species occurring in our study area. We estimated the volume and concentration of EFN production, sampled attending ants and documented the effectiveness of EFN-mediated plant protection services by ants by measuring attack on termites as simulated insect herbivore in 13 plots (50 m × 20 m) that varied in CAD intensity and aridity.

Results: We found that the volume of extrafloral nectar declined with increasing CAD but not aridity, and that its concetration was not reletede to either CAD or aridity. The composition of attendant ant species varied with aridity but not CAD, and ant protection services declined with increasing aridity, but were not related to CAD.

Main conclusions: Our results suggest that the decline in effectiveness of ant-mediated protection services in *P. moniliformis* is mediated by changes in the composition of attendant ant species rather than extrafloral nectar. Our findings highlight the vulnerability of the mutualism between ants and EFN-bearing plants to climate change due to replacement of ant partners by species that provide inferior protection services. This is likely to apply to the many other EFN-bearing plant species in our study system, resulting in a widespread increase in herbivory damage and consequently reduction in plant survival and reproductive success under climate change.

KEY WORDS: anti-herbivore defense, anthropogenic disturbance, climate change, extrafloral nectaries, plant-animal interactions, seasonally dry tropical forest.

INTRODUCTION

Chronic anthropogenic disturbance (CAD; s*ensu* Singh, 1998) is one of the main threats to biodiversity loss in developing countries, especially in the semi-arid tropics that support a high density of rural populations depending on forest resources for their livelihoods (Singh, Rawat, & Garkoti, 1997; Ribeiro, Arroyo-Rodriguez, Santos, Tabarelli, & Leal, 2015). CAD is characterized by a continuous removal of small portions of forest biomass due to activities such as livestock grazing, wood extraction and collection of non-timber products (Singh, 1998), and at the regional scale can have as great an impact on biodiversity services as acute disturbances such as deforestation and forest fragmentation (Martorell & Peters 2005; Ribeiro, Arroyo-Rodriguez, Santos, Tabarelli, & Leal, 2015; Ribeiro et al., 2016; Schulz et al., 2016; Sfair, Bello, França, Bauldauf, Tabarelli, 2018). Furthermore, most regions in the semi-arid tropics are threatened by declining rainfall and increasing temperatures due to climate change (Magrin et al., 2014). Such climatic change can mediate and intensify the effects of anthropogenic disturbance (Brook, Sodhi, & Bradshaw, 2008; Gibb et al., 2015; Frishkoff et al., 2016; Rito, Arroyo-Rodríguez, Queiroz, Leal, & Tabarelli, 2017).

Disturbance-mediated biodiversity loss can have broader ecological impacts through its cascading effects on species interactions (Tylianakis, Didham, Bascompte, & Wardle, 2008; Aizen, Sabatino, & Tylianakis, 2012), which mediate many aspects of ecosystem function (Valiente-Banuet et al., 2015; Dias et al., 2013). For instance, mutualisms play a key role in the functioning of ecosystems by providing services such as pollination, seed dispersal and nutrient transfer (Terborgh et al., 2008; Wilson, Rice, Riling, Springer, 2009; Potts et al., 2010), and are strongly affected by both anthropogenic disturbances and climate change (Tylianakis, Didham, Bascompte, & Wardle et al., 2008; Kiers, Palmer, Ives, Bruno, & Bronstein, 2010), either through changes in species composition (Jones, Berkelmans, Oppen, Mieog, & Sinclair, 2008;

Winfree, Aguilar, Vazquez, LeBuhn, & Aizen, 2009; Potts et al., 2010; Leal, Andersen, Leal, 2014), or by changing species behaviour (Brose et al., 2005, Tylianakis, Tscharntke, & Lewis, 2007).

This study addresses the effects of CAD and climate change on the mutualism between ants and plants producing extra-floral nectar. Extrafloral nectaries (EFNs) are indirect plant defenses produced by at least 4,000 plant species throughout the world (Weber & Keeler, 2013), whose function is to attract ants through the secretion of nectar. The ants then repel or kill insect herbivores (Rosumek et al., 2009; Heil, 2015; Del-Claro et al., 2016), potentially reducing plant herbivory and increasing plant growth and reproductive success (Nascimento & Del-Claro, 2010; Marazzi, Conti, Sanderson, McMahon, & Bronstein, 2013). Extrafloral nectar can be a particularly valuable resource for ants, and it can have an important effect on ant communities (Blüthgen & Fiedler, 2004; Lange, Dáttilo, & Del-Claro, 2013; Lange, Calix, & Del-Claro, 2017; Díaz-Castelazo, Chavarro-Rodríguez, & Rico-Gray, 2017). Interactions between EFN-bearing plants and attendant ants are typically facultative (Rico-Gray & Oliveira, 2007), such that the frequency and identity of ant partners are highly variable (Bechior, Sendoya, & Del-Calro, 2016; Fagundes, Dáttilo, Ribeiro, Rico-Gray, & Del-Claro, 2016; Del-Claro et al., 2016). A reduction in nectar production can reduce the frequency and change the identity of ants attending plants (Fagundes et al., 2016; Lange et al., 2017), and consequently reduce the effectiveness of plant protection services by ants (Fagundes et al., 2016).

Both CAD and climatic variation can lead to changes in the secretion of extrafloral nectar, with cascading effects on attendant ants and consequently plant protection services (Díaz-Castelazo, Chavarro-Rodríguez, & Rico-Gray, 2017). For example, EFNs are more active and produce nectar in higher concentration in conserved compared with disturbed areas (Hernandéz-Villanueva, 2010; Chavarro-Rodríguez, Díaz-Castelazo, Rico-Gray, 2013), with conserved areas

also showing a higher richness and visitation frequency of ants (Fernández-Martínez & Díaz-Castelazo, 2009; Leal, Andersen, Leal, 2015), which provide significant protection to plants (Evans et al., 2013). Similarly, EFN activity is sensitive to declining rainfall (Rico-Gray et al., 1998; Lange, Dáttilo, & Del-Claro et al., 2013). In spite of this, most of those studies focus only on the effects of anthropogenic disturbances and climate change on the EFNs traits and availability of ant partners. For better understanding the implications of anthropogenic disturbances, it is necessary to adopt mutualism effectiveness framework (i.e. combination of quantity and quality of the services, Schupp, Jordano, & Gómez, 2017) and the mechanism underlying them.

Our study investigates the impacts of increasing CAD and aridity on EFN-mediated plant protection services provided by ants in the Caatinga biome of semi-arid, north-eastern Brazil. Caatinga is an ideal study system for this purpose because a large proportion of its flora has EFNs (Reis, 2016; Rito, Arroyo-Rodriguez, Queiroz, Leal, & Tabarelli, 2017), the region suffers from high levels of CAD (Ribeiro, Arroyo-Rodriguez, Santos, Tabarelli, & Leal, 2015; Rito, Arroyo-Rodriguez, Queiroz, Leal, & Tabarelli, 2017), and it is forecast to experience a decrease in rainfall of about 22% by 2100 (Magrin et al., 2014). We focus on a single species of EFN bearing plant, *Pityrocarpa monilifromis* (Fabaceae), which attracts a variety of ants in our study system (Câmara et al., 2017), to address three key questions. First, what are the effects of CAD and aridity on the production of extrafloral nectar? Second, how does the composition of attendant ant species vary along the CAD and aridity gradients? Third, how do CAD and aridity influence the effectiveness of protection services provided by ants?

METHODS

Study Area

Our study was conducted in Catimbau National Park, which covers an area of nearly 640 km^2, located in Pernambuco State, north-eastern Brazil (8º24'00" and 8º36'35" S; 37º0'30" and 37º1'40" W) (Fig. 1). Annual rainfall varies markedly in Catimbau because of topographic influences, from 480 mm to 1100 mm per year, while the mean annual temperature is 23ºC. Quartzite sandy soils are predominant in the Park (approximately 70%), supporting a relatively open, low-stature vegetation in which Fabaceae, Euphorbiaceae and Cacataceae are the dominant families (Rito et al., 2017). EFN-bearing plants, mostly belonging to Fabaceae and Euphorbiaceae, representing nearly 30% of the total woody flora (Reis, 2016).

The Park remains occupied by low-income rural populations that depend on natural resources for their livelihoods, resulting in high levels of CAD (Rito, Arroyo-Rodriguez, Queiroz, Leal, & Tabarelli et al., 2017; Sfair, Bello, França, Baldauf, Tabarelli, 2018). The main activities are raising of livestock (goats and cattle), extraction of non-timber forest products and wood extraction (Arnan et al., unpublished data).

We selected thirteen 50 m × 20 m plots from the 20 permanent plots of the Catimbau ILTER project (https://www.peldcatimbau.org) where our focal plant species occur (Reis, 2016; Rito et al,. 2017). These plots cover a wide range of CAD and rainfall (Fig. 1). All plots were on sandy soil, on flat terrain, and supported old-growth vegetation. Plots were separated by a minimum of 2 km, and they all occurred within an area of 214.3 km^2 (Rito, Arroyo-Rodriguez, Queiroz, Leal, & Tabarelli, 2017).

Characterization of CAD and aridity gradients

We characterized the intensity of CAD in each plot by computing a global multimetric index that integrates five disturbance metrics that are related to the three main sources of chronic anthropogenic disturbance at Caatinga vegetation: livestock grazing, wood extraction and

extraction of non-timber forest products (Ribeiro, Arroyo-Rodriguez, Santos, Tabarelli, & Leal, 2015; Ribeiro-Neto, Arnan, Tabarelli, & Leal, 2016; Rito, Arroyo-Rodriguez, Queiroz, Leal, & Tabarelli, 2017). Livestock grazing and wood extraction were directly measured at field. To measure livestock grazing, we computed goat trail length and counted goat and cattle drops. Thus, we combined the two estimates of goat grazing (trail length and drop frequency) to obtain a single measure of goat grazing (see Appendix S1) and cattle drop frequency was considered a measure of cattle grazing. To measure wood extraction we computed the alive (stem cuts) and coarse woody debris extraction (litter) (see Appendix S1 for details on sampling of these variables at field). In addition to livestock grazing and wood extraction, local communities also harvest non-timber products (e.g., medicinal plants, animal and human foods) and hunt. We were not able to get direct measures at field to account for such a disturbance source and only indirect metrics were used. Thus, we particularly measured four variables that are related to the accessibility of human activities to the plots: proximity to the nearest house, proximity to the nearest village, proximity to the nearest road and number of people living in the houses with influence in the plots. These four variables were integrated in a new disturbance metric representing human pressure (see Appendix S1). Then, data from these five disturbance indicators (cattle grazing, goat grazing, live-wood extraction, coarse woody debris extraction, and human pressure) were integrated in an index. This index was computed by using the following formula (Legendre & Legendre 1998):

$$I = \frac{\sum_{i=1}^{n}(y_i - y_{\min})/(y_{\max} - y_{\min})}{n} \times 100$$

where I is the disturbance intensity index, y_i the observed value for one disturbance metric in plot *i*, y_{min} the minimum observed value for the disturbance metric considering all plots, y_{max} the maximum observed value for the disturbance metric considering all plots and *n* is the number of

individual disturbance metrics considered in the index. Thus, this formula first standardizes the values of each disturbance metric between 0 and 1, which makes disturbance metrics of different units comparable and easily to combine in the same index. The index ranges from 2 to 58 (from the lowest to the highest disturbance intensity) among the plots (Arnan et al., unpublished data). To characterize the aridity gradient, mean annual rainfall within each plot was obtained from the WorldClim database (www.worldclim.org) at a spatial resolution of 1 km extracted using the package *maptolls* (Bivand & Lewin-Koh, 2015) in the R software (R Core Team, 2016). Mean annual rainfall in our plots ranged from 940 mm to 510 mm, over a distance of just 18 km. Catimbau is thus an ideal study system for analysing ecological responses to variation in aridity. We also computed a global aridity index (Appendix S2), but since it was highly correlated with rainfall ($r = 0.98$; see Appendix S2 for more details) we retain rainfall as our measure of aridity because it is more commonly used in diversity studies (Hawkins et al., 2003; Dunn et al., 2009; Rito, Arroyo-Rodriguez, Queiroz, Leal, & Tabarelli, 2017).

Study species

Pityrocarpa moniliformis (Benth.) Luckow & R. W. Jobson (Fabaceae) is the most commom and widely distributed EFN-bearing plant species that occur in Catimbau (Reis, 2016; Rito, Arroyo-Rodriguez, Queiroz, Leal, & Tabarelli, 2017). It is endemic to Brazil, occurring primarily in Caatinga but also in Atlantic Forest (Maia-Silva et al., 2012; Morim, 2015). Its EFNs are an enclosed-concave type (Melo, Machado, & Alves, 2010), located singly on the rachis between the first pair of pinnae (Melo, Machado, & Alves, 2010; Reis, 2016).

Sampling

We selected 10 adult (height ≥ 1 m and a diameter at breast height ≥ 3 cm) plants per plot, all with similar size and architecture to control for possible ontogenic effects on nectar production (Villamil, Márquez-Guzmán, & Boege, 2013). Plants were separated from each other by a minimum of 10 m to ensure that most, if not all, attendant ants were from different colonies (Agosti & Alonso, 2000). For each of the total 130 plants, we estimated the volume and concentration of extrafloral nectar, sampled the attending ants, and documented the effectiveness of EFN-mediated plant protection services by ants as measured by rates of attack ant time taken to attack of simulated insect herbivores.

Extrafloral nectar volume and concentration: We selected three apical branches per plant with completely expanded leaves, and collected nectar from one EFN per branch (i.e. three EFNs per plant). Nectar was collected after 24h of EFNs being isolated from nectar-feeding insects by using bag of TNT non-woven fabric to cover the leaves and applying tanglefoot around each branch (Tanglefoot Company, Grand Rapids, Michigan USA) (Blüthgen, Stork, & Fiedler, 2004; Bixenman, Coley, & Kursar, 2011). Nectar volume was sampled with a 10µl Hamilton micro syringe and nectar concentration was measured using a Kasvi K52-032 portable Brix refractometer 0-32%. Extrafloral nectar was collected in nine plots (plots 17, 29, 28, 15, 14, 20, 4, 16 and 8) from May to July 2016 and in the remaining four plots (30, 22, 23 and 11) in May 2017 and both sampling periods included plots representing a range of variation in CAD and rainfall.

Attendant ants: Ant sampling was carried out once in one apical branch of each plant for up to 5 min as described by Leal, Andersen, Leal (2015) during the day (07-10h) from May to July of 2017. For each sample, we recorded the identity and the number of ants that contacted their mouthparts with EFNs. Ant species that could not be identified in the field were collected, placed in 70% ethanol and brought to the lab. Ants were identified to species, or sorted to

morphospecies when the species identification was not possible. Interactions were defined by the number of attendant-ant species interacts with EFN-bearing plant individuals, regardless of the total number of ant workers (Câmara et al, unpublished data).

Effectiveness protection services by ants: In the same day we had censured attendant ants, we selected another apical branch of each plant to conduct experimental observations of attack rates by ants. For each plant, we first observed and counted the initial abundance of ants on the selected branch before conduct. Experiments were not conducted if no ants were observed. Following previous studies (Oliveira, Silva, & Martins, 1987; Leal, Fischer, Kost, Tabarelli, & Wirth, 2006), we used live termites as simulated herbivores. Five termites were glued on the branch by the dorsum, each one in the middle of the foliole from different leaves as far distant as possible of each other. We observed ant behaviour (encounter, attack or no attack) in response to termite-baits during 10 min, and measured the time taken by each ant species to attack after termites were placed on the plant. We considered the attack succeeded when ants captured the termites. We used two measures of plant protection effectiveness: (1) attack rate (proportion of termites attacked of the total of five termites) and (2) time taken to attack. Additionally, we used and index of "protection effectiveness (PE)" for each ant species using the formula (modified from Fagundes et al., 2017):

$$\mathbf{PE} = \mathbf{n}[(\mathbf{t}^{-\mathbf{1}}\ (\mathbf{a})]$$

where n is the number of workers an ant species observed on the branch during the experiment of attack rates, t is the mean time taken to attack, and a is the ratio between number of interactions and number of attacks.

Statistical Analyses

We used generalized linear mixed models (GLMMs) to evaluate the effects of CAD and rainfall on the mean volume and concentration of extrafloral nectar per plant. Plot and year of sampling were included in the models as random factors and we used Gaussian error distributions.

We also used GLMMs to evaluate the effects of CAD and rainfall on the mean number of interactions between ants and EFN-bearing plants, ant attack rate and mean time taken to attack per plant. For attack rate and time taken to attack models, we included the mean of initial abundance of ants per plot as a covariate, since ant abundance is likely to influence the probability of ant attack. Plot was included in the models as a random factor and we used a Binomial error distribution for attack rate and a Gaussian error distribution for the number of interactions and the time spent to attack. Data that did not obey homoscedastic criteria were log(x) +1 transformed. We used *lme4* version 1.1-7 package (Bates et al., 2014) to build GLMM models in R.

The effects of CAD and rainfall on the composition of attendant-ant species were evaluated using canonical correspondence analysis (CCA) with *vegan* version 2.3 package (Oksanen, Blanchet, Kindt, Oksanen, & Suggests, 2015) in R. For this analysis, we considered the frequency that which each ant species attended EFN-bearing plants per plot. We performed a randomization test (10000 aleatorizations) to obtain the statistical significance of explanatory variables (Legendre, Oksanen, & Ter Braak, 2011).

RESULTS

Nectar volume of *Pityrocarpa moniliformis* decreased significantly with increasing CAD (Table 1), declining from 1.7 ± 0.22 µl (mean ± SE) in the least disturbed plot to 0.19 ±0.11µl in the most disturbed plot (Table 1, Fig. 2a). Nectar volume was not affected by rainfall (Table 1).

Nectar concentration ranged from zero to 15.26 ±0.41 Brix (mean ±SE), and did not vary significantly eith either CAD or rainfall (Table 1).

We observed 238 interactions involving 16 ant species attending *P. moniliformis* EFNs. *Camponotus crassus* occurred in all plots, and *Camponotus crassus* and *Cephalotes pusillus* were the most frequent ant species attending EFNs, involved in 40.7% of all interactions (Table 2). The mean number of interactions between ants and *P. moniliformis* per plot was strongly related to rainfall, ranging from 3.8 ± 0.44 (mean ± SE) in the least arid plot to 1.1 ± 0.18 in the most arid plot (Table 1, Fig. 2b. It was not related to CAD (Table 1).

The first and second axes of the CCA explained 28.1% and 9.5% of the variation in species composition, respectively (Fig. 3). However, only the first axis was significant (Table 3). The composition of attendant ant species composition varied significantly with rainfall but not with CAD (Table 3, Fig. 3). *Azteca* sp. A and *Camponotus* sp. D were associated with higher rainfall, whereas *Cephalotes* pr. *cordatus* and *Camponotus blandus* were more associated with lower rainfall (Fig. 3).

Eight (half) of the attendant ant species attacked experimanetal termites (Table 1). *Camponotus crassus* and *Crematogaster* pr. *evallans* were responsible for 41.6% and 30.5% of all attacks, respectively (Table 2). Overall rates of termite attack were low, only 5.5% (Table 2). Attack rate increased with increasing rainfall, ranging from 0.21 ±0.06 (mean ± SE) in the wettest plot to zero in the driest plot (Fig. 2c) and was positively correlated with the number of interactions between ants and EFNs (Spearman's $r = 0.46$, $p < 0.01$). Attack rate did not vary with CAD (Table 1). The mean time taken to attack decreased with increasing rainfall (Fig. 2d), and it was negatively correlated with the number of interactions (Spearman's $r = 0.38$, $p = 0.03$). Ants took on average 1.1 ± 0.27 minutes (mean ± SE) to attack termites in the wettest plot and 3.8 ± 0.40 minutes in the driest plot (Fig. 2d). There was no relationship between attack time and CAD (Table 1). *Crematogaster crinosa* and *Camponotus cingulatus* were the quickest ant species to attack (Table 2). The species with highest protection effectiveness were *Azteca* sp. A,

306 *Crematogaster* prox. *evallans* and *Camponotus cingullatus* (Table 2), all of which were
307 associated with higher rainfall (Fig. 3).
308
309 DISCUSSION
310 Our study investigated the effects of CAD and aridity on the mutualism between ants and EFN-
311 bearing plants in Brazilian Caatinga, which is forecast to receive substantial reductions in rainfall
312 over comunig decades. Our results show that CAD and aridity have largely independent effects.
313 We found a strong impact of aridity on the composition of attendant ant species and on the of
314 EFN-mediated plant protection services, but little evidence of impacts of CAD on this ant
315 protective mutualism.
316 Our first key question addressed the effects of CAD and aridity as factors influencing the
317 production of extrafloral nectar. We found that CAD but not aridity affected the volume of
318 extrafloral nectar, and that there were not effects of either CAD or aridity on its concentration.
319 Previous studies have shown negative effects of anthropogenic disturbance on the volume of
320 extrafloral nectar (Hernandéz-Villanueva, 2010; Chavarro-Rodríguez, Díaz-Castelazo,& Rico
321 Gray, 2013). However, these studies have attributed the reduction of extrafloral nectar to lower
322 water availability in disturbed areas, which is not consisten with our finding of no relationship
323 with aridity. An alternative explanation is that plants in disturbed areas, compensate for tissue
324 loss through faster relative growth rates (McNaughton et al., 1983; Richards, 1993), at the
325 expense of investing in defense against herbivores. Indeed, *Pityrocarpa moniliformis* is among
326 the most consumed plant by goats in our study area (Menezes et al., unpublished data) and these
327 plants has high regrowth capacity (Souza, 2017). Thus, the increasing CAD such as grazing by
328 goats could make the plant invest strongly in recomposing the lost structures trough regrowth and

mobilize less for nectar production/herbivory defense, which could explain the reduction of extrafloral nectar in our disturbed areas.

Our second key question asked how the composition of attendant ant species is affected by CAD and aridity. We found that aridity but not CAD affected the composition of ants attending EFNs of *P. moniliformis.* A study of all EFN-bearing species in Catimbau likewise found that the composition of attendant ants varied with aridity, but that it also varied with CAD (Câmara et al., unpublished data). In another Caatinga locality, Leal, Andersen, Leal (2015) showed that CAD changes the composition of attendant-ant species on 'loser' EFN-bearing plant species, but not on other EFN bearing plants. Since *P. moniliformis* is not a disturbance 'loser' (Rito, Arroyo-Rodriguez, Queiroz, Leal, & Tabarelli, 2017), this is consistent with our results showing no effect of CAD.

Finally, we asked about the effects of CAD and aridity on the effectiveness of EFN-mediated plant protection services provided by ants. We found that increasing aridity but not CAD reduced the effectiveness these services by ants. This constrasts with previous studies showing an increase in the effectiveness EFN-meidated ant protection services with declining rainfall (Pringle, Akçay, Raab, Dirzo, & Gordon, 2013; Leal & Peixoto, 2017). However, the rainfall gradients in these studies ranged up to 4000 mm/yr, and even our wettest sites (up to 940mm) would be considered at the drier end. Our results are consitest with those of Rico-Gray et al. (1998), who showed that the number of interactions between ants and EFN-bearing plants (a surrogate of the protection services provided; Cushman & Addicott, 1991; Bronstein, 1998; Di Giusto, Ansett, Dounias, & McKey, 2001; Rico-Gray & Oliveira, 2007) increased with increasing rainfall. Additionally, we found a replacement of less effective by more effective ant protectors with increasing aridity showing that the identity of attendant-ant species can determines the effectiveness of protection services (Fagundes et al., 2017). On the other hand, although CAD modified the volume of

extrafloral nectar, it did not affect the number of interaction between ants and EFN-bearing plants or the compostion of attendant ant species, and therefore had no influence of protection services provide by ants.

In conclusion, we found no evidence of CAD affecting EFN-mediated plant protection services provide by ants and in our Caatinga system. However, we found a major impact of aridity, due to replacement of ant partners by species that provide inferior protection services. This has important implication for the vulnerability of ant-mediated plant protection services under the forecast climate change scenario of increasing aridity. Considering that a large number of species of the Caatinga flora bears EFNs, the increasing aridity might influence negatively the anti-herbivory defence provided by ants to EFN-bearing plants, likely increasing herbivory damaged and reducing plant survival and reproductive success. Consequently, many plant species might have their abundance declined, which can influence on the successional trajectories of Caatinga flora (Arroyo-Rodriguez et al., 2017) under climate change.

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563

564 **Table 1** – Effects of chronic anthropogenic disturbance (CAD) and rainfall on the ant protection
565 effectiveness, nectar secretion and volume, and number of interactions with attendant-ant species
566 in *Pityrocarpa moniliformis* at Catimbau National Park, Pernambuco, Brazil. The ant protection
567 effectiveness was measured by evaluating attack rate and time spent to attack termites, and initial
568 ant abundance was used as a covariate. R^2 represents the coefficient of determination of the
569 whole statistical model.

Response variables	Explanatory variables	R^2	DF	F	P
Extrafloral nectar volume	CAD	0.60	1	6.8	**<0.01**
	Rainfall		1	2.3	0.12
	Residuals		35		
Extrafloral nectar concentration	CAD	0.18	1	0.1	0.80
	Rainfall		1	1.9	0.16
	Residuals		35		
Number of interactions	CAD	0.58	1	0.1	0.89
	Rainfall		1	43.4	**<0.01**
	Residuals		126		
Attack rate	CAD	0.29	1	0.8	0.38
	Rainfall		1	21.8	**<0.01**
	Ant abundance		1	0.2	0.88
	Residuals		125		
Time spent to attack	CAD	0.26	1	0.4	0.51
	Rainfall		1	15.6	**<0.01**
	Ant abundance		1	0.1	0.76

	Residuals	30

570

571

572 **Table 2** – Ant species attending and attacking termites on *Pityrocarpa moniliformis* over the
573 chronic anthropogenic disturbance (CAD) and rainfall gradients at Catimbau National Park,
574 Pernambuco, Brazil. PE is the index of protection effectiveness of each ant species.

Ant species	Number of plots	Number of interactions	Number of attacks	Mean time ±SD (min)	PE
Azteca sp. A	2	6	3	1.41 ± 1.1	5.31
Brachymyrmex sp. A	2	4	0	0	0
Camponotus blandus (Smith)	1	3	0	0	0
Camponotus cingullatus (Mayr)	1	1	1	1± 0	1
Camponotus crassus (Mayr)	13	67	15	3.5 ± 3.2	0.19
Camponotus fastigatus (Roger)	6	20	0	0	0
Camponotus sp. D	1	1	0	0	0
Camponotus vittatus (Forel)	3	9	2	2.5 ± 1.5	0.09
Cephalotes pr. *Cordatus*	4	10	0	0	0
Cephalotes pusillus (Klug)	7	30	1	3± 0	0.01
Crematogaster crinosa (Mayr)	3	7	2	1.66 ± 1.3	0.51
Crematogaster pr. *evallans*	8	22	11	2.0 ± 1.5	2
Dorymyrmex thoracicus (Gallardo)	4	17	0	0	0
Ecatomma muticum (Mayr)	2	2	1	5± 0	0.1
Pseudomyrmex acanthobius (Emery)	5	19	0	0	0
Pseudomyrmex gracilis (Fabricius)	6	20	0	0	0

575

576

577 **Table 3** – Results of the canonical correspondence analysis (CCA) used to test the influence of
578 chronic anthropogenic disturbance (CAD) and rainfall on the composition of ant species that
579 attend extrafloral nectaries of *Pityrocarpa moniliformis* at Catimbau National Park, Pernambuco,
580 Brazil. Significant values are in bold.

Source of variation	DF	χ^2	F	P
Axis				
CCA1	1	0.30	3.19	**<0.01**
CCA2	1	0.07	0.83	0.55
Variables				
CAD	1	0.08	0.9	0.42
Rainfalll	1	0.28	2.04	**0.04**
Residual	11	1.23		

581

582

583 **Figure Legends**

584 **Figure 1** - Map showing the study area in different scales: Caatinga vegetation in Brazil (A),
585 Catimbau National Park in Pernambuco State (B) and the distribution of the thirteen 50 m × 20 m
586 plots (gray circles) over the chronic anthropogenic disturbance (CAD) and rainfall gradients at
587 Catimbau National Park. Circles size represents the intensity of CAD, with largest circles
588 representing more disturbed areas.

589

590 **Figure 2** - Attack rates (A) and time taken to attack (B) by ants that attend extrafloral nectaries,
591 extrafloral nectar volume (C), and number of interactions (D) between ants and extrafloral
592 nectaries of *Pityrocarpa moniliformis* along the chronic anthropogenic disturbance (CAD) and
593 rainfall gradients at Catimbau National Park, Pernambuco, Brazil.

594

595 **Figure 3** - Representation of attendant- ant species and environmental gradients (chronic
596 anthropogenic disturbance – CAD and rainfall) at Catimbau National Park, on the first two axes
597 of the canonical correspondence analysis (CCA). Abbrevitation: AztA, *Azteca* sp. A; BraA,
598 *Brachymyrmex* sp. A; Cbla. *Camponotus blandus;* Ccin, *Camponotus cingullatus*; Ccra,
599 *Camponotus crassus*; Cfas, *Camponotus fastigatus*; CamD, *Camponotus* sp. D; Cvit,
600 *Camponotus vittatus*; Ccor, *Cephalotes* pr. *Cordatus*; Cpus, *Cephalotes pusillus*; Ccri,
601 *Crematogaster crinosa*; Ceva, *Crematogaster* pr. e*vallans*; Dtho, *Dorymyrmex thoracicus*; Emut,
602 *Ectatomma muticum*; Paca, *Pseudomyrmex acanthobius*; Pgra, *Pseudomyrmex gracilis*. Asterisk
603 represents ant species that attacked termites.

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605

606 **Figure 1**

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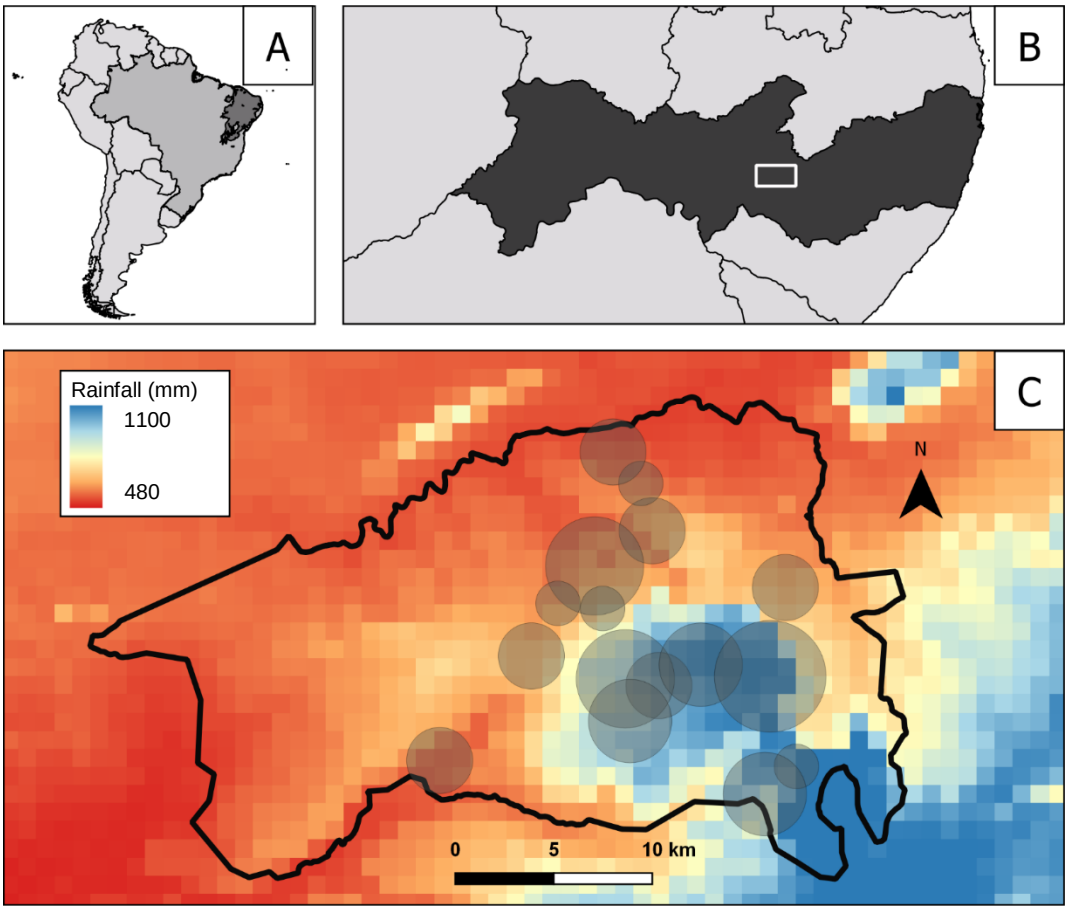

609 **Figure 2**

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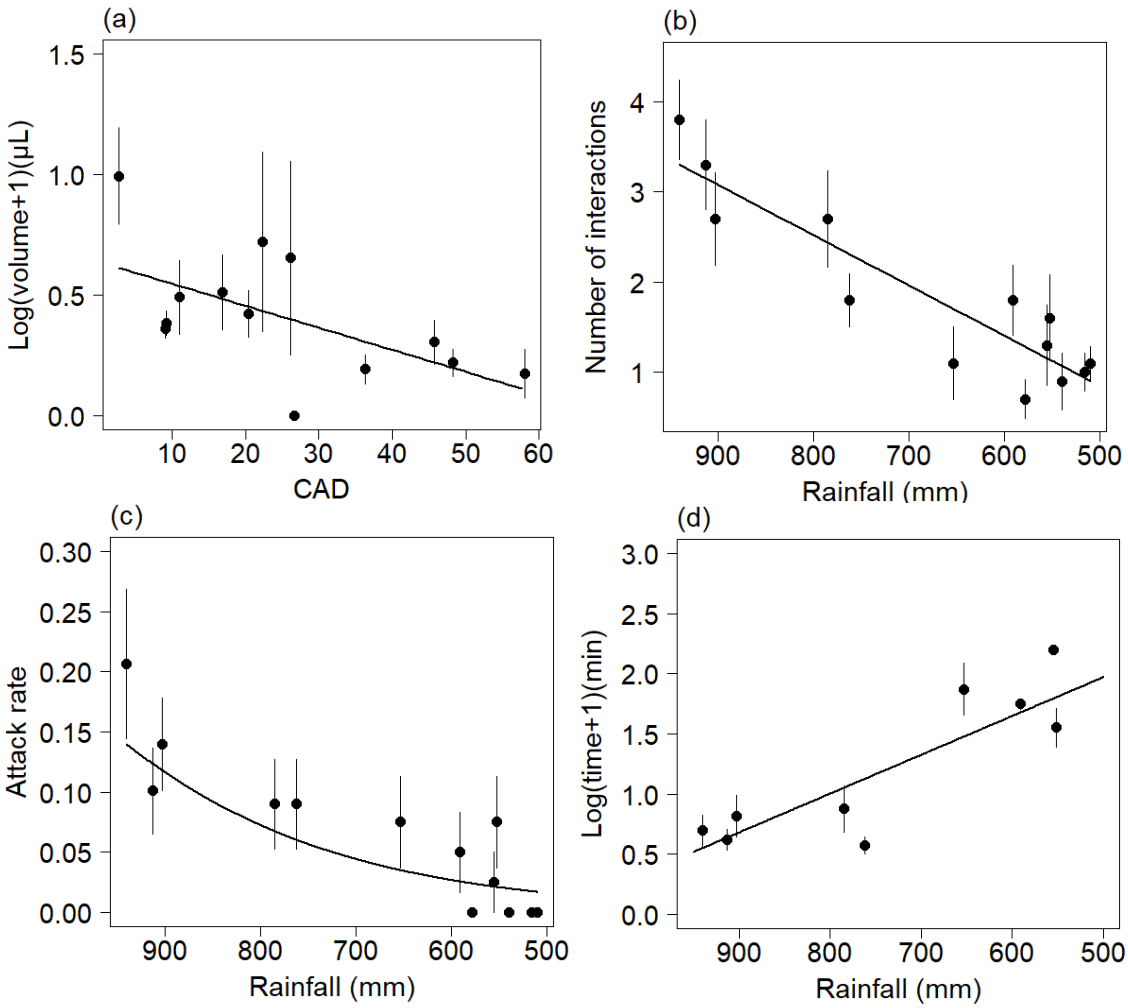
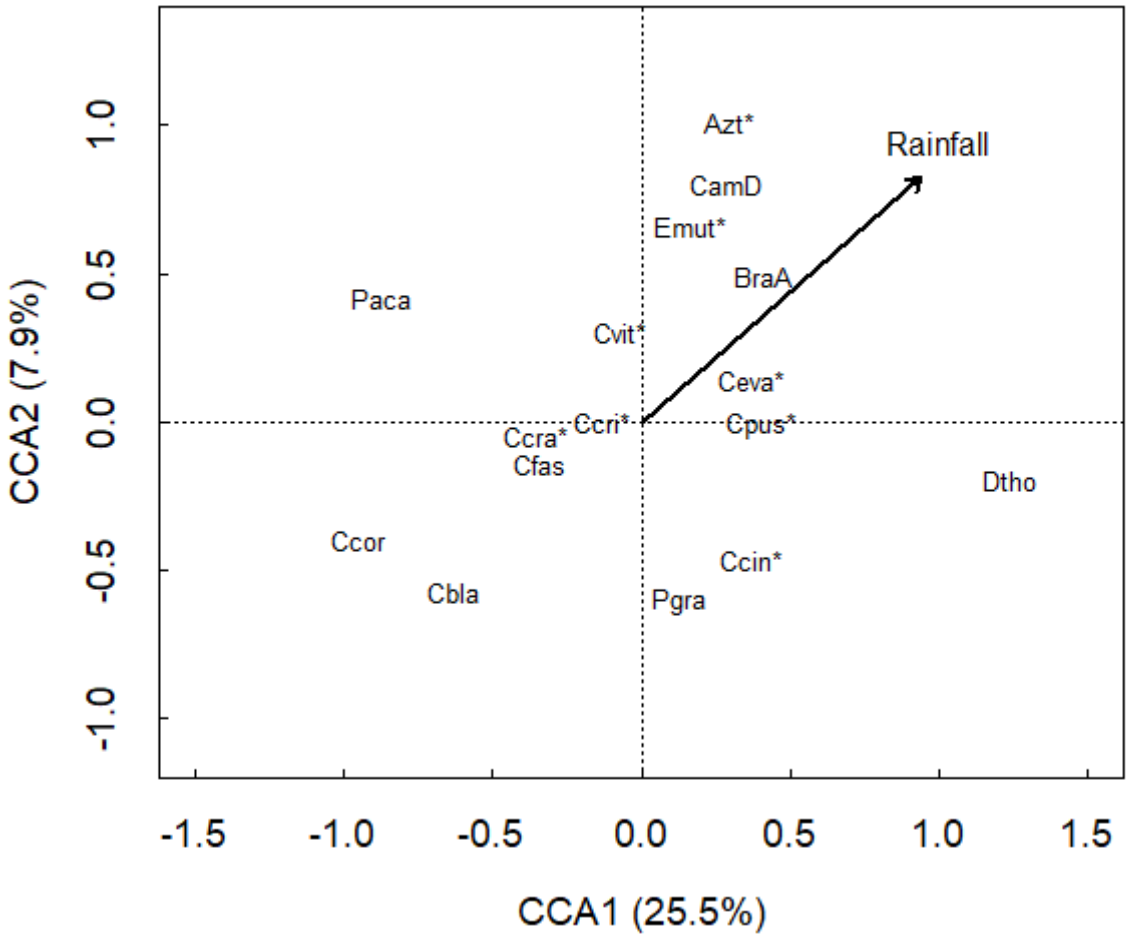


613 **Figure 3**



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SUPPORTING INFORMATION

Appendix S1. Chronic anthropogenic disturbance index measurement

The intensity of chronic anthropogenic disturbance (CAD) was measured by using a global multi-metric index computed from nine disturbances metrics. The variables used to describe a particular sub-index were computed at field or when not possible, using satellite imagery and interviews. Below, we describe the measurements of each variable for each sub-index.

A) Cattle grazing: it was measured through direct measures at field by counting the number of bovine and equine drops within each 0.1 ha plot.

B) Goat grazing: it was measured through two variables: (1) the length in meters of well-defined goat trails by using an odometer in each 0.1 ha plot and by (2) counting the number of goat drops within four subplots of 5 m x 5 m within each 0.1 ha plot. Then, we combined the two estimates of goat grazing (trail length and drops frequency) by means of PCA. Both measures were highly positively correlated ($r > 0.90$) with the first PCA axis, which explained 88% of variance. We therefore used its coordinates to obtain a single measure of goat grazing.

C) Live-wood extraction: it was quantified by counting the number of stem cuts within each 0.1 ha plot. Then, diameter of each stem cut was measured, so we can estimate the overall basal area extracted at each plot.

D) Coarse woody debris extraction: it was estimated by measuring the diameter (> 1cm) near the edges and the length (> 10 cm) of the dead stem laying on the ground within four 1m x 1m subplots in each 0.1 ha plot. Then, we calculated the volume of dead biomass using the volume of a frustum of a right circular cone. To tranform volume into a biomass, we used the mean wood density of tree species ($p = 0.634$) of the study area. The tree species density was measured at field according to the protocol of standardized measurements of Perez-Harguindeguy *et al*. (2013). For trees species that were not able to obtain the wood density at the field, we obtained

them by: WD, g cm-3 in http://datadryad.org/handle/10255/dryad.235. Since the amount of dead biomass is correlated with the total alive biomass available within of a given plot, we divided the dead biomass by total alive biomass for each plot. The total alive biomass for each plot was measured at field and computed by using an allometric equation for Caatinga vegetation ($Biomass_{kg} = 0.173\ DBH_{cm}^{\ 2.295}$; or $Biomass_{kg} = 0.1085\ (AB_{cm2} \times H_m)^{0,9497}$, where DBH is the diameter at breast height (Amorim *et al*. 2005). Because low values indicate high disturbance intensity, we used the multiplicative inverse of this sub-index in order to have the same direction of the others disturbance sub-indices or single metrics.

E) Human pressure: it was measured by using two approaches: satellite imagery and interviews. Based on satellite imagery, we computed proximity to the nearest house, proximity to the nearest village and proximity to the nearest road. Such metrics were computed to estimate the degree of human activities such as non-timber product extraction and hunting within a given plot. Because small distances indicate higher disturbance, we transformed them by using the multiplicative inverse; then, low values indicate low disturbance and high values indicate high disturbance. We also conducted 65 interviews to estimate the indirect influence of the people living in the villages within a given plot. To this aim, we gathered the information about how many people lives inside the house with influence in the plots.

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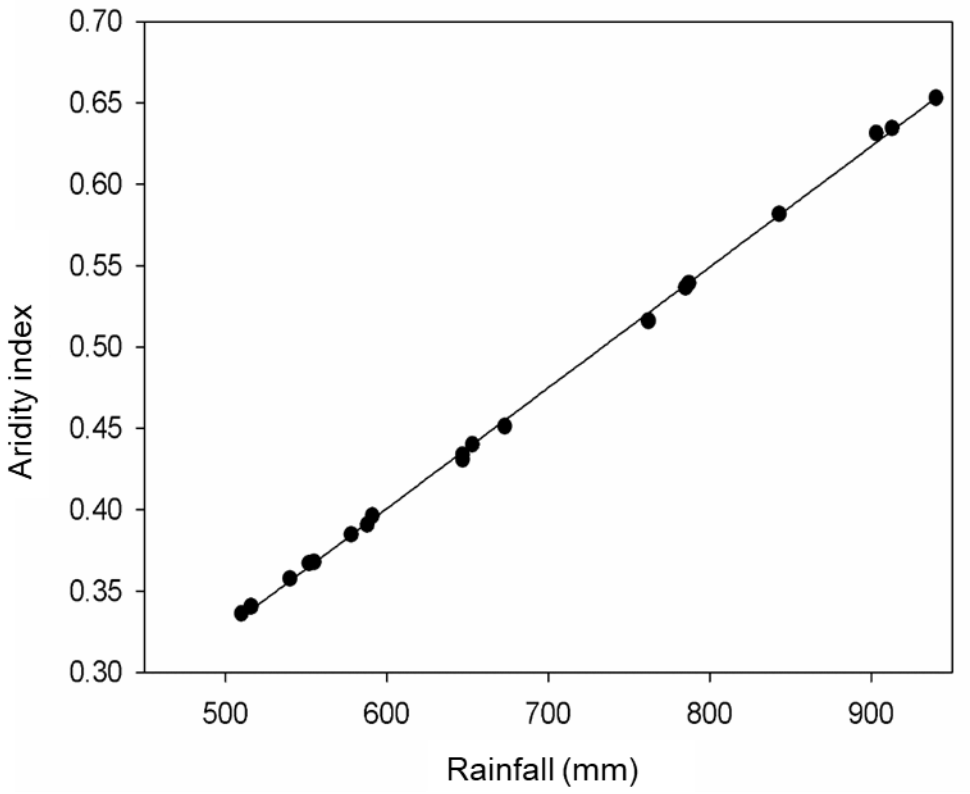
Appendix S2. Aridity measure and its correlation with rainfall

Global aridity index was obtained from CGIAR-CSI Global Aridity and PET Database (http://www.cgiar-csi.org, Zomer *et al*. 2007, 2008) where is calculated using the following formula: Aridity Index (AI) = MAR / MAE, where MAP is the Mean Annual Rainfall and MAE is the Mean Annual Potential Evapotranspiration. This index is modeled using the data available from WorldClim database (http://www.worldclim.org) and its values increase for more humid conditions, and decrease with more arid conditions (Global Aridity and Global PET Methodology available in http://www.cgiar-csi.org). Our index ranged from 0.33 to 0.65 per plot and was highly correlated with mean annual rainfall (Pearson's correlation; $r = 0.98$, $p < 0.001$):



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5 CONSIDERAÇÕES FINAIS

Os efeitos das atividades humanas e mudanças climáticas na biodiversidade de espécies é um tema bastante discutido na literatura. Além disso, atualmente existe uma preocupação de que os efeitos das mudanças climáticas podem potencializar os efeitos das perturbações antrópicas. Contudo, menos atenção tem sido dada sobre como esses efeitos isolados e interativos vão ser repercutidos nas interações mutualísticas e nos serviços providos por essas interações. Esse é um tema de extrema importância, uma vez que a modificação ou perda de serviços ecológicos deve estar diretamente relacionada à resiliência de um determinado ecossistema. Nesta tese, nós investigamos como perturbações antrópicas crônicas e precipitação atuam sobre dois importantes serviços providos por formigas às plantas através de interações mutualísticas na Caatinga: a dispersão de sementes e a proteção contra herbívoros em plantas com nectários extraflorais. Nossos resultados podem ser considerados pontos iniciais para prever a eficiência de importantes serviços ecológicos e, consequentemente, seus efeitos sobre a comunidade de plantas em um mosaico de paisagens com diferentes níveis de perturbação antrópica e diante de um cenário de redução da precipitação previsto para o final do século XXI.

No primeiro capítulo, não encontramos efeitos similares de perturbações antrópicas e precipitação sobre o serviço de dispersão de sementes por formigas, e encontramos pouca evidência que existam efeitos interativos entre esses dois fatores. Nós mostramos que embora existam muitas espécies de formigas dispersoras, não existe uma redundância funcional em relação às dispersoras de alta qualidade, o que pode limitar fortemente a resiliência desse serviço em relação à redução da precipitação. Em função dessa baixa redundância funcional, vimos que a precipitação afeta fortemente o serviço de dispersão de sementes através da redução na abundância de uma única espécie de formiga considerada dispersora de alta qualidade. Já no segundo capítulo, mostramos mais uma vez que perturbações antrópicas e precipitação atuam independentemente sobre o serviço de proteção contra herbívoros provido por formigas em plantas com nectários extraflorais. Nós mostramos mais uma vez o forte efeito da precipitação sobre o serviço provido por formigas. Mais interessante, encontramos que essa redução na eficiência do serviço com a diminuição da precipitação não é mediada via redução do néctar extrafloral e, consequentemente, mudanças na composição de formigas que visitam os nectários extraflorais como é sugerido na literatura. Essa redução é mediada diretamente pela substituição de formigas mais eficientes por formigas menos

eficientes com a redução da precipitação, independentemente da concentração e volume do néctar extrafloral.

Em síntese, nossos resultados mostram que os dois serviços analisados são resistentes a perturbações antrópicas, mas por outro lado são muito vulneráveis a reduções na precipitação. O mecanismo por trás da redução de ambos os serviços com a diminuição da precipitação está diretamente associado a mudanças na composição dos parceiros (formigas) disponíveis para as interações, seja pela redução de um parceiro que presta um serviço de alta qualidade ou pela substituição de parceiros mais eficientes por menos eficientes na prestação de serviços. Nossos resultados chamam atenção para as implicações dos efeitos de perturbações antrópicas e mudanças climáticas mudando a assembleia de parceiros disponíveis para as interações, e levando a um efeito em cascata que altera a eficiência dos serviços mantidos por essas interações. Dado que uma grande diversidade de espécies de plantas da Caatinga possui diásporos dispersos por formigas e/ou nectários extraflorais, a persistência dos serviços de dispersão de sementes e proteção contra herbívoros providos por formigas em áreas perturbadas pode ser importante para a manutenção da comunidade de plantas e para o funcionamento do ecossistema nessas áreas. Entretanto, a vulnerabilidade desses serviços à redução da precipitação pode ter implicações importantes para o recrutamento, a reprodução e o estabelecimento de plantas e, consequentemente, para a composição de plantas frente aos cenários futuros de mudanças climáticas.

Por fim, é importante saber de fato como a comunidade de plantas está reagindo às alterações nos serviços providos por formigas. Dessa forma, incentivamos a investigação das consequências dos nossos resultados para a comunidade de plantas e para o funcionamento da Caatinga. É necessário entender, por exemplo, quais são os efeitos da redução do serviço de dispersão de sementes sobre o recrutamento e distribuição das plantas, e se a redução do serviço de proteção contra herbívoros realmente leva a uma redução da aptidão e do sucesso reprodutivo de plantas com nectários extraflorais. Identificar estes padrões e mecanismos nos dará uma visão geral e mais completa de como a Caatinga está respondendo a mudanças ambientais e nos auxiliará a fazer previsões e traçar estratégias de conservação em relação aos cenários futuros previstos para esse ecossistema.

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Author Guidelines

Sections

1. SUBMISSION

- Please be advised that we experienced an unexpected issue that occurred on Saturday and Sunday January 20th and 21st that caused the site to be down for an extended period of time and affected the ability of users to