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VARIAÇÃO ESPAÇO-TEMPORAL DAS INTERAÇÕES ENTRE PLANTAS COM NECTÁRIOS EXTRAFLORAIS E FORMIGAS NA CAATINGA: efeito de perturbações antrópicas e mudanças climáticas

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

Orientadora: Profa. Dra. Inara Roberta Leal

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RESUMO

As perturbações antrópicas podem diminuir a qualidade dos serviços ecossistêmicos prestados pelas interações mutualísticas como também aumentar a instabilidade das comunidades ecológicas. A Caatinga é um dos ecossistemas que vem sendo negativamente afetada pela constante exploração dos recursos florestais como meio de subsistência humana. Além do mais, é previsto que haverá uma redução de 22% das chuvas na Caatinga, podendo acentuar ainda mais os efeitos das perturbações antrópicas. Esta tese teve como objetivo investigar os efeitos isolados e combinados das perturbações antrópicas crônicas (PACs) e precipitação influenciam as redes mutualísticas entre formigas e plantas com nectários extraflorais (NEFs) espacial e temporalmente. Para isso, este trabalho foi realizado no Parque Nacional do Catimbau em 16 parcelas permanentes 20 x 20 m nos anos de 2014 e 2016. Dentro de cada parcela foi realizado um levantamento de todas as plantas com NEFs e de suas formigas associadas. Para uma melhor avaliação dos efeitos das PACs e precipitação nestas redes mutualísticas, esta tese foi dividida em dois capítulos. No primeiro capítulo foi avaliado os efeitos isolados e combinados das PACs e precipitação na especialização das redes entre formigas e plantas com NEFs. As PACs foram caracterizadas em três índices de perturbações que são as principais fontes de perturbação na Caatinga: (1) pressão de pastagem, (2) extração de lenha e (3) utilização de recursos variados. Foram construídas, no total, 16 matrizes em que foram mensurados quatro tipos de especialização: (1) generalidade, (2) vulnerabilidade (3) equabilidade das interações e (4) especialização H_2'. Os resultados mostraram que as PACs podem influenciar de maneira positiva, neutra ou negativa ao longo dos gradientes de PACs. A precipitação também afetou a especialização das redes entre formigas e plantas com NEFs, ocasionando o aumento de sua especialização. Apesar de pressão de pastagem e precipitação ocasionar mudanças nas comunidades de plantas e formigas que interagem entre si, não foi o mecanismo que gerou mudança na especialização das redes. O segundo capítulo, por sua vez, investigou os efeitos isolados e sinérgicos das PACs e precipitação na estabilidade temporal das redes entre formigas e plantas com NEFs. Neste capítulo, foram construídas 32 matrizes (16 em cada ano). A estabilidade foi mensurada tanto no nível de comunidade como no nível de rede. Os resultados mostraram que a estrutura das comunidades de plantas com NEFs e formigas foram similarmente estáveis ao longo dos gradientes de PACs e precipitação.

Apenas a diversidade de plantas com NEFs mostrou ser afetada pela interação entre PAC e precipitação, em que a diversidade diminui à medida que aumentou PAC com esses efeitos mais acentuados em áreas úmidas. No entanto, a PAC e a precipitação modularam a estabilidade das redes. A PAC reduziu a estabilidade da generalidade com efeitos mais fortes nas áreas úmidas. A estabilidade da vulnerabilidade diminui com o aumento da PAC e diminuição da precipitação. Esta tese mostrou a vulnerabilidade das redes mutualísticas entre formigas e plantas com NEFs à redução de precipitação e PACs, porém a interação destes fatores mostrou ser mais preocupantes em áreas úmidas.

Palavras-chave: Defesa anti-herbivoria. Especialização. Estabilidade. Florestas Tropicais Sazonalmente Secas. Interações planta-animal. Perturbações antrópicas. Precipitação. Redes mutualísticas.

ABSTRACT

Anthropogenic disturbances can decrease the quality of ecosystem services provided by mutualistic interactions as well as increase the instability of ecological communities. Caatinga is one of the ecosystems that has been negatively affected by the exploit of forest resources for human subsistence. In addition, it is expected that there will be a 22% reduction in rainfall in Caatinga, which can exacerbate the anthropogenic disturbance effects. This thesis aimed to investigate how the isolated and combined effects of chronic anthropogenic disturbances (CAD) and precipitation influence the mutualistic networks between ants and plants with extrafloral nectaries (EFNs) spatial and temporal. To this end, this work was carried out in the Catimbau National Park in 16 permanent 20 x 20 m plots in 2014 and 2016. Within each plot a survey of all plants with EFNs and their associated ants was carried out. For a better evaluation of the CAD and precipitation effects on these mutualistic networks, this thesis was divided into two chapters. In the first chapter we evaluated the isolated and combined effects of CADs and precipitation on the specialization of networks between ants and plants with NEFs. CADs were characterized by three disturbance indices that are the main sources of disturbance in the Caatinga: (1) livestock pressure, (2) wood extraction and (3) miscellaneous resource use. A total of 16 matrices were constructed, in which four types of specialization were measured: (1) generality, (2) vulnerability (3) interaction equability and (4) H_2' specialization. The results showed that CAD can influence positively, neutrally or negatively along the gradient. Precipitation also affected the specialization of networks between ants and plants with NEFs, causing increasing in their specialization. Although livestock pressure and precipitation cause changes in interacting plant and ant communities, it was not the mechanism that led to changes in network specialization. The second chapter, in turn, investigated the isolated and synergistic effects of CADs and precipitation on the temporal stability of networks between ants and plants with NEFs. In this chapter, 32 matrices were built (16 each year). Stability was measured at both the community and network levels. Results showed that stability of both communities plants with EFNs and associated ants were stable over the CAD and precipitation gradients. Only plant diversity with EFNs has been shown to be affected by the interaction between CAD and precipitation, where diversity decreases as CAD increases with these more pronounced effects in wetter areas. However, CAD and precipitation have modulated network stability. The CAD has reduced overall stability of generality with stronger effects on wet areas. The stability of vulnerability decreases with increasing CAD and decreasing precipitation. This thesis showed the vulnerability of mutualistic networks between ants and plants with EFNs to the precipitation reduction and CAD, which interaction of these factors was more worrying in humid areas.

Key-words: Anti-herbivore defense. Anthropogenic disturbances. Mutualistic networks. Plant-animal interactions. Rainfall. Seasonally Dry Tropical Forests. Specialization. Stability.

SUMÁRIO

1 INTRODUÇÃO

As perturbações crônicas são remoções constantes de pequenas porções de biomassa vegetal (SINGH 1998). Embora os efeitos dessas perturbações sejam gradativos, pois não há perda de hábitat como aquelas geradas pelas perturbações agudas (e.g. desflorestamento), seus impactos se mostraram serem bastante deletérios (MARTORELL; PETERS, 2005, 2009). Por exemplo, atividades como criação de bodes e gados, extração de lenha e utilização de produtos não madeireiros são capazes de reduzir a riqueza de plantas lenhosas (RIBEIRO et al., 2015) e formigas (OLIVEIRA et al., 2017), conduzindo ambas comunidades a homogeneização biótica (RIBEIRO-NETO et al., 2016). De fato, as alterações dessas comunidades em ambientes perturbados podem acarretar ainda mudanças nos serviços ecossistêmicos, como observado para dispersão de sementes (LEAL; ANDERSEN; LEAL, 2014) e proteção contra os herbívoros (LEAL; ANDERSEN; LEAL, 2015).

Estes tipos de perturbações acontecem mais frequentemente em florestas tropicas sazonalmente secas (Seasonally Dry Tropical Forests, sensu MURPHY; LUGO, 1986), que suportam uma alta densidade populacional dependente de recursos florestais para a sobrevivência. Infelizmente, as previsões climáticas futuras indicam um aumento na temperatura média e redução nos regimes de chuvas (IPCC, 2014). Trabalhos de modelagem climática apontam que a estrutura e o funcionamento das florestas tropicais secas serão alterados à medida que há um prolongamento das secas e uma maior variabilidade anual das precipitações (ALLEN et al., 2017). Desta forma, acredita-se que, de uma maneira geral, as mudanças climáticas podem inclusive intensificar os efeitos das perturbações crônicas (RITO et al., 2017).

As interações mutualísticas são um dos principais mecanismos para a manutenção da diversidade global (BASCOMPTE; JORDANO, 2007). Todas as espécies estão diretamente ou indiretamente conectadas entre si através de serviços como polinização (POTTS et al. 2010), dispersão de sementes (TERBORGH et al., 2008; DONATTI et al., 2011) e fixação de nutrientes (WILSON et al., 2009), formando muitas vezes uma complexa rede (JORDANO; BASCOMPTE; OLESEN, 2003). Como parceiros podem variar quanto ao grau de dependência entre si, rupturas destas interações pelas perturbações e mudanças climáticas podem ocasionar extinções secundárias, acelerando ainda mais a perda de biodiversidade (AIZEN; SABATINO; TYLIANAKIS, 2012). Consequentemente, a perda destas interações pode influenciar toda estrutura e estabilidade das comunidades, aumentando ainda mais o processo de degeneração das paisagens perturbadas.

Nas últimas décadas, a teoria das redes ecológicas mostrou ser uma importante ferramenta para entender como a estrutura e a estabilidade das comunidades biológicas podem ser influenciadas ao longo de paisagens antropizadas e mudanças climáticas (TYLIANAKIS et al., 2010; KAISER-BUNBURRY; BLÜTHGEN, 2015; HARVEY, et al. 2017). Nesse sentido, esta tese teve como objetivo investigar os efeitos separados e sinérgicos das perturbações crônicas e precipitação das redes sobre variações espaço-temporal de interações facultativas entre plantas com nectários extraflorais e formigas na Caatinga. Esta tese consiste em uma fundamentação teórica e dois capítulos, cada um em forma de um artigo científico independente, mas que usam abordagens complementares. Na fundamentação teórica abordamos sobre os efeitos das perturbações antrópicas e mudanças climáticas nas interações mutualísticas, nas redes ecológicas e nas interações planta-formiga. No primeiro capítulo, investigamos como a especialização das redes de plantas com nectários extraflorais e formigas variam ao longo dos gradientes de perturbação e precipitação. Verificamos também se a resposta das espécies às variáveis ambientais está correlacionada com o grau de especialização com seus parceiros mutualistas. No segundo capítulo, avaliamos os efeitos das perturbações crônicas, precipitação e suas interações sobre a estabilidade temporal das redes de interação entre plantas com NEF e formigas. Neste capítulo, investigamos quais os possíveis mecanismos poderiam levar alteração na estabilidade temporal das interações ao longo dos gradientes, se pela alteração da estabilidade nas comunidades das plantas com nectários extraflorais e/ou formigas, ou simplesmente pela mudança no comportamento das formigas.

2 FUNDAMENTAÇÃO TEÓRICA

2.1 PERTURBAÇÕES ANTRÓPICAS E MUDANÇAS CLIMÁTICAS: MUTUALISMO OBRIGATÓRIO *VS* FACULTATIVO

Mutualismos são interações de cooperação que geram benefício (recurso/serviço) para ambos os parceiros envolvidos (BRONSTEIN, 1998). Estas interações são essenciais para a reprodução e sobrevivência dos organismos através dos serviços como polinização, dispersão de sementes (TERBORGH et al., 2008; POTTS et al., 2010). Apesar do mutualismo ser sempre visto como uma interação benéfica, os parceiros podem variar na qualidade (e.g. benefício recebido por um indivíduo) ou na quantidade (e.g. frequência com que duas espécies interagem) do serviço ao longo do espaço e do tempo (BRONSTEIN, 1994; NESS; MORRIS, BROSNTEIN, 2006). Esta diferença nos serviços varia de mutualistas, quando há efetivamente troca de benefícios, a ‘exploração’, quando a espécie consome o recurso fornecido pelo hospedeiro sem oferecer nenhum tipo de serviço em troca (IZZO; VASCONCELOS 2002; BARKER; BRONSTEIN, 2016). Infelizmente, esta variação na qualidade dos serviços entre os potenciais parceiros mutualísticos pode aumentar ainda mais com as modificações nas paisagens naturais geradas pelas perturbações antrópicas e mudanças climáticas, comprometendo o resultado geral do mutualismo.

De fato, nas últimas décadas, estudos vêm reportando que o aumento das atividades humanas em paisagens naturais e mudanças climáticas vêm causando rupturas nas interações mutualísticas (KIERS et al., 2010). A contínua perda de espécies, a alternância da abundância entre populações e a mudança na composição da assembleia que vem ocorrendo ao longo do espaço (MORITZ; AGUDO, 2013; HADDAD et al., 2015) e do tempo (BLÜTHGEN et al., 2016) são um dos principais mecanismos para o rompimento dos mutualismos (SCHLEUNING et al., 2016). Porém, além das mudanças nas estruturas das comunidades de plantas e animais, as mudanças climáticas também podem afetar o tempo de germinação, fenologia reprodutiva da planta, reprodução dos animais e suas atividades de forrageamento (PARMESAN; YOHE, 2003; ROOT et al., 2003; CLELAND et al., 2007; RAFFERTY; CARADONNA; BRONSTEIN, 2015). E devido às interações mutualísticas requererem parceiros que se localizem durante o mesmo tempo, essas mudanças fisiológicas nas plantas e animais podem alterar a quantidade e a qualidade dos serviços (MEMMOT, 2007; BURKLE; ALCARÓN, 2011; BURKLE; MARLIN; KNIGHT, 2013). Contudo, interações mutualísticas variam quanto à obrigatoriedade entre os parceiros, podendo os impactos destas perturbações variar em sua magnitude nos diferentes tipos de mutualismo.

Teoricamente, o mutualismo mais resiliente a estes eventos de perturbações são aqueles em que as espécies respondem às novas condições ambientais independentemente dos serviços oferecidos pelos seus parceiros mutualistas (KIERS et al., 2010). Quando as espécies são aptas a sobreviver temporariamente sem os serviços dos parceiros mutualistas, provavelmente terá uma maior chance de sobrevivência em áreas modificadas pelas perturbações e mudanças climáticas. Já as espécies que necessitam constantemente dos serviços dos parceiros podem estar mais ameaçadas. Dessa forma, no mutualismo obrigatório, há perda de um dos parceiros pode induzir a extinção do seu hospedeiro e vice-versa (DUNN et al., 2009). Entretanto, o mutualismo facultativo (interações não obrigatórias) apresenta uma maior flexibilidade quanto aos serviços dos seus parceiros (BRONSTEIN et al., 2004).

Independentemente do tipo de mutualismo, tanto o mutualismo obrigatório quanto o facultativo parecem ser negativamente afetados pelas perturbações nas diferentes relações entre plantas e animais (Tabela 1). Este fato parece ser claro para as interações obrigatórias em que a redução ou mudança na composição dos seus parceiros pode impedir a polinização, reduzir a dispersão e diminuir a proteção contra herbívoros. Apesar da troca de parceiros ser bastante frequente nas interações facultativas, esta intensidade acaba aumentando ainda mais em ambientes alterados pelas perturbações (BRONSTEIN et al., 2004). Espécies que apresentam uma baixa qualidade de serviço podem aumentar em ambientes perturbados e competir com os parceiros de alta qualidade. Dessa forma, plantas hospedeiras em áreas mais perturbadas podem estar mais suscetíveis a interagirem com parceiros de baixa qualidade, diminuindo a eficiência na polinização, dispersão e proteção contra herbívoros (AGUILAR; GALETTO 2004; LEAL, ANDERSEN; LEAL, 2014). Infelizmente, mensurar a qualidade desses serviços nem sempre é possível fazer em um contexto a nível de comunidades, o que dificulta muitas vezes encontrar padrões e fazer previsões acerca do funcionamento e estabilidade das comunidades biológicas.

Tabela 1. Efeitos das perturbações nas diferentes relações mutualísticas entre plantas e animais com diferentes níveis de obrigatoriedade com seus parceiros mutualistas.

Relações mutualísticas	**Obrigatoriedade**	**Respostas ecológicas à perturbação**
Planta-polinizador	Obrigatório	Diminuição do sucesso reprodutivo [1,2,3]
	Facultativo	Diminuição do sucesso reprodutivo[1]
Planta-dispersor	Obrigatório	Diminuição das sementes removidas e na distância[4]
	Facultativo	Diminuição de número de diásporos removidos e distância percorrida[5,6,7]
Planta-formiga	Obrigatório	Diminuição das plantas ocupadas pelos parceiros mutualistas, diminuição do crescimento das plantas e aumento da mortalidade das plantas hospedeiras[8]
	Facultativo	Aumento de danos causados por herbívoros[9]

Fontes: [1](AIZEN; LORENA; GALETTO, 2002), [2](AGUILAR et al., 2006), [3](KUDO; IDA, 2013) [3](MARKL et al., 2012), [4](BIEBER et al., 2014), [5](LEAL; ANDERSEN; LEAL, 2014), [6](NESS, 2004), [7](PALMER et al., 2008), [8](EVANS; TURLEY; TEKSBURY, 2013)

2.2 REDES ECOLÓGICAS E SUA APLICABILIDADE

Dentro das comunidades, as espécies estão interligadas umas às outras formando redes de interação complexas (BASCOMPTE et al., 2003). Descrever os padrões destas redes e os possíveis processos ecológicos e evolutivos por trás delas tem sido recorrente na literatura (BLÜTHGEN et al, 2007; GUIMARÃES et al., 2006; VAZQUEZ et al., 2009; DONATTI et al., 2011). Para isso, os estudos têm desenvolvido várias ferramentas e abordagens descritivas (Tabela 2). Dessa forma, vários progressos já foram realizados quanto à caracterização destas redes e à identificação das variáveis importantes que as moldam ao longo do espaço e do tempo (KAISER-BUNBURRY; BLÜTHGEN, 2015). Por exemplo, a distribuição da abundância (VÁZQUEZ; CHACOFF; CAGNOLO, 2009), a composição (VÁZQUEZ et al., 2009), a combinação dos traços morfológicos (STANG; KLINKHAMER; VAN DER MEIJEDEN, 2007; DONATTI et al, 2011) e fenológicos (OLESEN et al., 2008; LANGE et al., 2013) das espécies envolvidas já mostraram ser um dos principais mecanismos que moldam a estrutura destas redes. Tais descrições nos auxiliam a fazer previsões sobre as possíveis consequências para a estabilidade e o funcionamento dos ecossistemas quando estas redes estão perdendo espécies ou sofrendo alterações devido às mudanças ambientais.

Tabela 2. Descrição das métricas de redes dentro de diferentes níveis hierárquicos. Fontes: BERSIER; BANASEK-RICHTER; CATTIN (2002); BLÜTHGEN et al. (2008), DORMANN et al. (2009)

Métrica	Descrição
Nível de rede	
Conectância	Proporção de ligações observadas a partir de todas as ligações possíveis, em que valores maiores implicam em uma maior conectividade entre as espécies.
Aninhamento	Quando espécies com maior número de ligações interagem mais entre si, enquanto espécies com menor número de ligações interagem mais com aquelas com maior número de ligações.
Interação de equitabilidade	Frequências homogênea das interações ao longo de todas as ligações, em que valores maiores implicam em uma maior homogeneidade das interações entre espécies dentro de uma mesma comunidade. Esta métrica é análoga a conectância, porém esta métrica usa medidas quantitativas ao invés de medidas qualitativas.
Índice *H2’*	É o desvio da frequência das interações observadas dos valores esperados a partir de uma distribuição nula do total de interações. Este índice varia de 0 a 1, em quanto mais próximo de 1, maior o grau de especialização.
Nível de guilda	
Generalidade e Vulnerabilidade	A média de parceiros que interagem dentro de todos os parceiros possíveis de uma mesma guilda (plantas ou animais).
Nível de espécie	

Força de interação	Proporção de interações entre uma determinada espécie *i* e *j* a partir de todas as interações registradas para espécie *i*.
Índice *d'*	Representa a exclusividade de uma determinada espécie em relação ao seu recurso a partir do seu desvio das distribuições nulas.

Devido aos avanços em relacionar os padrões de redes observados com os principais processos envolvidos na manutenção das interações bióticas, cientistas vêm propondo o uso das redes ecológicas dentro dos estudos de ecologia de conservação (MEMMOTT et al., 2009; TYLIANAKIS et al., 2010; VAN DER PUTTEN; MACEL, VISSER, 2010; KAISER-BUBURRY; BLÜTHGEN, 2015, HARVEY et al., 2017). De fato, muitos estudos já investigaram como as perturbações antrópicas e mudanças climáticas influenciam nas estruturas das redes planta-polinizador (MEMMOT et al., 2009; SCHLEUNING et al., 2016; AINZEN; SABATINO; TYLIANAKIS, 2012), planta-dispersor (MENKE; BÖHNING-GAESE; SCHLEUNING, 2012; ALBRECHT et al, 2013) e planta-formiga (EMER; VENTICINQUE; FONSECA, 2013). No entanto, os efeitos destas perturbações nem sempre são intuitivos, gerando muitas vezes resultados contraditórios (SCHLEUNING et al., 2001; DÁTTILO et al., 2015). Para uma melhor estratégia de conservação, é também necessário identificar quais as espécies ou grupos funcionais mais suscetíveis às perturbações, e como elas afetam a organização das redes (HARVEY et al., 2017). Por exemplo, estudos apontam que tanto as perturbações antrópicas quanto as mudanças climáticas causam perdas não aleatórias onde espécies mais especialistas são mais suscetíveis a extinção do que espécies mais generalistas (AIZEN; SABATINO; TYLIANAKIS, 2012; SCHLEUNING et al., 2016). Como muitas vezes estas espécies especialistas apresentam uma maior dependência dos seus parceiros mutualistas, a perda destas espécies pode ocasionar extinções secundárias, perdendo concomitantemente funções importantes (WEINER et al., 2014).

Estudos teóricos têm sugerido que determinadas estruturas das redes pode afetar a estabilidade da comunidade (BASTOLLA et al., 2009; OKUYAMA; HOLLAND, 2008; THEBAULT; FONTAINE, 2010). Por exemplo, uma rede com maior diversidade de interação pode ser mais estável, uma vez que uma distribuição mais homogênea das frequências de interações aumenta a robustez da rede, além de aumentar a performance funcional (KAISER-BUNBURRY; BLÜTHGEN, 2015). No entanto, o conceito estabilidade é bastante amplo nos estudos ecológicos. Nesse sentido é importante primeiro definir estabilidade para então identificar quais atributos das redes precisam ser conservados. Por exemplo, uma rede ecológica estável já foi definida como aquela que é resistente a extinções secundárias a partir da perda de espécies (DUNNE; WILLIAMS; MARTINEZ, 2002; REZENDE et al., 2007). Outros estudos, por sua vez, definiram redes ecológicas estáveis como aquelas que mantêm a integridade da rede após um evento de perturbação (SOLÉ; MONTOYA, 2001; DUNNE; WILLIAMS, 2009). No entanto, a estabilidade das redes pode ser definida também quanto a sua variação ao longo do tempo (ALCARÓN, WASER, OLLERTON, 2008).

Para as interações ocorreram nem sempre é possível considerar a presença das espécies (TYLIANAKIS et al., 2010). No entanto, muitas vezes, é assumido que quando as espécies co-ocorrem em um determinado local, elas sempre interagem, independentemente do tempo e de onde elas ocorram (POISOT; STOUFFER; GRAVEL, 2015). Tal fato negligencia que a distribuição das espécies e a composição da comunidade podem variar entre os anos, interferindo na chance real de ocorrência dessas interações (HAVENS, 1992). Por exemplo, já foi demonstrado para interações planta-polinizador que a composição das espécies de polinizadores e o padrão de interações apresentam variações interanuais (DUPONT et al., 2009), afetando a estrutura das redes mutualísticas ao longo dos anos (ALCARÓN, WASER, OLLERTON, 2008). Devido às perturbações antrópicas direcionarem as comunidades florestais a estágios sucessionais iniciais, as condições abióticas e bióticas podem variar entre os anos, afetando a estabilidade temporal das interações. Já as mudanças climáticas podem causar variação na sazonalidade (e.g. aumento dos períodos de seca) e nos regimes de chuva (ALLEN et al., 2017), afetando as comunidades (ZELICOVA et al., 2014; DIAMOND et al., 2016) e o padrão fenológico interanual dos parceiros envolvidos (RAFFERTY et al., 2014), ocasionando, também, uma menor estabilidade temporal das redes de interações.

2.3 INTERAÇÕES ENTRE PLANTAS COM NECTÁRIOS EXTRAFLORAIS E FORMIGAS

Interações entre plantas e formigas costumam envolver diferentes espécies de formigas pertencentes a diferentes subfamílias, assim como, diversas espécies de plantas distantes filogeneticamente (DAVIDSON; MCKEY, 2003). As plantas podem oferecer diferentes tipos de recursos como abrigo (e.g. domácias) e alimentos ricos em carboidratos como, por exemplo, néctar produzido pelos nectários extraflorais (NEFs), e corpúsculos lipídico (RICO-GRAY; OLIVEIRA, 2007). As formigas, por sua vez, defendem as plantas hospedeiras contra os inimigos naturais, como herbívoros, patógenos, pilhadores de néctar e até plantas trepadeiras (JANZEN, 1966; ROSUMEK et al., 2009). No entanto, este mutualismo de proteção entre plantas e formigas varia quanto a sua obrigatoriedade. As plantas com domácias, também denominadas de mirmecófitas, são habitadas permanentemente por espécie de formigas especializadas, através de associações simbióticas (FONSECA, 1994). As plantas com NEFs, ao contrário, não são ocupadas por colônias de formigas, interagindo de uma maneira facultativa e oportunista com suas atendentes (ROSUMEK et al., 2009).

Ainda que as formigas interajam de maneira facultativa com as plantas com NEFs, a literatura já mostrou diversos benefícios que elas conferem as suas plantas hospedeiras (RICO-GRAY; OLIVEIRA, 2007, ROSUMEK et al., 2009). De maneira geral, elas diminuem os danos causados por herbívoros ou por insetos pilhadores de néctar, aumentando o sucesso reprodutivo e a sobrevivência das plantas hospedeiras (BRONSTEIN, 1998; DEL-CLARO; BERTO; REU, 1996; LEAL et al., 2006). No entanto, também há estudos demonstrando o resultado neutro destas interações, em que as formigas usam o recurso oferecido pela planta, mas não oferecem nenhum benefício em troca (RASHBROOK; LAWTON, 1992; NOGUEIRA et al., 2011) ou até mesmo negativo, como (PEREIRA; TRIGO, 2013). Por estas interações envolverem um terceiro componente (presença de herbívoros), o resultado desta interação é mais dependente do contexto em que ela está inserida (CHAMBERLAIN; HOLLAND, 2009).

O resultado destas interações também pode variar tanto com as condições abióticas e bióticas ao longo do espaço e no tempo (KERSH, FONSECA 2005; RUDGERS, STRAUSS 2004). Mais especificamente, a qualidade de proteção das formigas às plantas com NEFs, pode variar por fatores como: (1) mudança na abundância dos parceiros (DI GIUSTO et al., 2001; RUDGERS; STRAUSS, 2004); (2) identidade dos parceiros (DEL-CLARO; MARQUIS, 2015; FAGUNDES et al., 2017); (3) disponibilidade e qualidade de recursos (BLÜTHGEN; FIEDLER 2004, NESS et al., 2006); e, por fim, (4) pela abundância e identidade dos herbívoros (BARTON, 1986). Como as perturbações antrópicas causam mudanças na assembleia de formigas (RIBEIRO-NETO et al., 2016; OLIVEIRA et al., 2017), das plantas com NEFs (CÂMARA et al., 2016) e herbívoros (WIRTH et al., 2008), o serviço de proteção prestados pelas formigas as plantas hospedeiras podem ser alterados tanto no espaço quanto no tempo. Ainda mais alarmante, esta mudança pode ser ainda intensificada pelas mudanças climáticas. Comunidades de formigas já mostraram sofrer variações temporais com a diminuição da temperatura (DIAMOND et al., 2016), enquanto a produção de néctar pode estar correlacionada com a sazonalidade (DÁTTILO et al., 2015b, DEL-CLARO et al., 2016).

Apesar das interações entre plantas com nectários extraflorais e formigas ocorrerem em diferentes ecossistemas que variam desde regiões temperadas até as regiões tropicais (RICO-GRAY; OLIVEIRA, 2007), há evidencias que o mutualismo, de fato, é mais frequente nas áreas áridas (LEAL; PEIXOTO 2016). A Caatinga é classificada como uma floresta tropical sazonalmente seca (sensu PENNIGTON; PRADO; PENDRY, 2000), inserida completamente no território brasileiro, caracterizada por clima tropical semiárido com baixa precipitação (250 – 1000 mm, concentrada entre 3-5 meses) e temperaturas médias que variam entre 23 a 27°C (SAMPAIO, 1995). 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).

Esta região semiárida do Brasil é uma das mais populosas do mundo (GARGLIO et al., 2010), povoada principalmente por pessoas de baixa-renda, que ainda necessitam de recursos florestais para a sua subsistência (SPECHT et al., 2015). Atividades como criação de caprino e gado, extração de lenha e coleta de produtos florestais não-madeireiros são frequentes nessa região (LEAL; ANDERSEN; LEAL, 2014; RIBEIRO et al.; 2015; RIBEIRO-NETO et al., 2016). E diferente das perturbações agudas (remoção completa de biomassa florestal), o uso destes recursos ocorrem de maneira gradativa, mas constantes, por isso eles são classificados como perturbações crônicas (SINGH, 1998; MARTORELL; PETERS, 2005). O efeito destas perturbações crônicas sobre a biota apenas recentemente começou a era avaliado, mas os resultados destes estudos indicam efeitos deletérios similares às perturbações agudas, como empobrecimento taxonômico (RIBEIRO et al., 2015), funcional (OLIVEIRA et al., 2017) e filogenético (RIBEIRO et al., 2016), que podem levar a uma homogeneização biótica, já observado para comunidades de plantas e formigas (RIBEIRO-NETO et al., 2016). Já foram registrados também perda de interações entre plantas e formigas como dispersão de sementes (LEAL; ANDERSEN; LEAL, 2014) e proteção de plantas contra herbívoros (LEAL; ANDERSEN; LEAL, 2015). Adicionalmente, a Caatinga pode ainda sofrer alterações com as mudanças climáticas, em que as previsões apontam um aumento da temperatura que pode variar de 1,7 a 6,7°C e uma redução da precipitação de 22% a 40% (IPCC, 2014; MAGRIN et al., 2014). Como a Caatinga cobre áreas com diferentes regimes de precipitação, ela propicia uma paisagem interessante para investigar efeitos sinérgicos entre perturbações antrópicas crônicas e mudanças climáticas, usando uma abordagem de substituição de espaço por tempo. De fato, Rito e colaboradores (2017) mostraram que a precipitação media os efeitos das perturbações antrópicas crônicas na assembleia de plantas lenhosas da Caatinga, sendo estes efeitos mais drásticos em áreas perturbadas com baixa precipitação.

Diante do exposto nessa fundamentação teórica, o objetivo geral desse estudo foi investigar os efeitos das perturbações antrópicas crônicas, precipitação e suas interações nas redes de interação entre plantas com nectários extraflorais e formigas ao longo do espaço e no tempo, no intuito de fazer previsões acerca da estabilidade e do funcionamento deste ecossistema.

3 EFFECTS OF CHRONIC ANTHROPOGENIC DISTURBANCE AND RAINFALL ON THE SPECIALIZATION OF ANT-PLANT MUTUALISTIC NETWORKS IN THE CAATINGA, A BRAZILIAN DRY FOREST

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Effects of chronic anthropogenic disturbance and rainfall on the specialization of ant-plant mutualistic networks in the Caatinga, a Brazilian dry forest

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Summary

1. Anthropogenic disturbance and climate change might negatively affect the ecosystem services provided by mutualistic networks. However, the effects of such forces remain poorly characterized. They may be especially important in dry forests, which (1) experience chronic anthropogenic disturbances (CADs) as human populations exploit forest resources and (2) are predicted to face a 22% decline in the rainfall under climate change.

2. In this study, we investigated the separate and combined effects of CADs and rainfall levels on the specialization of mutualistic networks in the Caatinga, a seasonally dry tropical forest typical of northeastern Brazil. More specifically, we examined interactions between plants bearing extrafloral nectaries (EFNs) and ants. We analyzed whether changes in network specialization could arise from environmentally mediated variation in the species composition, namely via the replacement of specialist by generalist species.

3. We characterized these ant-plant networks in 15 plots (20 x 20 m plots) that varied in CAD intensity and mean annual rainfall. We quantified CAD intensity by calculating three indices related to the main sources of disturbance in the Caatinga: livestock grazing (LG), wood extraction (WE), and miscellaneous resource use (MU). We determined the degree of ant-plant network specialization using four metrics: generality, vulnerability, interaction evenness, and H_2'.

4. Our results indicate that CADs differentially influenced network specialization: we observed positive, negative, and neutral responses along LG, MU, and WE gradients, respectively. The pattern was most pronounced with LG. Rainfall also shaped network specialization, markedly increasing it. While LG and rainfall were associated with changes in network species composition, this trend was not related to the degree of species specialization. This result suggests that shifts in network specialization might be related to changes in species behavior, not species composition.

5. Our study highlights the vulnerability of such dry forest ant-plant networks to climate change. Moreover, dry forests experience highly heterogeneous anthropogenic disturbances, creating a geographic mosaic of selective forces that may shape the coevolution of interactions between ants and EFN-bearing plants.

Keywords: anti-herbivore defense, anthropogenic disturbance, climate change, extrafloral nectaries, mutualistic network, plant-animal interactions, seasonally dry tropical forest, specialization

Introduction

Seasonally dry tropical forests (SDTFs) are the most threatened type of major tropical forest (Miles *et al*. 2006). The dry tropics are home to large human populations that depend on natural resources for subsistence (Singh, Rawat & Garkoti 1997). These populations continuously remove small quantities of forest biomass via livestock grazing, firewood collection, and the exploitation of miscellaneous resources, which each lead to chronic anthropogenic disturbance (CAD; *sensu* Singh 1998). The consequence is the emergence of heterogeneous landscapes of resource use (Martorell & Peters 2005; Ribeiro *et al*. 2015). Although the effects of CADs have only recently started to be evaluated, some studies have already revealed they are significant for plants (Hernández-Oria, Chavez & Sánchez 2006; Ribeiro *et al.* 2015, 2016; Rito *et al*. 2017), animals (Ribeiro-Neto *et al*. 2016; Oliveira *et al*. 2017), and plant-animal interactions (Leal, Andersen & Leal 2014, 2015). Moreover, in the dry tropics, it has been predicted that climate change will increase temperatures and decrease precipitation by 2100 (Magrin *et al*. 2014), which will threaten natural biota (Miles *et al*. 2006; Feng *et al*. 2013). There is particular concern that climate change could aggravate CAD effects on biodiversity in the dry tropics (Hirota *et al*. 2011; Gibb *et al*. 2015; Frishkoff *et al*. 2016).

SDTFs also harbor a great diversity of mutualistic species networks (Machado & Lopes 2004; Leal *et al*. in press), which contribute to multiple ecosystem functions by driving processes as diverse as pollination, dispersal, plant defense, and nutrient transfer (Kiers *et al*. 2010). While the specialization of mutualistic networks plays a central role in species coexistence and, possibly, speciation (Dynesius & Jansson 2000; Dyer *et al*. 2007), it has received relatively little attention in conservation biology. However, it is widely accepted that anthropogenic disturbances are major drivers of specialist-generalist replacement (McKinney & Lockwood 1999; Clavel, Julian & Devictor 2011; Tabarelli, Peres & Melo 2012), which can lead to biotic homogenization (Devictor *et al*. 2010) and loss of functionality (Girão *et al*. 2007; Lopes *et al*. 2009), both alarming trends. The root cause is that specialists have a narrower breadth of resource use than do generalists, which means they tend to be more sensitive to changes in habitat, food availability, and food quality (Futuyama & Moreno 1988; Devictor *et al*. 2010). Thus, if species form specialized mutualisms (Blüthgen *et al*. 2007), the disturbance-related extinction or decline of one partner could threaten the other (Weiner *et al*. 2014). Therefore, even though a species may survive a disturbance event, the resulting changes in resource availability could have detrimental effects on specialist populations.

Species' responses to environmental change might thus be tightly linked to the degree of specialization within mutualisms (Vázquez & Simberloff 2002). Moreover, disturbance could leave species abundance unaffected but change behavioral interactions in an environmentally dependent fashion (Brose *et al*. 2005; Tylianakis, Tscharntke & Lewis 2007).

To date, anthropogenic disturbances have been found to have contrasting effects on the specialization of mutualistic networks. While some studies have shown that disturbance decreases specialization in plant-pollinator (Aizen, Sabatino & Tylianakis 2012), plant-frugivore (Menke, Böhning-Gaese & Schleuning 2012), and ant-plant networks (Emer, Venticinque & Fonseca 2013), others have found no effects at all (plant-frugivore network, Schleuning *et al*. 2011; Dáttilo *et al*. 2015; ant-plant network, Falcão *et al*. 2017). Disturbance type appears to matter. For instance, network specialization may be affected by habitat fragmentation (Aizen, Sabatino & Tylianakis 2012) but not necessarily by land-use change (Weiner *et al*. 2014) or by the introduction of exotic species (Emer *et al*. 2016). Such patterns could result from different anthropogenic disturbances having different effects on resource availability and quality. Furthermore, there may be interactions between disturbances and climatic conditions. For example, plant-hummingbird networks are more specialized in regions with high precipitation and low temperatures (Abrahamczyk & Kessler 2010; Dalsgaard *et al*. 2011), but the opposite is true for plant-insect pollinator networks (Dalsgaard *et al*. 2009). In general, theory predicts that biotic specialization should be favored as precipitation and temperature increase because of the opportunities afforded by high levels of productivity (Srivastava & Lawton 1998; Schemske 2002).

In this study, we focused on the facultative mutualistic networks established between plants bearing extrafloral nectaries (EFN) and the ants that attend them. EFN-bearing plants produce carbohydrate-rich resources, which attract ants that often then protect the plants against herbivores (Bentley 1977; Fagundes *et al*. 2017). Although such networks occur in many different ecosystems (Rico-Gray & Oliveira 2007), the protection provided by ants to EFN-bearing plants appears to be particularly effective in arid environments (Leal & Peixoto 2016). However, arid environments usually experience significant anthropogenic disturbance (Miles *et al*. 2006), which can lead to declines in the abundance of specialist EFN-bearing plants (Leal, Andersen & Leal 2015), the abundance of specialist arboreal ants (Oliveira *et al*. 2017), and ant visitation rates (Leal, Andersen & Leal 2015).

We aimed to investigate the separate and combined influences of different CADs and rainfall levels on the specialization of networks formed by ants and EFN-bearing plants in the

Caatinga, a SDTF typical of northeastern Brazil. The Caatinga biome is found in the world’s most populated semi-arid region and sustains over 27 million people (Gariglio *et al*. 2010). The rainfall gradient within the Caatinga is broad (Sampaio 1995), and the biome supports a high diversity of mutualisms (Leal *et al.*, in press). Increasingly, though, the Caatinga is being exposed to different CADs (livestock grazing, wood extraction, and miscellaneous resource use). It thus represents an excellent study system for examining the influences of CADs and climate change on the specialization of ant-plant mutualisms in SDTFs. We tested the following hypotheses: (1) the level of network specialization will decrease with increasing CAD intensity and decreasing rainfall; (2) networks will become less specialized due to the interactive effects of increased CAD intensity and decreased rainfall; and (3) decreases in network specialization will largely arise from changes in the species composition of networks, as a result of specialist-generalist replacement in dry highly disturbed areas.

Materials and methods

STUDY AREA

We conducted our study in Catimbau National Park (State of Pernambuco, northeastern Brazil, 8°24’00” and 8°36’25” S; 37°09’30” and 37°09’30” W), a natural reserve covering nearly 64,000 ha. The climate is hot and semi-arid; annual rainfall varies from 480 to 1100 mm; and the mean annual temperature is 23°C (Sociedade Nordestina de Ecologia, 2002). Deep sandy soils predominate (quartzite sand: 70% of area), but planosols (15% of area) and lithosols (15% of area) are also present (Sociedade Nordestina de Ecologia, 2002). Catimbau contains typical Caatinga taxa: the shrubs and trees mostly belong to the families Fabaceae, Euphorbiaceae, Boraginaceae, and Burseraceae, while the herbaceous understory plants are largely in the Cactaceae and Bromeliacae (Rito *et al*. 2017). There are many EFN-bearing plants—those in Fabaceae and Euphorbiaceae are the most common (Reis 2016). Catimbau became a national park in 2002, but it is still inhabited by rural populations that rely on its natural resources for subsistence (Rito *et al*. 2017). Their main activities include livestock farming (mainly goats and cattle), firewood collection, and the harvesting of miscellaneous forest resources (e.g., medicinal plants, edible fruit, or animal game) (Rito *et al*. 2017).

CHARACTERIZING CHRONIC ANTHROPOGENIC DISTURBANCE AND RAINFALL

We established 15 plots (20 x 20 m; separated by at least 2 km) across 214.3 -km². The study area was dominated by old-growth vegetation, and the plots experienced different CAD intensities and rainfall levels (Figure 1).

Chronic anthropogenic disturbance. We characterized disturbance intensity by calculating three different indices that corresponded to the main sources of CADs within the Caatinga, and particularly in Catimbau: (1) livestock grazing (LG)—consumption of vegetation, trampling, and other physical damage caused by goats and cattle; (2) wood extraction (WE)—the extraction of dead and live wood for fuel, fence construction, and artisanal production; and (3) miscellaneous resource use (MU)—the use of non-wood resources by humans (e.g., medicinal plants, animal game) (Leal et al. 2014, 2015; Ribeiro et al. 2015). Index values were calculated using the following formula:

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

where I is disturbance intensity; y_i is the observed value for a given disturbance metric in plot i; y_{min} is the minimum observed value for the disturbance metric across all plots; y_{max} is the maximum observed value for the disturbance metric across all plots; and n is the number of individual disturbance metrics incorporated in the index. This formula thus standardizes the metrics (sometimes of different units) to take on a value between 0 and 1, allowing them to be combined in the same index. Index values ranged from 0 to 100 (from no disturbance to maximum-intensity disturbance). Both the LG and WE indices quantified disturbances that were directly measured in the field. For the LG index, we estimated grazing levels by measuring the length of goat trails and the frequency of goat and cattle dung (see Appendix 1 for details). Then, we combined the two estimates of goat grazing (trail length and dung 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. The LG index was then calculated by inputting measures of goat grazing and cattle dung frequency into the formula above. For the WE index, we estimated the extraction of live wood and the collection of firewood (Appendix 1) and plugged them directly into the formula above. Finally, the MU index was determined using three indirect variables that are proxies for local anthropogenic pressure and habitat accessibility. More specifically, we determined two relevant geographic distances—plot proximity to the nearest house and plot proximity to the nearest road (using satellite imagery and ArcGis 10.1 software)—as well as a socioecological variable—the number of people living in the area that influence the plot (Appendix 1). Then, the values of these metrics were inputted into the formula above to obtain the MU index. The three indices were not highly correlated (LG vs. WE: r = 0.05, LG vs. MU: r = 0.65, and MU vs. WE: r = 0.003), which underscores that they are independent and measure different forms of anthropogenic disturbance.

Rainfall. Mean annual rainfall was obtained for each plot using the WorldClim database (Rito *et al*. 2017), which contains spatial climate data from 1950 to 2000. Spatial resolution was 1 km, and mean annual rainfall was extracted using ArcGIS. Values ranged from 510 mm to 940 mm, indicating the presence of a steep rainfall gradient in Catimbau.

CHARACTERIZING INTERACTIONS BETWEEN ANTS AND EFN-BEARING PLANTS

We characterized interactions between ants and EFN-bearing plants in 2014 and 2016 during the wet season (March-July), when EFN activity is high (TC, personal observation). To determine which plant species bear EFNs and to identify study plants, we carried out preliminary observations of all the plants in a given plot in early 2014 (Table S1). Then, once in 2014 and once in 2016, we carried out a census of all the EFN-bearing plants with a height ≥ 1 m and a diameter at breast height (DBH) ≥ 3 cm that were found within the plots. Plants were observed for at least 10 min. They were considered to be attended by ants when the ants' mouthparts came in contact with the EFNs. All observations occurred between 6:00 am and 10:00 am. During each census, we noted all interacting ant and EFN-bearing plant species. We attempted to identify all the species involved. However, when this was not possible in the field, samples were collected and brought to the laboratory for identification. Samples that could not be identified to species were classified to morphospecies.

CHARACTERIZING NETWORK SPECIALIZATION

For each plot, we built a matrix using all the interactions observed between EFN-bearing plants and attendant ants in 2014 and 2016. More specifically, we used the number of interactions between individual EFN-bearing plants and attendant ant species; the total number of ant workers involved was ignored. To characterize network specialization, we used four complementary quantitative metrics: (1) weighted generality (Gw), which expresses the degree of specialization at the highest trophic level and is defined as the mean effective number of EFN-bearing plants visited by each ant species weighted by ant species interaction frequency; (2) weighted vulnerability (Vw), which expresses the degree of specialization at the lowest trophic level and is defined as the mean effective number of ants per EFN-bearing plant species weighted by EFN-bearing plant species interaction frequency; (3) interaction evenness (IE), which measures whole-network specialization by quantifying the equitability of interaction frequencies between EFN-bearing plant species and attendant ant species; and (4) the network specialization index H_2', which measures whole-network specialization by determining the difference between realized and expected interaction frequencies (Blüthgen, Menzel & Blüthgen 2006). For more details, see Appendix 2 and Dormann *et al*. (2009). In summary, low values of Gw, Vw, and interaction evenness indicate that networks are highly specialized; Gw and Vw reveal the relative specialization of the ant species and plant species, respectively. In contrast, larger values of H_2' (range: 0–1) indicate greater network specialization.

Since metric values could be influenced by sampling effects (i.e., interaction number and network size [the sum of EFN-bearing plant species and attendant ant species]), we also calculated specialization metrics using data from null models (Dalsgaard *et al*. 2017). We generated 10,000 randomized matrices for each observed matrix using the Patefield algorithm, which constrains both interaction number and network size and assumes that all network partners have the same probability of interacting with each other (Blüthgen *et al*. 2008). We used the following Z-transformation formula:

$$Z = \frac{(x_i - \mu)}{\sigma}$$

where x_i is the observed value of a given metric for given plot *i*, μ is the mean metric value obtained from the 10,000 randomized matrices for a given plot *i*, and σ is the metric’s standard deviation from the 10,000 randomized matrices for a given plot *i.* We calculated observed and null-model metric values using the *bipartite* package (Dormman *et al*. 2009) in R (R Development Core Team 2016).

For both plants and ants, we characterized species-specific levels of specialization in each plot using d_i’, which expresses the exclusivity of partnerships engaged in by particular EFN-bearing plant species and attendant ant species (Blüthgen *et al*. 2006). Then, we calculated the weighted per-plot mean of d_i' (by determining species *i*’s number of interactions in a given plot compared to its total interactions across all plots). As for H_2', higher values of d_i' (range: 0–1) indicate greater specialization.

STATISTICAL ANALYSES

We used general linear models to test the separate and combined effects of the CADs (LG, WE, and MU) on the network specialization metrics. For each analysis, we started with a full model that included LG, WE, MU, and rainfall as the main independent variables and the interactions between each disturbance index and rainfall (LG x rainfall, WE x rainfall, and MU x rainfall). The response variables were the metrics calculated from the observed and null-model data. Then, we used a backward-selection procedure to choose the best-fit model (a single model containing a maximum of three terms, excluding the intercept). The best-fit models were those with the lowest Akaike information criterion values (ΔAICc < 2; Burnhnam & Anderson 2002). We then applied model averaging to make inferences about how CADs and rainfall influenced ant-plant network specialization. First, for each variable, we averaged coefficients and 95% confidence intervals across the best-fit models. Second, we considered variables to be significant when the 95% confidence intervals did not include 0. Model selection and averaging were carried out using the *MuMIn* package in R.

We also tested the effects of the CADs and rainfall on community composition (separately for the plants and the ants) using canonical correspondence analysis (CCA), implemented with the *vegan* package in R. In these analyses, we used the abundance of EFN-bearing species (i.e., plant species observed interacting with attendant ants) and the frequencies of attendant ant species (i.e., ant species observed attending EFN-bearing plants. Plant and ant species with frequencies of less than five were excluded from the analysis to prevent bias introduced by rare species (Russildi *et al*. 2016).

The species-specific CCA scores associated with significant CCA axes were taken to be the environmental responses of the plant and ant species to CADs or rainfall. To test whether these responses were dependent on species specialization, we carried out separate Spearman rank correlations between the CCA scores and the d_i' values for the plants, the ants, and each significant CCA axis.

Results

We recorded 555 interactions between 23 EFN-bearing plant species and 33 attendant ant species. There were between two and nine EFN-bearing plant species per plot. Eight were rare (recorded in just one plot), while two were common (*Cenostigma microphylla*: 8 plots; *Tacinga palmadora*: 10 plots). *Pityrocarpa moniliformis*, *C. microphylla*, and *T. palmadora* accounted for encompassed most of the interactions (47.6%) (Fig. 1). There were between 5 and 13 attendant ant species per plot. Eleven were rare (recorded in just one plot), while one was extremely common (*Camponotus crassus*: all plots). *C. crassus* and *Cephalotes pusillus* accounted for most of the interactions (53.3%) (Fig. 1).

Overall, the best-fit models indicated that network specialization was indeed influenced by CADs and rainfall. However, results differed for the different metrics (Table 1). In the analyses based on the observed data, LG and MU were retained in the best-fit models for Vw and H_2' but were only significant in the latter case (Table 1). While H_2' increased with increasing LG (Figure 2a), it declined with increasing MU (Fig. 2b). Rainfall was retained in the best-fit models for Gw and H_2' but was only significant in the latter case. H_2' increased with increasing rainfall (Fig. 2c).

In the analyses based on the null-model data, LG and rainfall were retained in the best-fit models for all the metrics (Table 1). Both Gw and IE were significantly negatively associated with LG (Figs. 3a-b) and rainfall (Figs. 3c-d). LG, WE, and rainfall were retained in the best-fit model for Vw, but only rainfall was significant (Fig. 3e). Although LG, WE, MU, rainfall, and the LP x rainfall interaction were retained in the best-fit model for H_2', none were significant (Table 1).

In the plant-specific CCA, the first and second axes explained 41% and 28% of the variation in species composition, respectively (Figure 4a); however, only the first axis was significant (Table S4). Both WE and rainfall were significant (Table 3). Axis 1 differentiated plant communities that were favored by wood extraction and increased rainfall from plant communities that were harmed by wood extraction and decreased rainfall. For example, *Cenostigma pyramidalis* was more abundant in plots with higher levels of wood extraction, while *Senna velutina* was more abundant in plots with higher rainfall (Fig. 4a). In the ant-specific CCA, the first and second axes were significant, explaining 40% and 36% of the variation in community composition, respectively (Fig. 4b). Both LG and rainfall were significant (Table 3) and associated with axis 1; rainfall was also associated with axis 2. *Dolichoderus quadridenticulatus* and *Crematogaster crinosa* were common in plots with high LG levels, while *Pheidole radoskowiskii* was common in plots with low LG levels. *Pseudomyrmex elongatus* and *Azteca* sp. A were common in wetter plots, while *Brachymyrmex* sp. A and *Cephalotes* pr. *cordatus* were common in drier plots (Figure 4b).

In EFN-bearing plant species, there was no relationship between the response to WE and rainfall (i.e., CCA1 scores) and specialization (mean d' ± SD: 0.17 ± 0.09; Spearman r_s= -0.27, P = 0.284). Similarly, in attendant ant species, neither the response to LG and rainfall (i.e., CCA1 scores) (Spearman r_s= 0.27, P = 0.314) nor the response to rainfall only (i.e., CCA2 scores) (Spearman r_s= 0.4822, P = 0.071) was correlated with specialization (d' = 0.21 ± 0.22).

Discussion

We found that CADs and rainfall separately influenced the degree of specialization in ant-plant networks in the Caatinga. Livestock grazing and, in particular, rainfall were most strongly associated with increased specialization. To a lesser degree, miscellaneous resource use was associated with declines in specialization. There was no relationship between wood extraction and specialization. The composition of plant and ant communities varied with disturbance and rainfall. However, such changes were not related to the degree of species specialization, which means that the pattern cannot be explained by specialist-generalist replacement. Furthermore, these changes were not due to CAD-related effects on species richness and/or the abundance of EFN-bearing plants and ant attendants (Leal, Andersen & Leal 2015; Oliveira *et al*. 2017) since results were consistent using both the observed and null-model-based metrics.

Previous research has shown that, along gradients of anthropogenic disturbance, the degree of specialization in mutualistic plant-animal networks can either decrease (plant-frugivore networks: Menke, Böhning-Gaese & Schleuning 2012; plant-pollinator networks: Aizen, Sabatino & Tilianakis 2012) or remain unaffected (plant-frugivore networks: Schleuning *et al*. 2011; plant-pollinator networks: Weiner *et al*. 2014). However, most of these studies were focused on acute disturbances such as forest fragmentation (Albrecht *et al*. 2013), logging (Schleuning *et al*. 2011; Menke, Böhning-Gaese & Schleuning 2012), and land-use change (Weiner *et al*. 2014). Here, we demonstrate that chronic disturbances (sensu Singh 1998) may also influence the degree of specialization in mutualistic networks. More interestingly, we have shown that different forms of anthropogenic disturbance occurring within the same landscape may have contrasting effects on network specialization. For example, the relationship was strongly positive for livestock grazing, slightly negative for miscellaneous resource use, and non-existent for wood extraction.

It has been reported that EFN-bearing plants experiencing high levels of herbivory produce more nectar, thus attracting more ants (Huang *et al*. 2015; Hernandez-Cumplido *et al*. 2016)—a strategy that better defends the plants. Moreover, disturbance could leave species abundance unaffected but change behavioral interactions in an environmentally dependent fashion (Brose *et al*. 2005; Tylianakis, Tscharntke & Lewis 2007). against herbivores. Indeed, in savanna forests, large herbivores shape ant-plant interactions. Palmer *et al*. (2008) showed that, in areas from which large herbivores had been excluded for ten years, nectar production declined and colonization by less aggressive ants increased, triggering higher tree mortality. The Caatinga has no native large herbivores—they are believed to have gone extinct more than 11,000 years ago (de Vivo & Carmignotto 2004). However, non-native large herbivores, such as goats and cattle, were introduced into the Caatinga at the time of European colonization, in the 16th century (MMA 2011); they might currently be serving similar functional roles to the extinct species. Since extrafloral nectar production is an induced defense response (Huang *et al*. 2015), herbivory might activate EFNs and thus strengthen interactions with particular ant species. However, wood extraction and miscellaneous resource use probably do not modify resource availability (i.e., nectar availability) in a manner that mediates this mutualism. That said, miscellaneous resource use might alter the interaction behavior of either plants or ants; it was not associated with community composition changes.

Some studies have already shown that current climatic conditions are shaping the degree of specialization in mutualistic networks of pollinators and seed-dispersers across the globe (Dalsgaard *et al*. 2011; Schleuning *et al*. 2012). We found some support for our first hypothesis: rainfall levels were associated with specialization in networks of EFN-bearing plants and attendant ants within a Caatinga forest. Other studies have found that intra-annual variation in rainfall might also influence such networks (Rico-Gray *et al*. 2012; Lange, Dáttilo & Del-Claro 2013). The mechanism could be water availability, which could affect nectar secretion and, subsequently, network structure. Indeed, the number of active EFNs is associated with interannual variation in rainfall (Rico-Gray *et al*. 1998). In Catimbau, EFN size increases as rainfall increases (Reis 2016), which may lead to greater nectar production. If so, nectar production might be highest in the wettest parts of the Caatinga, resulting in more specialized species interactions. Moreover, in the Caatinga, productivity is highest where rainfall is highest (Sampaio 2003), and higher productivity might generate more opportunities for species to specialize (Scrivastava & Lawton 1998; Schemske 2002).

As far as we know, our study is the first to look for evidence that anthropogenic disturbance and rainfall act in tandem to influence the specialization of mutualistic networks, our second hypothesis. We found no support for this idea. Several recent studies have discovered that disturbance intensity and climatic variation interact to modulate biodiversity responses (Gibb *et al*. 2015; Frishkoff *et al*. 2016). However, most of these studies were conducted at larger spatial scales than that of our study. For example, Gibb and collaborators (2015) found that anthropogenic disturbance and climatic variation interact to structure ant communities: in disturbed regions, there was a greater reduction in ant species diversity and evenness when conditions were hot and arid than when they were wet. It is worth noting that, in the latter study, mean annual rainfall ranged from 500 mm to 3000 mm. In our study, it ranged from 580 mm to 940 mm.

Some studies have found that CADs and rainfall influence plant (Ribeiro *et al*. 2015, 2016; Rito *et al*. 2017) and ant (Ribeiro-Neto *et al*. 2016; Oliveira *et al*. 2017) community structure and composition in the Caatinga. We also observed that CADs and rainfall levels were associated with changes in the compositions of EFN-bearing plant communities and attendant ant communities, supporting part of our third hypothesis. Plant community composition varied with wood extraction intensity; ant community composition varied with livestock grazing intensity; and both plant and ant community composition varied with rainfall levels. However, contrary to the other part of our third hypothesis, we did not find a correlation between the environmental responses of plants or ants and their degree of specialization, suggesting that compositional changes are not behind the changes in network specialization. One explanation may be that ant-plant interactions involving extra-floral nectaries are often generalized and facultative (Heil & McKey 2003; Rico-Gray & Oliveira 2007; Blüthgen *et al*. 2007). Studies that focused on more specialized mutualisms, such as those between plants and frugivor (Albrecht *et al*. 2013) and plants and pollinators (Weiner *et al*. 2014), found that, in disturbed habitats, specialist frugivores and pollinators were more negatively affected than were generalist frugivores and pollinators. Here, the two ant species that accounted for more than 50% of the interactions (*Camponotus crassus* and *Cephalotes pusillus*) did not respond to the environmental factors we studied. Another explanation might be that ant species behave differently in different environments (Brose *et al*. 2005; Tylianakis, Tscharntke & Lewis 2007). For example, protection by ants is enhanced when plants invest more in nectar rewards (Fagundes *et al*. 2017), and changes in network specialization can largely be attributed to increased nectar production due to increased livestock grazing and rainfall. Thus, in the most disturbed and rainy parts of Catimbau, where plants produce more extra-floral nectar (Reis 2016), ants' protective roles might change in tandem with their interaction-related behavior (i.e., interaction number and strength, partner identity). Unfortunately, there were not enough commonly occurring ant species to test this hypothesis.

Our main finding—that different CADs and rainfall levels are associated with different levels of specialization in mutualisms involving ants and ENF-bearing plants—has various implications. First, and according to the specialist-generalist evolutionary paradigm (Levins 1968, Devictor *et al*. 2010), human activities can compromise the quality of plant protection services in SDTFs. According to this paradigm, specialist species are good at a few services, while generalists are mediocre at many services. However, a recent study on the plant protection services provided by ants showed that the most protective ant species might be the most generalist as well (Fagundes *et al*. 2017). Unfortunately, this study examined protection against non-natural plant enemies, and we still need to learn more about the effectiveness of mutualisms protecting against natural enemies before making predictions about how protection services change depending on environmental conditions. Moreover, changes in species composition, by themselves or in combination with changes in network specialization, change service quality because attendant ant species differ in the protection they afford to hosts (Leal *et al*. 2006; Del-Claro & Marquis 2015; Fagundes *et al*. 2017). Second, the large heterogeneity in anthropogenic disturbance and rainfall levels in Catimbau National Park has created a mosaic of ant-plant interactions—and the degree of specialization differs, as do interaction identity, interaction strength, and plant protection quality. This mosaic may result in different selective forces that operate on the coevolution of species involved in these mutualisms, especially in dry environments. Although we lack information on the effects of such variation on the success of plant protection services, we can imagine that the scenario is one in which a human-driven selection mosaic exists (Thompson 2005) and in which the local adaptive responses of plants might arise because of local variation in community composition and function. Finally, despite great spatial variation in specialization responses, the strong influence of rainfall suggests that the predicted 22% decline in precipitation in the Caatinga by 2100 (Magrin *et al*. 2014) could trigger the loss of the most specialized ant-plant networks, which would have implications for related ecosystem services.

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Authors' contributions

TC, XA, and IRL conceived the ideas and designed the experiments. TC and FMPO collected the data. NB contributed to the network analysis. TC conducted the analyses and coordinated the writing of the manuscript. All the authors significantly contributed to the manuscript drafts and gave their final approval for submission.

Data accessibility

The data are available from the Dryad Digital Repository: (XXXXXX)

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Table 1. Results of the best-fit models (ΔAICc< 2) examining the separate and combined influences of chronic anthropogenic disturbances (livestock grazing, LG; wood extraction, WE; and miscellaneous resource use, MU) and rainfall levels on the specialization of networks formed by ants and EFN-bearing plants. The network specialization metrics were weighted generality (Gw), weighted vulnerability (Vw), interaction evenness (IE), and H_2*'*. Each metric was calculated twice, once using observed data (obs) and once using data from null models (null). For each variable retained in the best-fit model, we have indicated the mean coefficient (β), the unconditional standard error (SE), the 95% confidence intervals (95% CI), the P-value, and relative variable importance (RVI). Significant variables (according to 95% confidence intervals) are in bold. Observed IE does not appear because no variables were retained in its best-fit model.

			95% CI			
Model factors	**$\beta/10^{-3}$**	**$SE/10^{-3}$**	**$Lower/10^{-3}$**	**$Upper/10^{-3}$**	**P-value**	**RVI**
Gw_{obs}						
Rainfall	1.00	1.49	-0.831	5.444	0.519	0.44
Vw_{obs}						
LG	16.39	20.88	-11.01	71.48	0.448	0.54
MU	-8.58	18.61	-82.90	9.91	0.656	0.24
$H_2'_{obs}$						
LG	4.74	0.95	-83.85	-32.71	**<0.001**	1.00
MU	-4.84	1.13	0.19	0.58	**0.001**	1.00
Rainfall	0.49	0.09	-35.26	-54.74	**<0.001**	1.00
Gw_{null}						
LG	-23.99	9.79	32.65	557.46	**0.031**	1.00
Rainfall	-3.60	1.28	41.43	328.56	**0.016**	1.00
Vw_{null}						
LG	-3.15	7.87	-38.37	9.77	0.703	0.22
WE	2.14	5.29	-6.45	25.62	0.700	0.22
Rainfall	-4.43	1.47	-7.60	-1.26	**0.006**	1.00
IE_{null}						
LG	-30.54	10.20	-52.66	-8.42	**0.007**	1.00
Rainfall	-2.97	1.27	-5.72	-0.21	**0.034**	0.71

$H_2{}'_{null}$

LG	35.32	27.29	-24.41	95.04	0.247	1.00
MU	-19.16	17.03	-56.64	18.31	0.316	0.32
WE	-1.25	6.78	-16.19	13.68	0.870	0.15
Rainfall	3.19	1.51	-0.13	6.50	0.060	1.00
LG x rainfall	-0.01	0.08	-0.20	0.16	0.870	0.15

Table 2. Results of the canonical correspondence analyses (CCAs) used to test the influence of livestock grazing (LG), wood extraction (WE), miscellaneous resource use (MU), and rainfall on the species composition of EFN-bearing plant communities and attendant ant communities. Significant values are in bold.

Source of variation	**df**	χ^2	**F**	***P***
EFN-bearing plant species				
LG	1	0.248	1.245	0.254
WE	1	0.376	1.886	**0.021**
MU	1	0.200	1.001	0.501
Rainfall	1	0.331	1.660	**0.038**
Residual	10	1.996		
Attendant ant species				
LG	1	0.176	1.745	**0.047**
WE	1	0.126	1.243	0.253
MU	1	0.145	1.745	0.150
Rainfall	1	0.255	2.557	**0.001**
Residual	10	1.010		

Figure legends

Fig. 1. Map of the 15 study plots (20 m x 20 m; gray circles) in Catimbau National Park, along with graphs of their ant-plant networks. The width of the links between species denotes the interaction frequency between EFN-bearing plants (bottom bars) and ants (top bars). Bar width is proportional to the number of interactions per species, revealing a species' relative contribution to the network. *Pityrocarpa moniliformis* (white bars), *Cenostigma microphylla* (dark gray bars), and *Tacinga palmadora* (light gray bars) were the plant species involved in the most interactions. *Camponotus crassus* (blue bars) and *Cephalotes pusillus* (red bars) were the ant species with the highest interaction frequencies.

Fig. 2. Influence of (a) livestock grazing, (b) miscellaneous resource use, and (c) mean annual rainfall on the observed network specialization index H_2'. The metric values and 95% confidence intervals (in gray) were calculated by averaging estimates across the best-fit models (ΔAICc< 2).

Fig. 3. Influence of livestock grazing on (a) null-model-based weighted generality (Gw_{null}) and (b) interaction evenness (IE_{null}), and the influence of mean annual rainfall on (c) Gw_{null}, (d) IE_{null}, and (e) weighted vulnerability (Vw_{null}). The metric values and 95% confidence intervals (in gray) were calculated by averaging estimates across the best-fit models (ΔAICc< 2).

Fig. 4. Results of the canonical correspondence analyses examining the associations between three chronic anthropogenic disturbances (LG, WE, and MU), rainfall, and the species composition of (a) EFN-bearing plant communities and (b) attendant ant communities in Catimbau National Park, Brazil. The abbreviations for the EFN-bearing plant species are as follows: Cfol = *Chloroleucon foliolosum*, Chel = *Croton heliotropiifolius*, Cmic = *Cenostigma microphylla*, Cnep = *Croton nepetifolius*, Cpyr = *Cenostigma pyramidalis*, Ctri = *Croton tricolor*, Cfle = *Cynophalla flexuosa*, Ptub = *Pilosocereus tuberculatus*, Psti = *Piptadenia stipulacea*, Pmon = *Pityrocarpa moniliformis*, Sgla = *Sapium glandulosum*, Sbah = *Senegalia bahiensis*, Spia = *Senegalia piahuiensis*, Ssp = *Senegalia* sp., Sriz = *Senna rizzinii*, Sspl = *Senna splendida*, Svel = *Senna velutina*, Tpal = *Tacinga palmadora*, and Vcur = *Varronia curassavica*. The abbreviations for the attendant ant species are as follows: AztA

= *Azteca* sp. A, BraA = *Brachymyrmex* sp. A, BraC = *Brachymyrmex* sp. C, Ccra = *Camponotus crassus*, Ccor = *Cephalotes* pr. *cordatus*, Cpus = *Cephalotes pusillus*, Ccri = *Crematogaster crinosa*, Ceva = *Crematogaster* pr. *evallans*, Cobs = *Crematogaster* pr. *obscurata*, Dqua = *Dolichoderus quadridenticulatus*, Dtho = *Dorymyrmex thoracicus*, Prad = *Pheidole radoskowiskii*, Paca = *Pseudomyrmex acanthobius*, Pelo = *Pseudomyrmex elongatus*, Pgra = *Pseudomyrmex gracilis*, and Svir = *Solenopsis virulens*.

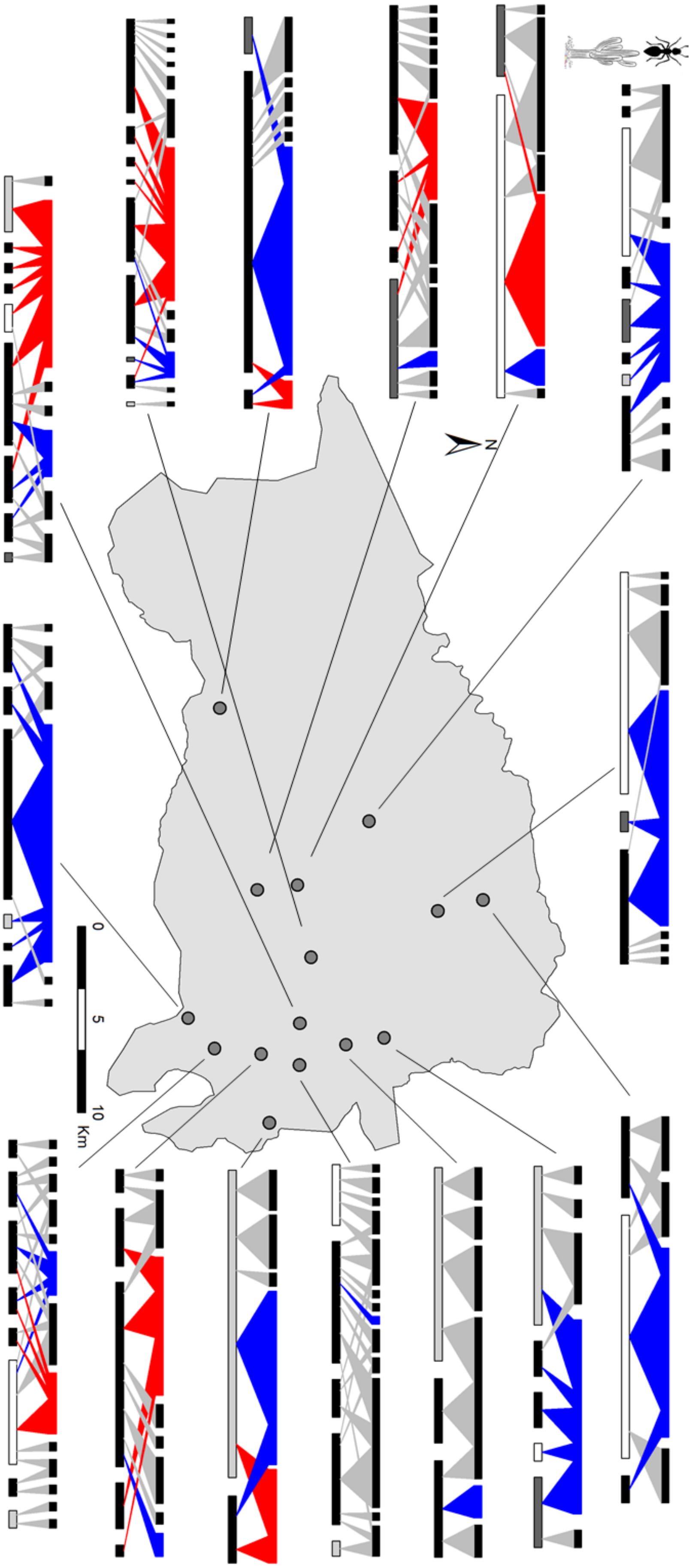


Fig. 1

Fig. 2

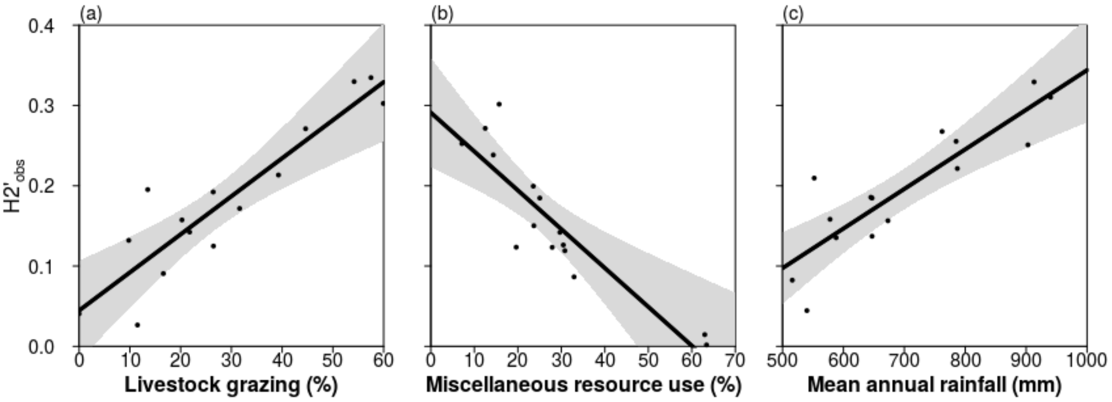
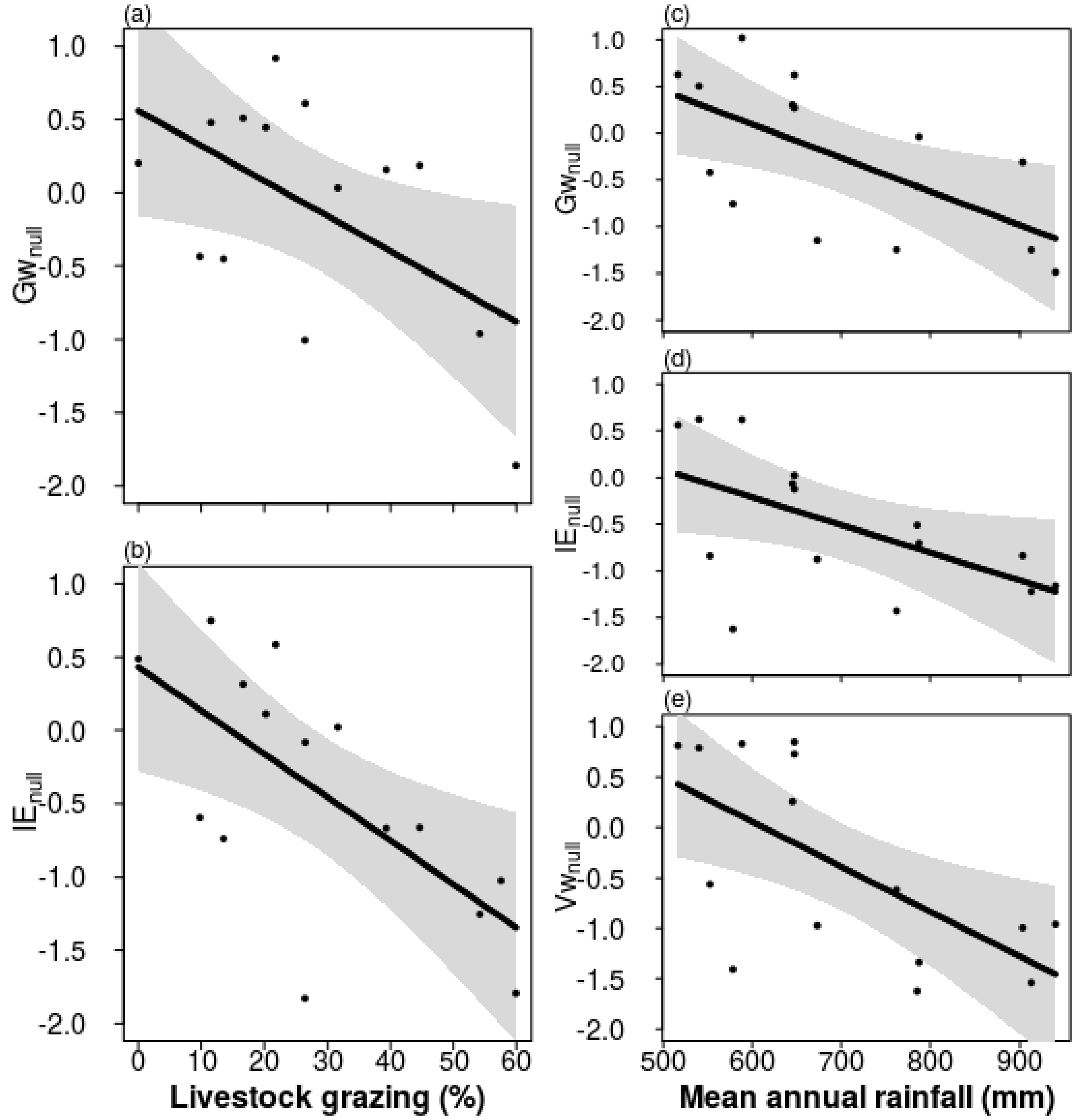

(a)
(b)
(c)
H2'$_{obs}$
0.0
0.1
0.2
0.3
0.4
0
10
20
30
40
50
60
Livestock grazing (%)
0
10
20
30
40
50
60
70
Miscellaneous resource use (%)
500
600
700
800
900
1000
Mean annual rainfall (mm)

Fig. 3


(a)
(b)
(c)
(d)
(e)
Gw$_{null}$
IE$_{null}$
Vw$_{null}$
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
0
10
20
30
40
50
60
Livestock grazing (%)
500
600
700
800
900
Mean annual rainfall (mm)

Supplementary material

Appendix 1. *Individual chronic anthropogenic disturbance index measurement*

Different indices of chronic anthropogenic disturbance were calculated by using direct variables, *i.e.* data obtained at the field, and indirect variables, *i.e.* data obtained through satellite imagery and interviews. For example, the livestock pressure index (LP) was only computed from direct variables: (1) we counted the number of bovine and equine drops within each 0.1 ha plot, (2) we counted the number of goat drops within four subplots of 5 m x 5 m within the 0.1 ha plots; and 3) we measured the length in meters of well-defined goat trails by using an odometer in each 0.1 ha plot. Similarly, the wood extraction index (WE) was computed from direct variables: live-fuel wood extraction (LFWE) and fuel-wood collection.LFWE was obtained by counting the number of stem cuts within the 0.1 ha plot; for each cut we measured the diameter, so we can estimate the overall basal area extracted at each plot. Fuel-wood collection 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.We, then, 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 we were not able to obtain the wood density at the field, we obtained density values from 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 ($\text{Biomass}_{\text{Kg}} = 0.173\ \text{DBH}_{\text{cm}}^{2.295}$, where DBH is 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 than the others disturbance sub-indices or single metrics. Finally, the people pressure index (PP) was only measured using indirect variables. We used two approaches: satellite imagery and interviews. Through satellite imagery, we computed proximity to the nearest house (PNH) and proximity to the nearest road (PNR). Because small distances indicate higher disturbance, we transformed them by using the multiplicative inverse, so low values indicate low disturbance while high values indicate high disturbance. Using 65 interviews, we gathered information about how many people lives inside proximate houses with influence in the plots (NP)

Appendix 2. Quantitative specialization network metrics.

A) **Interaction evenness**: it quantifies the equitability of the interaction frequency between ant species and EFN-plant species, as:

$$E_S = \frac{-\sum_i \sum_j p_{ij} ln p_{ij}}{lnL}$$

Where p_{ij} is the proportion of interactions in given plot *k* between ant species *j* and EFN-plant species *i* ($p_{ij}= a_{ij}$/m) and *L* is the number of realized links in a network.

B) **Weightedgenerality**: we first calculated the Shannon diversity of interactions for ant species *j* and EFN-plant species *i*, respectively, as:

$$H_j = -\sum_{i=l}^{I} \left(\frac{a_{ij}}{A_j} . ln \frac{a_{ij}}{A_j}\right)$$

where a_{ij} is the number of interactions of ant species *j* visiting EFN-plant species *i*,and A_j is the sum of interaction of ant species *j* (Bersier *et al.* 2002, Blütghen *et al.* 2008). Weighted generality reflects the mean of effective number of EFN-plants visited per ant species weighted by the interaction frequency of ant species, as:

$$G_{qw} = \sum_{j=1}^{J} \frac{A_j}{m} 2^{H_j}$$

where *Aj* is the sum of interactions of ant species *j* and *m* is the total number of interactions in the network.

C) **Weighted vulnerability** is analogous to the generality index, reflecting the mean of effective number of ants per EFN-plant species weighted by the interaction of EFN-plant species. For computations, we just need to replace *j* for *i* and *J* by *I* in the Generality equation.

D) **Index H_2'**: it measures specialization based on the difference between realized and expected associations generated by null frequency distribution of the total interaction given in a plot *k* (Blütghen *et al.* 2006). First, we calculated the Shannon diversity of the entire network:

$$H_2 = -\sum_{i=1}^{J} \sum_{j=1}^{I} (p_{ij} . \ln p_{ij})$$

where p_{ij} is the proportion of interactions in a cell between ant species *j* and EFN-plant species *i* as showed above. Then, we calculated the standardized network specialization:

$$H_2' = \frac{H_{2\,max} - H_2}{H_{2\,max} - H_{2\,min}}$$

Table S1. List of EFN-bearing plants species, their abundance, the occurrence and the degree of specialization (*d'*) in relation to their associated attendant-ants species in fifteen plots distributed along chronic anthropogenic disturbance and rainfall gradients in Caatinga dry forest, Brazil. Attendant-ant species interacting with each EFN-bearing plant species are indicated by numbers (see Table S2).

Family/EFN-bearing plant species	**Abundance**	**Number of plots**	***d'***
Anacardiaceae			
Anacardium occidentale	1	1	0
Boraginaceae			
Varronia curassavica	14	2	0.1835
Cactaceae			
Pilosocereus tuberculatus	3	1	0.2872
Tacinga palmadora	71	10	0.1626
Capparaceae			
Cynophalla flexuosa	5	2	0.2665
Euphorbiacae			
Cnidosculus bahianus	1	1	0.1540
Croton heliotropiifolius	10	4	0.4037
Croton nepetifolius	35	5	0.1807
Croton tricolor	26	4	0.1634
Sapium glandulosum	5	3	0.2850
Fabaceae			
Chloroleucon foliolosum	19	3	0.1367
Piptadenia stipulaceae	30	5	0.2254
Pityrocarpa moniliformis	89	8	0.1890
Poincianella microphylla	46	8	0.2568
Poincianella pyramidalis	7	2	0.1693
Senna rizzinii	30	4	0.2124
Senna splendida	7	2	0.1864
Senna velutina	6	1	0.1964

Senegalia bahiensis	6	1	0.1647
Senegalia piahuensis	5	4	0.0130
Senegalia cf. *polyphylla*	1	1	0.0651
Senegalia sp.	8	2	0.0962

Table S2. List of attendant-ant species, their abundance, the occurrence and their degree of specialization (*d'*) in fifteen plots along chronic anthropogenic disturbance and rainfall gradients in Caatinga dry forest, Brazil.

Attendant-ant species	**Abundance**	**Number of plots**	**d'**
1- *Azteca* sp. A	15	4	0.1116
2- *Brachymyrmex* sp. A	6	3	0.0611
3- *Brachymyrmex* sp. B	4	3	0.2048
4- *Brachymyrmex* sp. C	9	3	0.0936
5- *Camponotus blandus*	1	1	0.2500
6- *Camponotus crassus*	173	15	0.0672
7- *Camponotus fastigatus*	3	3	0.1474
8- *Camponotus* sp. C	1	1	0.7211
9- *Camponotus* sp. G	1	1	0
10- *Cephalotes clypeatus*	2	1	0.2790
11- *Cephalotes persimilis*	1	1	0.4103
12- *Cephalotes* pr. *cordatus*	22	4	0.2339
13- *Cephalotes pusillus*	123	8	0.1248
14- *Crematogaster abstinens*	2	2	0
15- *Crematogaster crinosa*	5	2	0.3151
16- *Crematogaster* pr. *evallans*	15	7	0.0728
17- *Crematogaster* pr. *obscurata*	14	6	0.1377
18- *Crematogaster* sp. D	2	2	0.1250
19- *Crematogaster* sp. E	1	1	0.0745
20- *Dolichoderus quadridenticulatus*	7	3	0.2502
21- *Dorymyrmex goeldii*	2	2	0.0519
22- *Dorymyrmex thoracicus*	57	8	0.2258
23- *Ectatomma muticum*	3	3	0.1290

24- *Gnamptogenys sulcata*	1	1	0
25- *Linephitema neotropicum*	1	1	1
26- *Pheidole radoskoviskii*	5	3	0.1561
27- *Pheidole* sp. D	1	1	0.7500
28- *Pheidole* sp. E	3	2	0.2229
29- *Pseudomyrmex acanthobius*	31	9	0.1701
30- *Pseudomyrmex elongatus*	7	1	0.1061
31- *Pseudomyrmex gracilis*	30	12	0.2019
32- *Pseudomyrmex laevifrons*	2	1	0.2016
33- *Solenopsis virulens*	5	2	0.1728

Table S3. Best-fit models (ΔAICc < 2) of the isolated and combined effects of different chronic anthropogenic disturbance pressures (livestock pressure (LP), wood extraction (WE) and people pressure (PP)) and rainfall variation on the observed (obs) and null model corrected specialization (Z-transformation) characterized by generality, vulnerability, interaction evenness and H_2'. The number of estimated parameters (k), Akaike information criterion (AIC) and AIC corrected for small sample size difference (ΔAICc) are indicated.

Best-fit models	**k**	**AIC**	**ΔAICc**
Obs-Generality			
~1	2	40.2	0.00
Rainfall	3	40.8	0.52
Obs-Vulnerability			
~1	2	45.7	0.00
LP	3	46.5	0.18
LP + PP	4	47.0	0.14
Obs-Interaction evenness			
~1	2	-32.9	0.00
Z-Generality			
LP + Rainfall	4	39.3	0.00
Z-Vulnerability			
Rainfall	3	41.1	0.00
WE + Rainfall	4	42.9	1.83

LP + WE + Rainfall	4	42.9	1.86
Z-Interaction evenness			
LP + Rainfall	4	38.9	0.00
LP	3	40.8	1.84
Z-H_2’			
LP + Rainfall	4	35.2	0.00
LP + PP + Rainfall	5	35.6	0.37
LP + Rainfall + LP x Rainfall	5	37.2	1.95
LP + WE + Rainfall	5	37.2	1.95

4 ANTHROPOGENIC DISTURBANCE AND RAINFALL VARIATION THREATEN THE STABILITY OF PLANT-ANT INTERACTIONS IN THE BRAZILIAN CAATINGA

MANUSCRITO PUBLICADO NO JORNAL ECOGRAPHY

Original Paper - Ecography

Anthropogenic disturbance and rainfall variation threaten the stability of plant-ant interactions in the Brazilian Caatinga

Abstract

Climate change is projected to exacerbate the effects of anthropogenic disturbance, with negative impacts on ecosystem stability and functioning. We evaluate the additive and combined effects of chronic anthropogenic disturbance (CAD) and rainfall variation on the temporal stability of mutualistic EFN-bearing plant-ant networks in a Caatinga dry forest. We evaluated whether changes in the stability of these interactions are driven by changes in the stability of the communities of partners involved and/or in ant behavior. We sampled EFN-bearing plant-ant networks in sixteen 20m×20m plots distributed across CAD and rainfall gradients. The stability of EFN-bearing plant and attendant-ant communities were measured as the inverse of temporal differences in their community structure and composition. We also computed the stability of EFN-bearing plant-ant networks by measuring the inverse of temporal differences in network specialization metrics. We found that, in general, the structure and composition of plant and ant interacting communities were similarly stable along both environmental gradients. Only CAD and its interaction with rainfall affected the temporal stability of EFN-bearing plant diversity, which declined as CAD increased, with a more pronounced relationship in wetter areas. However, variation in levels of CAD and, to a lesser extent, rainfall greatly modulated the stability of EFN-bearing plant-ant network specialization. CAD reduced the stability of network generality (specialization at the ant level), an effect that was much stronger in wetter areas. Meanwhile, the stability in network vulnerability (specialization at the plant level) decreased with the increase of CAD and the decrease of rainfall levels. Finally, there was a trend of decreasing stability in specialization of the overall network with increasing CAD. Our results suggest that changes in the structure of interaction networks are mainly driven by a switch in ant behavior rather than by changes in the structure and composition of plant and ant communities between years.

Key-words: climate change, chronic anthropogenic disturbance, ecosystem stability, environmental fluctuation, mutualisms, plant-animal interactions, seasonally dry tropical forest

Introduction

Ecosystem stability, *i.e.* the invariability in ecosystem function over time, is often beneficial for the reliable provision of ecosystem functioning and services, and is important to the ability of ecosystems to deal with future disturbance events (Holling 1973, Carpenter et al. 2001, Colwell et al. 2008, Magurran et al. 2010, Mori 2016). Thus, insights about potential improvements to conservation efforts can be gleaned from our understanding of temporal dynamics of ecological communities (Butchart et al. 2010). Global climate projections have been becoming increasingly concerning, with not only increases in global mean temperature and changes in global rainfall regimes, but also increasingly variable conditions and a higher frequency of extreme weather events (IPCC 2014, Otzurk et al. 2015). Moreover, climate change can also affect ecosystems by modifying disturbance regimes (Dale et al. 2001). In the face of this pessimistic scenario, assessing the stability of ecological communities and ecosystems under human-driven environmental change is becoming a major goal in conservation ecology (Mori et al. 2013, 2017, Fischer et al. 2016).

Globally, human populations have been responsible for acute changes in land-use, fire regimes, and increases in intensity and severity of droughts over vast swaths of land, likely affecting many aspects of ecosystem functioning, especially ecosystem productivity, stability, and biodiversity (Vitousek et al. 1997, Sala et al. 2000, Hooper et al. 2012, Hautier et al. 2015). However, our current knowledge of ecosystem stability in areas affected by chronic anthropogenic disturbance (CAD) is limited. CAD is especially prevalent in dry areas of the tropics, where very dense human populations are dependent on forest ecosystems and resources (Singh 1998, Specht et al. 2015). In these areas, it is essential to understand how CAD may harm ecosystem stability, and consequently, compromise the future use of these ecosystem resources by humans. Thus, in areas where people are continuously extracting natural resources, ecological communities might be in a constant process of secondary succession, and species colonizations and extinctions might also occur continuously (Lehtilä et al. 2016). Consequently, ecosystem stability would be lower in more disturbed areas than in relatively undisturbed areas. In tropical dry areas, aridity is a relevant factor that might also affect ecosystem stability, where harsh environmental conditions in the driest areas may harbor more dynamic communities than wetter areas, where environmental conditions are more favorable for stability (Diamond et al. 2016). Moreover, aridity may interact with disturbance to intensify ecosystem instability (Pulla et al. 2015, Puig-Gironés et al. 2017).

The study of mutualistic ecological interaction networks has contributed to our understanding of the mechanisms that maintain ecosystem stability (Benadi et al. 2013, Rohr et al. 2014). Plants bearing extrafloral nectaries (EFNs) produce high carbohydrate-rich resources, which attract several ant species (*i.e.* attendant ants) that potentially defend their hosts from herbivores (Bentley 1977). Such mutualisms form stable networks of interacting species which are likely resilient to disturbance (Díaz-Castelazo et al. 2010, Díaz-Castelazo et al. 2013). However, some studies have reported that the decline in abundance of some EFN-bearing plants in human-disturbed habitats is related to decreases in the number of species of arboreal dominant ants (Câmara et al. 2017) and ant visitation rates (Leal et al. 2015). As most plant and ant species are vulnerable to climate change (*e.g.* Moritz and Agudo 2013, Resasco et al. 2014, Diamond et al. 2016), the combined effects of disturbance and climate change might cause an impoverishment of plant and ant communities in the driest disturbed habitats (Rito et al. 2017, Gibbs et al. 2015). It is unclear, however, whether changes in plant and ant communities across gradients of CAD and rainfall might alter EFN-bearing plant-ant mutualism networks over time.

The mechanisms that shape the stability of free-living mutualistic networks are complex; even when both mutualistic partners co-occur, they may not necessarily interact (Poisot et al. 2015). Thus, environmental change might not only affect the temporal stability of ecological networks by altering community structure and composition of mutualistic partners, but also by climate-induced changes in the behavior of mutualist partners (Kiers et al. 2010). Ant preferences for EFN-bearing plants depend on EFN nectar amount and composition (Blüthgen and Fiedler 2004a,b, Bixenman et al. 2011), and nectar production is highly dependent on abiotic and biotic factors (Bixenman et al. 2011, Alves-Silva and Del-Claro 2014). In addition, the physical conditions of microhabitats determine the spatial and temporal foraging patterns of ants (Fitzpatrick et al. 2014, Arnan and Blüthgen 2015). Thus, in more environmentally unstable areas (probably the most disturbed and arid areas), shifts in ant foraging patterns and plant preferences may be more pronounced from year to year, thus increasing temporal instability in interaction networks.

Here, we investigate the additive and combined effects of CAD and rainfall on the temporal stability of mutualistic EFN-bearing plant-ant networks in a Caatinga dry forest. Caatinga is a typical seasonally dry tropical forest that supports a high density of EFN-bearing plants (Melo et al. 2010, Leal et al. 2017). Despite the wide range of ecosystems where EFN-bearing plants interact with ants (Rico-Gray and Oliveira 2007), there is some evidence that this protective service is more effective in arid environments (Leal and Peixoto 2016).

However, the Caatinga is continuously degraded by human activities such as wood extraction, overgrazing by livestock (cattle and goats) and collection of non-timber forest products (Albuquerque et al. 2007, Ramos and Albuquerque 2012, Ribeiro et al. 2015, Arnan et al. 2018a). These human activities can threaten important ecosystem services provided by mutualists, such as ant-mediated seed-dispersal (Leal et al. 2014) and plant protection against herbivores (Leal et al. 2015, Câmara et al. 2018). In addition, the Caatinga is also threatened by climate change, with an increase of mean annual temperature between 1.7°C and 6.7°C and a reduction in rainfall of 22-40% predicted for the end of the twenty-first century (Magrin et al. 2014, IPCC 2014). Because the Caatinga encompasses different rainfall regimes (Sampaio 1995), even within small geographic ranges (Rito et al. 2017), it offers an excellent opportunity to study the potential effects of CAD and rainfall reduction on the stability of plant-ant mutualistic networks. We tested the following two hypotheses: (1) the additive effect of increasing CAD and decreasing rainfall will reduce the temporal stability of EFN-bearing plant-ant networks, and (2) the combined effects of increasing CAD and decreasing rainfall will negatively affect the temporal stability of EFN-bearing plant-ant networks, whereby the temporal stability will be lowest in the most arid and disturbed sites. We then investigated three non-exclusive mechanisms that might explain changes in temporal stability of EFN-bearing plant-ant networks along the gradients: (1) changes in the interacting EFN-bearing plant community, (2) changes in the attendant-ant community, and/or (3) changes in attendant-ant behavior.

Materials and methods

Study area

The study was conducted in the Catimbau National Park, Pernambuco state, northeastern Brazil (8º24’00’’and 8º36’35’’S; 37º09’30’’and 37º14’40’’W; Figure 1). The Park covers an area of 607 km² dominated by low stature (6-8 m) Caatinga vegetation. The climate is semi-arid, with an average temperature of 23ºC and mean annual rainfall ranging from 480 mm to 1100 mm, mostly received between March and July (Rito et al. 2017). Predominant soils are quartzite sandy soils (72.3% of the Park), but planosols, latosols and vertisols are also present (Rito et al. 2017). The most representative plant families are Fabaceae, Euphorbiaceae and Cactaceae (Rito et al. 2017). Such families are the most dominant EFN-bearing plants in the world (Weber et al. 2015), and together with other EFN-bearing plant families such as

Anacardiaceae, Capparaceae, Passifloraceae, and Turneraceae, they comprise 15% of woody species and 39% of individuals in the Catimbau flora (Leal et al. 2017).

Catimbau National Park has been protected by law since 2002; however, there are still low-income rural populations living inside the park boarders who use the forest resources for their survival (Rito et al. 2017). These populations contribute to CAD through, for example, extraction of non-timber forest products (*e.g.* exploitation of tree bark for medicinal purposes and hunting), animal husbandry (especially goats and cattle) and wood extraction (*e.g.* firewood, for the construction of houses, fences and handy crafts) (Rito et al. 2017, Arnan et al. 2018a). These varied sources of disturbance spread out across the Park, show high and independent spatial variability, and point to complex patterns of resource use by local communities with different areas targeted for different resources (Arnan et al. 2018a). We established sixteen 20 m × 20 m plots with a minimum 2-km distance within a 214 km² landscape (Figure 1). 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. These plots were exposed to varying levels of CAD and rainfall, thus forming gradients of both CAD and rainfall.

Characterization of disturbance and rainfall gradients

We characterized the level of CAD in each plot by computing a global multi-metric index that integrates eight disturbance indicators related to the three main sources of CAD in the Catimbau National Park: livestock pressure (herbivory by goats and cattle), wood extraction (live and dead wood) and exploitation of non-timber forest products (poaching/hunting, medicinal plants, collection of food items for human consumption and livestock fodder) (Rito et al. 2017, Arnan et al. 2018a). Livestock pressure and wood extraction were directly measured in the field through assessments of goat trail length, goat dung frequency, cattle dung frequency, live wood extraction (stem cuts) and coarse woody debris extraction (litter) within each plot (Arnan et al. 2018a). Non-timber products were estimated via three variables related to the accessibility and influence of human activities in each plot: proximity to the nearest house, proximity to the nearest road and number of people living in each house that engage in the practices described above (Arnan et al. 2018a). These three indirect disturbance indicators were integrated into a single metric—*people pressure*—by means of PCA analysis (Arnan et al. 2018a). Data from the single disturbance metrics (livestock pressure, wood extraction and people pressure) were integrated into a compound, additive index in which different kinds of disturbance contribute to an overall level of chronic anthropogenic disturbance. The compound index ranged from 2 to 58 (from the lowest to the highest level of disturbance) among the plots. For more details on the characterization of disturbance and calculation of the global multi-metric index, see Arnan et al. (2018a).

Data on mean annual rainfall was obtained from the WorldClim global climate data repository Version1 (http://www.worldclim.org, Hijmans et al. 2005), which contains spatial climate data from 1960 to 1990. We downloaded the dataset at 30 arc seconds resolution, and the mean annual rainfall at each plot was extracted using the *maptools* package **(**Bivand & Lewin-Koh 2015) in the R software v.3.3.1 (R Core Team 2016). This resulted in a spatial resolution of 1 km^2, which provides climatic data that are directly applicable to the scale of sampling where interactions between EFN-bearing plants and ants were observed and avoids overlapping in climatic conditions among plots (plots were separated by at least 2 km). Mean annual rainfall ranged from 510 to 940 mm, representing almost a 50% variation in rainfall over a small geographic area. Past studies conducted in the same study area using the same plots and Worldclim data, showed strong effects of climate gradients on plant (Rito et al. 2017) and ant (Arnan et al. 2018b) communities, and in their interactions (Câmara et al. 2018, Oliveira et al., in press). Thus, the Catimbau National Park provides an excellent opportunity to investigate the effects of rainfall variation on the stability of interaction networks. CAD and rainfall gradients were not significantly correlated ($r = 0.23$, $p > 0.05$), and therefore were statistically independent.

EFN-bearing plant-ant networks

We observed attendant-ant species visiting EFN-bearing plants in all plots from March to July in 2014 and March to April in 2016. These months comprise the rainy season in the Caatinga, when extrafloral nectar secretion is high (T. Câmara, personal observation). First, we performed preliminary censuses using direct observations to determine which plant species bear EFN. Then, we performed censuses twice in all plots (once in 2014 and once in 2016) on all EFN-bearing plants with height ≥ 1 m and diameter basal height (DBH) ≥ 3 cm in the morning, from 6:00 to 10:00 a.m. Each EFN-bearing plant was inspected for up 10 min and ants were considered feeding nectar when mouthparts were in contact with EFNs. These procedures have been widely adopted in studies describing EFN-bearing plant and attendant-ant interactions (*e.g.* Leal et al. 2015, Câmara et al. 2018). EFN-bearing plant and attendant-ant species that were not identified in the field were collected and transported to our laboratory where they were identified to the species level or sorted into morphospecies whenever this was not possible. We only considered interacting plants and ants and not the entire plant and ant communities.

For each of the sixteen plots, we constructed a matrix based on the records of interactions between EFN-bearing plant species and attendant-ant species in 2014 and 2016. Since ants are social insects, to avoid bias due to the proximity between plants and ant trails or nests (Gotelli et al. 2011), interactions between ants and EFN-bearing plant species were considered as the number of individual EFN-bearing plants on which an ant species was recorded, regardless of the total number of ant workers. That is, when two different ant species visited a single EFN-bearing plant, or if one ant species visited two individuals of the same EFN-bearing plant species, we considered both cases as two different interactions.

Data analysis

The temporal stability of EFN-bearing plant and attendant-ant communities was computed for each plot using four different parameters that characterize community structure and composition. First, we computed the absolute difference in abundance of EFN-bearing plant and attendant-ant species between years. Considering again the social nature of ant colonies (Gotelli et al. 2011), the abundances of EFN-bearing plant species were estimated by the number of individuals interacting with attendant-ant species while the abundances of ant species were estimated by the frequency of each ant species interacting with an individual of a EFN-bearing-plant species. Second, we computed the absolute difference in richness of EFN-bearing plant and attendant-ant species between years. Third, we computed the absolute difference in diversity of EFN-bearing plant and attendant-ant species. Diversity was computed as the exponential of Shannon entropy ($e^{H'}$) which estimates the effective number of species present in a particular community (Jost 2006). Fourth, we computed the Bray-Curtis dissimilarity index, comparing plant and ant (both involved in EFN-bearing plant-ant interactions) community compositions between years. The Bray-Curtis dissimilarity is defined as:

$$d_{BC} = -1\,\frac{B+C}{A+B+C}$$

where A is the relative abundance of each species found in both communities (2014 and 2016), while B and C are the relative abundance of unique species found in 2014 and 2016, respectively. This index ranges from 0 to 1, where 0 represents the lowest dissimilarity and 1 the highest dissimilarity in species composition.

In order to evaluate the stability of the interaction networks, we used four specialization network metrics: (1) interaction evenness (IE), which quantifies the equitability of the interaction frequency between EFN-bearing plant and attendant-ant species; (2) weighted quantitative generality (Gw), which is the mean of the effective number of EFN-plants visited per ant species weighted by the interaction frequency of ant species (*i.e.* specialization at the level of ants); (3) weighted quantitative vulnerability (Vw), that is analogous to generality, but instead of focusing on the highest trophic level, it focuses on the lowest—it is thus the mean of the effective number of ants per EFN-plant species weighted by the interaction frequency of EFN-plant species (*i.e.* specialization at the level of plants); and, (4) network specialization index H_2*'*, which provides information about functional complementarity and redundancy among ant and EFN-bearing plant species at the community level (*i.e.* specialization at the overall network level). This index estimates specialization based on differences between realized and expected associations generated by null frequency distributions of the marginal totals (Blüthgen et al. 2006). For more details on each network metric, see Dormann et al. (2009) and Appendix 1. Temporal stability of community interaction networks was then computed (similarly to ant and plant community structure) as the absolute difference of each network between the two years of study (*i.e.* $\Delta IE_{obs,}$ $\Delta Gw_{obs,}$ $\Delta Vw_{obs,}$ $\Delta H_2'_{obs}$).

Since the stability of network metrics can be affected by richness and sampling effort (Dormann et al. 2009), we also computed the same network specialization metrics controlled for changes in species occurrences and abundances between years to remove network size effects. Given that the effects of different species occurrence and/or species abundance were removed, this approach allowed us to detect changes in stability due to factors other than changes in ant or plant community structure, *i.e.* changes in species identity (with different interacting behaviors) and/or changes in species behavior. Thus, we first performed 10,000 randomizations of each interaction network matrix in 2014 and 2016 by using the Patefield algorithm (Blüthgen et al. 2008). This algorithm fixes the marginal totals (*i.e*. total number of interactions recorded per EFN-bearing plant species and attendant-ant species) and produces random interaction networks. The mean value of each specialization metric was computed from all randomized matrices per plot and year (*i.e.* we computed 32 random values for each specialization metric). We then computed the absolute difference in the random specialization metrics between the two years of study for each plot (*i.e.* $\Delta IE_{rand,}$ $\Delta Gw_{rand,}$ $\Delta Vw_{rand,}$ $\Delta H_2'_{rand}$). Finally, the stability in abundance- and richness-controlled specialization network metrics were computed as the difference between the observed and the random network metrics: (1)

$\Delta[\Delta IE] = \Delta IE_{obs} - \Delta IE_{rand}$, (2) $\Delta[\Delta G_w] = \Delta Gw_{obs} - \Delta Gw_{rand}$, (3) $\Delta[\Delta Vw] = \Delta Vw_{obs} - \Delta Vw_{rand}$ and (4) $\Delta[\Delta H_2] = \Delta H_2'_{obs} - \Delta H_2'_{rand}$. Observed and abundance- and richness-controlled specialization metrics were computed using the *Bipartite* package (Dormann *et al*. 2009) in R.

For all response variables, low differences between years mean high stability. Therefore, we standardized all response variables according to the following formula:

$$S = -\frac{(y_i - y_{min})}{(y_{max} - y_{min})}$$

where S is temporal stability, y_i is the observed value for each response variable found in plot *i* (*e.g.* Δ[ΔIE]), y_{min} is the minimum observed value found for this variable across all plots and y_{max} is the maximum observed value across all plots. This standardization puts all variables on the same scale and the stability gradient from low to high values. Thus, temporal stability for each response variable ranged from -1 to 0, where zero is the highest stability (no change between years) and negative values up to -1 represent lower stabilities. Because the difference in EFN-bearing plant richness had few discrete values (ranging between 0 and 2, except one plot with a value of 6) and many zeros, we transformed this variable into a binary variable. Therefore, plant richness with high temporal stability were those that had no differences between years, represented by 0, while plant richness with low temporal stability were those that had some variation in species richness (*i.e.* values such as 1, 2 or 6) between years, and were represented by -1.

We analyzed the effects of CAD and rainfall (and their interaction) on the stability of EFN-bearing plant (with the exception of richness) and ant communities, and on network specialization (either observed and abundance- and richness-controlled metrics) using general linear models. In turn, the effects of CAD, rainfall and their interaction on stability of species richness of EFN-bearing plants were analyzed using a generalized linear model with a Binomial distribution and a logit-link function. All models were rerun only adding CAD and rainfall (and not adding their interaction) as fixed factors when the interaction between CAD and rainfall were initially not statistically significant ($p < 0.05$). We tested the normality of all model residuals using Shapiro-Wilk tests. All analyses were conducted in R.

Results

We observed 312 interactions between 17 EFN-bearing plant and 25 ant species in 2014, and 243 interactions between 19 EFN-bearing plant and 26 ant species in 2016 (a total of 555 interactions during the two years of study, involving 23 EFN-bearing plant and 33 ant species, see Table S1 and Table S2). Almost half of the EFN-bearing plant (43% of 23 species) and attendant-ant species (45% of 33 species) interacted exclusively in only one year of the survey (Figure 2). *Pityrocarpa moniliformis* and *Tacinga palmadora* were the most common EFN-bearing plant species interacting with attendant-ant species, encompassing near 50% of the interactions in 2014, while *P. moniliformis*, *T. palmadora* and *Piptadenia stipulaceae* were the most abundant plant species encompassing ~52% of the interactions in 2016. In turn, *Camponotus crassus* and *Cephalotes pusillus* were the ant species that visited the most EFN-bearing plants: both were responsible for 62% and 58% of the interactions in 2014 and 2016, respectively (Figure 2).

Overall, both EFN-bearing plant and attendant-ant communities were similarly stable along CAD and rainfall gradients. From the four parameters used to measure temporal stability (abundance, richness, diversity and composition) of EFN-bearing plant communities, only diversity was affected by CAD and its interaction with rainfall (Table 1). Thus, stability in plant diversity decreased as CAD increased along the entire gradient, with greater reductions in the wetter rather than in the driest areas (Figure 3a). Moreover, all four parameters used to measure the temporal stability of attendant-ant communities were not affected by CAD, rainfall or their interaction (Table1). However, the temporal stability of interaction networks was shaped by environmental change. The stability of observed generality (*i.e.* stability of specialization at the ant level) was strongly affected by CAD, rainfall and their interaction (Table 2). Overall, stability decreased with increasing CAD, and the reduction was greater in the wettest areas (Figure 3b). The observed stability in vulnerability (*i.e.* stability of specialization at the plant level) was significantly affected by CAD and rainfall when the interaction effect from the model was excluded (Table 2, Appendix 2): an increase in CAD led to a decrease in temporal stability of observed vulnerability (Figure 4a) while a reduction in annual rainfall resulted in a decline in temporal stability of vulnerability (Figure 4b). The observed stability in interaction evenness and H_2*'* (*i.e.* stability of specialization at the overall network level) were not affected by CAD, rainfall or their interaction (Table 2, Appendix 2). The stability in the abundance- and richness-controlled vulnerability was only affected by CAD (Table 2); that is, an increase in CAD resulted in a reduction in temporal stability of vulnerability (Figure 4c). The abundance- and richness-controlled H_2*'* were only marginally affected by CAD when the interaction effect was excluded from the model (Table 2, Appendix 2), thus the stability of H_2*'* decreased as CAD increased (Figure 4d). However, the stability in the abundance- and richness-controlled interaction evenness and generality were not affected by CAD, rainfall or their interaction (Table 2, Appendix 3). Since we were only able to compute the observed and abundance- and richness-controlled stability of *H_2'* for 11 interaction networks due to small network sizes, we repeated the analyses for the other specialization metrics using the same 11 networks. We found similar results to those found when using all sixteen plots (Appendix 2).

Discussion

We have shown that the increase in human disturbance and a decrease in rainfall do not affect the stability in the structure of interacting plant and ant communities in a consistent manner, but that they (especially CAD) reduce the temporal stability of the structure of EFN-bearing plant-ant mutualistic interaction networks in Caatinga vegetation. Emer and collaborators (2013) showed that changes in the structure of interacting plant and animal communities are important for interaction network structure. Previous studies reported relevant negative effects of land-use changes, on temporal stability of plant and animal communities (Yang et al. 2012, Blüthgen et al. 2016). Meanwhile, climate variation has been highlighted as an important factor shaping plant and animal communities across spatial and temporal scales (Zelicova et al. 2014, Diamond et al. 2016). In general, it is widely accepted that environmental conditions in wetter areas are more favorable for community stability than in drier areas (Diamond et al. 2016), which is also believed to be the case for seasonally dry tropical forests (Allen et al. 2017). However, recent studies have proposed that plant and ant communities appear to be stable temporally even under climate change scenarios (Zelicova et al. 2014, Donoso 2017). In support of this, we found disturbance effects on the temporal stability in the diversity of interacting plant communities only, and no effects on the stability in the structure of interacting ant communities or the composition of interacting plant and ant communities. In addition, both interacting EFN-bearing plant and attendant-ant communities were similarly stable along rainfall gradients. We thus demonstrate that despite the stability of community structure of interacting organisms is similar, there are large changes in the stability of the structure of their interactions along the environmental gradients. This is manifested by the consistent negative effects that increasing CAD impose on the stability of network specialization at the ant (generality), plant (vulnerability) and overall network (H_2') levels. Furthermore, variation in rainfall levels affect differently the components of the stability of network specialization: a decrease in rainfall related to a reduction in the stability of the specialization at the plant level (stability of vulnerability) but an increase in the stability of specialization at the ant level (stability of generality).

Interestingly, these changes in the temporal stability of interacting EFN-bearing plant communities and their interactions appear to be mostly driven by changes in ant behavior rather than by changes in the structure of interacting communities across the environmental gradients. First, changes in the stability of interaction networks almost parallels changes in the stability in diversity of interacting plants. However, our EFN-bearing plant communities are mostly composed of long-lived shrubs and trees. Although previous studies have reported changes in the structure of woody plant communities at different levels (taxonomic, functional and phylogenetic) along gradients of CAD in the Caatinga (Ribeiro et al. 2015, 2016, *in press*; Ribeiro-Neto et al. 2016, Rito et al. 2017), these changes were measured along spatial gradients where disturbed areas were subjected to long periods of disturbance (> 50 years) rather than short periods. It is thus difficult to envision strong effects of CAD on plant communities in two years. And second, we found effects of CAD on the stability of abundance- and richness-controlled interaction network metrics, particularly on the stability of abundance- and richness-controlled vulnerability (*i.e.* specialization at the plant level) and H_2' (*i.e.* specialization at the overall network level), although only marginally significant effects for the latter. All these results taken together makes it plausible to think that changes in the stability of both the diversity of interacting EFN-bearing plants and interaction network structure along the CAD gradient are driven by temporal changes in ant behavior in response to different abiotic conditions between years. If ant species from the most disturbed areas behave more differently from year to year than species from the least disturbed areas (*i.e.* they interact more or less intensively with more or less plant species in different years), this implies that temporal changes in ant behavior determine temporal changes in network structure (*e.g.* generality, vulnerability). Alternatively, although temporal changes in ant composition are constant along the CAD gradient, they might also be relevant and might involve different changes in species identity (and consequently, behavior) at different ends of the gradient, respectively.

Temporal changes in ant behavior might be explained either by temporal changes in abiotic conditions that regulate the availability of nectar, *i.e.* the basal resource that mediates these interactions, or by direct effects on ant activity. Vegetation in areas that are frequently disturbed might be in constant early-successional stages, and consequently, their habitat conditions will quickly change. As the secretory activity of EFNs are also induced by abiotic conditions (Bixenman et al. 2011, Lange et al. 2017), nectar production and quality in more disturbed areas might be more variable among years, thus greatly changing plant individual attractiveness to ants from year to year. In fact, these changes might be responsible for changes in the stability of the diversity of interacting plants, because ants might choose to interact more or less intensively with a plant depending on nectar quality and quantity. Similarly, nectar production and quality are largely affected by water availability (Lange et al. 2013, Dáttilo et al 2015). If the driest areas are unstable environments that experience a great variation in water availability for plants from year to year, this probably will affect the temporal secretory activity of EFNs, and might explain larger inter-annual variations in the ants interacting with a particular plant species (*i.e.* vulnerability) in most arid areas. Also, Fitzpatrick and collaborators (2014) showed that physical conditions such as temperature on plants' surfaces might also determine temporal ant foraging patterns. If abiotic conditions on plants' surfaces change between years, which is more likely to occur in more unstable disturbed areas, this might lead to changes in ant foraging activity. Unfortunately, we do not have temperature and/or precipitation measurements for our plots during the collection of interaction data, but it is apparent that microclimatic instability is higher in most disturbed open areas (Chen et al. 1995; Laurance 2002).

In line with our second hypothesis, our results showed synergistic effects between CAD and rainfall on the temporal stability of observed network generality (*i.e.* the effective number of plant species visited by ant species or specialization at the ant level). Thus, CAD effects on stability were higher in wetter than in drier areas of the park, and rainfall variation only affected network stability in most disturbed areas. Puig-Gironés and collaborators (2017) reported rainfall effects on the post-fire recovery patterns of plant and bird populations in a Mediterranean region. They found plant and bird populations recovered more slowly in arid areas compared to wet environments. Similarly, Salvatierra and collaborators (2017) showed that drier deforested areas had slower plant recover than wetter deforested areas in the Caatinga. These studies thus suggest that communities that are constantly in early-successional stages will be more similar from year to year in the driest areas. Moreover, these studies were focused on acute disturbances (*i.e.* complete loss of forest biomass), whereas our study targeted chronic anthropogenic disturbance (constant removal of small fractions of forest biomass). If the post-disturbance recovery of vegetation is faster in wetter areas than in drier ones, wet areas are probably important sources of forest products and become increasingly used by local populations. Thus, wet areas might be subjected to a more continuous exploitation of forest resources over time than dry areas, which may make them more unstable.

Although two years might not seem long for a study of ecosystem stability, we provide several pieces of clear evidence that inter-annual changes in the structure of the interaction networks follow spatial patterns driven by variations in disturbance and rainfall levels. Our study highlights the fact that CAD keeps the system continually in the early stages of secondary succession, that is, the more unstable stages that are less resilient to future disturbances. Several studies have found that plant-animal interactions are altered by anthropogenic disturbance and climate change, compromising the quality of the provided services in disturbed areas (Kiers et al. 2010 and references therein). However, most studies focus on spatial patterns between disturbed and undisturbed habitats. Since biotic interactions are not static but highly dynamic over time, it is essential to consider how plant-animal interactions vary through time (Poisot et al. 2015) along environmental gradients. Our results showing inter-annual variation in EFN-bearing plant-ant networks along chronic anthropogenic disturbance and rainfall gradients complement our understanding about potential impacts of human activities and climate change on biodiversity, and especially on ecosystem functioning. Anthropogenic disturbance and decreasing rainfall are important drivers that might cause destabilization of EFN-bearing plant-ant interactions, compromising the quality of the anti-herbivore defense service. High inter-annual variation in the number and abundance of ant species visiting a particular plant species in disturbed habitats and in more arid areas might compromise the protection service, since ant species vary markedly in the quality of the defensive service they provide to their host plants (Del-Claro and Marquis 2015; Fagundes et al. 2017). It is thus essential to expand protected areas in the Caatinga for the maintenance of ecosystem functioning and stability. Since our results show that rainfall variations mediate anthropogenic disturbance effects by reducing the temporal stability of mutualistic interactions in wetter disturbed areas, conservation policies should give special priorities to wet areas.

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Table 1. Effects of chronic anthropogenic disturbance (CAD), mean annual rainfall and their interaction on the stability of EFN-bearing plant and ant communities, measured using abundance, richness, diversity and species composition dissimilarity between the years 2014 and 2016 in the Caatinga dry forest, Brazil (n = 16 networks). Significant values are in bold.

Source of Variation	**t**	***P***
Stability of EFN-bearing plant species abundance		
CAD	1.588	0.141
Rainfall	0.870	0.403
CAD*Rainfall	-1.751	0.108
Stability of EFN-bearing plant species richness		
CAD	1.648	0.099
Rainfall	1.176	1.205
CAD*Rainfall	-1.596	-1.535
Stability of EFN-bearing plant species diversity		
CAD	2.999	**0.012**
Rainfall	1.660	0.125
CAD*Rainfall	-3.360	**0.006**
Stability of EFN-bearing plant community composition		
CAD	0.751	0.467
Rainfall	-0.388	0.705
CAD*Rainfall	-0.594	0.563
Stability of attendant-ant abundance		
CAD	0.927	0.374
Rainfall	0.834	0.422

CAD*Rainfall	-1.199	0.256
Stability of attendant-ant species richness		
CAD	0.066	0.948
Rainfall	0.749	0.469
CAD*Rainfall	0.177	0.862
Stability of attendant-ant species diversity		
CAD	-0.884	0.396
Rainfall	-0.274	0.789
CAD*Rainfall	0.852	0.412
Stability of attendant-ant community composition		
CAD	-1.771	0.1020
Rainfall	-1.000	0.3369
CAD*Rainfall	1.870	0.0847

Table 2. Effect of chronic anthropogenic disturbance (CAD), mean annual rainfall and their interaction on stability of the observed interaction evenness, generality, vulnerability, H_2' and their abundance- and richness-controlled equivalents between the years 2014 and 2016 in the Caatinga dry forest, Brazil (n = 16 networks). Statistical outputs for independent factors and not their interaction were shown when the initial model failed to find significant interaction effects (for the statistical outputs for complete models, see Appendix 2). Significant values (p < 0.05) are in bold.

Source of Variation	**t**	***P***
Observed interaction evenness		
CAD	0.887	0.394
Rainfall	1.561	0.147
CAD*Rainfall	-0.987	0.345
Observed generality		
CAD	3.305	**0.006**
Rainfall	2.205	**0.048**
CAD*Rainfall	-3.717	**0.003**
Observed vulnerability		
CAD	-2.582	**0.023**
Rainfall	2.251	**0.042**
Observed index **H_2'**†		
CAD	1.299	0.235
Rainfall	0.735	0.486
CAD*Rainfall	-1.707	0.132
Controlled interaction evenness		
CAD	0.458	0.656
Rainfall	0.349	0.733

CAD*Rainfall	-0.656	0.526
Controlled generality		
CAD	1.241	0.238
Rainfall	0.847	0.414
CAD*Rainfall	-1.421	0.181
Controlled vulnerability		
CAD	-2.548	**0.024**
Rainfall	0.709	0.491
***Controlled index* H_2'[†]**		
CAD	-2.252	0.054
Rainfall	-0.892	0.398

[†] We analyzed the temporal stability of observed and controlled index H_2' only with 11 networks due to the impossibility of generating values from null modelling in five networks in 2016.

Figure legends

Figure 1. Representation of the study area at different scales: distribution of the sixteen 50 m × 20 m plots (circles) over rainfall and chronic anthropogenic disturbance (CAD) gradients in the Catimbau National Park (map with white outline) (A) and the localization of the Catimbau National Park (white star) in Brazil (dark grey) (B). The proportion of black within each circle represents the level of CAD with the higher proportion of black indicating more disturbance. The background black and white color scale depicts the mean annual rainfall gradient.

Figure 2. Quantitative EFN-bearing plant-ant networks surveyed during the years 2014 and 2016 across sixteen plots in the Caatinga forest, Brazil. Box width is proportional to the total number of interactions recorded per species, indicating the contribution of each species within the network. Width of links denotes interaction frequency. Upper boxes are represented by attendant-ant species, where black boxes are attendant-ant species that interacted in both years of survey while gray boxes represent attendant-ant species that interacted in only one year of the survey. Lower boxes represent EFN-bearing plant species, while black boxes represent plant species that interacted in both years of survey and white boxes represent plant species that interacted in only one year. The name of the species with the highest contribution to the total number of interactions per year is shown.

Figure 3. Contour plots showing the interaction effect between chronic anthropogenic disturbance (CAD) and rainfall variation on the stability of EFN-bearing plant diversity (a) and observed generality in EFN-bearing plant-ant networks (b) in the Caatinga dry forest, Brazil.

Figure 4. Effect of chronic anthropogenic disturbance (CAD) (a) and rainfall variation (b) on the temporal stability of observed network vulnerability, and the effect of chronic anthropogenic disturbance on the temporal stability of abundance- and richness-controlled network vulnerability (c) and index H_2' (d) in EFN-bearing plant-ant networks in the Caatinga dry forest, Brazil.

Figure 1.

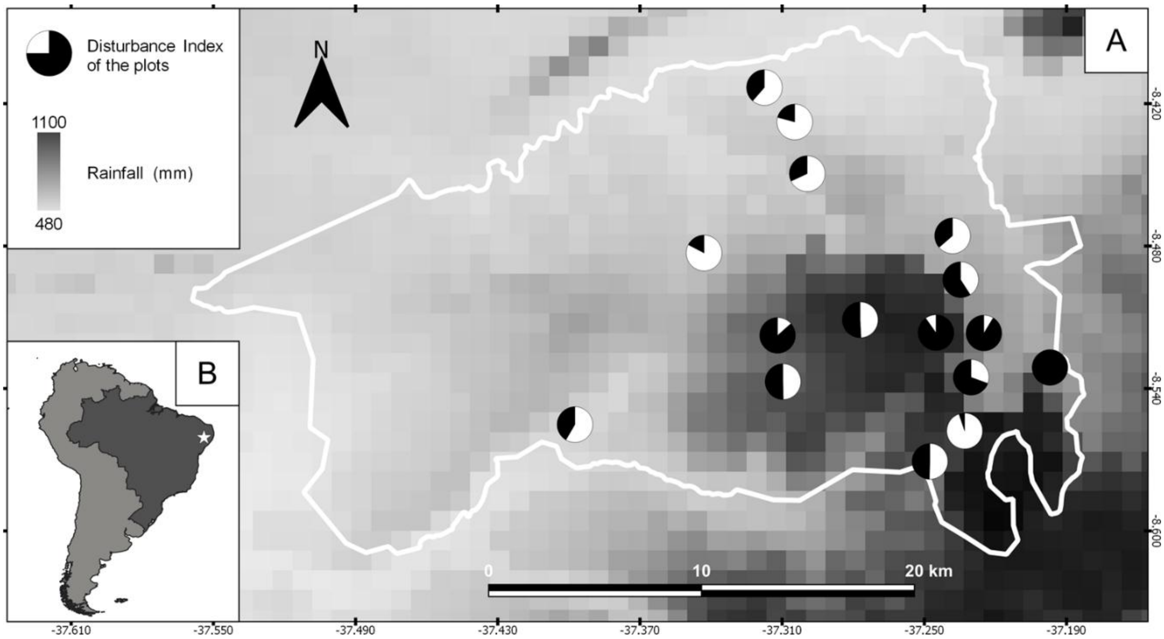
Disturbance Index
of the plots
1100
Rainfall (mm)
480
N
A
B
0
10
20 km
-8.420
-8.480
-8.540
-8.600
-37.610
-37.550
-37.490
-37.430
-37.370
-37.310
-37.250
-37.190

Figure 2.

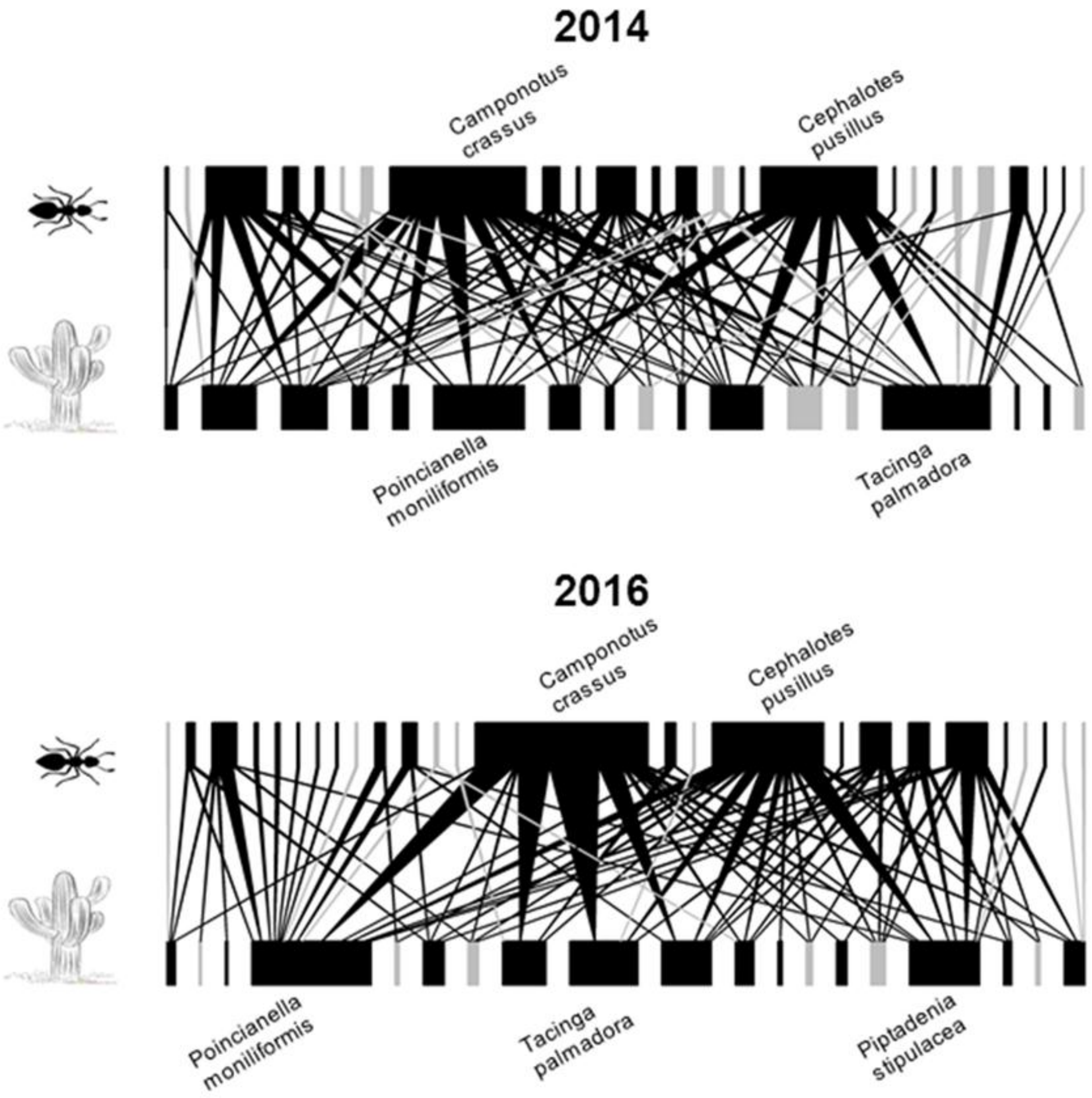
2014
Camponotus crassus
Cephalotes pusillus
Poincianella moniliformis
Tacinga palmadora
2016
Camponotus crassus
Cephalotes pusillus
Poincianella moniliformis
Tacinga palmadora
Piptadenia stipulacea

Figure 3**.**

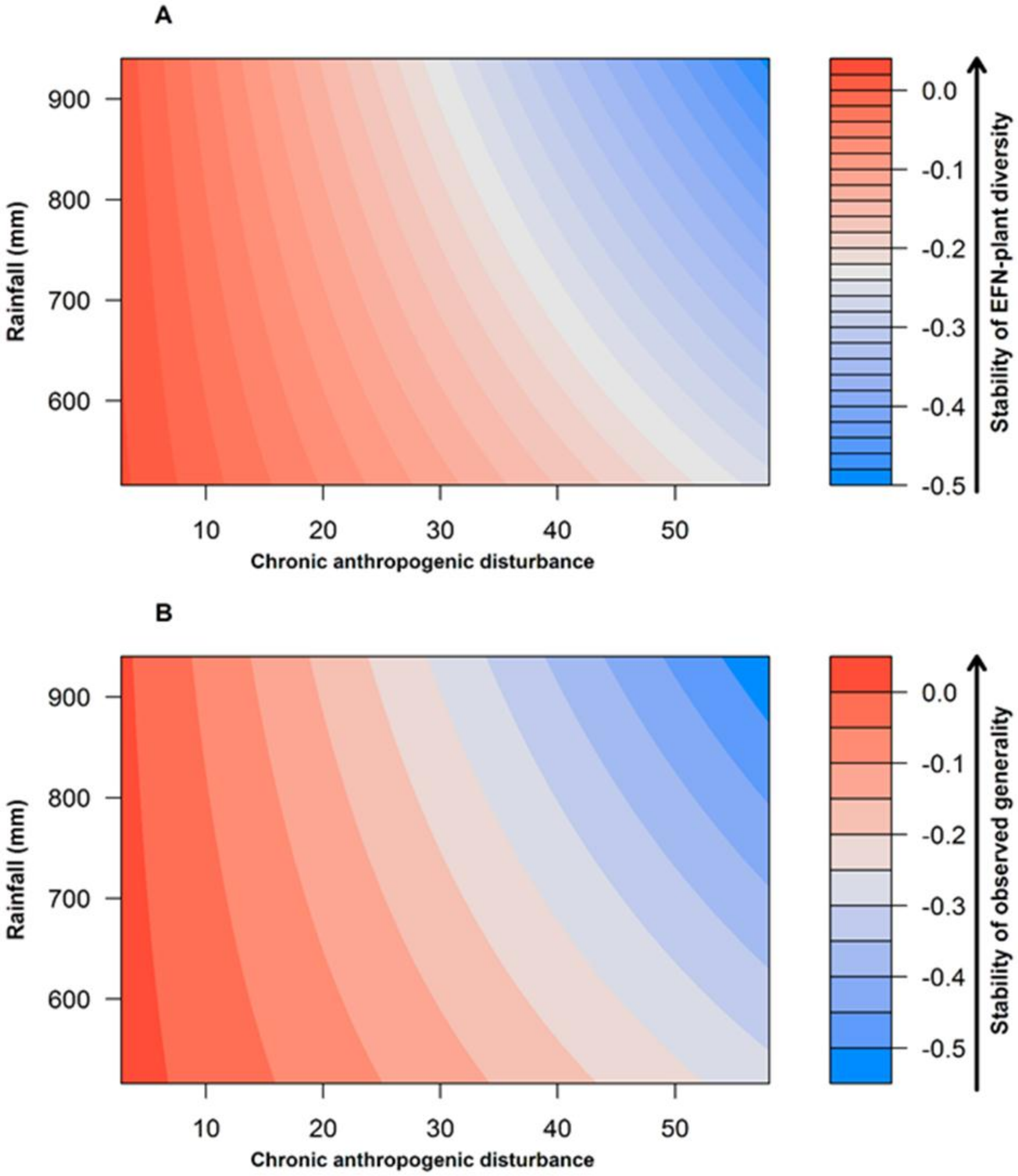
A
Rainfall (mm)
900
800
700
600
10
20
30
40
50
Chronic anthropogenic disturbance
0.0
-0.1
-0.2
-0.3
-0.4
-0.5
Stability of EFN-plant diversity
B
Rainfall (mm)
900
800
700
600
10
20
30
40
50
Chronic anthropogenic disturbance
0.0
-0.1
-0.2
-0.3
-0.4
-0.5
Stability of observed generality

Figure 4.

Supporting Information. Anthropogenic disturbance and rainfall variation threaten the stability of plant-ant interactions in the Brazilian Caatinga

Appendix 1. Measurements of the quantitative specialization network metrics.

To investigate the effects of chronic anthropogenic disturbance and rainfall on specialization of ant-plant mutualism, we used the following metrics:

A) **Interaction evenness**: it quantifies the equitability of the interaction frequency between ant species and EFN-plant species, as:

$$E_S = \frac{-\sum_i \sum_j p_{ij} ln p_{ij}}{lnL}$$

Where p_{ij} is the proportion of interactions in a cell between ant species *j* and EFN-plant species *i* ($p_{ij}= a_{ij}/\text{m}$) and *L* is the number of realized links in a network.

B) **Weighted generality**: we first calculated the Shannon diversity of interactions for ant species *j* and EFN-plant species *i*, respectively, as:

$$H_j = -\sum_{i=l}^{I} \left(\frac{a_{ij}}{A_j} . ln \frac{a_{ij}}{A_j}\right)$$

where a_{ij} is the number of interactions of ant species *j* visiting EFN-plant species *i*,and A_j is the sum of interaction of ant species *j* (Bersier *et al.* 2002, Blütghen *et al.* 2008). Weighted generality reflects the mean of the effective number of EFN-plants visited per ant species weighted by the interaction frequency of ant species, as:

$$G_{qw} = \sum_{j=1}^{J} \frac{A_j}{m} 2^{H_j}$$

where *Aj* is the sum of interactions of ant species *j* and *m* is the total number of interactions in the network..

C) **Weighted vulnerability** is analogous to the generality index, reflecting the mean of the effective number of ants per EFN-plant species weighted by the interaction of EFN-plant species. For quantifying this index, we just need to replace *j* for *i* and *J* by *I* in the Generality equation.

D) **Index H_2'**: it measures specialization based on the difference between realized and expected associations generated by null frequency distribution of the marginal totals (Blütghen *et al.* 2006). First, we calculated the Shannon diversity of the entire network:

$$H_2 = -\sum_{i=1}^{J} \sum_{j=1}^{I} (p_{ij} . \ln p_{ij})$$

Where p_{ij} is the proportion of interactions in a cell between ant species j and EFN-plant species i as showed above. Then, we calculated the standardized network specialization index:

$$H_2' = \frac{H_{2\,max} - H_2}{H_{2\,max} - H_{2\,min}}$$

Appendix 2. Summary of the general linear models accounting for the effects of chronic anthropogenic disturbance (CAD), annual mean rainfall and their interaction on temporal stability in the observed interaction evenness, generality, vulnerability, index H_2' and the 'abundance- and richness-controlled' temporal stability of interaction evenness, generality, vulnerability and index H_2' among the years 2014 and 2016 in Caatinga dry forest, Brazil. Statistical models were performed with 16 and 11 plots to show that the results are consistent as regards the number of plots. The statistical outputs conducted with 16 plots are similar to those in Table 2, but only results from completed models are here shown. Significant values are in bold.

Source of Variation	**Statistical models (n = 16 plots)**		**Statistical models (n = 11 plots)**	
	t	***P***	**t**	***P***
Observed interaction evenness				
CAD	0.887	0.3939	0.163	0.147
Rainfall	1.561	0.1469	0.959	0.369
CAD*Rainfall	-0.987	0.3448	-1.975	0.089
Observed generality				
CAD	3.305	**0.006**	2.400	**0.047**
Rainfall	2.205	**0.048**	1.291	0.238
CAD*Rainfall	-3.717	**0.003**	-2.824	**0.026**
Observed vulnerability				
CAD	-1.733	0.109	-1.271	0.244
Rainfall	0.400	0.696	-0.080	0.939
CAD*Rainfall	1.259	0.232	0.906	0.395
Observed index H_2'				
CAD			1.299	0.235
Rainfall			0.735	0.486
CAD*Rainfall			-1.707	0.132
Controlled interaction evenness				
CAD	0.458	0.656	0.388	0.710
Rainfall	0.349	0.733	0.169	0.870
CAD*Rainfall	-0.656	0.526	-0.595	0.571
Controlled generality				

CAD	1.241	0.238	0.348	0.738
Rainfall	0.847	0.414	0.459	0.660
CAD*Rainfall	-1.421	0.181	-0.579	0.581
Controlled vulnerability				
CAD	-0.833	0.421	-1.271	0.244
Rainfall	0.118	0.908	-0.080	0.939
CAD*Rainfall	0.375	0.714	0.906	0.395
Controlled index H_2*’*				
CAD			0.701	0.506
Rainfall			0.256	0.805
CAD*Rainfall			-1.101	0.307

5 CONCLUSÃO

A discussão sobre os efeitos das atividades humanas e mudanças climáticas nas interações mutualistas tem sido recorrente na literatura, porém pouco se conhece sobre os efeitos sinérgicos entre estas duas principais fontes de perturbações. Acredita-se que as mudanças climáticas podem potencializar os efeitos das perturbações antrópicas, aumentando a ruptura das interações mutualistas, afetando nos serviços e na estabilidade ecológica. Nesta tese, nós buscamos conhecer os efeitos das perturbações antrópicas crônicas, precipitação e seus efeitos sinérgicos nas variações espaço-temporal das interações entre plantas com nectários extraflorais e formigas. Acreditamos que os resultados apresentados nesta tese são pontos iniciais para prever osserviços e a estabilidade ecológica em um mosaico de áreas com diferentes graus de perturbação na Caatinga diante de um cenário de mudanças climáticas previsto para o final do século XXI.

No primeiro capítulo, demostramos que as perturbações antrópicas crônicas estão provavelmente afetando a qualidade dos serviços e gerando mosaico de diferentes forças seletivas, provavelmente interferindo no processo de coevolução entre plantas com NEFs. Enquanto a pressão de pastagem (criação de caprinos e gados) favorece uma maior especialização, a pressão de pessoas (coleta de produtos não madeireiros) ocasiona uma generalizaçãodestas interações. A extração de lenha, por sua vez, foi a única que não implicou em nenhum efeito nas interações entre plantas com NEFs e formigas. Além disso, mostramos também a propensão da generalização destas interações com a redução da precipitação. No entanto, o mecanismo por trás destas mudanças mostrou-se não ser pela substituição de espécies especialistas e generalistas, mas pela mudança no comportamento das espécies ao longo dos gradientes. Já no segundo capítulo, mostramos que o aumento das perturbações crônicas está ocasionando uma menor estabilidade temporal das interações entre plantas com NEFs e formigas. A diminuição da precipitação, por sua vez, pode ocasionar uma menor estabilidade das interações, mas em áreas mais perturbadas seus efeitos são menores do que em áreas úmidas. Mostramos neste capítulo também que a estabilidade temporal destas interações provavelmente está sendo ocasionada pela mudança na atividade de forrageamento das formigas do que pela variação interanual das estruturas das comunidades das plantas e formigas que estão interagindo.

De um modo geral, nossos resultados mostram que as interações mutualistas facultativas entre plantas com NEFs e formigas são afetados tanto espacialmente quanto temporalmente pelas perturbações antrópicas crônicas e pela precipitação.De acordo com a literatura, muitas destas variações ocorrem pela mudanças espaço-temporal das identidades dos parceiros mutualistas. Nossos resultados apontam um outro mecanismo: a mudança no comportamento dos parceiros mutualistas. Sugerimos dois mecanismos não mutuamente exclusivos para estas mudanças no comportamento das formigas associadas às plantas com NEFs: (1) variações na quantidade e na qualidade do néctar produzida pelas plantas hospedeiras ao longo do espaço e no tempo e (2) restrições fisiológicas das formigas à determinadas condições abióticas. Seja qual for o mecanismo responsável pela mudança das interações mutualistas, as diferentes fontes de perturbação provocadas pelas atividades humanas na Caatinga estão provocando uma variação nos resultados das interações, comprometendo a estabilidade destas interações. Já a redução da precipitação esperada para Caatinga até o final deste século provavelmente levará uma maior generalização destas interações, também diminuindo sua estabilidade. Ao considerar os efeitos sinérgicos das perturbações crônicas e precipitação, áreas perturbadas e mais úmidas são as que mais se encontram ameaçadas.

Por fim, para uma melhor compreensão de como mutualismo são afetados pelas perturbações antrópica e mudanças climáticas nas interações mutualísticas, é importante considerar diferentes tipos de mutualismos levando em consideração sua obrigatoriedade e especificidade. Mutualismos são variareis quanto ao grau de dependência entre os parceiros mutualistas, podendo ser extremamente especialista, onde os parceiros não sobrevivem sem a presença do outro, até mais generalistas.Quando consideramos estas diferenças nos tipos de mutualismos em um contexto de perturbações e mudanças climáticas, provavelmente estas interações podem responder de formar diferentes através de diferentes mecanismos. E identificar estes mecanismos podem auxiliar a criar estratégias para a manutenção destas interações bióticas que estão sendo perdidas nestas paisagens submetidas a diferentes ações humanas.

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