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INTERAÇÕES ENTRE PLANTAS E INSETOS HERBÍVOROS AO LONGO DE GRADIENTES DE PRECIPITAÇÃO E PERTURBAÇÃO ANTRÓPICA CRÔNICA

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

Orientador: Dr. Bráulio Almeida Santos

Coorientador: Dr. Jean Carlos Santos

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Mudam-se os tempos, mudam-se as vontades,
Muda-se o ser, muda-se a confiança:
Todo o mundo é composto de mudança,
Tomando sempre novas qualidades.

Continuamente vemos novidades,
Diferentes em tudo da esperança:
Do mal ficam as mágoas na lembrança,
E do bem (se algum houve) as saudades.

O tempo cobre o chão de verde manto,
Que já coberto foi de neve fria,
E em mim converte em choro o doce canto.

E afora este mudar-se cada dia,
Outra mudança faz de mor espanto,
Que não se muda já como soía.
(CAMÕES, 1595)

Se a educação sozinha, não transforma a sociedade, sem ela tampouco a sociedade muda.
(FREIRE, 2000)

RESUMO

A herbivoria por insetos é responsável pela maior parte da remoção de biomassa vegetal em florestas tropicais. No entanto, pouco se sabe sobre como as mudanças ambientais causadas pelo homem podem afetar a interação, sobretudo em florestas sazonalmente secas perturbadas cronicamente e sujeitas à alta vulnerabilidade climática, como a Caatinga. Seguindo a Hipótese da Disponibilidade de Recursos proposta por Coley e colaboradores, que prediz que plantas submetidas à alta disponibilidade de recursos (e.g. água no solo) apresentam maiores taxas de herbivoria, avaliamos se a redução na precipitação e o aumento nas perturbações antrópicas crônicas aumentam os níveis de herbivoria em comunidades de plantas herbáceas e lenhosas no Parque Nacional do Catimbau, PE. Adicionalmente, avaliamos os efeitos subjacentes de características intrínsecas das plantas – como área foliar específica (AFE) e presença de nectários extraflorais (NEFs) – e da estrutura da comunidade – abundância, riqueza e identidade das plantas. Monitoramos a frequência, a magnitude e os tipos de dano foliar das principais guildas tróficas de insetos herbívoros exógenos (mastigadores, raspadores e furadores) e endógenos (minadores e galhadores). Plantas herbáceas e lenhosas apresentaram um terço de folhas intactas. No estrato herbáceo, o dano médio acumulado foi de 4,4% de tecido foliar removido (em 21 dias), enquanto no estrato lenhoso foi 10,2% (em 121 dias). Em ambos os estratos da vegetação, os insetos mastigadores foram os herbívoros mais frequentes e com maior taxa de remoção de tecido foliar. Plantas herbáceas e lenhosas apresentaram padrões de herbivoria semelhantes, os quais aumentaram em função da aridez, opondo-se ao esperado. Contudo, perturbações crônicas não apresentaram nenhum efeito sobre os padrões de herbivoria. Além disso, o dano foliar não variou em função da AFE, da presença de NEFs, da densidade e riqueza de plantas, e foi fracamente relacionado à composição taxonômica das plantas. Os resultados não apoiam a Hipótese da Disponibilidade de Recursos e indicam um baixo controle ascendente (*bottom-up*) da herbivoria na Caatinga. Evidências recentes mostram que a aridez favorece a proliferação de insetos mastigadores na região estudada. Em virtude disso, sugerimos que o aumento da herbivoria nas áreas mais secas seja causado pelo enfraquecimento dos controles descendentes (*top-down*) da herbivoria, tais como a redução da predação e parasitismo sobre os herbívoros. Se as estiagens na Caatinga se tornarem mais severas e prolongadas, como previsto pelo Painel Brasileiro de Mudanças Climáticas, as interações inseto-planta podem ser alteradas permanentemente, culminando no aumento substancial da herbivoria em comunidades de plantas herbáceas e lenhosas.

Palavras-Chave: Aridez. Caatinga. Mudanças Climáticas. Gradientes Ambientais. Precipitação. Perturbação Crônica.

ABSTRACT

Insect herbivory is responsible for most plant biomass removal in tropical forests. Following the Resource Availability Hypothesis proposed by Coley and collaborators, which predicts that plants subjected to high resource availability (e.g. water in the soil) have higher herbivory rates because they have greater ability to compensate for leaf damage, we assessed whether the reduction in rainfall and the increase in chronic anthropogenic disturbances reduce herbivory levels in herb and woody plant communities at Parque Nacional do Catimbau, PE. Additionally, we evaluated the underlying effects of foliar traits - as specific leaf area (SLA), presence of extrafloral nectários (ENFs) - and community structure – plant density, richness and plant identity. We monitor the frequency, magnitude and types of foliar damage of the main trophic guilds of exogenous herbivorous insects (chewers, scrapers and drillers) and endogenous insects (miners and gallows). Herbs and woody plants showed one third of intact leaves. In the herb stratum, the daily foliar damage was 4.4% along 21 days, while in the woody stratum it was 10.2% along 121 days. In both vegetation strata, chewing insect was the most frequent trophic guild showing the highest rate of foliar tissue removal. In Caatinga, different plant life-forms present similar herbivory patterns, which increase as a function of aridity, opposing what was expected. However, chronic anthropogenic disturbances had no effect on herbivory patterns. In addition, leaf damage did not vary due to SLA, presence of NEFs, plant density and richness, and was poorly related to the taxonomic composition of the plants. The results do not support the Resource Availability Hypothesis and indicate a low bottom-up herbivory control in Caatinga. Recent evidence shows that aridity favors the proliferation of chewing insects in the region studied. Because of this, we suggest that the increase in herbivory in the drier areas is caused by the weakening of the top-down herbivory controls, such as reduced predation and parasitism on herbivores. If droughts in the Caatinga become more severe and prolonged as predicted by the Brazilian Panel on Climate Change, insect-plant interactions may be permanently altered, culminating in a substantial increase in herbivory in herbaceous and woody plant communities.

Keywords: Aridity. Caatinga. Climate Change. Environment Gradients. Rainfall. Chronic Disturbance.

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INTRODUÇÃO

A herbivoria por insetos é uma das interações ecológicas mais importantes dos ecossistemas, uma vez que os insetos são responsáveis pela maior parte da remoção de biomassa vegetal em florestas tropicais (COLEY; BARONE, 1996). Esse grupo apresenta grande diversidade nas formas de utilização das plantas (SCHOWALTER, 2006). Embora sejam altamente diversas, as interações inseto-planta são mediadas por mecanismos de controle das plantas hospedeiras e dos inimigos naturais, os quais influenciam a distribuição e o comportamento alimentar dos insetos herbívoros (HUNTER et al., 1992). Nesse sentido, tanto as plantas afetam as comunidades de herbívoros, por meio de defesas intrínsecas, como os inimigos naturais (como predadores, parasitas e parasitoides) controlam as populações de insetos herbívoros. Contudo, os mecanismos que medeiam às interações inseto-planta podem sofrer graves alterações em virtude das mudanças climáticas e de modificações nas paisagens naturais, geradas pelas perturbações antrópicas, com consequências nos diferentes níveis de organização biológica, o que pode comprometer o equilíbrio de interações multitróficas, o fluxo de energia no sistema, as cadeias alimentares e a ciclagem de nutrientes.

Para que as interações inseto-planta ocorram é necessário que as condições do ambiente sejam adequadas para o estabelecimento de plantas hospedeiras e dos insetos herbívoros (COLEY; BRYANT; CHAPIN III, 1985). O aumento da aridez e das perturbações antrópicas crônicas e agudas (LEAL; ANDERSEN; LEAL, 2015) configuram um filtro importante no estabelecimento de interações biológicas. Estima-se que as mudanças climáticas serão mais severas nas regiões áridas e semiáridas do planeta (FENG; PORPORATO; RODRIGUEZ-ITURBE, 2013; MAGRIN et al., 2014; SALAZAR; NOBRE; OYAMA, 2007), como a Caatinga. Para esse ecossistema, as previsões são de reduções de até 50% no volume médio anual de chuvas e aumento de até 4,5º C na temperatura média até 2100 (PBMC, 2016). Além disso, essa floresta tropical sazonalmente seca (sensu PENNINGTON; LAVIN; OLIVEIRA, 2009) contém um dos maiores contingentes de populações humana em florestas tropicais secas, grande parte dependente de recursos naturais (BANDA-R et al., 2016). Assim, as formas de subsistência somadas ao manejo da terra configuram cenários de perturbações antrópicas crônicas (SINGH, 1998) a partir da remoção contínua de pequenas quantidades de biomassa florestal (ARNAN; LEAL; et al., 2018; SINGH, 1998).

Embora os efeitos do aumento da aridez e das perturbações antrópicas crônicas sejam aparentemente gradativos, estes podem afetar a diversidade em diferentes grupos e níveis de organização biológica. Os efeitos isolados ou sinérgicos desses eventos são refletidos nas interações inseto-planta, principalmente, através da disponibilidade de recursos (i.e.: água, tecido vegetal) e propiciam alterações em características funcionais das plantas (GROSSIORD et al., 2017; PEARSE; HIPP, 2012), assim como na estrutura de comunidades vegetais (GROSSIORD et al., 2017; RIBEIRO-NETO et al., 2016; RITO; TABARELLI; LEAL, 2017), de insetos herbívoros e de seus inimigos naturais (AYRES; LOMBARDERO, 2000; RODRÍGUEZ-CASTAÑEDA, 2013; TERBORGH et al., 2001; ALMEIDA et al., 2008). Embora haja evidências de que as reduções na precipitação e o aumento das perturbações antrópicas alteram os grupos biológicos supracitados, ainda se sabe pouco sobre seus efeitos nos padrões de interação em grupos de plantas com diferentes formas de vida.

Plantas herbáceas e lenhosas são diferentes não apenas em termos de tamanho, crescimento secundário ou longevidade (EWEL; BIGELOW, 1996), mas também em relação as suas contribuições ecológicas. O componente lenhoso das comunidades biológicas consiste no principal meio para sequestro e estocagem de carbono (NIKLAS, 1997). Enquanto o estrato herbáceo apresenta grande parte da área foliar disponível (EWEL; BIGELOW, 1996) e contém alta diversidade de espécies, principalmente em ambientes restritivos, como as florestas tropicais secas (MORO et al. 2015). Assim, as formas de vida englobam diferentes estratégias adaptativas frente às condições adversas do meio (INGROUILLE; EDDIE, 2006), como aridez (MORO et al. 2015) e perturbações (DENSLOW, 1996). Comunidades de plantas herbáceas, por exemplo, apresentam altas taxas de substituição de espécies e adaptações evolutivas em comparação às plantas lenhosas em ambientes com restrição de recursos (SMITH; DONOGHUE, 2008).

Sabendo que plantas de diferentes formas de vida respondem de formas distintas à disponibilidade de recursos e à qualidade do meio, objetivamos investigar como a redução da precipitação e o aumento das perturbações antrópicas crônicas medeiam a herbivoria em comunidades de plantas herbáceas e lenhosas em uma floresta tropical seca. Assim, no primeiro capítulo (*Rainfall reduction increases insect herbivory in tropical herb communities*), investigamos os padrões de herbivoria em comunidades de plantas herbáceas distribuídas ao longo de um gradiente de precipitação. No segundo capítulo (*Rainfall shortage increases insect herbivory on woody plants of the Brazilian Caatinga*), avaliamos os padrões de herbivoria em comunidades de plantas lenhosas distribuídas ao longo de um gradiente de precipitação e outro de perturbação humana crônica.

FUNDAMENTAÇÃO TEÓRICA

ASPECTOS GERAIS DAS INTERAÇÕES ENTRE INSETOS HERBÍVOROS E PLANTAS HOSPEDEIRAS

Embora a maior parte dos debates em ecologia e conservação seja centrada no componente taxonômico da biodiversidade, a extinção das interações precede ou acompanha a perda de espécies, funções e serviços ecossistêmicos (VALIENTE-BANUET et al., 2016). Interações são intrínsecas aos indivíduos, permeiam todos os níveis de organização biológica (SCHOWALTER, 2006) e apresentam papel fundamental na origem, manutenção e funcionamento da biodiversidade em ecossistemas terrestres e aquáticos (ANDERSEN; ARROYO-RODRÍGUEZ; ESCOBAR, 2018). Assim, entender como as espécies se relacionam no espaço e no tempo é uma questão chave para a conservação das interações, principalmente em cenários de mudanças climáticas e alterações antrópicas nas paisagens naturais.

Dentre os diversos tipos de interações, aquelas protagonizadas por consumidores e recursos merecem destaque, uma vez que afetam a distribuição espacial das espécies, organizam as comunidades em redes ou cadeias alimentares e promovem o fluxo de energia e a ciclagem de nutrientes ao longo dos sistemas biológicos (CHAPIN; MATSON; MOONEY, 2002). Assim, os consumidores primários, tais como os insetos herbívoros, podem se beneficiar individualmente da extração de recursos, aumentando seu desempenho e, consequentemente, o tamanho de suas populações (MORIN, 2011) e exercendo grande pressão sobre suas plantas hospedeiras. Este grupo opera na estruturação das comunidades vegetais, influenciando o sucesso reprodutivo (LEHTILÄ; STRAUSS, 1999) e o estabelecimento (CONNELL, 1971; JANZEN, 1970) das plantas hospedeiras no espaço e no tempo. Por outro lado, as plantas afetam as comunidades de herbívoros por meio de uma série de mecanismos ascendentes de defesa, influenciando assim a distribuição e o comportamento alimentar dos herbívoros (HUNTER et al., 1992).

Da grande amplitude de herbívoros, os insetos merecem especial atenção, uma vez que são responsáveis pela maior parte da remoção de biomassa vegetal em florestas tropicais (COLEY; BARONE, 1996). Insetos herbívoros podem ser categorizados de acordo com o tipo de recurso vegetal que exploram, como: 1) folívoros, os quais se alimentam de folhas; 2) radicívoros, de raízes; 3) brocadores, do caule e sementes (ver GULLAN; CRANSTON, 2012); 4) florívoros, de botões florais, flores ou de suas partes (sépalas, pétalas, estigma ou estames); 5) frugívoros, de frutos em desenvolvimento ou maduros; 6) granívoros, de sementes; 7) polínívoros, pólen e, por fim, 8) nectarívoros, os quais se alimentam de néctar (DEL-CLARO, 2012).

Os insetos herbívoros podem ser classificados não apenas em relação ao tipo de recurso que exploram, mas se o uso do recurso ocorre externa (insetos de vida livre) ou internamente (insetos endógenos) aos tecidos vegetais (SINCLAIR; HUGHES, 2010). Tais formas de vida, muitas vezes, estão relacionadas à fase de desenvolvimento. Insetos galhadores, por exemplo, apresentam fase endógena (fase de ovo até pupa) e de vida livre (fase adulta) (FERNANDES; SANTOS, 2014). Em adição, insetos herbívoros apresentam diferentes níveis de especificidade em relação aos recursos. Tal especificidade é fruto de processos coevolutivos e consistem na capacidade de os insetos herbívoros sobrepujarem as defesas vegetais, ao passo que quanto mais específica, mais restrita é a relação de uso dos recursos (COLEY, 1987; ENDARA et al., 2017). Nesse sentido, insetos herbívoros considerados especialistas apresentam uma estreita amplitude de nicho e dependem de poucas espécies hospedeiras, geralmente muito próximas taxonômica e filogeneticamente (ALI; AGRAWAL, 2012). Contrariamente, os insetos considerados generalistas apresentam maior amplitude de nicho e exploram espécies pouco aparentadas ou até quimicamente distintas (FEENY, 1976; FORKNER; MARQUIS; LILL, 2004). Assim, como exemplo, insetos herbívoros endógenos como galhadores, são considerados altamente especializados na exploração dos recursos, sendo consideradas indicadoras de táxons de plantas (FERNANDES; SANTOS, 2014).

A categorização dos insetos herbívoros pode ser ainda mais refinada, abrangendo aspectos funcionais, independente do tipo de recurso explorado, forma de vida ou das relações espécie-específicas. Diferentes guildas de insetos herbívoros, ainda que utilizando as mesmas plantas hospedeiras em uma comunidade local, podem apresentar diferenças significativas na repartição do uso dos recursos (NOVOTNY et al., 2010). Tal especialização alimentar foi potencialmente ocasionada por relações de competição, o que propiciou a coexistência de diferentes consumidores, não apenas morfofisiologicamente (SCHOWALTER, 2006), mas também funcionalmente distintos. Nesse sentido, a classificação proposta por NOVOTNY et al., (2010) considera as principais guildas de alimentação de insetos herbívoros, como mastigadores – jovens e adultos com alimentação interna e externa, respectivamente – de folhas, frutos, raízes, fungos, xilema e floema; sugadores de folhas, xilema e floema (alimentação interna) e minadores de folhas – alimentação interna ao mesolfilo na fase jovem. Adicionalmente, os tipos de dano observados nos tecidos vegetais, especificamente nas folhas, podem ser um indicador do tipo de guilda presente na comunidade. Nesse sentido, LORANGER et al. (2014) classificaram quatro guildas tróficas, de acordo com os tipos de danos foliares, sendo mastigadores; sugadores; raspadores e minadores, embora não tenham classificado os herbívoros indutores de galhas.

Independente das guildas tróficas, a herbivoria confere inúmeros prejuízos às plantas hospedeiras ao promoverem injúrias nos tecidos vegetais fotossintetizantes, mesmo não as removendo das populações hospedeiras (SCHMITZ, 2008; ZANGERL et al., 2002). A intensidade dessas interações, no entanto, pode ser controlada por fatores intrínsecos às comunidades de plantas e insetos, como mecanismos ascendentes (através de defesas vegetais) e descendentes (por meio de predadores patógenos dos herbívoros). Além disso, fatores regionais (temperatura, precipitação anual) e locais (perturbação natural e antrópica) também podem exercer efeitos sobre a estrutura da comunidade de plantas e de inimigos naturais dos insetos herbívoros. Tanto os fatores intrínsecos às comunidades de plantas e insetos, como os fatores regionais e locais serão detalhados nas próximas seções.

MECANISMOS REGULADORES DAS INTERAÇÕES ENTRE INSETOS HERBÍVOROS E SUAS PLANTAS HOSPEDEIRAS

Plantas podem “escapar” da ação de seus inimigos naturais, reduzindo a capacidade dos herbívoros de encontrá-las (CONNELL, 1971; JANZEN, 1970). A dessincronização da fenologia de populações vegetais ou de múltiplas espécies permite o escape temporal (MURALI; SUKUMAR, 1993). Para a região tropical úmida, por exemplo, o principal período de vulnerabilidade de folhas ocorre durante a janela de expansão foliar (COLEY; BARONE, 1996). Nessa fase, os tecidos são bem defendidos, mas os grupos de herbívoros especialistas apresentam a capacidade de sobrepujar tais defesas (AIDE, 1993; QUINTERO; BOWERS, 2018). Assim, a produção tardia ou antecipada de tecidos vulneráveis pode resultar na redução do ataque de herbívoros (AIDE, 1992; MURALI; SUKUMAR, 1993).

As variações no meio abiótico podem ser refletidas nas interações entre insetos e plantas através da disponibilidade de recursos. Condições e recursos ambientais, como a temperatura, a disponibilidade hídrica, e fertilidade do solo têm efeitos na riqueza, desenvolvimento e susceptibilidade das plantas aos herbívoros (GARIBALDI; KITZBERGER; RUGGIERO, 2011). Assim, os recursos consistem em um fator limitante ao balanço nutricional, crescimento e diferenciação de plantas hospedeiras e, assim, intensificam as demandas conflitantes entre crescimento/reprodução e a produção de defesas contra a herbivoria (COLEY; BRYANT; CHAPIN III, 1985; ENDARA; COLEY, 2011; STAMP, 2003). COLEY et al., (1985) predizem que à medida que ocorre redução na taxa de crescimento máximo (com disponibilidade ideal de recursos), o nível de defesas aumenta entre as espécies vegetais. Assim, a taxa de crescimento líquido das plantas se dá pela a relação entre os custos de crescimento e defesa contra herbívoros. Em ambientes com restrição de recursos, como o sub-bosque de florestas tropicais chuvosas e locais com baixa precipitação em florestas secas, a tendência é de haver menor crescimento e maior proteção dos tecidos produzidos. Assim, através de um maior investimento em defesas, a herbivoria em espécies de crescimento tardio (características conservativas) é menor do que aquele suportado pelas espécies de crescimento inicial (características aquisitivas) (ENDARA; COLEY, 2011).

A hipótese de Coley et al. (1985) ainda pavimenta diversas discussões relacionadas às características das plantas, as quais tanto são respostas às condições do meio abiótico, como podem contribuir para defesas vegetais (CINGOLANI; POSSE; COLLANTES, 2005; ENDARA; COLEY, 2011). Essa discussão evoca a qualidade do meio ou a disponibilidade de recursos como indicador preponderante de características das plantas, as quais estão submetidas ao balanço entre crescimento e sobrevivência (STERCK; POORTER; SCHIEVING, 2006). Em ambientes com recursos abundantes, prosperam plantas com características aquisitivas, as quais produzem folhas baratas, com menor conteúdo de matéria seca por cm², ao passo que apresentam crescimento rápido, altas taxas fotossintéticas e de substituição tecido vegetal danificado, configurando assim baixa resistência (i.e. capacidade de evitar ser consumida) e alta tolerância à herbivoria – i.e.: capacidade de compensar o dano (CARMONA; LAJEUNESSE; JOHNSON, 2011; GROSSIORD et al., 2017; POORTER et al., 2009; WIGLEY et al., 2016). Em contraponto, nos ambientes com recursos limitados, prosperam plantas com características conservativas, as quais apresentam folhas onerosas, com maior conteúdo de massa seca por área e crescimento lento, configurando alta resistência ao ataque de herbívoros e baixa tolerância à herbivoria (CARMONA; LAJEUNESSE; JOHNSON, 2011; GROSSIORD et al., 2017; POORTER et al., 2009; WIGLEY et al., 2016). Dos atributos utilizados para categorizar as plantas em aquisitivas ou conservativas, destaca-se aqueles relacionados às folhas (e.g. pubescência, espessura e tenacidade foliar, conteúdo de massa seca e área foliar específica), uma vez que apresentam alta plasticidade fenotípica, sendo bons modelos para representar as demandas conflitantes entre crescimento e defesas. Além disso, esses atributos configuram uma importante barreira física que reduz o acesso dos herbívoros aos tecidos vegetais (CINGOLANI; POSSE; COLLANTES, 2005).

A maioria dos estudos de interações inseto-plantas foca nos mecanismos intrínsecos de defesa das plantas, como a qualidade dos tecidos e os compostos do metabolismo secundário. Contudo, é razoável considerar um terceiro nível trófico, os inimigos naturais dos herbívoros, como agentes controladores da herbivoria. Diversos grupos são “inimigos naturais” dos herbívoros e podem atuar como controladores da ação destes: aves, aranhas, formigas, lagartos, dentre outros (RODRÍGUEZ-CASTAÑEDA, 2013; TERBORGH et al., 2001). Embora os efeitos descendentes também interajam com os mecanismos ascendentes de controle da herbivoria (DENNO et al., 2013), são em grande parte direta ou indiretamente determinados por condições do meio (RODRÍGUEZ-CASTAÑEDA, 2013; TERBORGH et al., 2001). Nesse último caso, os inimigos naturais dos insetos herbívoros variam em abundância (BOMMARCO; BANKS, 2003), diversidade (CASTAGNEYROL; JACTEL, 2012) e efetividade no controle das populações (JACTEL et al., 2006) em função da riqueza de espécies hospedeiras. Dessa forma, comunidades de plantas hospedeiras mais ricas e diversas representam maior amplitude de dieta para os herbívoros generalistas, os quais são mais susceptíveis à predação, uma vez que os herbívoros são mais expostos aos seus inimigos naturais durante o forrageamento (CASTAGNEYROL et al., 2017; MOONEY; PRATT; SINGER, 2012).

Além das interações multitróficas entre plantas, herbívoros e seus inimigos naturais, outras relações podem evidenciadas com plantas que desenvolveram defesas biológicas contra herbívoros, como estruturas morfológicas que podem ser utilizadas como abrigo ou secretar recursos alimentares. Tais estruturas compreendem as domáceas, (IZZO; VASCONCELOS, 2002) e, principalmente, os nectários extraflorais (LANGE; DÁTTILO; DEL-CLARO, 2013; FREITAS, 2004). Nectários extraflorais, comumente encontrados na base do pecíolo, produzem substâncias ricas em açúcares, importantes como suprimento alimentar de muitas formigas. Nessas relações, a exploração do néctar extrafloral ocorre ao mesmo tempo em que as formigas protegem as plantas da incidência de outros herbívoros, conferindo uma defesa indireta ou biológica (NESS; MORRIS; BRONSTEIN, 2009).

A disponibilidade de recursos é um fator determinante para a ocorrência das interações multitróficas (SCHOWALTER, 2006) como as relações entre plantas, insetos herbívoros e formigas (DÁTTILO et al., 2015). A oferta de água e a qualidade do ambiente têm efeitos sobre a produção de néctar extrafloral em termos de quantidade e qualidade da secreção em comparação aos ambientes com condições mais severas (CHAVARRO-RODRÍGUEZ et al., 2013). Como evidenciado em comunidade de plantas do Cerrado (LANGE et al., 2013) e em florestas secas mexicanas (RICO-GRAY et al.1998), a produção do néctar extrafloral pode variar de acordo com a sazonalidade de ambientes, tendo efeitos também na comunidade de formigas visitantes e na efetividade da proteção contra herbívoros (LANGE et al. 2013; LEAL; ANDERSEN; LEAL, 2015). Assim, reduções na oferta de néctar ou a exclusão de formigas podem resultar na redução das defesas biológicas providas por esses grupos e, consequentemente, contribuir para o aumento do ataque por herbívoros (IZZO; VASCONCELOS, 2002).

EFEITOS DAS MUDANÇAS CLIMÁTICAS E PERTURBAÇÕES ANTRÓPICAS SOBRE AS INTERAÇÕES INSETO-PLANTA NA CAATINGA

Os mecanismos de controle da herbivoria citados acima são sensíveis à qualidade do meio e à disponibilidade de recursos. Condições ambientais extremas, proporcionadas pelas alterações climáticas (como o aumento da aridez) e pelas perturbações antrópicas crônica e aguda, por exemplo, configuram um filtro importante no estabelecimento de interações inseto-planta. Isso ocorre por meio de alterações em diversas características adaptativas das plantas (GROSSIORD et al., 2017; PEARSE; HIPP, 2012), assim como na estrutura das comunidades vegetais (GROSSIORD et al., 2017; RIBEIRO-NETO et al., 2016; RITO; TABARELLI; LEAL, 2017), de insetos herbívoros (RIBEIRO-NETO et al., 2016) e de seus inimigos naturais (AYRES; LOMBARDERO, 2000; RODRÍGUEZ-CASTAÑEDA, 2013; TERBORGH et al., 2001).

Estima-se que as mudanças climáticas serão mais severas nas regiões áridas e semiáridas do planeta (FENG; PORPORATO; RODRIGUEZ-ITURBE, 2013; MAGRIN et al., 2014; SALAZAR; NOBRE; OYAMA, 2007), como a Caatinga. Para esse ecossistema, as previsões são de reduções de até 50% no volume médio anual de chuvas e aumento de até 4,5º C na temperatura média até 2100 (PBMC, 2013). A Caatinga é ainda a floresta tropical sazonalmente seca (sensu PENNINGTON et al., 2009) com um dos maiores contingentes de populações humanas – aproximadamente 27 milhões de pessoas (GARIGLIO et al., 2010) – grande parte dependente de recursos naturais (BANDA-R et al., 2016). As formas de subsistência somadas ao manejo da terra configuram cenários de perturbações antrópicas crônicas (SINGH, 1998). Nesse sentido, a constante remoção de pequenas quantidades de biomassa florestal, via sobrepastoreio, corte seletivo de madeira e ciclos de corte e queima da vegetação nativa, causa alterações aparentemente imperceptíveis, porém severas no ecossistema (RIBEIRO et al., 2016, 2015, 2019). Embora os efeitos das perturbações antrópicas crônicas sejam aparentemente gradativos, podem afetar a diversidade biológica em diferentes níveis (LEAL et al., 2015; VILLARREAL-BARAJAS; MARTORELL, 2009), principalmente quando potencializados pela redução nos níveis de precipitação. A soma desses eventos configura um importante filtro no estabelecimento de interações inseto-planta (LEAL et al., 2015) e pode resultar em processos de desertificação em regiões semiáridas (SALAZAR; NOBRE; OYAMA, 2007).

A precipitação é um fator chave para a manutenção das interações biológicas (WU et al., 2011). De acordo com a hipótese de disponibilidade de recursos postulada por COLEY et al., (1985), o padrão de associação entre as características vegetais (e.g. atributos foliares) e o meio abiótico é, em grande parte, consistente com uma combinação de limitações de recursos e pode estar relacionado com diferentes pressões de herbivoria. Sabe-se que a disponibilidade de água medeia às interações inseto-planta (COLEY et al., 1985; HUBERTY; DENNO, 2004) e os efeitos da redução da precipitação podem reduzir diretamente a oferta de recursos aos insetos herbívoros (BARTON; BECKERMAN; SCHMITZ, 2009). De fato, a baixa disponibilidade hídrica no solo tem efeitos negativos na produtividade primária líquida através da redução nas taxas fotossintéticas e condutância estomática (GROSSIORD et al., 2017; LOUGHNAN; WILLIAMS, 2019). Como resultado, a redução na produção de biomassa (WU et al., 2011) limita os recursos disponíveis aos herbívoros.

Contudo, a redução no acesso e assimilação do conteúdo vegetal também precariza a disponibilidade de recursos aos herbívoros (ENDARA; COLEY, 2011). Nesse sentido, tal limitação ocorre através da redução na qualidade dos tecidos (palatabilidade), a qual varia em função da oferta de recursos hídricos (POORTER et al., 2009) e dos níveis de perturbação do meio (SFAIR et al., 2018). Alterações no estado de atributos foliares, como o aumento na densidade de tricomas, na dureza foliar, no conteúdo de massa seca e redução da área foliar específica, são respostas funcionais às adversidades do meio. No entanto, a combinação dos atributos nesse estado tem natureza conservativa e seus efeitos limitam o acesso dos insetos herbívoros aos tecidos vegetais (PEARSE; HIPP, 2012; POORTER et al., 2009). Em florestas secas, atributos nesse estado são relacionados a determinados grupos de plantas herbáceas heliófilas (VIEIRA et al., 2017) e plantas lenhosas como algumas espécies da família Euphorbiaceae (RIBEIRO et al., 2016) adaptadas às condições de aridez e aos altos níveis de perturbações antrópicas.

Os efeitos negativos da baixa disponibilidade hídrica e de altos níveis de perturbação crônica também podem ser evidenciados em componentes da estrutura de comunidades vegetais (RIBEIRO-NETO et al., 2016; RIBEIRO et al., 2016, 2019). Perdas na riqueza e aumento na abundância de espécies adaptadas às condições extremas do ambiente, como os grupos supracitados, podem ocasionar declínios nas diversidades taxonômicas (RITO et al., 2017) ou filogenéticas (RIBEIRO et al., 2016), culminando na homogeneização de comunidades de plantas (RIBEIRO-NETO et al., 2016). A perda na diversidade e alterações na composição das comunidades vegetais pode levar à perda de interações espécie-especificas e têm efeitos que atingem tanto os herbívoros, como seus predadores, em múltiplas escalas (RODRÍGUEZ-CASTAÑEDA, 2013; TERBORGH et al., 2001).

Embora em ambientes com forte limitação de recursos e alto nível de perturbação haja proliferação de plantas com atributos foliares conservativos (SFAIR et al., 2018), ainda assim, pode haver disfunções nas interações inseto-planta na perspectiva multitrófica (RODRÍGUEZ-CASTAÑEDA, 2013). A limitação dos inimigos naturais dos herbívoros (grupos de parasitas e parasitoides), os quais são sensíveis às condições extremas, pode reduzir a pressão de predação e o parasitismo em áreas mais secas (CONNAHS et al., 2011) e perturbadas (ALMEIDA; WIRTH; LEAL, 2008; TERBORGH et al., 2001), enfraquecendo o controle descendente das populações de insetos herbívoros. Somado a isso, ou em paralelo, da mesma forma que os ambientes secos e perturbados propiciam a proliferação de plantas adaptadas às condições mais severas, o mesmo ocorre com grupos de insetos herbívoros. A expressiva abundância e riqueza de insetos mastigadores são relacionadas à aridez e ao nível de perturbação antrópica em uma região de Caatinga (SANTOS-NETO et al., 2016). O mesmo ocorre com a densidade de ninhos de formigas do gênero *Atta* (Formicidae: Myrmicinae), as quais mantêm colônias vivas em regiões de menor cobertura vegetal (SIQUEIRA et al., 2018).

Além do enfraquecimento dos controles descendentes e da proliferação de insetos herbívoros, o estresse fisiológico sofrido pelas plantas expostas à menor disponibilidade de água e maior incidência de luz (JAMIELSON et al., 2012) também contribuem para a disfunção das interações inseto-planta. Sabe-se que o estresse hídrico evoca preferências alimentares entre distintos grupos de herbívoros (HUBERTY; DENNO, 2004;

NYKANEN; KORICHEVA, 2004), tais como formigas cortadeiras (RIBEIRO-NETO et al., 2012), ortópteras (BARTON; BECKERMAN; SCHMITZ, 2009) e insetos minadores (MAZÍA et al., 2012), os quais priorizam plantas submetidas a estresse hídrico. No entanto, ainda não são conhecidos os impactos provenientes da redução da precipitação e do aumento das perturbações antrópicas na Caatinga sobre os padrões e intensidade das interações entre plantas e insetos herbívoros, os quais ainda são controversos (SIQUEIRA et al., 2018).

Por fim, também já foi relatado que as mudanças na composição de espécies de formigas (e das defesas biológicas mediadas por elas) em virtude das perturbações crônicas, leva ao enfraquecimento dos serviços de proteção de plantas portadoras de nectários extraflorais (LEAL et al. 2015). Nesse último mutualismo, a qualidade do serviço prestado pelas formigas, ou mesmo a taxa de visitação aos nectários extraflorais, declinam com o aumento da perturbação crônica. Esse declínio é ainda mais severo para assembleias de plantas menos adaptadas às condições mais adversas (LEAL et al., 2015).

A compreensão dos efeitos isolados ou sinérgicos da redução da precipitação e das perturbações antrópicas sobre as interações inseto-planta é uma questão chave em ecologia e conservação, dado que esses fenômenos causam impactos severos nas comunidades biológicas e nos seus atributos em diversos níveis de organização. Sabe-se que perturbações antrópicas, como a perda e fragmentação de habitat, podem alterar a magnitude da herbivoria (SANTOS; BENÍTEZ-MALVIDO, 2012) e a abundância e riqueza de herbívoros (ROSSETTI et al., 2017; SOUZA et al., 2013). Contudo, ainda se sabe pouco a respeito dos efeitos da perturbação antrópica crônica sobre as interações entre insetos herbívoros e plantas hospedeiras, quando comparado aos efeitos da perturbação aguda. Dessa forma, a Caatinga, com um histórico de perturbações antrópicas crônicas e com grande variação espacial de precipitação, configura-se como um excelente modelo natural de investigação dos efeitos isolados e interativos da aridez e das perturbações antrópicas crônicas sobre as interações entre plantas e insetos herbívoros.

RESULTADOS

ARTIGO 1: RAINFALL REDUCTION INCREASES INSECT HERBIVORY IN TROPICAL HERB COMMUNITIES

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APÊNDICE A

ARTIGO 2: RAINFALL SHORTAGE INCREASES INSECT HERBIVORY ON WOODY PLANTS OF THE BRAZILIAN CAATINGA

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Basic and Applied Ecology – Research Article

Rainfall shortage increases insect herbivory on woody plants of the Brazilian Caatinga

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Abstract

Chronic anthropogenic disturbance and extreme environmental conditions triggered by climatic change, such as aridity of seasonally dry tropical forests, can disrupt multi-trophic interactions and alter herbivory patterns. Because plants in low resource environments are expected to invest more in defense, we tested whether rainfall reduction and chronic disturbance increase reduces community-level insect herbivory on woody plants of the Caatinga. We sampled 19 woody plant communities across a natural rainfall (510 mm to 940 mm) and chronic disturbance (2.74 to 58.07) gradients. We monitored for four months the frequency, magnitude and type (feeding guild) of insect damage on young, fully expanded leaves. We related the herbivory levels to local rainfall and chronic disturbance and examined potential confounding effects of plant traits (specific leaf area – SLA and presence of extrafloral nectaries – NEFs), plant density, richness and floristic composition on foliar damage. We monitored 855 leaves from 285 plants belonging to 17 species. A third of the leaves escaped from herbivory but all species was attacked. Chewing and rasping insects were the most frequent herbivores removing 6.7% and 3.3% of leaf tissues, respectively. Contrary to expectations, cumulative foliar damage was greater in drier areas and did not respond to chronic disturbance. Also frequency and magnitude of herbivory did not vary with SLA, NEFs, plant abundance, richness and composition. Rainfall shortage increases insect folivory on woody plants in the Catimbau National Park, possibly by weakening the top-down control of leaf-chewing and rasping insects rather than changing plant community attributes. Chronic anthropogenic disturbance plays a secondary role on plant-herbivory interactions, but their effects on other biotic interactions must not be ignored. If the Caatinga becomes up to 50% drier and 4.5°C warmer by 2100, it is likely that the woody flora faces a substantial increase in foliar damage.

Key-words: aridity, Caatinga, chronic anthropogenic disturbance, climate change, environmental gradient, folivory, plant-insect interaction, precipitation.

Introduction

Herbivory is one of the most important ecological interactions of terrestrial ecosystems (Scherber, Heimann, Köhler, Mitschunas, & Weisser, 2010; Schmitz, 2008), but it is very sensitive to changes in biotic and abiotic conditions. Extreme environmental conditions derived from climate change, such as increased aridity in seasonally dry tropical forests, as well as altered conditions generated by chronic anthropogenic disturbances may change plant-herbivore interactions permanently (Rodríguez-Castañeda, 2013; Valiente-Banuet et al., 2015; Wirth, Meyer, Leal, & Tabarelli, 2008). Such changes may rise as a response to modifications in the abundance, distribution, and quality of host plants (bottom-up control) (Ribeiro-Neto, Arnan, Tabarelli, & Leal, 2016), but also due to the presence or absence of predators and parasitoids that regulate herbivore populations (top-down control) (Almeida, Wirth, & Leal, 2008; Ayres & Lombardero, 2000; Barrera, Becker, Elizalde, & Queiroz, 2017). If we are interested in conserving ecosystem functions and ecological interactions rather than species per se (Valiente-Banuet et al., 2015), thus we should understand how bottom-up and top-down controls of herbivory may be altered by rainfall and disturbance.

Rainfall shortage is projected to be more intense in tropical dry forests than in other regions (Magrin et al., 2014; Salazar, Nobre, & Oyama, 2007). In the Brazilian Caatinga, a 1,000,000-km^2 seasonally dry tropical forest (SDTF) that homes 1,112 woody plant species (Banda-R et al., 2016), by 2100 it is expected an increase of up to 4.5°C in mean air temperature and a reduction of up to 50% in mean annual rainfall (PBMC, 2016). In addition, over 30 million people live in the region (Gariglio, Smpaio, Castro, & Kageyama, 2010), most of them are extremely dependent on natural resources and monetarily deprived (Silva, Leal, & Tabarelli, 2017; Specht et al., 2019). These human populations continuously remove small quantities of forest biomass and use them for food, energy, livestock farming and other purposes, chronically degrading the forest (Arnan et al., 2018; Singh, 1998) and driving some locations to desertification (Salazar et al., 2007).

The effects of increased disturbance and/or reduced rainfall on Caatinga biodiversity are relatively well known, but important knowledge gaps remain. For instance, there are evidence of taxonomic (Rito, Arroyo-Rodríguez, Queiroz, Leal, & Tabarelli, 2017), functional (Ribeiro et al., 2019; Julia C. Sfair, De Bello, De Frana, Baldauf, & Tabarelli, 2018) and phylogenetic (Ribeiro et al., 2016) impoverishment of plant communities in response to rainfall shortage or chronic disturbance. Insect communities, which concentrate the herbivores in the Caatinga, have been less studied, but evidence so far indicate homogenization of ant communities (Ribeiro-Neto et al., 2016) and disruption in seed dispersal provided by ants (Oliveira et al., 2019). The interaction between plants and insect herbivores has been evaluated only recently and exclusively on herb communities (Andrade et al., 2020). Main findings suggest that herbivory levels are greater in drier sites possibly due to relaxation of top-down control of chewing insects; bottom-up forces play a minor role. On the other hand, woody plants have been not yet assessed from this perspective.

As an alternative to the resource availability hypothesis proposed by Coley et al. (1985), we suggest that drier environments have higher herbivory rates as already seen for herbaceous communities (Andrade et al. 2020). According to resource availability for plants, such as light in tropical rainforests and water in dry forests, determine the strength of the bottom-up mechanism (see also Endara & Coley et al. 2011). Plants that establish under shady conditions of rainforests or dry conditions of dry forests grow slowly due to resource limitation and thus invest more to protect their tissues. In contrast, plants that grow up in treefall gaps of rainforests or wetter sites of dry forests grow rapidly and invest less in defense because they can compensate for herbivory damage by producing new leaves (Coley et al. 1985; Loughnan & Williams 2019). Consequently, plant communities in drier areas of the Caatinga are expected to exhibit smaller levels of foliar damage than those in wetter areas. Because disturbance also decreases water supply by desiccating the soil, the same trend is expected for highly disturbed areas.

When bottom-up forces govern the interaction, the frequency and magnitude of foliar damage depend on plant characteristics such as plant density, identity and quality. Drought and disturbance may affect host quality for herbivores by altering their levels of direct and indirect defenses (Kessler & Baldwin, 2002). Foliar characteristics such as low specific leaf area, which estimates the content of dry matter per unit area, may confer resistance against herbivore and drought (Grossiord et al., 2017; Poorter, Niinemets, Poorter, Wright, & Villar, 2009; Wigley et al., 2016), resulting in small levels of herbivory in drier and disturbed sites. Contrarily, indirect defenses offered by ants that explore extrafloral nectaries may be weakened in disturbed (Leal, Andersen, & Leal, 2015) and drier environments (Dáttilo et al., 2015; Lange, Dáttilo, & Del-Claro, 2013), resulting in greater levels of herbivory in these sites due to reduced predation on herbivores (Izzo & Vasconcelos, 2002). Functionally, this indirect plant defense works as a top-down control of herbivores, but the true top-down forces are independent of plant characteristics – they are direct responses of predators and parasitoids to new conditions. The insect feeding guild, e.g. chewing, rasping, galling, mining, and sap-sucking, may respond differentially to environmental conditions (Andrade et al., 2020). Endogenous insects such as mining and galling usually benefit from drought (Mazía, Chaneton, Dellacanonica, Dipaolo, & Kitzberger, 2012; Price et al., 1998) while exogenous insects such as chewing, rasping and sap-sucking exhibit the opposite

(Huberty & Denno, 2004; Koricheva, Larsson, & Haukioja, 1998). Thus, their relative damage should be estimated along the rainfall and disturbance gradients.

In this study we evaluated the effects of rainfall shortage and chronic disturbance on community-level insect herbivory on woody plants of the Catimbau National Park, which is one of largest Caatinga reserves in Northeast Brazil. It represents an excellent study system to understand the effects of rainfall reduction and anthropogenic disturbances on plant-insect interactions, with a view to future desertification predictions. Following the bottom-up perspective of herbivory control (Coley's hypothesis), we expected that: (*i*) wetter and conserved areas showed greater levels of foliar damage, once they provide larger amounts of water for plants to tolerate herbivory; (*ii*) relative damage by exogenous insects (chewing, rasping and sap-sucking insects) was greater than that by endogenous insects (leaf-mining and galling insects) and smaller in drier and disturbed areas due resource scarcity, with the opposite trend for endogenous insects; (*iii*) plant communities with low mean specific leaf area or greater proportion of species bearing extrafloral nectaries showed small levels of herbivory due to increased defensive levels, and (*iv*) plant communities with smaller plant abundance and greater species richness showed reduced levels of herbivory (Castagneyrol, Giffard, Péré, & Jactel, 2013; Root, 1973). Finally, we assessed if taxonomically similar communities exhibited similar levels of damage to account for potential confounding effects of plant species composition on herbivory.

Methods

Study area

We performed the study in the 640-km^2 Catimbau National Park (hereafter, Catimbau), Northeast Brazil (8 ° 24'00 "and 8 ° 36'35" S, 37 ° 0'30 "and 37 ° 1'40" W). The climate in Catimbau is predominantly semi-arid (Koeppen's classification Bsh) with annual rainfall variation from 400 to 1100 mm. The rainy season usually occurs from March to June and the average annual temperature is approximately 23 °C. The soil is predominantly quartz-type regosol with coarse granulation. The vegetation is composed of herb, shrub and tree species; Fabaceae and Euphorbiaceae are the most common botanical families in the woody strata (Rito et al., 2017). The insect community is composed mainly by Coleoptera, Hemiptera, Orthoptera, Hymenoptera, Lepidoptera and Phasmatodea (Santos-Neto, 2016). These orders are very diverse with representatives on different trophic levels and, within these, diverse in feeding guilds (Rafael, 2012). There are approximately 300 families living inside the Catimbau (Arnan et al., 2018; Specht et al., 2019); their livelihoods are mainly based on goat farming and subsistence agriculture (Specht et al., 2019).

Rainfall and chronic anthropogenic disturbance gradients

Mean annual rainfall was estimated for 19 plots of 20 m x 50 m using the WorldClim database (www.worldclim.org) for the period between 1960 and 1990 (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). Data were at the spatial resolution of 1 km^2 and were extracted in Arcgis. Plots were at least 2 km apart from each other (Fig. 1). Values of rainfall ranged from 510 mm to 940 mm between the plots, indicating a clear rainfall gradient in Catimbau. On the other hand, temperature varied similarly across the plots and thus no temperature gradient is observed (see also Andrade et al., 2020).

We estimated the chronic anthropogenic disturbance index using 12 metrics from three different approaches (Arnan et al., 2018): (a) indirect measures based on the geographic context; (b) indirect measures based on the socio-ecological context; and (c) direct measures taken in the plots. From these approaches we integrated the chronic disturbance metrics into a fully-integrated global multimetric metric – the Chronic

Anthropogenic Disturbance Index (GMDI) according to Arnan et al. (2018). The GMDI varied from 0 (no disturbance) to 100 (maximum disturbance). Importantly, gradients of rainfall and disturbance are not correlated.

Herbivory and plant monitoring

We gathered the data of woody plant communities from Rito et al. (2017), who carried out the floristic inventory in the same plots. In each plot, all shrubs and trees with diameter at soil height ≥ 3 cm and with a height ≥ 1m were recorded and identified following the botanical nomenclature of APG III (Bremer et al., 2009). Among this set of plants, we selected the 17 most frequent and abundant woody species of all plots and haphazardly drew 15 individuals according to species abundance. From these plants we selected three healthy, young, and completely expanded leaves to be monitored over 120 days – from the beginning to end of the rainy season of 2018 (March to June).

To monitor foliar damage by leaf-chewing, rasping, sap-sucking, leaf-mining and unknown insects, if any, we used a 10-megapixel digital camera (Nikon Coolpix P80) and a white background panel. At intervals of about 40 days, we took digital photographs of all leaves marked (with maximum focal length 84.2 mm, 2 x 2 cm scales) and processed them with ImageJ software (Rasband 2006). We considered as damage any injury present in leaf blade caused by herbivorous insects, following Filip et al. (1995). After image processing, we estimated the frequency of herbivory, measured as the proportion of leaves attacked in the plot, and the magnitude of herbivory, estimated as the percentage of leaf area removed from the plot.

Frequency ranged from 0, when all leaves remained intact at the end of the monitoring, to 1, when all leaves were damaged. Magnitude was estimated as daily rate of damage (% leaf area day^{-1}) relative to each leaf lifetime. Rates of 40 days were used to support our repeated measures analyses on damage evolution. We used cumulative foliar damage over the four months to compare herbivory levels among feeding guilds across the rainfall and chronic disturbance gradients. It is important to notice that the leaf lifetime varied across species and plots; 349 leaves dropped before monitoring ends. In those cases, herbivory level was assumed the same recorded before leaf falling. We eventually lose some damage by herbivores, but certainly avoided overestimations by not assigning 100% of damage to herbivores.

Feeding guilds

We visually categorized foliar damage into six main types [see Loranger et al. (2013) and (Andrade, Batista, Pereira, Fernandes, & Santos, 2018)]: 1) chewing damage – any completely missing area in the in the border or center of the leaf blade that presents regular (e.g., leaf-cutting ants) or irregular shape (e.g., caterpillars, beetles); 2) rasping damage – a kind of damage that only the abaxial or adaxial blade surface is removed, and no hole is formed (e.g., young caterpillars); 3) sap-sucking damage – regular or irregular shape scores or small holes on the leaf blade; 4) leaf-mining damage – the removal of the foliar mesophyll conserving both surfaces (e.g., some Lepidoptera); 5) galling damage – protuberances on the abaxial and/or adaxial surfaces, smooth or covered by trichomes; and 6) unknown damage – caused by insects that did not fit the categories above. In addition, we did not include in this category any change in leaf color or necrosis.

Plant traits and extrafloral nectaries

As foliar characteristics that confer resistance to drought and consequently to herbivore attack, we considered only the specific leaf area (SLA), following Pérez-Harguindeguy et al. (2013). We sampled all individuals of the most representative species in the plots and calculated their mean SLA values (cm²/g). Additionally, we examined all species of the plots for the presence/absence of extrafloral nectaries (NEF). We compared the species in our inventory with the data bank of species bearing NEF (http://www.extrafloralnectaries.org/the-list.html) and specific literature (Y. Melo, Machado, & Alves, 2010). Then we calculated the proportion of individuals bearing extrafloral nectaries in the plots.

Plant density, richness, and composition

Although our sampling based on the most representative plant species ensured a reliable description of the herbivory at the community level, the differences in plant density, richness, and composition from one plot to another could have confounded the role of rainfall and disturbance on herbivory patterns. We accounted for this possibility by evaluating statically *a posteriori* the effect of plant density, richness and composition on foliar damage (see statistical analysis).

Statistical analyses

We used linear mixed model (LMM) to test for differences in frequency and magnitude of foliar damage across the rainfall and chronic disturbance gradients. We set rainfall, disturbance, time and their interactions of second order as fixed effects, and plot identity (ID) as random effect. The response variable (damage accumulated per 40 days) was arcsine square-root transformed prior to analyses to satisfy model assumptions (Crawley, 2007). We performed the LMM in JMP 7 (SAS Institute Inc.) using the restricted maximum likelihood method to separate the variance of fixed effects from that of the random effects (Bolker et al., 2009).

We also performed LMMs to test for differences in herbivory levels by feeding guilds across the rainfall and chronic disturbance gradients. Models had rainfall, chronic disturbance, feeding guild, and their interactions as fixed effects, and plot ID as random effect. Because damage by leaf-chewing and rasping insects was much more frequent than the other feeding guilds, we considered only these two feeding guilds. The data of frequency and magnitude of herbivory (response variables) were also arcsine square-root transformed to satisfy model assumptions.

We performed a multiple linear regression to assess the effect of SLA, proportion of individuals bearing extrafloral nectaries, plant density and richness on herbivory levels. The response variables (frequency and magnitude of foliar damage) were arcsine square-root transformed. Finally, to evaluate the effect of species composition on herbivory frequency and magnitude, we performed Mantel tests in PRIMER 6.0 Software (Clarke & Gorley, 2006). Species abundance was square root transformed to reduce discrepancies caused by hyperdominant species, standardized, and then used to construct a similarity matrix based on Bray–Curtis index. Frequency and magnitude of foliar damage data were used to construct Euclidian-distance based matrices, which were correlated with the compositional matrix.

Results

Overview of herbivory pattern

We monitored 285 individuals from 17 woody species, 14 genera, and seven families across the rainfall and chronic disturbance gradients. All woody species showed damage by herbivorous insects, although approximately 35% of the leaves remained intact throughout the monitoring period (120 days). *Cenostigma microphyllum* (Fabaceae), *Trischidium molle* (Fabaceae), *Pityrocarpa moniliformis* (Fabaceae), *Croton heliotropiifolius* (Euphorbiaceae) and *Neocalyptrocalyx longifolium* (Capparaceae) were the most frequent and abundant species. *Senegalia piauinsis* (Fabaceae) and *C. microphyllum* (Fabaceae) presented the highest frequency of herbivory with 93% and 91% of leaves attacked, respectively (Fig. 2). On the other hand, *Commiphora leptophloeos* (Burseraceae), *Jatropha mutabilis* (Euphorbiaceae), and *Croton tricolo* (Euphorbiaceae) were the plant species with the highest magnitude of herbivory with 60%, 48% and 22.6% of leaf area removed, respectively (Fig. 2; Tab. SA).

Chewing insects were the most frequent feeding guild attacking 53.5% of the leaves, followed by rasping (35.2%) and unknown insects (9.6%). The frequency of the other guilds (sap-sucking, leaf-mining and galling insects) did not surpass 1.6%. Surprisingly, galling insects were present only in one individual of *Cnidoscolus obtusifolius* (Euphorbiaceae) and one individual of *T. molle*. Over the 120 days, chewing insects removed approximately 6.7% of leaf tissue and rasping insects 3.3%, while the other trophic guilds combined (leaf mining, sap-suckers, galling insects and unknown insects) removed 2.2% of leaf tissues.

Effects of rainfall and chronic disturbance on herbivory levels

The daily rates of herbivory varied from 0.0047%/d (plot with 843 mm and 22.44 GMDI) to 0.43%/d (plot with 510 mm and 20.38 GMDI) (Fig. 3). Along the monitoring period, these huge differences in herbivory rates also resulted in large variation in cumulative damage across the plots (0.6% to 43%). Contrary to expectations, the magnitude of foliar damage recorded at intervals of 40 days significantly increased from wetter to drier areas (Tab. 1; Fig. 3), but did not vary in function of chronic disturbance (Tab. 1). Regarding the damage by different feeding guilds, chewing insects were more frequent and removed more leaf tissue than rasping insects did (Tab. 2), but the relative damage of both guild did not vary consistently with rainfall and chronic disturbance (Tab. 2; Fig. 4).

Effects of plant characteristics on herbivory levels

The frequency and magnitude of herbivory did not vary significantly with any of the plant characteristics analyzed, i.e. specific leaf area and proportion of plants bearing extrafloral nectaries (Tab. SB; Fig SA). Despite the variation in plant density (120 to 440 plants/0.1 ha) and richness (13 to 47 species/0.1 ha) across plots, plant density and richness did not affect herbivory levels either (Tab. SB; Fig. SB). Moreover, floristic dissimilarity across the plots was not significantly correlated with differences in herbivory frequency (Rho = 0.162; p = 0.053) and magnitude (Rho = 0.071; p = 0.235), suggesting little influence of plant characteristics on herbivory levels.

Discussion

Our findings do not support the hypothesis that wetter and conserved areas of the Caatinga provide more resource for plant growth and development and, consequently, are more attacked by herbivore insects. In fact, the pattern is reversed along the rainfall gradient as wetter areas show smaller levels of herbivory, and neutral along the disturbance gradient, because plants in highly disturbed areas are as attacked as those in highly conserved areas. Such patterns are unexpected from the perspective of bottom-up control of insect herbivory (Coley's hypothesis) and also evident from the analyses involving SLA, NEFs, plant density, richness and composition, which do not respond to rainfall shortage and chronic disturbance. Jointly, these results suggest that insect herbivory on woody flora of the Catimbau is unlikely to be controlled by bottom-up forces, which has been already demonstrated for herb communities across rainfall gradient (Andrade et al. 2020) and woody communities at different successional stages (Alencar et al. 2019).

Several studies have supported Coley's Growth Rate or Resource Availability Hypothesis (Coley et al. 1985) based on the premise that plant species have more conservative traits in resource-poor environments and can resist more to herbivore attack (Endara & Coley, 2011; Loughnan & Williams, 2019). Despite the high variation across plots in SLA and NEFs, our results do not support this assertion. Instead, they suggest that the environmental variation in rainfall and disturbance observed in the Catimbau is not sufficient to consistently alter the effectiveness of plant defensive strategies. This is supported by Sfair et al. (2018), who worked in the Catimbau and found no relationship of rainfall shortage and chronic disturbance with leaf traits related to plant defense SLA, leaf thickness and leaf dry matter content (see also Grossiord et al., 2017; Wigley et al., 2016). They argue that intraspecific variability in leaf traits of most abundant species interacts with species turnover at the community level, making the functional profile of woody plant communities similar across the environmental gradients (Sfair et al. 2018).

Apparently, the herbivory patterns in our study region are driving by top-down forces, as recently proposed for folivory on herbs (Andrade et al. 2020). There is empirical evidence in the literature demonstrating how herbivorous insects distribution (Rodríguez-Castañeda 2013) and predation pressure on them (Connahs et al. 2011) drive herbivory patterns. In the drier areas of Catimbau it has been reported an increase in abundance and richness of chewing insects (Santos-Neto, 2016), which account for most of total damage in our study. Additionally, leaf-cutting ants also represent a substantial source of foliar damage and, at Catimbau, their colonies are related to the drier (Tabarelli, Siqueira, Backé, Wirth, & Leal, 2017) and disturbed regions (Siqueira et al., 2018). Although we have grouped the damage by chewing insects and leaf-cutting ants in the same feeding guild, the characteristic damage of the leaf-cutting ants (regular or half-round cuts on the leaf blade edges) was common in the plots (J.F.A., personal observation). Rasping insects were apparently more common in drier sites too, but further studies on the distribution of chewing and rasping insects are needed to understand their role in plant-herbivore interactions.

Besides the apparent beneficial conditions of drier areas for exogeneous insect herbivores, these herbivores can also benefit from reduced predation and parasitism by vertebrates and invertebrates in the same areas (Greenberg et al., 2000). This potential weakening of top-down control in drier areas has been recently proposed to explain increased foliar damage on native herbs in drier areas of Catimbau (Andrade et al., 2020). The natural enemies of the herbivores are very sensitive to environmental conditions, rapidly responding to changes in temperature, humidity and disturbances (Terborgh et al., 2001). In forest fragments, for instance, the higher temperature and low humidity of forest edges have been attributed to the lower incidence of phorid flies and consequent increased activity of leaf-cutting ants (Almeida et al., 2008; Barrera et al., 2017). Insectivorous birds and mammals respond similar as well. Without pressure by natural enemies, the exogenous herbivores improve their performance, reproduce more and damage more foliar tissue (Greenberg et al., 2000; Rodríguez-Castañeda, 2013; Terborgh et al., 2001). Thus, it is reasonable to expect that extreme conditions can contribute to the reduction of natural enemies of herbivorous insects and indirectly increase herbivory in drier areas(Rodríguez-Castañeda, 2013). Disturbed areas are likely to be facing the same process given the proliferation of leaf cutting ants (Siqueira et al., 2018), but their outcome on herbivory levels are less clear.

Overall, our findings indicate that rainfall shortage in the Caatinga may change the structure of plant-herbivore interactions. The herbivore patterns seem to be more related to the insect abundance and distribution than to the characteristics of host plants. Although we have not sampled the insect communities, the underlying mechanism is likely to be the weakening of top-down control of exogenous herbivore insects due to aridity, which lead to the increase of foliar damage. Chronic anthropogenic disturbance plays a secondary role on plant-herbivory interactions, but their effects on other biotic interactions must not be ignored. If the Caatinga becomes up to 50% drier and 4.5°C warmer by 2100, it is likely that the woody flora faces a substantial increase in foliar damage. Further experimental studies should assess the effects of drought and chronic anthropogenic disturbances on multi-trophic interactions involving insect herbivores and natural enemies.

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Tables

Table 1. Fixed effects of linear mixed models fitted for repeated measures of magnitude of foliar damage (damage at 40 days) as a function of rainfall, chronic disturbance and time in the Catimbau National Park, Northeast Brazil.

	Df	*F*-ratio	*P*-value	R^2 (%)
Rainfall	1	4.60	0.048*	91%
GMDI	1	1.151	0.237	
Rainfall*GMDI	1	0.047	0.830	
Time	2	53.41	<0.001*	
Rainfall*Time	2	3.263	0.0514	
GMDI*Time	2	1.014	0.373	

Table 2. Fixed effects of linear mixed models fitted for frequency (proportion of leaves damaged) and magnitude (cumulative damage) as a function of rainfall, chronic disturbance and feeding guild (chewing and rasping insects) in the Catimbau National Park, Northeast Brazil.

	Error	*F*-ratio	*P*-value	R^2 (%)
Herbivory frequency				67%
Rainfall	1	2.264	0.151	
GMDI	1	0.153	0.700	
Feeding guild	1	19.288	<0.001*	
Rainfall*feeding guild	1	0.368	0.552	
GMDI*feeding guild	1	0.162	0.692	
Herbivory magnitude				52%
Rainfall	1	0.145	0.707	
GMDI	1	0.422	0.524	
Feeding guild	1	6.075	0.025*	
Rainfall*feeding guild	1	0.266	0.612	
GMDI*feeding guild	1	0.422	0.524	

List of figures

Figure 1. Location of the study region in Northeast Brazil, Catimbau National Park, indicated by the small red square on the left and enlarged on the right. Different tones of blue describe the rainfall gradient in which the 19 woody communities were monitored. Circles size represents the intensity of CAD, with largest circles representing more disturbed areas.

Figure 2. Herbivory frequency (proportion of leaves damaged) and magnitude (daily rate of damage) by woody species along a rainfall and disturbance in the Catimbau National Park, Northeast Brazil. Jat – *Jatropha mutabillis* (Euphorbiaceae); Com – *Commiphora leptophloeos* (Burseraceae); Cni – *Cnidoscolus obtusifolius* (Euphorbiaceae); Tri – *Croton tricolor* (Euphorbiaceae); Lip – *Lippia gracilis* (Verbenaceae); Hel – *Croton heliotropiifolius* (Euphorbiaceae); Nep – *Croton nepetifolius* (Euphorbiaceae); Neo – *Neocalyptrocalyx longifolium* (Capparaceae); Eri – *Erythroxylum revolutum* (Erythroxylaceae); Pit – *Pityrocarpa moniliformis* (Fabaceae); Bau – *Bauhinia acuruana* (Fabaceae); Ano – *Annona leptopetala* (Annonaceae); Mol – *Trischidium molle* (Fabaceae); Cen – *Cenostigma microphylla* (Fabaceae); Pia – *Senegalia piauhiensis* (Fabaceae); Pip – *Piptadenia stipulacea* (Fabaceae); Bai – *Senegalia bahiensis* (Fabaceae).

Figure 3. Mean herbivory magnitude accumulated over three months on 19 woody communities in the Catimbau National Park, Northeast Brazil. Each line represents a community with its respective annual rainfall. Note that wetter sites (blues) accumulated less foliar damage. Statistics are shown in Table 1.

Figure 4. Herbivory frequency and magnitude on woody communities distributed across rainfall and disturbance gradients in the Catimbau National Park, Northeast Brazil. Statistics are shown in Table 2.

Figures

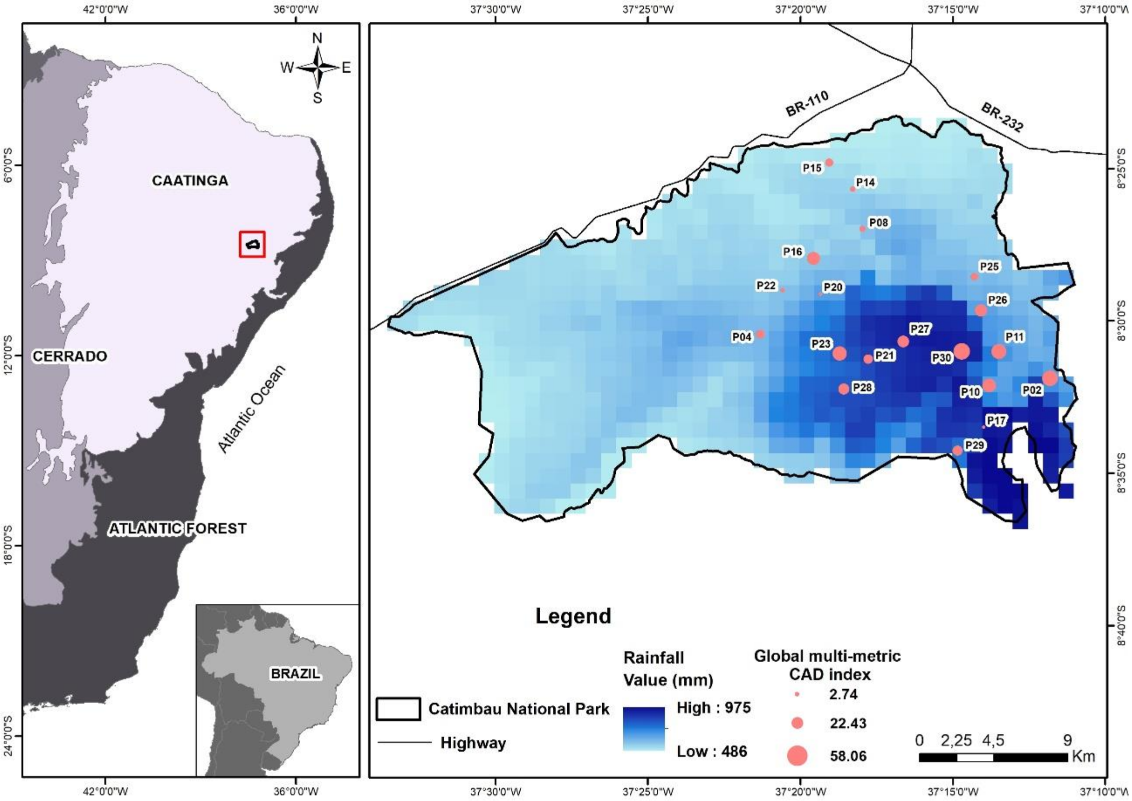
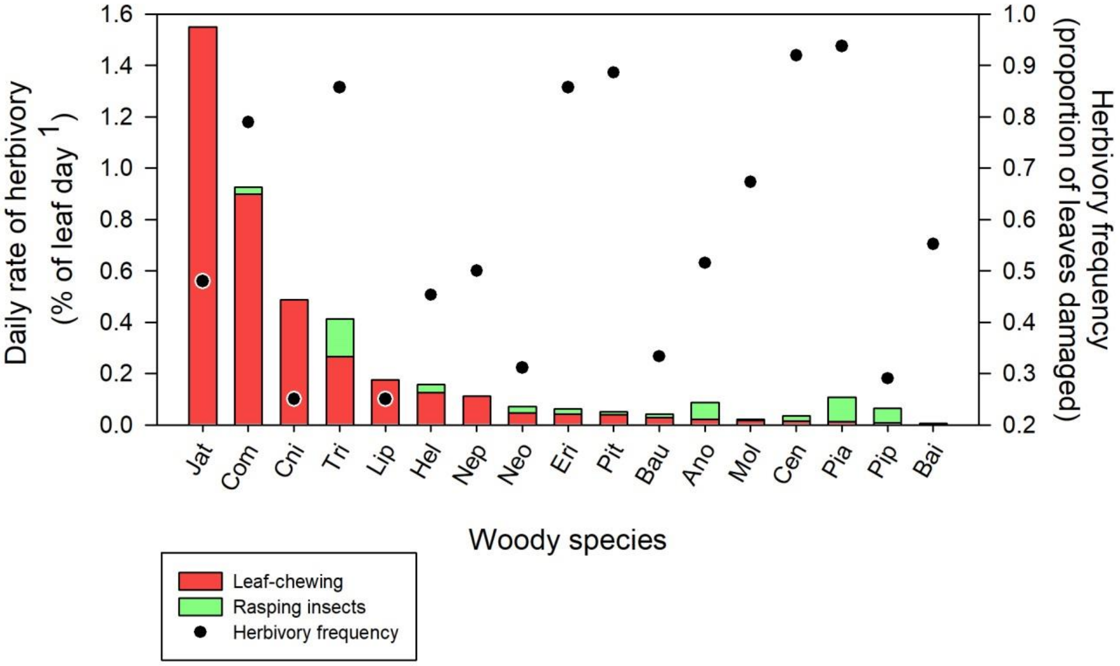


Figure 1.



656

657 **Figure 2.**

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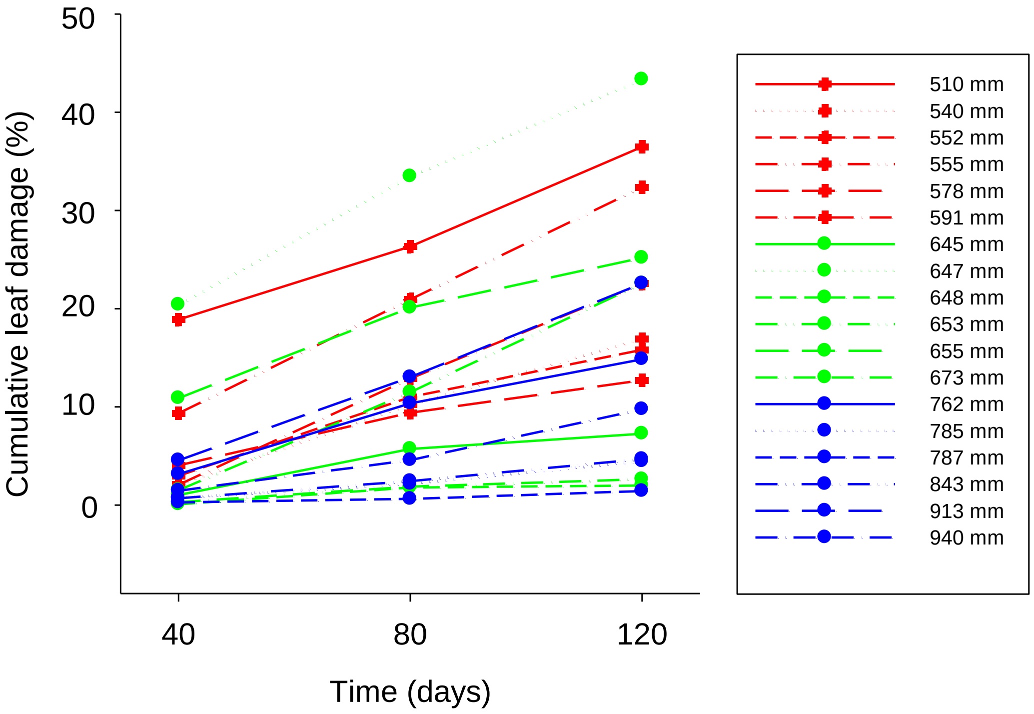
Cumulative leaf damage (%)
50
40
30
20
10
0
40
80
120
Time (days)
510 mm
540 mm
552 mm
555 mm
578 mm
591 mm
645 mm
647 mm
648 mm
653 mm
655 mm
673 mm
762 mm
785 mm
787 mm
843 mm
913 mm
940 mm

Figure 3.

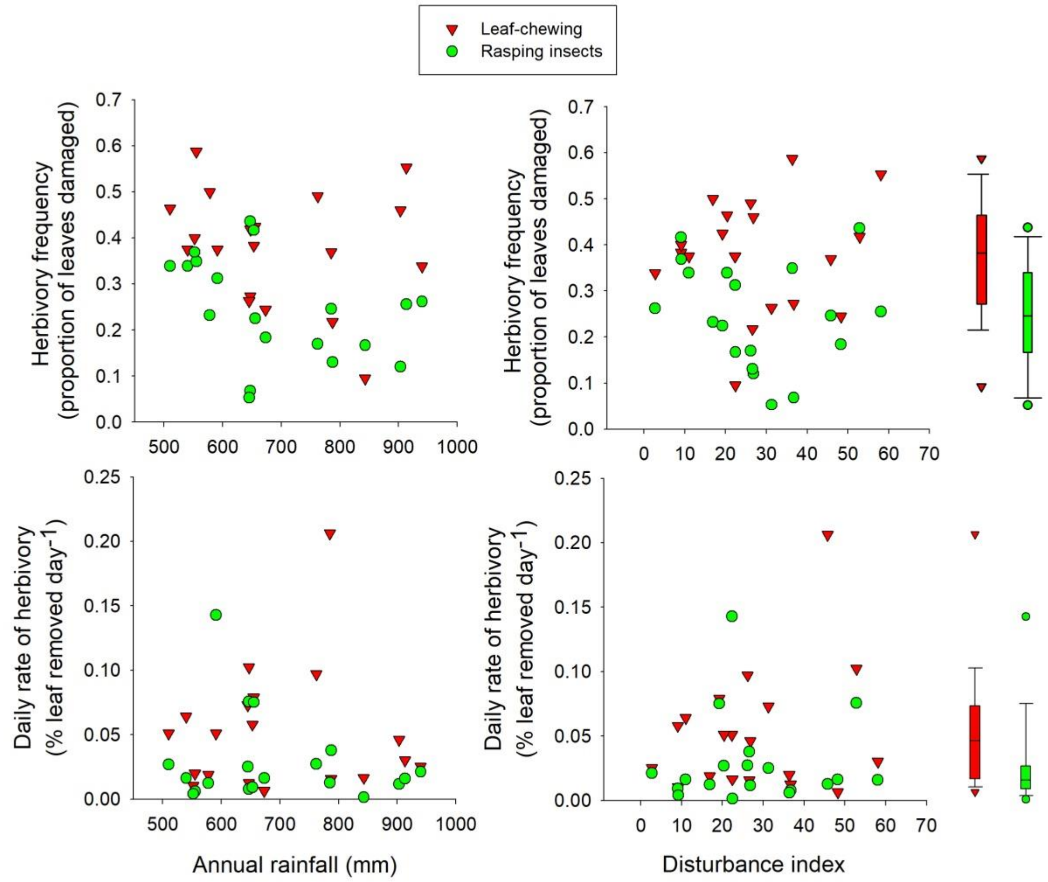
Leaf-chewing
Rasping insects
Herbivory frequency (proportion of leaves damaged)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
500
600
700
800
900
1000
0
10
20
30
40
50
60
70
Daily rate of herbivory (% leaf removed day^{-1})
0.00
0.05
0.10
0.15
0.20
0.25
Annual rainfall (mm)
Disturbance index

Figure 4.

Supporting material

Table 3. Woody species recorded across rainfall and chronic disturbance gradients in the Catimbau National Park, Northeast Brazil. Herbivory frequency refers to proportion of leaves damaged removed tissues refers to total foliar area removed along 120 days in 19 plots.

Species	**Family**	**Herbivory frequency**	**Removed tissues (%)**	**Total abundance**
Senegalia piauhiensis	Fabaceae	93%	6.23%	171
Cenostigma microphylla	Fabaceae	92%	1.96%	204
Pityrocarpa moniliformis	Fabaceae	88%	2.9%	207
Croton tricolor	Euphorbiaceae	85%	22.6%	202
Erythroxylum revolutum	Erythroxylaceae	85%	3.74%	36
Commiphora leptophloeos	Burseraceae	78%	60%	26
Trischidium molle	Fabaceae	67%	1.2%	61
Senegalia bahiensis	Fabaceae	55%	0.50%	155
Annona leptopetala	Annonaceae	51%	1.86%	19
Croton nepetifolius	Euphorbiaceae	50%	5.8%	126
Jatropha mutabillis	Euphorbiaceae	47%	48%	156
Croton heliotropiifolius	Euphorbiaceae	45%	6.6%	126
Bauhinia acuruana	Fabaceae	33%	1%	70
Neocalyptrocalyx longifolium	Capparaceae	31%	1%	85
Piptadenia stipulacea	Fabaceae	29%	0.84%	105
Lippia gracilis	Verbenaceae	25%	4.1%	77
Cnidoscolus obtusifolius	Euphorbiaceae	25%	14.7%	61

Table 4. Liner model of foliar damage frequency and magnitude (cumulative damage) as a function of rainfall, chronic disturbance (GMDI), specific leaf area, proportion of individuals bearing extrafloral nectaries, woody density, and species richness in Catimbau National Park, Northeast Brazil.

Explanatory variables	Df	*F*-ratio	*P*-value	R^2 (%)
Herbivory frequency				8%
Specific leaf area (cm²/g)	1	1.139	0.256	
Plants with NEF (%)	1	0.721	0.410	
Woody density	1	1.555	0.232	
Species richness	1	2.435	0.140	
Herbivory damage magnitude				12%
Specific leaf area (cm²/g)		0.140	0.713	
Plants with NEF (%)		0.883	0.363	
Woody density	1	3.519	0.081	
Species richness	1	0.065	0.801	

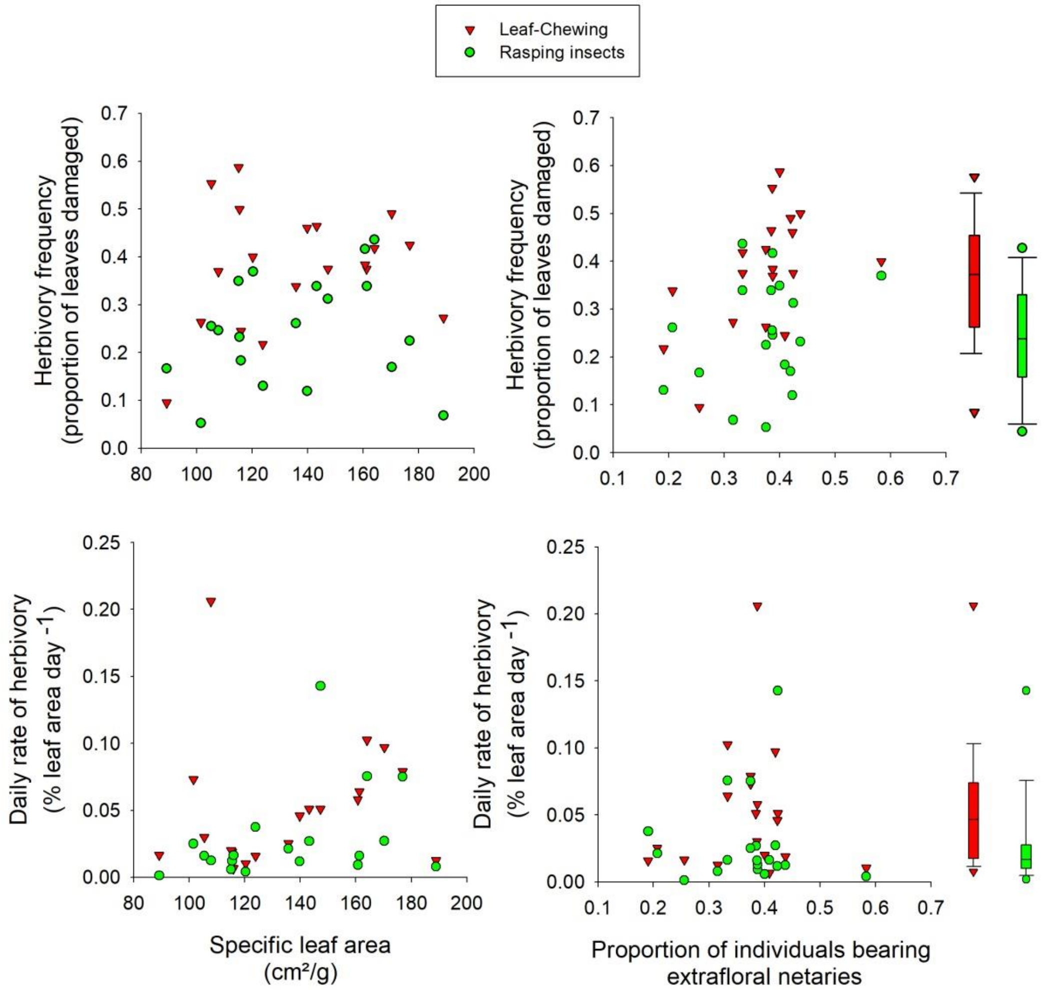

Figure 5: Herbivory frequency and magnitude in function of specific leaf area and proportion of plants bearing extrafloral nectaries per plot across a rainfall and chronic disturbance gradients in the Catimbau National Park, Northeast Brazil. Statistics are shown in Table S1.

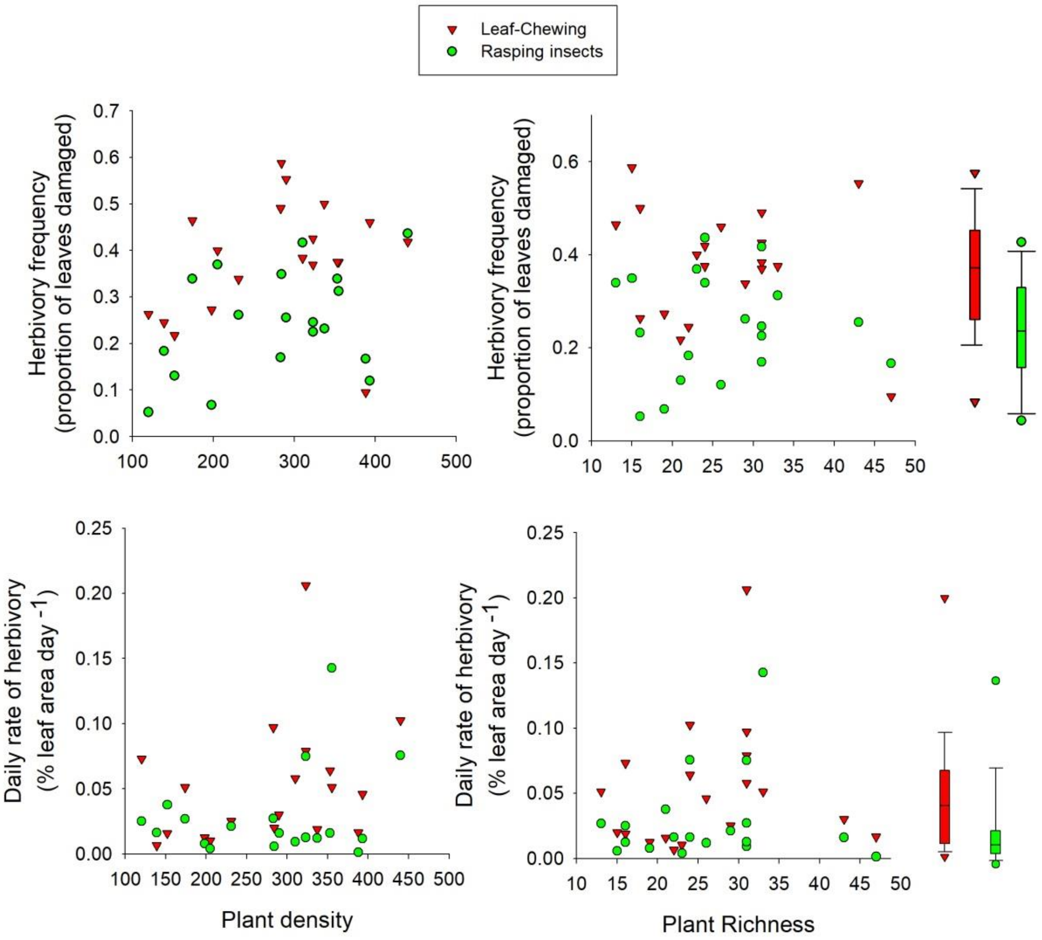

Figure 6: Herbivory frequency and magnitude in function of community plant abundance and richness across a rainfall and chronic disturbance gradients in the Catimbau National Park, Northeast Brazil. Total abundance and plant richness indicate the abundance of each woody species recorded in 19 plots of 1,000m^2. Statistics are shown in Table S1.

CONSIDERAÇÕES FINAIS

As mudanças climáticas e as perturbações antrópicas têm sido foco de diversas discussões na literatura, embora ainda sabe-se pouco dos efeitos isolados ou interativos desses eventos sobre interações antagonistas em múltiplos níveis. Na Caatinga, plantas herbáceas e lenhosas, apresentam padrões de herbivoria semelhantes, os quais aumentam em função da aridez, opondo-se ao proposto na Hipótese da Disponibilidade de Recursos, proposta por Coley et al. (1985). Por outro lado, perturbações antrópicas crônicas podem estar desempenhando um papel secundário sobre as interações inseto-planta, os quais não podem ser ignorados e precisam ser avaliados de forma mais detalhada.

No primeiro capítulo, verificamos que a redução na precipitação altera os níveis de dano foliar em comunidades de plantas herbáceas. Nessas comunidades, a composição florística esteve fracamente subjacente a esse padrão de herbivoria, enquanto outros elementos como a densidade e a riqueza das plantas não influenciaram o mesmo. A guilda trófica mais expressiva foi dos insetos mastigadores, apresentando quase o dobro da frequência de dano e de tecido foliar removido. Adicionalmente, no segundo capítulo observamos que a herbivoria variou positivamente em função do aumento da aridez e ao longo do tempo. Não encontramos efeitos isolados ou interativos das perturbações antrópicas sobre os padrões de dano foliar. Além disso, a baixa área foliar específica e a presença de NEFs, bem como a densidade, a riqueza de plantas e a composição florística não tiveram efeitos sobre a frequência e magnitude de dano foliar. Embora insetos mastigadores tenham sido mais frequentes, esses juntamente com os raspadores apresentaram contribuição semelhante em relação à magnitude de dano causado.

Assim, nossos resultados mostram que na Caatinga a redução da precipitação tem efeitos significativos sobre a remoção de área foliar em plantas com diferentes formas de vida. Contudo, tais efeitos não apresentaram relação com os aspectos intrínsecos às plantas e às comunidades vegetais – como os atributos foliares, presença de NEFs, densidade, riqueza de plantas e identidade das mesmas. Acreditamos que a redução da disponibilidade hídrica medeie às interações inseto-planta, possivelmente, através do enfraquecimento dos controles descendentes da herbivoria por inimigos naturais dos herbívoros. Assim, em cenários extremos, a aridez pode propiciar a proliferação massiva de insetos mastigadores, alterando o equilíbrio das interações multitróficas e os processos ecológicos, como é amplamente discutido que, tanto a aridez como as mudanças nas paisagens naturais têm efeitos negativos nas populações de predadores e patógenos de insetos herbívoros. Assim, se as secas na Caatinga se tornarem mais severas, com aumento de até 50% previsto para 2100, é possível que as comunidades de plantas herbáceas e lenhosas sofram um aumento substancial na herbivoria e que as interações inseto-planta sejam alteradas permanentemente.

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APÊNDICE A – ARTIGO PUBLICADO: RAINFALL REDUCTION INCREASES INSECT HERBIVORY IN TROPICAL HERB COMMUNITIES

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RESEARCH ARTICLE

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Rainfall reduction increases insect herbivory in tropical herb communities

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Abstract

Questions: Climate change is dramatically altering rainfall patterns and species distribution around the world. However, little is known about how rainfall reduction may affect plant–herbivore interactions that are crucial to the of input energy and nutrients into terrestrial ecosystems. Following Coley's growth rate hypothesis, we assessed whether rainfall reduction in a seasonally dry tropical forest decreases community-level herbivory owing to water shortage in drier areas.

Location: Catimbau National Park, Northeast Brazil.

Methods: We sampled 16 herb communities along a rainfall gradient (564–917 mm). Using digital photographs, we monitored for 3 weeks the frequency, magnitude and type (feeding guild) of insect damage on young, fully expanded, short-lived leaves (lifespan <1 month). We related herbivory levels to local rainfall and examined potential confounding effects of herb abundance, richness and floristic composition on such relationships.

Results: We monitored 290 leaves from 202 plants belonging to 28 species. About one-third of the leaves and six species escaped from herbivory. Leaf-chewing insects were the most frequent herbivores, attacking 17 species, 44% ± 15% of the leaves and removing the same amount of foliar tissue as all the other insects combined removed (sap-sucking, rasping, leaf-mining and 'unknown'). Contrary to expectations, foliar damage accumulated more in drier areas following the increase in the frequency of leaf-chewing damage. In addition, frequency and magnitude of herbivory did not vary with herb abundance and richness and were weakly influenced by floristic composition.

Conclusions: Our findings suggest that rainfall underlies community-level herbivory by mechanisms not related to plant availability, identity and diversity. Based on recent evidence that aridity favours leaf-chewing proliferation in the study region, we hypothesize that rainfall reduction may weaken the top-down control of herbivores, increasing folivory pressure on herbs. If prolonged droughts become more frequent in the coming decades, plant–herbivore interactions may be altered permanently.

KEYWORDS
aridity, Caatinga, climate change, dry forest, environmental gradient, folivory, plant–insect interaction, precipitation

1 | INTRODUCTION

The effects of global warming and climate change are no longer debatable: the question now is how plants and animals will adapt to these (if they do so) and how this will impact on our ecosystems (Bonan & Doney, 2018; Rogelj et al., 2018). In South America, the emissions of greenhouse gases are expected to raise mean air temperatures from +1.7°C to +6.7°C during this century (Magrin et al., 2014), drastically affecting the rainfall regime (Weltzin et al., 2006). This warming is predicted to be more severe in regions with arid and semi-arid climate (Feng, Porporato, & Rodriguez-Iturbe, 2013) such as north-east Brazil, which in turn should face a 22% decrease in annual average rainfall and an increase from 2% to 6% in dry season spell (Magrin et al., 2014). This region is home to over 30 million people, most of whom depend upon forest resources for food and energy, and covers about 1 million km^2 with unique seasonally dry tropical forests (Silva et al., 2017; Specht et al., 2019). Understanding how species will interact to each other under the new drier conditions is therefore critical for the region.

Plant–insect interactions are the basis of terrestrial food chains (Scherber, Heimann, Köhler, Mitschunas, & Weisser, 2010; Schmitz, 2008) and herbivory is amongst the most important ecological interactions because it represents the first entry of energy and matter into consumer trophic levels (Coley & Barone, 1996). To be established, herbivory requires not only the host (palatable) plant and the insect, but also suitable conditions for both. Unsuitable environmental conditions such as shade in tropical rainforests and aridity in dry forests may disrupt, strengthen or weaken the interaction by modifying the establishment and performance of plants (Moro et al., 2015) and insects (Ayres & Lombardero, 2000). Rainfall reduction is likely to reduce soil moisture and, consequently, plant ability to tolerate or resist to herbivore attack; physical, chemical, and nutritional foliar characteristics may change in response to drought or warming (Santos & Benítez-Malvido, 2012; Zhang et al., 2018). Similarly, rainfall reduction may reduce air humidity and rise air temperature, modifying insect growth, dispersal and feeding intensity on their host plants (Weltzin et al., 2006; Wilf, Labandeira, Johnson, Coley, & Cutter, 2001). Thus, the level of foliar damage (i.e. the frequency and magnitude of herbivore attack) will be ultimately driven by the environment (Santos & Benítez-Malvido, 2012).

One of the most acceptable hypotheses to explain patterns of insect herbivory in tropical forests is Coley's Growth Rate or Resource Availability hypothesis (Coley, Bryant, & Chapin, 1985). It assumes that fast-growing species have short-lived leaves because energy acquisition in nutrient-rich environments is maximized by rapid leaf turnover, whereas slow-growing species have long-lived leaves because slow turnover is advantageous in a nutrient-poor environment where (re)growth is constrained (Stamp, 2003). Among its predictions, is that in low-resource environments (e.g. dry or shaded habitats), resource limitation favours slow-growing plant species that bear conservative traits and allocate more resources to avoid being attacked (Coley et al., 1985; McBranch et al., 2016; Wigley et al., 2016). Conversely, high-resource environments (e.g. wet and sunny habitats) favour plants with more acquisitive characteristics that allow them to tolerate and compensate for herbivore damage (Coley et al., 1985; Endara & Coley, 2011). These responses are expected to scale up from populations to the whole community, making herbivore damage less frequent and intense in low-resource (drier) habitats (Coley et al., 1985; Loughnan & Williams, 2019; Rodríguez-Castañeda, 2013).

The herbivorous insects also respond to environmental conditions (Weissflog, Markesteijn, Lewis, Comita, & Engelbrecht, 2018) depending on their feeding habits (Anstett, Naujokaitis-Lewis, & Johnson, 2014; Huberty & Denno, 2004). In wetter environments, damage by free-living insects such as leaf-chewing and sap-sucking may be more prominent owing to increased insect survivorship in such areas (Mazía, Chaneton, Dellacanonica, Dipaolo, & Kitzberger, 2012). In contrast, drier environments can improve the performance of leaf-mining (Mazía et al., 2012) and galling insects (Lara & Fernandes, 1996; Price et al., 1998), increasing their foliar damage. In a multi-trophic perspective, it is also possible to observe changes in the interaction between herbivorous insects and their natural enemies. As shown by Connahs, Aiello, Van Bael, and Rodríguez-Castañeda (2011), parasite and parasitoid species that are limited by water scarcity may reduce predation and parasitism in drier seasons, relaxing the top-down control of insect herbivore populations they prey on. Similarly, insectivory by birds, bats and other vertebrates may be weakened in response to anthropogenic modifications that make the environment drier and warmer, increasing the frequency of herbivory (Greenberg et al., 2000; see also Roslin et al. (2017) for global patterns of arthropod, bird and mammal predation along latitude and elevation gradient).

In the present study, we assessed whether rainfall reduction in the Caatinga decreases community-level insect herbivory owing to water shortage in drier areas (sensu Coley's hypothesis). We took advantage of the natural variation in annual rainfall observed in one of the largest protected areas of north-east Brazil (480–1,100 mm), the Catimbau National Park (see also Rito, Arroyo-Rodríguez, Queiroz, Leal, & Tabarelli, 2017). We focused on the herb stratum, which is known to concentrate the plant species diversity of the Caatinga (Moro et al., 2015), and used non-destructive methods (digital photographs) to monitor the frequency and magnitude of foliar damage by leaf-chewing, sap-sucking, rasping, leaf-mining and galling insects along the rainfall gradient. We expected that wetter areas would present more foliar damage such as leaf-chewing, rasping, and sap-sucking by free-living insects, while endogenous insects such as leaf-mining and galling insects would damage more leaf tissue in drier areas (Mazía et al., 2012). We also examined potential confounding effects of herb abundance, richness and floristic composition on herbivory patterns across the rainfall gradient.

2 | METHODS

2.1 | Study area

The study was performed in the 640-km^2 Catimbau National Park, north-east Brazil (8°24′00″ and 8°36′35″S, 37°0′30″ and 37°1′40″W). The climate is predominantly semi-arid (Koeppen's classification Bsh), with an average annual temperature of approximately 23°C. Rainfall decreases sharply from east to west, from 1,100 mm to 480 mm annually, and the rainy season usually occurs from March to June (Rito et al., 2017). The soil is predominantly quartz-type regosol with coarse granulation. The vegetation varies from herbaceous, shrub to arboreal with deciduous species. Herbaceous is the most representative plant growth form, with 33% (202 species) of the total Catimbau flora (Rito et al., 2017). Fabaceae and Euphorbiaceae are the most common botanical families in the woody strata (Rito et al., 2017). The herbaceous stratum is mainly composed of Poaceae, Asteraceae, Cyperaceae, Bromeliaceae, and Fabaceae (Athiê-Souza et al., 2019) and the most common species are *Commelina erecta* (Commelinaceae), *Mollugo verticillata* (Molluginaceae) and *Urochloa mollis* (Poaceae) (Vieira, 2017). Most of them have very short life spans (<2 months), germinating, growing and reproducing within the short rainy season (Vieira, 2017). The insect community is dominated by representatives from Coleoptera, Hemiptera, Orthoptera, Hymenoptera, Lepidoptera and Phasmatodea (Santos-Neto, 2016). These orders are very diverse with representatives in different trophic levels, including many herbivores (Rafael et al., 2012).

2.2 | Plant sampling and herbivory monitoring

We started our fieldwork in June 2017 at the end of the rainy season. This year was the first following a long drought period between 2012 and 2016, which possibly collapsed herb and insect populations across the entire Caatinga. At our study sites, the first rains started in March and April 2017. Threrefore, we waited some weeks to allow herbs to fully expand their leaves and insects to recover their populations. We then proceeded with our survey by sampling herb communities in 16 plots of 20 m × 20 m (400 m^2). Plots were at least 1 km away from each other and encompassed an annual rainfall gradient that varied from 564 to 917 mm (Figure 1). Annual average temperature is quite constant among the plots, usually reaching 21°C in July (coldest month) and 25°C in December (warmest month). Plots were protected against herbivorous mammals with barbed wire fences, including livestock (mainly goats) raised extensively within the park (Specht et al., 2019). Rainfall data was extracted from WordClim global climate data repository at 1 km^2 scale (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) (www.worldclim.org), which calculated averages for the 1960–1990 period. In each plot, we systematically established five equidistant subplots of 0.25 m^2 (0.5 m × 0.5 m) and randomly marked representatives of the most abundant herb species to be monitored (N = 202 across the 80 subplots). Species were selected from a previous study on the herb communities of the Catimbau National Park (Vieira, 2017). Subplots were needed to capture the patchy distribution of many herb species within the plots, but all statistical analyses were performed at the plot level (N = 16) by collapsing subplot data, thus avoiding pseudoreplication.

To estimate the frequency and magnitude of foliar damage (i.e. proportion of leaves attacked and percentage of leaf area damaged, respectively), in the first week (time 0) we randomly sampled one to six young, healthy, fully expanded leaves (N = 297 leaves) from each plant and monitored them weekly for the next three weeks. The number of leaves varied between plants, species, subplots and plots because many leaves did not match our conservative criteria at time 0. To monitor the injuries by leaf-chewing, rasping, sap-sucking, leaf-mining and unknown insects, if any, we used a 10-megapixel digital camera (Nikon Coolpix P80) and a white background panel. We took digital photographs with maximum focal length of 84.2 mm and a scale of 2 cm × 2 cm. The images were then processed and analysed with the ImageJ software (Rasband 1997–2006). We considered as damage any injury present in leaf blade caused by herbivorous insects, following Filip, Dirzo, Maass, and Sarukhan (1995).

Because herbivore attack by different feeding guilds may be infrequent but very intense (low frequency and high magnitude) and vice versa (high frequency and low magnitude), we examined herbivory levels in several complementary ways. We used herbivory frequency to describe the prevalence of folivory on Caatinga herbs. Frequency reached 1 when all leaves were attacked and was 0 when all remained intact by the end of the monitoring. Second, we estimated herbivory magnitude as daily rates (% day^{-1}) to allow comparisons with other studies and across plant species (Coley & Barone, 1996). Weekly rates were used to support our repeated measures analyses on damage evolution, given that our sample size was not large enough to perform analyses by day; this would imply 21 levels within the factor time and require dozens of plots. Finally, we used the damage accumulated over the three weeks to compare herbivory levels among feeding guilds across the rainfall gradient. In that case, time was controlled instead of being considered a source of variation. It is important to note that the leaf lifetime varied across species: 86 leaves dropped before monitoring ended, so those cases, herbivory level was assumed to be the same recorded in the last week.

2.3 | Feeding guilds

To quantify the relative damage caused by leaf-chewing, rasping, sap-sucking, leaf-mining and unknown insects, we classified the injuries into six main types of damage following Loranger et al. (2014) and Andrade, Batista, Pereira, Fernandes, and Santos (2019): (a)

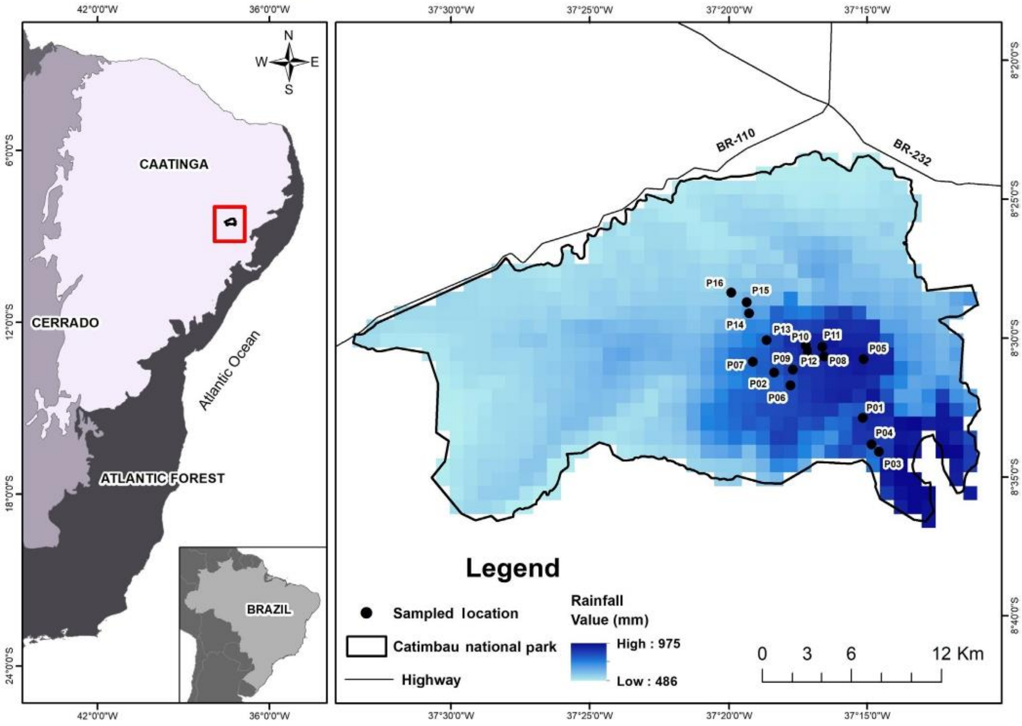


FIGURE 1 Location of the study region in Northeast Brazil, Catimbau National Park, indicated by the small red square on the left and enlarged on the right. Different shades of blue describe the rainfall gradient in which the 16 herb communities were monitored [Colour figure can be viewed at wileyonlinelibrary.com]

leaf-chewing damage – any completely missing area of the leaf blade with regular (e.g. leaf-cutting ants) or irregular shape (e.g. caterpillars, beetles) in the border or in centre of the leaves; (b) sap-sucking damage – regular or irregular shape scars, as well as small holes in the leaf blade (e.g. Hemiptera, Thysanoptera); (c) rasping damage – a kind of damage that only part of the leaf blade is removed from the abaxial or adaxial blade surface but leaving the ribs, and no hole is formed (e.g. young caterpillars); (d) leaf-mining damage – the removal of the leaf mesophyll conserving abaxial and adaxial surfaces causing a serpentine or blotched dead areas in the leaves (e.g. larval stages of Coleoptera, Diptera, Hymenoptera and Lepidoptera); (e) galling damage – protuberances on the abaxial and/or adaxial surfaces, smooth or covered by trichomes (e.g. Diptera, Coleoptera, Hymenoptera, Hemiptera, Thysanoptera and Lepidoptera); and (f) unknown damage – caused by insects that did not fit the categories above.

2.4 | Herb density, richness and composition

Working with the most abundant species of each plot ensured a reliable description of the herbivory at the community level, but resulted in strong differences in plant composition that could underlie herbivory patterns along the gradient. We solved this problem statistically by assessing a posteriori the effect of plant composition on herbivory levels (see Section 2.5). To that end, we first counted and identified all herb plants recorded in the subplots following the botanical nomenclature of APG III (Angiosperm Phylogeny Group, 2009). We identified the species by consulting experts and comparing the records with previously identified material from our research team (Vieira, 2017). Specimens that we were not able to identify at the family level were treated as morphospecies. These variables were finally used to decouple the effects of herb density, richness and species composition from the effect of rainfall on herbivory.

2.5 | Statistical analyses

To test whether herbivory levels decreased with rainfall as time advances, we used generalized linear mixed model (GLMM) (Bolker et al., 2009). We set rainfall, time (weeks) and their interaction as fixed effects and plot identity (ID) as random effect. The response variable (damage accumulated per week) was arcsine square-root transformed to satisfy model assumptions (Crawley, 2007). We performed the GLMM in JMP 7 (SAS Institute Inc.) using the restricted maximum likelihood method to separate the variance of fixed effects from that of the random effects (Bolker et al., 2009).

We also performed GLMMs to assess if wetter areas presented more foliar damage by free-living insects and less damage by endogenous insects. In these cases, we set rainfall, feeding guild and their interaction as fixed effect and plot identity (ID) as random effect. Because damage by leaf-chewing insects was much more frequent than the other feeding guilds (see Section 3), we collapsed damage by the other feeding guilds into a single category and compared it against leaf-chewing insects. The response variables of these GLMMs (herbivory at the end of the sampling period) were also arcsine square-root transformed to satisfy model assumptions.

To explore the effects of herb density and richness on herbivory levels, we modelled the cumulative damage as a function of herb density and richness per plot using multiple linear regression. Finally, to assess how herb species composition affected herbivory levels, we performed Mantel tests in PRIMER 6.0 Software (Clarke & Gorley, 2006). We constructed a species similarity matrix based on Bray–Curtis abundance-based index to describe the variation in species composition across the plots. Then we constructed similar matrices based on the Euclidian distance of cumulative frequency and cumulative magnitude of damage, which were then correlated to the species similarity matrix.

3 | RESULTS

We recorded 28 herb species belonging to 21 genera and 17 families (Table 1). Approximately 36% of the leaves remained intact throughout the monitoring period. Surprisingly, no leaf was damaged by galling insects, even in the driest plots. Only six species escaped herbivore attack.

While some species had all their leaves damaged (frequency of 1.0) or showed daily rates of herbivory as high as 2.7% per day (Figure 2), herbivores removed <12% of the herb community tissue by the end of the monitoring (Figure 3). Leaf-chewing insects were the most frequent herbivores, attacking 17 species, 44% ± 15% (mean ± SD) of the leaves and removing the same amount of foliar tissue damaged by the other insects combined (sap-sucking, rasping, leaf-mining, and unknown together).

Contrary to expectations, herb communities in drier areas accumulated significantly more foliar damage than communities in wetter areas (Table 2; see also the red and green lines above blue ones in Figure 3). This pattern followed the increase in the frequency of leaf-chewing damage in the drier areas, which was twice that of all other guilds together (Table 3; Figure 4). However, the magnitude of the damage by leaf-chewing insects did not vary consistently with rainfall (Table 3; Figure 4).

With regard to the effects of herb density and richness on herbivory levels, both frequency and magnitude of foliar damage varied irrespective of these variables (Appendix S1). This pattern was also supported by rare and abundant plant species that presented similar herbivory levels (Figure 2), as well as by herb species with similar density but contrasting damage levels, for example *Urochoa mollis* (Poaceae) and *Talinum paniculatum* (Talinaceae). Furthermore, floristic composition did not affect the frequency of foliar damage ($\rho = -0.002$; $p = 0.43$) and weakly influenced herbivory magnitude ($\rho = 0.244$; $p = 0.042$), as indicated by the low ρ value.

TABLE 1 Herb species and morphospecies recorded along a rainfall gradient in the Catimbau National Park, north-east Brazil.

Species	Family	Total abundance
Richardia sp.	Rubiaceae	103
Herissantia sp.	Malvaceae	89
Portulaca mucronata	Portulacaceae	51
Commelina sp.	Commelinaceae	45
Galactia sp.	Fabaceae	23
Urochloa mollis	Poaceae	19
Sida sp.	Malvaceae	19
Talinum paniculatum	Talinaceae	18
Morphospecies M21	–	10
Zornia grandiflora	Fabaceae	8
Chamaecrista rotundifolia	Fabaceae	7
Pavonia sp.	Malvaceae	7
Alternanthera brasiliana	Amaranthaceae	5
Ayenia erecta	Malvaceae	4
Aeschynomene viscidula	Fabaceae	3
Bidens pilosa	Asteraceae	2
Morphospecies M20	–	2
Marsypienthes chamaedrys	Lamiaceae	1
Boehavia coccinea	Nyctaginaceae	1
Jacquemontia sp.	Convolvulaceae	1
Kallstroemia grandiflora	Zygophyllaceae	1
Morphospecies M11	–	1
Morphospecies M14	–	1
Pombalia sp.	Violaceae	1
Schwendia americana	Solanaceae	1
Tarenaya spinosa	Cleomaceae	1
Tragos bertonianum	Poaceae	1

Note: Total abundance refers to the total number of individuals observed in 80 subplots of 0.25 m^2. Their herbivory levels are described in Figure 2.

4 | DISCUSSION

Our findings do not support Coley's Growth Rate hypothesis as a plausible explanation to describe community-level patterns of insect herbivory on native Caatinga herbs. To support it, the frequency and

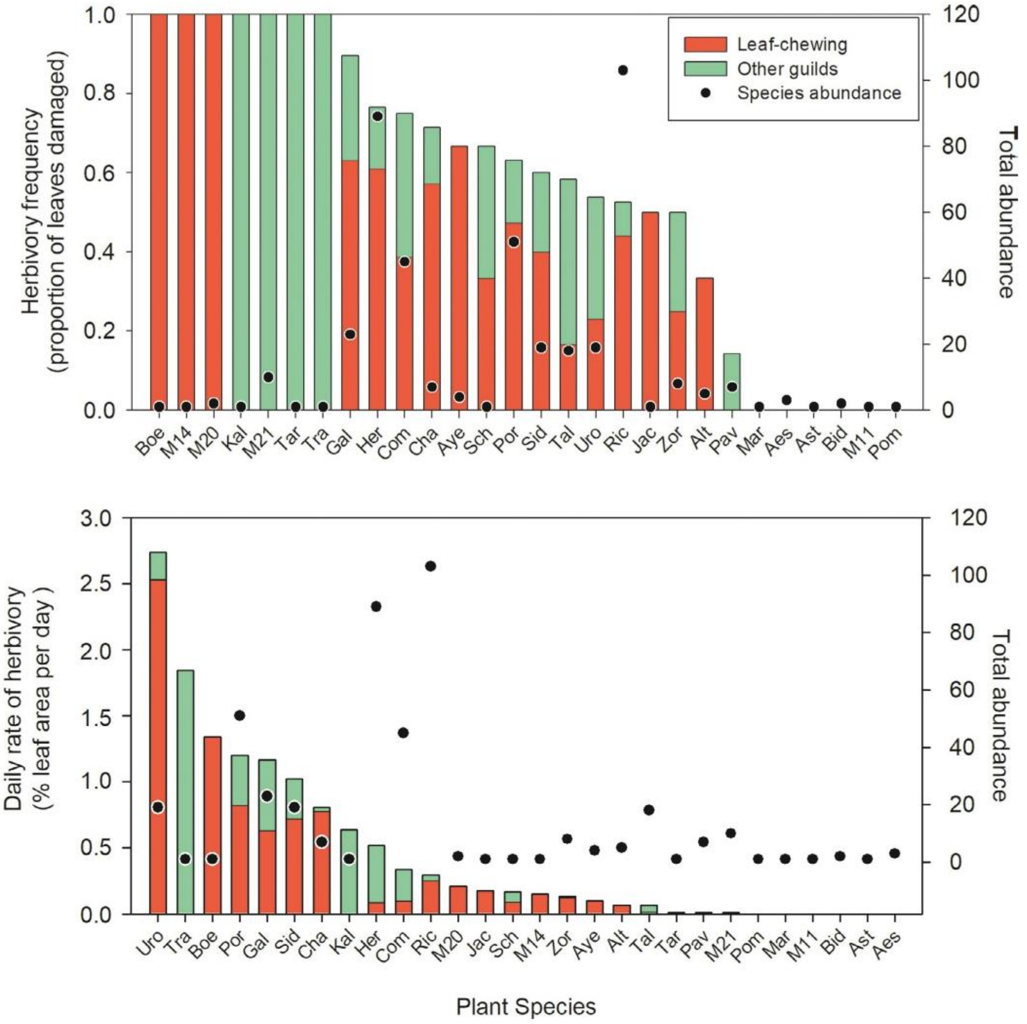
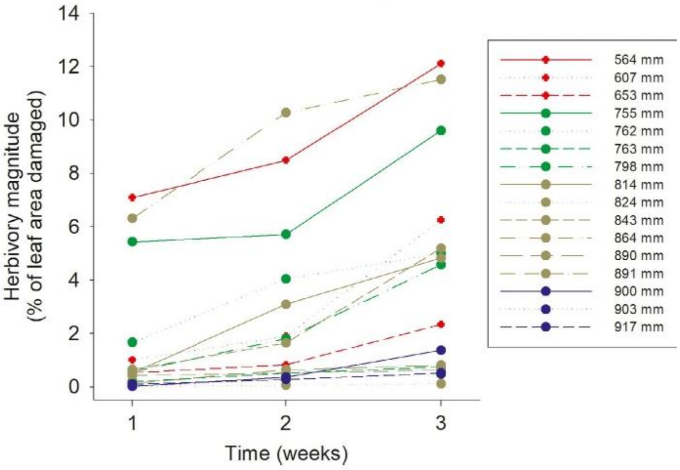


FIGURE 2 Herbivory frequency and magnitude (daily rate of damage) by herb species in the Catimbau National Park, north-east Brazil. 'Other guilds' refer to the damage caused by sap-sucking, rasping, leaf-mining and unknown insect herbivores combined. Total abundance indicates the abundance of each herb species recorded in 80 subplots of 0.25 m^2. Gal, *Galactia* sp. (Fabaceae); Por, *Portulaca mucronata* (Portulacaceae); Uro, *Urochloa mollis* (Poaceae); Her, *Herissantia* sp. (Malvaceae); Ric, *Richardia* sp. (Rubiaceae); Com, *Commelina* sp. (Commelinaceae); Sid, *Sida* sp. (Malvaceae); Cha, *Chamaecrista rotundifolia* (Fabaceae); Boe, *Boehavia coccinea* (Nyctaginaceae); Tra, *Tragos bertonianum* (Poaceae); Kal, *Kallstroemia grandiflora* (Zygophyllaceae); Zor, *Zornia grandiflora* (Fabaceae); Tal, *Talinum paniculatum* (Talinaceae); M20, Morph-specie 20; Aye, *Ayenia erecta* (Malvaceae); Jac, *Jacquemontia* sp. (Convolvulaceae); M14, Morphospecies 14; Alt, *Alternanthera brasiliana* (Amaranthaceae); Sch, *Schwendia americana* (Solanaceae); Mar, *Marsypienthes chamaedrys* (Lamiaceae); Aes, *Aeschynomene viscidula* (Fabaceae); Ast, *Astrea lobata* (Euphorbiaceae); *Bidens pilosa* (Asteraceae); M11, Morphospecies 11; M21, Morphospecies 21; Pav, *Pavonia* sp. (Malvaceae); Pom, *Pombalia* sp. (Violaceae); and Tar, *Tarenaya spinosa* (Cleomaceae) [Colour figure can be viewed at wileyonlinelibrary.com]

magnitude of herbivory should have been smaller in drier areas where the limiting resource water is scarce and plants should be better defended. However, we observed not only a similar high frequency of herbivory across the entire rainfall gradient, but also a significantly greater magnitude of herbivory in the drier areas (the opposite). The explanation seems to be related to weak plant responses to rainfall at the Catimbau National Park and strong response of leaf-chewing insects to aridity, which we detail below.

FIGURE 3 Mean herbivory magnitude accumulated over 3 weeks on 16 herb communities in the Catimbau National Park, Northeast Brazil. Each line represents a community with its respective annual rainfall. Note that wetter sites (blue) accumulated less foliar damage. Statistics are shown in Table 2 [Colour figure can be viewed at wileyonlinelibrary.com]



That plants from dry sites bear several conservative foliar characteristics (McBranch et al., 2016; Wigley et al., 2016) that contribute to defence against herbivore attack has been exhaustively discussed (Endara & Coley, 2011; Loughnan & Williams, 2019). Although there is no doubt that water is the main resource affecting the biological dynamics at the Caatinga (Silva et al., 2017), apparently the rainfall range of our gradient (564 to 917 mm annually) has been not enough to sort out defensive strategies against insect herbivores across the plots (Endara & Coley, 2011; Scherber et al., 2010). Consequently, herbs in drier plots may be as well defended as they are in wetter plots, violating the premise of Coley's hypothesis of more defence in poor environments. Although we have not measured any kind of defence, this statement is supported by Sfair and colleagues' study at the Catimbau National Park (Sfair, de Bello, de França, Baldauf, & Tabarelli, 2018), who found no relationship between environmental gradients and conservative or acquisitive plant traits (but see Moreira et al. (2018) and Cao, Li, and Chen (2018) for examples of significant environmental effects on leaf traits).

The weak effect of plant characteristics as a driver of herbivore damage also appeared in the analyses of the effects of herb density, richness and floristic composition on herbivory levels. Plant abundance is known to affect damage by leaving the host plants more visible to insects [plant appearance hypothesis sensu Feeny (1976)]. Plant species richness may buffer foliar attack by providing alternative hosts to herbivores, thus avoiding the typical outbreaks seen in monocultures (Scherber et al., 2010; Weissflog et al., 2018). Even with host density and richness being equal, herbivory levels might be also influenced by plant composition membership, which will determine palatability and herbivory at the community level (Ruiz-Guerra, Guevara, Mariano, & Dirzo, 2010). However, our findings indicate that plots with greater herb density or richness do not exhibit greater herbivory levels than those with smaller density and richness. In addition, they show that floristic composition is a poor predictor of differences in damage caused. Asynchrony in leaf flushing might also have influenced the results, but the first rains of the rainy season synchronize herb growth across the study region.

TABLE 2 Fixed effects of generalized linear mixed models fitted for repeated measures of magnitude of herbivory (weekly rate of damage) as a function of rainfall and time (3 weeks) in the Catimbau National Park, north-east Brazil.

	df	F-ratio	*p*-value	Model R^2 (%)
Rainfall	1,14	4.802	0.045*	95.7
Time	2,28	47.591	<0.001*	
Rainfall*Time	2,28	2.404	0.108	

Note: Refer to Figure 3 for graphical representation. The random factor (Plot ID) accounted for 8.5% of the residual variance.

TABLE 3 Fixed effects of generalized linear mixed models fitted for herbivory frequency and magnitude (damage accumulated over 3 weeks) as a function of rainfall and feeding guild (leaf-chewing insects vs. other guilds) in the Catimbau National Park, north-east Brazil. Other guilds combine the damage by sap-sucking, rasping, leaf-mining and unknown insect herbivores (see Figure 4). The random factor (Plot ID) accounted for 5.1% and 3.3% of the residual variance of the frequency and magnitude models, respectively

	df	F-ratio	*p*-value	Model R^2 (%)
Herbivory frequency				
Rainfall	1,14	7.192	0.017*	24.1
Feeding guild	1,14	20.094	<0.001*	
Rainfall*feeding guild	1,14	0.831	0.377	
Herbivory magnitude				
Rainfall	1,14	2.533	0.133	12.8
Feeding guild	1,14	0.001	0.972	
Rainfall*feeding guild	1,14	0.706	0.414	

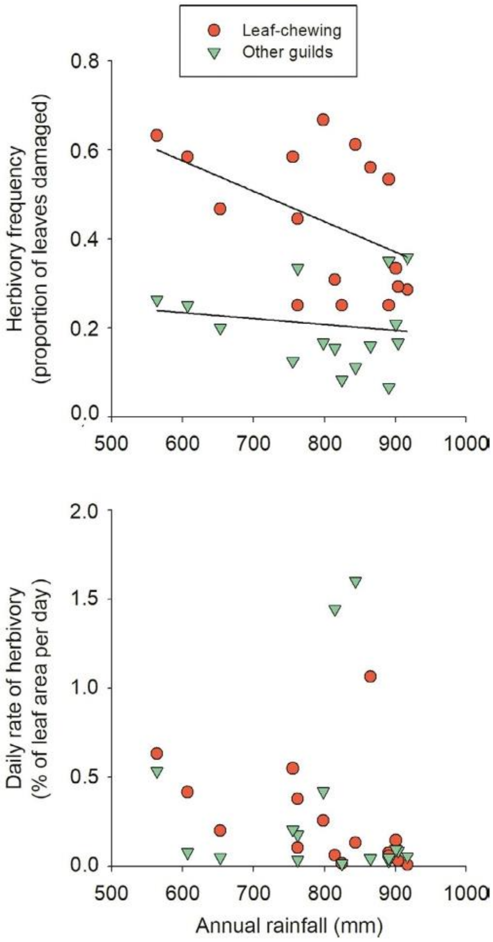


FIGURE 4 Herbivory frequency and magnitude on herb communities distributed across a rainfall gradient in the Catimbau National Park, north-east Brazil. Other guilds refer to sap-sucking, rasping, leaf-mining and unknown insect herbivores combined. Statistics are shown in Table 3 [Colour figure can be viewed at wileyonlinelibrary.com]

Jointly, these findings suggest that the interaction between herbs and herbivorous insects in the Caatinga is driven little by plant community characteristics.

We argue that herbivory patterns on herb communities are mainly ruled from top to bottom, with insects being the best predictor of damage levels. Although we have not been able to collect the herbivores and therefore describe insect dynamics at our plots, it is obvious that the interaction depends on insect abundance and feeding habits (Coley & Barone, 1996). Fortunately, a comprehensive assessment of herbivore insects has been conducted at the Catimbau National Park (Santos-Neto, 2016). In the drier areas of Catimbau, there was an increase in abundance and richness of leaf-chewing insects such as Coleoptera, Orthoptera, and Lepidoptera (Santos-Neto, 2016), which clearly matches the increased frequency of damage we documented for this feeding guild in the drier areas. Our interpretation is that the leaf-chewing insects do not remove more tissue per leaf in the drier areas, but attack more leaves (i.e. increase their damage frequency) in the areas where they are more abundant.

The mechanisms underlying the leaf-chewing proliferation under drier conditions are not completely understood, as insect response to water availability is controversial in the literature (Huberty & Denno, 2004; Rodríguez-Castañeda, 2013). On one hand, dominance by leaf-chewing insects in wetter environments and by leaf-mining in xeric ones (Mazía et al., 2012), reduced grasshopper performance with increasing humidity (Barton, Beckerman, & Schmitz, 2009) and increase in damage by leaf-chewing insects from rain to dry forest has been documented (Brenes-Arguedas, Coley, & Kursar, 2009). On the other hand, in dry forests the rates of wasp parasitism, which control the populations of free-living insects, decrease sharply in dry season (Connahs et al., 2011) and predation on herbivorous insects decreases gradually with reducing rainfall (Rodríguez-Castañeda, 2013). Insectivory by birds, bats and other vertebrates, which are critical to control insect herbivore populations (Greenberg et al., 2000), might also be weaker in the drier areas. This phenomenon of reduced vertebrate predation and parasitism on insect herbivores has been described in forest remnants as ecological meltdown (sensu Terborgh et al., 2001), resulting in increased herbivory levels because of the relaxation of top-down control of herbivore populations.

Thus, we hypothesize that rainfall reduction in Catimbau National Park may weaken the top-down control of leaf-chewing herbivores, increasing folivory pressure on herbs. Such an increased impact of herbivores in drier environments has also been documented elsewhere. For example, Barton et al. (2009) observed that reduced water availability strengthened the herbivorous effect on the overall plant total biomass. In another study, leaf-cutting ants preferentially attacked plants from habitats with water limitation (Ribeiro-Neto, Pinho, Meyer, Wirth, & Leal, 2012), and at our study area, leaf-cutting ants pressure on woody plants (leaf consumption and herbivory rate) is higher in the dry season (Siqueira et al., 2018). The challenge arises in predicting the outcome of increased herbivory on the long-term persistence of herbs and the insects themselves. If prolonged droughts become more frequent in the coming decades (Magrin et al., 2014), plant–herbivore interactions may be altered permanently. Possible synergies with chronic anthropogenic disturbances may also impose additional threats (Rito et al., 2017). Further studies should investigate how rainfall drives insect development, dispersal and feeding strategies in the increasingly drier Caatinga. They should also deepen our understanding of the relative contribution of bottom-up and top-down drivers of insect herbivory, as both may be influenced by climatic factors.

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DATA AVAILABILITY STATEMENT

Raw data were generated at Long-Term Ecological Research (*Programa Ecológico de Longa Duração*) PELD Catimbau. Derived data supporting the findings of this study are available from the corresponding author (BAS) on request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Effect of herb density and species richness on herbivory frequency and magnitude (damage accumulated over 3 weeks) in the Catimbau National Park, Northeast Brazil

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