UNIVERSIDADE FEDERAL DE PERNAMBUCO

CENTRO DE BIOCIÊNCIAS

DEPARTAMENTO DE BOTÂNICA

PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA VEGETAL

MÁRCIA EMANUELLE MADRUGA FORTUNATO

FENOLOGIA E DIVERSIDADE FUNCIONAL REPRODUTIVA DE UMA COMUNIDADE EM GRADIENTE DE PRECIPITAÇÃO E PERTURBAÇÃO

Recife

2018

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

Orientadora: Drª Isabel Cristina Sobreira Machado

Co-orientador: Dr Marcelo Tabarelli

Recife

2018

Dados Internacionais de Catalogação na Publicação (CIP) de acordo com ISBD

Fortunato, Márcia Emanuelle Madruga
Fenologia e diversidade funcional reprodutiva de uma comunidade em gradiente de precipitação e perturbação / Márcia Emanuelle Madruga Fortunato. – 2018.

107 f. : il.

Orientadora: Isabel Cristina Sobreira Machado.
Coorientador: Marcelo Tabarelli.
Tese (Doutorado) – Universidade Federal de Pernambuco. Centro de Biociências. Programa de Pós-graduação em Biologia Vegetal, Recife, 2018.
Inclui referências e anexos.

1. Fenologia vegetal 2. Plantas – Reprodução I. Machado, Isabel Cristina Sobreira (orientadora) II. Tabarelli, Marcelo (coorientador) III. Título.

571.82 CDD (22.ed.) UFPE/CB – 2018 - 182

Elaborado por Bruno Márcio Gouveia - CRB-4/1788

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Aprovada em: __28__/__02__/_2018__

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Às mulheres que me inspiram...

Ana (in memória) e *Elizabeth Madruga*

Pelo exemplo de força e sabedoria!

AGRADECIMENTOS

Aos órgãos de financiamento, Fundação de Amparo à pesquisa e Tecnologia de Pernambuco (FACEPE) pela concessão da bolsa de Doutorado (IBPG-0820-2.03/13); à Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (Capes) pela concessão da bolsa de Doutorado Sanduíche no México (PDSE-88881.133050/2016-01) e à Universidade Federal de Pernambuco (UFPE) pela concessão de ajuda de custo para participação e apresentação de trabalhos em eventos científicos.

À Universidad Nacional Autónoma de México (UNAM) e ao Laboratorio de Ecología de Paisajes Fragmentados pela acolhida e infraestrutura disponível no período de Doutorado Sanduíche no país.

Ao PELD Catimbau (Projeto Ecológico de Longa Duração) pelo apoio logístico e financiamento das atividades de campo, através dos projetos financiados pelo Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) – processo PELD 403770/2012-2 e Processo Universal 470480/2013-0.

À Francisco de Assis Araújo chefe da unidade do Parque Nacional do Catimbau por disponibilizar o carro da instituição em algumas coletas de campo.

À colaboração de orientação da Drª Isabel Machado, de coorientação do Dr Marcelo Tabarelli e de coorientação do estágio sanduíche do Dr Víctor Arroyo-Rodríguez pelos ensinamentos e avanços na pesquisa.

À equipe do Laboratório de Biologia Floral e Reprodutiva (Polinizar) e Laboratório de Ecologia Vegetal Aplicada (LEVA) pela infraestrutura e apoio de pesquisa.

Ao querido Natan Almeida do céu pelo apoio e companheirismo na montagem do experimento de campo e troca de experiências, pelas conversas agradáveis e momentos divertidos, que nossa parceria seja sempre próspera e duradoura.

Ao querido amigo Diego Sotero pela ajuda e companhia em campo e por compartilhar momentos de suor, sofrimento, sucessos e sorrisos. *Ó meu Pai... Me ajude!*

À querida Kátia Rito por disponibilizar seus dados de composição de espécies das parcelas do Peld Catimbau e por toda a ajuda no manuscrito de diversidade funcional.

Aos amigos que ganhei neste processo Nando Albuquerque, Camila Miranda, Caio Félix, Lucas Costa, Rafael Farias, Nayara Albuquerque, Arthur Domingos pelas trocas de ideias e experiências acadêmicas, sempre me apoiando e dando forças nos momentos mais difíceis. *"Amigos são anjos disfarçados de humanos, que trocaram as asas por pernas para tornar nossa vida um lugar mais bonito e feliz!"* (Autor desconhecido)

Aos tantos colegas de trabalho que me acompanharam neste processo, estudantes assim como eu do Programa de Pós-Graduação em Biologia Vegetal (PPGBV), do Curso de Campo: Ecologia e Conservação da Caatinga (ECCA) e do PELD Catimbau, que serão sempre boas lembranças da vivência e dos conhecimentos adquiridos.

À minha linda família, que é a razão de meu esforço, pelo incentivo ao conhecimento e apoio em todas as circunstâncias. *"Quando somos amados por nossa família conseguimos sentir um pouco da felicidade do paraíso!"*

Ao meu amado Raphael, pelo seu amor e apoio em todas as decisões de minha vida. Por sempre estar presente em todos os momentos, sendo a minha fortaleza, ombro amigo e braço acolhedor.

Pela fé em Deus que sempre me guia, me ajudando a superar todas as adversidades da vida, me fortalecendo nos momentos difíceis e me dando sabedoria para seguir em frente!

RESUMO

Os serviços ecossistêmicos que envolvem floração e frutificação são importantes na disponibilidade de recursos de flores e frutos e para a manutenção de polinizadores e dispersores de sementes. Fatores externos como variação de precipitação e atividades humanas podem alterar os eventos reprodutivos das plantas e comprometer os processos de estrutura e funcionamento de comunidades. A tese tem o objetivo de avaliar a distribuição espacial e temporal e a funcionalidade de flores e frutos em espécies lenhosas de Caatinga em gradientes de precipitação e perturbação antrópica crônica. Para isso, o estudo foi desenvolvido no Parque Nacional do Catimbau, pois possui variação na disponibilidade de precipitação e apresenta diferentes níveis de pressão antrópica. As coletas foram realizadas em parcelas permanentes delineadas no PELD Catimbau (20 x 50 m), com amostragem das espécies lenhosas. Os indivíduos lenhosos (217 de 56 espécies) foram acompanhados por 24 meses e foram realizadas coletas de flores e frutos (101 espécies) para avaliação dos atributos funcionais. A fenologia foi testada com estatística circular, aplicados os índices funcionais (FRic, FEve, FDiv, FDis e FD) e avaliados os efeitos dos gradientes com GLM. Floração e a frutificação ocorreram ao longo dos anos, com picos em ambas fenofases, indicando a sazonalidade dos eventos, principalmente em áreas com menor precipitação. Perturbação humana e sua interação com a precipitação atuam como filtro ambiental limitando a frequência de floração e frutificação. A funcionalidade reprodutiva se mantém ao longo de ambos os gradientes, devido à distribuição homogênea das síndromes de polinização e dispersão que contribui para a manutenção de atributos reprodutivos. Em síntese, precipitação e perturbação antrópica atuam na ocorrência de eventos reprodutivos de floração e frutificação, mas a funcionalidade de flores e frutos se mantém nas espécies lenhosas da Caatinga.

Palavras-chave: Atributos funcionais. Floração. Frutificação.

ABSTRACT

Ecosystem services involving flowering and fruiting are important in the availability of flower and fruit resources for the maintenance of pollinators and seed dispersers. External factors such as precipitation variation and human activities can alter reproductive events of plants and compromise the processes of structure and functioning of communities. This thesis aims to evaluate the spatial and temporal distribution and functionality of flowers and fruits in Caatinga woody species in precipitation and chronic human disturbance gradients. For this, study was developed in Catimbau National Park, because it has variation in the availability of precipitation and presents different levels of anthropogenic pressure. The collections were carried out in permanent plots delineated in the Catimbau PELD (20 x 50 m), with sampling of the woody species. The woody individuals (217 of 56 species) were followed for 24 months and flower and fruit collections (101 species) were performed to evaluate the functional traits. Phenology was tested with circular statistics, functional indexes (FRic, FEve, FDiv, FDis and FD) were applied and effects of GLM gradients were evaluated. Flowering and fruiting occurred along of years, with peaks in both phenophases, indicating the seasonality of events, especially in areas with minor precipitation. Human disturbance and its interaction with precipitation act as environmental filter limiting the frequency of flowering and fruiting. Reproductive functionality is maintained along both gradients, due to the homogeneous distribution of pollination and dispersal syndromes that contributes to the maintenance of reproductive traits. In summary, precipitation and anthropogenic disturbance act in the occurrence of reproductive events of flowering and fruiting, but the functionality of flowers and fruits is maintained in the Caatinga woody species.

Keywords: Flowering. Fruiting. Functional Traits.

SUMÁRIO

1 INTRODUÇÃO

Mudanças climáticas e distúrbios antrópicos crônicos (por exemplo, sobrepastoreio e extração de lenha) ameaçam cada vez mais a manutenção da biodiversidade global, em particular nas Florestas Tropicais Sazonalmente Secas (DIRZO et al., 2011). Portanto, entender a resposta das espécies a tais ameaças é importante para nortear ações de conservação. De particular interesse é o impacto potencial que as alterações climáticas e a perturbação ambiental podem ter no funcionamento do ecossistema.

Diante das ameaças atuais, é necessário realizar estudos focados na compreensão do funcionamento dos ecossistemas, os quais incluem os serviços de polinização e de dispersão de sementes. Além desses, os estudos que abordam fenologia reprodutiva nos mostram a ocorrência e a disponibilidade de recursos de flores e frutos nas comunidades ecológicas, em escala espacial e temporal (MORELLATO, 2003) e também podem revelar um panorama das interações planta-animal, de acordo com a polinização e dispersão de sementes (JOHANSSON et al., 2015; MORELLATO et al., 2016). Além de classificar diferentes grupos funcionais de espécies, a polinização e a dispersão de sementes são importantes serviços ecossistêmicos que contribuem para a disponibilidade de recursos florais e de frutos (NEUSCHULZ et al., 2016; QUESADA et al., 2011). Portanto, a classificação das síndromes de polinização e de dispersão são tão importantes para entender os processos em estudos de comunidades.

Estudos recentes estão interessados em compreender o funcionamento das comunidades e para isso foram desenvolvidos vários índices para calcular a diversidade funcional (DÍAS; CABIDO, 2001; MASON et al., 2013; MOUCHET et al., 2010; PETCHEY; GASTON, 2006). A avaliação da diversidade funcional a partir de atributos florais e de frutos é uma problemática crescente nos últimos anos. Os trabalhos mais atuais têm utilizado diferentes filtros para explicar a diversidade funcional, como habitat em regeneração (SOBRINHO et al., 2016), habitat fragmentado (GIRÃO et al., 2007; LOPES et al., 2009), sucessão ecológica (WARRING et al., 2016) e gradiente altitudinal (ARAÚJO, 2016). De forma geral, a disponibilidade de recursos florais e de frutos está relacionada à capacidade das espécies e suas inter-relações de fornecerem serviços ecossistêmicos (FONTAINE et al., 2006; GIRÃO et al., 2007; MAYFIELD et al., 2006).

Desta maneira, compreender o funcionamento de comunidades vegetais é um grande desafio para ecólogos, inclusive quando os trabalhos abordam parâmetros reprodutivos, que incluem atributos de flores e frutos. Comumente, os estudos de reprodução vegetal focam no conhecimento da biologia floral e reprodutiva e da história natural das espécies, mas não levam em consideração os aspectos ambientais e a composição total das espécies das comunidades (ALMEIDA et al., 2013; NADIA et al., 2007a; 2007b). Diante disso, buscamos apontar direções que facilitem estudos mais aplicados e completos para entender como comunidades vegetais podem ser organizadas a partir de uma óptica reprodutiva, através da inclusão de estudos de fenologia e diversidade funcional reprodutiva. Mostraremos como exemplos, estudos fenológicos e funcionais em Florestas Tropicais Sazonalmente Secas, no Brasil, a Caatinga.

1.1 FENOLOGIA

O termo fenologia foi primeiramente utilizado por Morren em 1853 (ver HOPE, 1974) e mais tarde Lieth (1974) o definiu como o estudo da ocorrência de eventos biológicos repetitivos, das causas de sua ocorrência em relação a fatores bióticos e abióticos e das interrelações entre as fases caracterizadas por esses eventos, da mesma ou de diferentes espécies. Posteriormente, Morellato (2003) sintetizou o conceito de fenologia como sendo o estudo de eventos cíclicos que ocorrem na vida dos vegetais, influenciados por fatores bióticos e abióticos. O estudo da fenologia pode ser empregado para compreender os processos cíclicos e as interações ecológicas, através de eventos de floração e frutificação (MORELLATO, 2003).

Os fatores bióticos que podem influenciar na fenologia tem origem interior (ou seja, desencadeados por características filogenéticas e fisiológicas) ou exterior (ou seja, relacionados com as interações biológicas com animais herbívoros, frugívoros, polinizadores e dispersores (MACHADO; SEMIR, 2006; MANTOVANI; MARTINS, 1988). Dentre os fatores abióticos que podem atuar como gatilhos na ocorrência das fenofases reprodutivas citam-se luminosidade, temperatura, umidade, fotoperíodo e pluviosidade (CALLE et al., 2010; LIEBSCH; MIKICH, 2009; MORELLATO; LEITÃO-FILHO, 1990). Aliado às características climáticas, a sazonalidade também é um fator importante que influencia a organização temporal de árvores e de polinizadores (BELO et al., 2013; FISOGNI et al., 2016; MORELLATO, 1992).

No âmbito da biologia de populações e comunidades o estudo da fenologia é um componente importante porque atua em vários fatores, como por exemplo, na composição e estrutura da vegetação (CARADONNA et al., 2014; FARRER et al., 2010) e nas interações ecológicas entre plantas e animais, tais como polinização, herbivoria, frugivoria e dispersão de sementes (LOPEZARAIZA-MIKEL et al., 2014). De tal forma, a fenologia de floração é altamente relevante para a organização e estrutura das comunidades de plantas, a conservação das espécies mutualistas e suas interações e a manutenção de serviços essenciais dos ecossistemas (CARADONNA et al., 2014; GARIBALDI et al., 2013). Além de nos mostrar uma perspectiva de mudanças nos ciclos vegetativos e reprodutivos com as atuais ameaças de alterações climáticas globais (CHAMBERS et al., 2013; MORELLATO et al., 2016).

Assim como fatores climáticos (por exemplo, a precipitação) que atuam na ocorrência das fenofases, distúrbios humanos também podem afetar negativamente as fenofases (ver QUESADA et al., 2011). Distúrbios antrópicos crônicos são intensificados por alterações climáticas, ou seja, o aumento da perturbação induzida pelo clima poderia, por sua vez, alterar significativamente a biomassa total e a resposta composicional das florestas a um possível aquecimento futuro (OVERPECK et al., 1990). As mudanças ambientais causadas pela atividade humana também podem desencadear mudanças na fenologia da floração e da frutificação (QUESADA et al., 2011).

1.1.1 Fenologia numa Perspectiva de Caatinga

A bioma Caatinga é caracterizado como Floresta Tropical Sazonalmente Seca com vegetação adaptada a longos períodos de déficit hídrico, abrange uma área de cerca de 844.453 km², o equivalente a 11% do território nacional e engloba os estados Alagoas, Bahia, Ceará, Maranhão, Pernambuco, Paraíba, Rio Grande do Norte, Piauí, Sergipe e o norte de Minas Gerais (ANDRADE et al., 2004; FIGUEIREDO et al., 2000; MMA, 2017; PRADO, 2003; RODAL et al., 1998). O clima semi-árido da Caatinga (BSh de KÖPPEN), apresenta temperaturas elevadas, altas taxas de evaporação e evapotranspiração, precipitação média anual inferior a 620 mm, distribuição irregular de chuvas e longo período de seca (AB’SABER, 1974; ARAÚJO et al., 2007; REIS, 1976). O padrão temporal de disponibilidade hídrica é provavelmente o fator determinante na reprodução de plantas em regiões tropicais, especialmente em florestas tropicais secas, como a Caatinga (GRIZ; MACHADO, 2001). Diferentes estratégias reprodutivas já foram registradas na Caatinga, como a ocorrência de floração e frutificação na estação chuvosa, floração na estação chuvosa e frutificação na seca, floração na estação seca e frutificação na chuvosa, floração e frutificação na estação seca e floração e frutificação duas vezes por ano (ARAÚJO et al., 2007; NADIA et al., 2007a; 2007b). Em síntese, o padrão fenológico reprodutivo em áreas de Caatinga é sazonal, relacionado com a ocorrência da estação chuvosa, a qual estimula os eventos de floração e frutificação (BARBOSA et al., 2003; GRIZ; MACHADO 2001; MACHADO et al., 1997; QUIRINO; MACHADO, 2014). Apesar dos picos reprodutivos serem mais frequentes na estação chuvosa, é comum o registro de espécies em floração e frutificação ao longo do ano (BARBOSA et al., 2003; GRIZ; MACHADO, 2001; MACHADO et al., 1997; QUIRINO; MACHADO, 2014). Mudanças climáticas globais alteram os padrões de temperatura e ocorrência de chuvas e também podem afetar negativamente a fenologia e a produção de flores e frutos (QUESADA et al., 2011). Aumento da temperatura e diminuição da precipitação em regiões semi-áridas ocasionam perda na capacidade reprodutiva de vegetais, devido à perda de insetos polinizadores e simplificação das interações ecológicas (LESICA; KITTELSON, 2010).

A resposta das plantas xerófilas à precipitação está relacionada à disponibilidade de água, tanto pelas chuvas, como por meio do armazenamento de água nos caules e nas raízes em períodos de aridez (BORCHERT, 1994; BORCHERT; RIVERA, 2001; LIMA; RODAL, 2010). De uma forma geral, a variação sazonal no estado da água da árvore parece ser o principal determinante na fenologia e distribuição de espécies arbóreas em Florestas Tropicais Secas (BORCHERT, 1994), sendo possível a utilização e armazenamento de água na planta de diferentes maneiras, como nos tecidos vegetais (LIMA et al., 2012). Entretanto, a redução da pluviosidade tende a diminuir a cobertura vegetal, simplificar as interações ecossistêmicas (HIROTA et al., 2011; NOBRE; BORMA, 2009) e, além disso, áreas mais secas apresentam plantas funcionalmente empobrecidas que se tornam mais sensíveis à perturbação antrópica (RITO et al., 2017).

1.1.2 Floração

A floração é uma fenofase no ciclo dos vegetais na qual se inicia a reprodução sexuada e é importante pela produção de recursos florais (MACHADO et al., 1997; MACHADO; LOPES, 2004). Associar o período de floração com a fenologia do polinizador pode garantir o processo de polinização e sucesso reprodutivo da espécie (FORTUNATO; QUIRINO, 2016), principalmente em períodos de escassez de recursos, como na Caatinga (QUIRINO; MACHADO, 2014; SANTANA; MACHADO, 2010). O padrão de floração pode variar de acordo com as espécies (características endógenas) e com o ambiente (características exógenas), sendo estimulada pela ocorrência de chuvas (BIANCHINI et al., 2006; MANTOVANI et al., 2003), temperatura (MORELLATO et al., 2000) e comprimento do dia (CALLE et al., 2009; MORELLATO et al., 2000). No caso da Caatinga, as espécies e indivíduos tendem a sincronizar a floração com o período chuvoso da região, desencadeado pela ocorrência de chuvas, devido à disponibilidade de água para iniciar a reprodução – desenvolver botões florais e flores (BARBOSA et al., 2003; QUIRINO; MACHADO, 2014). A sincronia de floração entre os indivíduos é comum em florestas tropicais, as quais dependem do período chuvoso para garantir seu processo de reprodução (LOCATELLI; MACHADO, 2004; QUIRINO; MACHADO, 2014).

Nas espécies perenifólias de Caatinga a floração pode ocorrer preferencialmente na estação seca, por exemplo, *Licania rigida* Benth. (Chysobalanaceae), *Spondias tuberosa* Arruda (Anacardiaceae), *Ximenia americana* L. (Olacaceae) e *Ziziphus joazeiro* Mart. (Rhamnaceae) as quais utilizam a água disponível no solo para o desenvolvimento reprodutivo (BARBOSA et al., 2003; NADIA et al., 2007a; 2007b). Neste caso a disponibilidade de chuvas não é um fator limitante, pois a planta consegue captar a água necessária para o processo de reprodução devido às suas estratégias de coleta e armazenamento de água na seca (BARBOSA et al., 2003). Por sua vez, as espécies com alta densidade de madeira são fortemente dependentes da precipitação para iniciar a floração, uma vez que são capazes de armazenar apenas quantidades limitadas de água em seus troncos (LIMA; RODAL, 2010).

De uma forma geral, a floração em espécies de Caatinga ocorre sazonalmente relacionada com a estação chuvosa (GRIZ; MACHADO, 2001; MACHADO et al., 1997; QUIRINO; MACHADO, 2014). Mas é comum encontrar espécies em floração na estação seca, normalmente relacionada com as diferentes estratégias adaptativas ou ao hábito (BARBOSA et al., 2003; LIMA; RODAL, 2010; QUIRINO; MACHADO, 2014). As diferentes estratégias de floração, tanto na estação seca quanto na estação chuvosa, são importantes para garantia de recursos florais na manutenção de animais polinizadores durante todo o ano (FORTUNATO; QUIRINO, 2016).

1.1.3 Frutificação

Apesar do padrão sazonal da floração, na estação chuvosa, a frutificação na Caatinga possui um padrão contínuo, devido à maior duração dos indivíduos nesta fenofase e às diferentes épocas de maturação de frutos (BARBOSA et al., 2003; GRIZ; MACHADO, 2001; MACHADO et al., 1997). Também é encontrada variação no período de frutificação, de acordo com o tipo de fruto produzido, isto é, a produção de frutos zoocóricos é mais frequente na estação chuvosa, enquanto a produção de frutos anemocóricos e autocóricos é mais comum na estação seca (BARBOSA et al., 2003; GRIZ; MACHADO, 2001; MORELLATO; LEITÃO–FILHO, 1992). A produção de frutos zoocóricos está relacionada com a disponibilidade de água no ambiente, ou seja, em regiões com alta sazonalidade climática, o período úmido contribui para o desenvolvimento dos frutos carnosos (MARCOS; PAÉZ, 2002). Relacionando a classificação das síndromes de dispersão com a deciduidade das espécies de Caatinga, Barbosa e colaboradores (2003) observaram que as espécies perenifólias foram exclusivamente zoocóricas, enquanto as espécies decíduas foram preferencialmente autocóricas, seguidas de anemocóricas. Isto corrobora que os padrões de dispersão de diásporos e as síndromes de dispersão na Caatinga são similares a outros ecossistemas com alta sazonalidade (GRIZ; MACHADO, 2001), o que, por sua vez, garante a ocorrência de frutos durante todo o ano na Caatinga.

A maior duração da fenofase de frutificação ocorre pelo longo período de maturação dos frutos (QUIRINO, 2006). Em ambientes de elevada sazonalidade, a grande proporção de fruto imaturo ocorre pela redução na disponibilidade de água, impedindo o amadurecimento de todos os frutos formados (QUIRINO, 2006). Por sua vez, os diásporos zoocóricos são mais frequentes durante a estação chuvosa em ambientes sazonal de Caatinga, enquanto os diásporos anemocóricos e autocóricos se dispersam preferencialmente na estação seca quando são favorecidos por grande incidência de ventos e queda de folhas, aumentando as distâncias de dispersão (GRIZ; MACHADO, 2001).

1.2 DIVERSIDADE FUNCIONAL

As medidas tradicionais de diversidade que levam em conta apenas o número de espécies e suas contribuições relativas, tem se mostrado pouco preditivas da estrutura e do funcionamento das comunidades (CIANCIARUSO et al., 2009). Medidas de diversidade que incorporem informações sobre as relações filogenéticas das espécies ou suas características funcionais tem se mostrado mais sensíveis para detectar respostas das comunidades às mudanças ambientais do que as medidas tradicionais de diversidade (CIANCIARUSO et al., 2009; PETCHEY; GASTON, 2006; RICOTTA et al., 2005).

Em 2001, Tilman propôs um conceito para diversidade funcional que pode ser traduzido como o valor e a variação das espécies e de suas características que influenciam o funcionamento das comunidades. A diversidade funcional, portanto, estima as diferenças entre os organismos a partir de características funcionais, as quais devem levar em consideração os atributos funcionais que influenciam os processos da comunidade, independentemente da filogenia dos organismos (CIANCIARUSO et al., 2009). Isso também ajuda a esclarecer os processos que determinam o funcionamento das comunidades, na medida em que associa organismos e comunidades através de mecanismos como a complementaridade no uso de recursos e facilitação (PETCHEY; GASTON, 2006).

Estudos anteriores, mostram que ecossistemas com alta diversidade de características funcionais tem maior eficiência no uso de água, nutrientes e luz e aumento da produtividade (HOOPER; VITOUSEK, 1997; TILMAN et al., 1997), além de serem mais resistentes (TILMAN; DOWNING, 1994). Entretanto, as práticas humanas que alteram a diversidade funcional possuem grande impacto em processos ecossistêmicos, podendo causar perda de espécies ou de grupos funcionais (TILMAN et al., 1997). A erosão de grupos funcionais ocorre pela perda de habitat e de espécies e afeta a comunidade de árvores como: espécies tolerantes à sombra (OLIVEIRA et al., 2004; SANTOS, *et al.* 2008), do estrato emergente (OLIVEIRA et al., 2004), polinizadas por vertebrados (GIRÃO et al., 2007) e com sementes grandes e dispersas por vertebrados (MELO et al., 2006; SANTOS et al., 2008). Principalmente os níveis tróficos mais altos podem ser afetados pela perda de diversidade funcional (FONTAINE et al., 2006).

A formação de grupos ecológicos independe dos padrões filogenéticos das espécies, as condições adversas favorecerão a co-ocorrência de espécies filogeneticamente distantes e as condições favoráveis removerão a associação sistemática (WEBB et al., 2002; WEBB et al., 2006). Desta forma, as características que culminam na convergência adaptativa podem agrupar espécies filogeneticamente diferentes e desagregar funcionalmente espécies próximas (WEBB et al., 2006).

A utilização de parâmetros reprodutivos para determinação da diversidade funcional de uma comunidade ainda é um campo novo para a ciência. Os atributos reprodutivos contribuem para a compreensão da heterogeneidade morfológica e funcional de ecossistemas

(MACHADO; LOPES, 2004), mas o cálculo preciso e atuais da diversidade funcional ainda não foi aplicado para estes parâmetros nas espécies de Caatinga. Os estudos com abordagem funcional já realizados na Caatinga abordam parâmetros de diversidade tradicionais e exploram atributos específicos que podem responder a um determinado parâmetro ambiental (MACHADO; LOPES, 2004; SOBRINHO et al., 2016).

1.2.1 Atributos Funcionais

Atributos funcionais são características do organismo que afetam seu fitness, respondendo ao ambiente abiótico e suas interações, os quais podem estar relacionados às tolerâncias a condições e a competição por recursos (DÍAZ; CABIDO, 2001). Os atributos funcionais são importantes nos processos estruturadores de comunidades, pois tanto tolerância ao ambiente quanto competição por recursos são fundamentais para entender organização de comunidades (DÍAZ; CABIDO, 2001).

A disponibilidade de água favorece a diversidade de espécies nos ambientes (O'BRIEN et al., 2000) e consequentemente a diversidade de atributos das plantas (DÍAZ et al., 1998), os quais estão relacionados com os vínculos entre os filtros ambientais e os principais traços funcionais da vegetação dominante (DÍAZ et al., 1997).

Os atributos florais atuam como sinais atrativos para os animais polinizadores que, por sua vez, norteiam seu comportamento de forrageio (SCHAEFER et al., 2004). O conjunto de atributos florais, relacionados às características morfológicas, fisiológicas e ecológicas, que reunidas podem ajudar na previsão dos vetores de polinização, é conhecido como síndromes de polinização, as quais podem ser mediadas tanto por vetores bióticos quanto por abióticos (FAEGRI; VAN DER PIJL, 1979). Desta maneira, a classificação das espécies em síndromes de polinização facilita a organização da diversidade taxonômica de Angiospermas a partir de seus atributos florais e ajuda a inferir o vetor de polinização de determinada espécie (OLLERTON et al., 2009).

Os frutos também apresentam atributos funcionais que, reunidos, podem ajudar na predição de dispersores de diásporos, conhecidas como síndromes de dispersão (VAN DER PIJL, 1982). Os atributos dos frutos usados na dispersão estão relacionados à consistência do pericarpo, mecanismos de deiscência, presença de estruturas aladas, aderentes. Assim, os atributos de flores e frutos que apresentam respostas ambientais e efeitos nos serviços ecossistêmicos, como na interação planta-polinizador e planta-dispersor, atuam no funcionamento dos ecossistemas e ajudam a compreender a organização das comunidades vegetais (DÍAZ; CABIDO, 2001).

1.2.2 Síndromes de Polinização e de Dispersão de Sementes

Atualmente, a utilização da classificação das síndromes de polinização é bastante questionada devido ao seu valor preditivo, muitos autores argumentam que a inclusão das espécies em síndromes é superficial, pois a maioria das espécies apresenta polinização generalista (KINGSTON; MC QUILLAN, 2000; MCCALL; PRIMACK, 1992). O valor preditivo das síndromes de polinização determina a confiabilidade da predição a partir das características florais, quando comparadas com as observações realizadas em campo. Apesar das inconsistências, o uso de síndromes é importante para a organização e inferências dos vetores de polinização (OLLERTON et al., 2009), o que norteia inicialmente os estudos taxonômicos e de polinização. Diante das inconsistências no uso das síndromes de polinização, Rosas-Guerreiro e colaboradores (2014) em revisão sistemática das síndromes encontraram que a evolução floral convergente está relacionada à adaptação ao grupo polinizador mais eficaz e a previsibilidade das síndromes de polinização é maior em espécies que dependem de polinizadores e em plantas de regiões tropicais. Os estudos que testam quantitativamente a eficiência dos polinizadores, enfim, comprovam que os polinizadores mais eficientes correspondem consistentemente aos previstos pela síndrome e o valor preditivo da síndrome tende a ser maior para espécies polinizadas exclusivamente por um grupo funcional do que para espécies polinizadas por mais de um grupo funcional (ASHWORTH et al., 2015).

Nós baseamos a classificação das espécies nas síndromes tradicionais de polinização, de acordo com os atributos florais relacionados com a atração de polinizadores (FAEGRI; VAN DER PIJL, 1979; VAN DER PIJL, 1960; 1961; VOGEL, 1954), os quais os principais vetores de polinizadores incluem abelhas (síndrome de *melitofilia*), borboletas (*psicofilia*), mariposas noturnas e esfingídeos (*falenofilia* e *esfinfofilia*), aves (*ornitofilia*), morcegos (*quiropterofilia*) e vento (*anemofilia*), as quais são classificadas de acordo com a antese, tipo floral, coloração, presença de guias de recursos, tipo de recurso floral e emissão de odores.

Por sua vez, as síndromes de dispersão de sementes são organizadas em três grandes grupos fundamentais, de acordo com as características morfológicas dos frutos (STEVENS et al., 2013; VAN DER PIJL, 1982), sendo eles: *anemocoria* (cujos diásporos são dispersos pelo vento e apresentam características que facilitam a ação do vento, como pericarpo seco e leve e estruturas aladas), *autocoria* (os diásporos podem ser dispersos por ação do peso/gravidade ou por mecanismos de explosão e apresentam atributos funcionais como, pericarpo seco, deiscentes e as sementes podem ser pesadas) e *zoocoria* (cujos diásporos são dispersos por animais, tanto aderidos ao pelo quanto por ingestão para longe da planta-mãe e variam de pericarpo seco a carnoso).

1.2.3 Diversidade Funcional Reprodutiva

A diversidade funcional das interações planta-animal atua analisando a estrutura da comunidade e o funcionamento do ecossistema (FONTAINE et al., 2006; GIRÃO et al., 2007; MAYFIELD et al., 2006), visto que a disponibilidade de recursos de flores e frutos está relacionada com a capacidade de prover serviços ecossistêmicos de polinização e dispersão. A redução da diversidade funcional reprodutiva ameaça a permanência das comunidades planta-polinizador, sendo necessário manter a funcionalidade das redes de polinização a fim de evitar a perda de biodiversidade (FONTAINE et al., 2006; GIRÃO et al., 2007). A relação fruto-dispersor envolve as características nutritivas dos frutos e a capacidade de consumo dos dispersores. De uma forma geral, a presença de grandes sementes está relacionada com a presença de vertebrados dispersores (MELO et al., 2006; SANTOS et al., 2008).

A polinização mediada por animais é um dos serviços ecossistêmicos mais importantes, pois os polinizadores garantem a formação de frutos consumidos pela humanidade (COSTANZA et al., 1997; FONTAINE et al., 2006). A relação planta-polinizador aumenta a diversidade funcional destas espécies por complementaridade entre os grupos funcionais de polinizadores e de plantas; e tende a aumentar o recrutamento das comunidades vegetais (FONTAINE et al., 2006). Na Caatinga, os atributos florais foram estudados com base na classificação das síndromes de polinização (MACHADO; LOPES, 2004; QUIRINO; MACHADO, 2014) e comparados com outros tipos de vegetação. Os estudos revelaram que os sistemas de polinização na Caatinga são diversificados, com baixa porcentagem de flores generalistas e semelhante a outras comunidades de florestas tropicais secas e úmidas. Os atributos de frutos em Caatinga também foram estudados e relacionados com as síndromes de dispersão, sendo a zoocoria mais frequente, seguida da anemocoria e da autocoria (GRIZ; MACHADO, 2001; QUIRINO, 2006). Neste sentido, é necessário um estudo mais abrangente que caracterize um padrão de diversidade funcional da comunidade de

Caatinga, em relação aos seus atributos reprodutivos para polinização e dispersão (ver SOBRINHO et al., 2016).

Uma característica encontrada em ambientes extremos é a adaptação e manutenção dos atributos funcionais, relacionados com a dinâmica compensatória, que por sua vez é um importante componente na estabilidade de comunidades e atua na diversidade de respostas às mudanças ambientais (GONZALEZ; LOREAU, 2009). Evidências mostram que a perda ou declínio de espécies tolerantes pode ser compensado pelo crescimento de outras espécies (IVES; CARDINALE, 2004). Desta forma, a dinâmica compensatória envolve modos de compensação de crescimento e declínio entre espécies em respostas às mudanças ambientais ocorrendo em uma ou mais escalas temporais (KEITT, 2008; VASSEUR; GAEDKE, 2007). A estabilidade da comunidade e resiliência do ecossistema são difíceis de detectar porque a dinâmica de populações é governada por efeitos diretos na demografia e interação de espécies (GONZALEZ; LOREAU, 2009).

De uma forma geral, a diversidade funcional reprodutiva em espécies de Caatinga é um campo ainda inexplorado, mas com potencial para determinação de padrões reprodutivos para florestas tropicais secas. Diante da crescente busca em compreender a dinâmica funcional reprodutiva de comunidades vegetais, nosso estudo focará em testar as hipóteses apresentadas a seguir.

2 HIPÓTESES E OBJETIVOS

2.1 HIPÓTESES

1. A frequência de espécies e indivíduos em floração e frutificação nas espécies lenhosas da Caatinga é proporcional à disponibilidade de água, seja relacioda ao período chuvoso quanto em áreas com maior precipitação.

2. A reprodução das espécies lenhosas da Caatinga é afetada por distúrbios antrópicos crônicos, pois diminui a frequência de floração e frutificação na comunidade.

3. A diversidade funcional reprodutiva aumenta com o gradiente de precipitação em comunidades de plantas lenhosas de Caatinga, devido à grande variedade de atributos funcionais em áreas com maior pluviosidade.

4. A diversidade funcional reprodutiva diminui com o aumento de perturbação crônica em espécies lenhosas da Caatinga, devido à simplificação das espécies nas áreas perturbadas.

5. A diversidade das síndromes de polinização e de dispersão por animais é maior em áreas com grande quantidade de chuvas, devido ao desenvolvimento dos atributos especializados de flores e de frutos que estão relacionados à interação planta-animal nestas áreas.

2.2 OBJETIVO GERAL

Avaliar a disponibilidade de recursos florais e de frutos em escalas espacial e temporal, as síndromes de polinização e de dispersão e a diversidade funcional reprodutiva em uma comunidade de plantas lenhosas de Caatinga nos gradientes de precipitação e de perturbação antrópica crônica.

2.3 OBJETIVOS ESPECÍFICOS

Para as espécies arbustivas e arbóreas de uma comunidade de Caatinga distribuídas nos gradientes de precipitação e de perturbação antrópica crônica, pretendeu-se:

- Avaliar a ocorrência, a periodicidade e a sincronia de eventos de floração e frutificação, em escala espacial e temporal;
- Analisar os atributos qualitativos e quantitativos/mensuráveis de flores e frutos;
- Determinar os tipos e a frequência das síndromes de polinização e de dispersão;
- Calcular e analisar a diversidade funcional.

3 COMMUNITY-LEVEL PLANT PHENOLOGY RESPOND TO PRECIPITATION AND HUMAN DISTURBANCE IN A CAATINGA DRY FOREST

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Running headline: Community-level plant phenology respond

Artigo a ser submetido ao Journal of Ecology (Fator de Impacto = 6.13, Qualis = A1, esta seção segue a norma da revista, com normas em anexo A)

Summary

1. Phenological cycles are a key attribute of plant communities as they control the resources for plant attendants such as herbivores, pollinators and seed dispersers, and consequently patterns of biodiversity organization and persistence. Although phenological cycles usually correlate with climatic variables, it is unknown how they would respond to the combined effect imposed by changes in annual rainfall and chronic human disturbances.
2. In this paper we examine how reproductive phenology of woody plant assemblages respond to a 500-mm variation on average annual rainfall and disturbances imposed by goats, firewood collection and timber exploitation in a Caatinga dry forest. A total of 217 woody plants (56 species of 19 families) across 10 permanent forest plots were monitored through two whole year between (Aug/2014 and Jul/2016) regarding reproductive phenophases of flowering and fruiting. Plots were located along a precipitation (500-1000 mm) and chronic disturbance gradients in the Catimbau National Park, Northeast Brazil. We assessed the reproductive seasonality using circular statistics and the effects of gradients using general linear models.
3. Flowering and fruiting was continuous and with two seasonal peaks throughout the year. Production of flowers and fruits increased through the precipitation gradient, while individuals' synchrony in flowering and fruiting was higher across assemblages exposed to lower precipitation levels. Both flowering and fruiting patterns were negatively affected by human disturbance and by interaction of both gradients.
4. *Synthesis*. Caatinga woody plant assemblages support flowering and fruiting through the whole year. However, precipitation acts as an important trigger for reproductive development, while chronic human disturbance acts as an environmental factor limiting flowering and fruiting of woody species of Caatinga. These findings reinforce the

notion that climate change and chronic disturbances are able to alter phenological patters of dry forests with unanticipated impacts on biodiversity organization and persistence.

Keywords: Caatinga, flowering, fruiting, chronic human disturbance, precipitation, seasonality, woody species

INTRODUCTION

Phenological patterns related to the availability of leaves, flowers and fruits in plants at the community level are important for the support of plant-animal interactions, such as herbivory, pollination and seed dispersal (Aide, 1993; Johansson, Kristensen, Nilsson, & Jonzén, 2015; Rafferty, CaraDonna, & Bronstein, 2015). Ecological interactions maintain the ecological complexity at the community level, particularly in tropical forests (Carlo & Morales, 2016; Leal, Lopes, Machado, & Tabarelli, 2017). Changes in phenological patterns cause mismatches in the maintenance and conservation of mutualistic interactions between interdependent species, related to the absence of available resources (Morellato et al. 2016; Rafferly et al. 2015). Phenological cycles also maintain biodiversity, caused by the significant relationship between floristic and phenological similarities (Viña, Liu, Zhou, Huang, & Liu, 2016). In addition, phenological patterns directly influence the functioning of ecosystems by shaping the occurrence of events and the availability of resources, especially associated to environmental and climatic changes (Cleland, Chiariello, Loarie, Mooney, & Field, 2006).

In dry forests, the occurrence of phenological events is shaped mainly by abiotic conditions, *i.e.* precipitation (Griz & Machado, 2000; Justiniano & Fredericksen, 2000; Quirino 2006). The response of dry forest plants to precipitation is related to water availability by rainfall as well as by water storage in stems and roots during periods of aridity

(Borchert, 1994; Borchert & Rivera, 2001). Increased temperature and reduced precipitation in semi-arid regions cause decrease in plant reproductive capacity due to loss of insect pollinators and simplification of ecological interactions (Lesica & Kittelson, 2010). In general, seasonal variation in tree water status seems to be the main determinant in phenology and distribution of tree species in Tropical Dry Forests (Borchert, 1994), enabling water use and storage in different ways such as inside tissues (Lima et al., 2002). The rainfall reduction tends to decrease vegetation cover, simplifying the ecosystem interactions (Nobre & Borma, 2009; Hirota, Holmgren, Van Nes, & Scheffer, 2011).

Chronic human disturbance is the continuous removal of small fractions of forest biomass through the extraction of forest products in pastures, firewood and non-timber (Singh, 1998). Chronic human disturbance can disrupt ecological processes from population to ecosystem level, and consequently the provision of ecosystem services (Malhi, Gardner, Goldsmith, Silman, & Zelazowski, 2014), such as pollination and seed dispersal (Arroyo-Rodríguez et al., 2017). At community level, chronic disturbances have proved to anthropogenic activities may also result in simplification and homogenization of plant communities, which alter ecosystem functioning and its ecological capacity (Singh, 1998). However, drier areas have functionally impoverished plants that become more sensitive to anthropogenic disturbance (Rito, Arroyo-Rodríguez, Queiroz, Leal, & Tabarelli, 2017). The exploitation of forest resources in the Caatinga dry forest (i.e. chronic human disturbances), such as firewood collection, timber extraction and livestock production via native fodder, have significant impacts on the structure of woody plant assemblages (Leal, Tabarelli, & Silva, 2003), including the decrease on diversity and structure of tree species in Caatinga (Ribeiro, Arroyo-Rodríguez, Santos, Tabarelli, & Leal, 2015; Ribeiro, Santos, Arroyo-Rodríguez, Tabarelli, & Leal,2016). Combined to the effects of precipitation on plant species, chronic human disturbances also tend to alter phenological dynamics of species and ecosystems (Rito et al. 2017).

In a dry forest environment such as Caatinga, precipitation is a key factor on plant development and reproduction (Andrade, Lima, Rodal, Encarnação, & Pimentel, 2008; Machado, Barros, & Sampaio, 1997; Quirino & Machado, 2014). Thus, the reproductive phenological pattern in Caatinga area is often seasonal, related to the occurrence of a rainy season, which stimulates flowering and fruiting events (Barbosa, Barbosa, & Lima, 2003; Griz & Machado, 2001; Machado et al., 1997; Quirino & Machado, 2014). Although reproductive peaks are more frequent in the rainy season, it is common to record species in flowering and fruiting stages throughout the year (Barbosa et al., 2003; Griz & Machado, 2001; Machado et al., 1997; Quirino & Machado, 2014). A common fact in limiting environments is the synchrony of the reproductive events in the most favorable period to trigger the flowering and fruiting (Augspurger, 1983; Bencke & Morellato, 2002), in the Caatinga for example, some of the species concentrate the reproductive period in a specific season, dry or rainy season (Barbosa et al., 2003; Nadia et al. 2007).

In synthesis, community-level phenological patterns are expected to respond to a combination of forces, including climatic variables, soil conditions but also local human disturbances, such as those imposed by local human population dependent of forest resources. Here we examine how changes on average annual rainfall and chronic disturbances affect community-level patters of plant reproductive phenology in a Caatinga dry forest. We examined the following hypotheses: (1) the availability of rainfall favors the events of flowering and fruiting in woody species of semi-arid environment; (2) chronic human disturbance acts as environmental pressure on the frequency of reproductive events in the community of Caatinga woody plants; and (3) the synchrony of the reproductive events is greater when allied with hydric deficit in the Caatinga woody plants. We expect that (1) the frequency of flowering and fruiting individuals will increase in areas with higher precipitation, (2) chronic human disturbance will act as environmental pressure limiting the reproductive events in the Caatinga woody plants, and (3) the synchrony of flowering and fruiting will be greater in areas that rains less.

MATERIAL AND METHODS

Study area

The study was carried out in the Catimbau National Park (Figure 1), located in the semi-arid of Pernambuco State, Northeastern Brazil (8°24’00” and 8°36’35” S; 37°0”30” and 37°1’40” W). The National Park has an arboreal-shrub xerophytic vegetation, with a very heterogenous physiognomy, characteristic of Caatinga, varying with the formation type and soil structure from sedimentary to crystalline (Rodal, Andrade, Sales, & Gomes, 1998). This work was conducted exclusively in a region with sedimentary soil formation. The climate of the region is BSh (hot and dry climate) (Köppen, 1948), with annual average temperature of 26 °C and annual rainfall ranging between 650 and 1100 mm, with more intense rains between April and June (SUDENE 1990, SNE 2002).

The Catimbau National Park covers an area of over 62 000 ha, consisting in a vegetation mosaic in a natural precipitation gradient, according to the topography of the region (SNE, 2002), and a human disturbance gradient. Despite being a preservation area, there is a chronic disturbance due to land use, wood extraction, animal husbandry and hunting by the residents of the region (Rito et al., 2017).

Annual precipitation and disturbance index

The sites were delineated in the Projeto Ecológico de Longa Duração (PELD / CNPq) – Catimbau National Park and were distributed in a precipitation and chronic human disturbance gradient. Precipitation gradient varies from 510 to 940 mm of mean annual precipitation (see Rito et al., 2017) and a chronic human disturbance gradient that is based on the Global Multi-metric Chronic Anthropogenic Disturbance Index (GMDI) by Arman et al., (in prep.).

We used the average historical precipitation of each site to obtain the updated global climate data repository of the WorldClim for all sites, at a 1 km spatial resolution along the equator (following Rito et al., 2017). The plots were established in areas with no record of acute disturbance in the last 80 years, confirmed by aerial photographs and interviews with the local community. We classified the precipitation gradient in following categories: 1) low precipitation P1 = 510mm, P2 = 540mm, P3 = 588mm, 2) mean precipitation P4 = 645mm, P5 = 647mm, P6 = 653mm and 3) high precipitation P7 = 762mm, P8 = 787mm, P9 = 843mm and P10 = 940mm to facilitate the understanding of phenological results.

We used the index of chronic disturbance gradient proposed by Arman et al., (Supporting Information). Succinctly, the Global Multi-metric Chronic Anthropogenic Disturbance Index (GMDI) was calculated from three indicators of chronic disturbance (people pressure index – PPI, livestock pressure index – LPI and wood extraction index – WEI). These indices individually are composed of independent (i.e. not correlated) chronic disturbance metrics related to: herbivory and physical damages caused by cattle and goats; extraction of living and dead wood, and; nature resources used by people, respectively. Disturbance indicators were based on indirect measures based on geographic context, indirect measures based on the socio-ecological context, and direct measures based on local fieldwork. We tested if the single metrics that compose the GMDI were correlated among each other (Spearman’s correlation test), to avoid redundancy among disturbance metrics, but we found no significant correlation between variables. Finally, these three individual indices were integrated in the global GMDI index using fully-integrated formula of Legendre & Legendre

(1998) for single pressure indices (Arnan et al., Supporting Information). The overall index varies from 0 (zero values for all pressure metrics) to 100 (maximum values of all pressure metrics). This index has been successfully used in previous assessments about the effect of chronic disturbance on biodiversity (Arnan et al., Supporting Information).

Data collection

We monitored monthly 217 plants between August 2014 and July 2016 (24 months), corresponding to 56 species of 19 families (see Table S1, Supporting Information). We observed the reproductive phenophases of flowering (floral bud and anthesis) and fruiting (unripe and ripe fruit). We recorded the presence and absence of flowers and fruits in plants located in 10 permanent plots (50 x 20m) along precipitation and chronic human disturbance gradients that are > 2 km apart.

For the experiment assembly, we marked woody species (shrub and tree) for monitoring present in the plots with CSL (Circumference at the Soil Level) equal to or greater than 10 cm. We used the presence of flowers and fruits to analyze the frequency, synchrony and periodicity of the reproductive resources availability per month. We analyzed the species at community level according to their phenological pattern and phenophases synchrony. Species considered common (those that presented in more plots along the gradients, from six to seven plots) were analyzed individually for phenological pattern and synchrony, in order to observe spatial and temporal distribution of flowers and fruits of the species distributed in most of the gradients.

Phenological analysis

We analyzed the frequency of reproductive phenophases to determine the temporal distribution of flower and fruit resources between gradients areas and the occurrence of flowering and fruiting peaks. According to the frequency of occurrence of reproductive events, we classified the community pattern, as stated by Newstrom, Frankie, & Raker, (1994) and these were associated with precipitation events in the region. The synchrony index of the phenophases was calculated (adapted from Augspurger, 1983), considering individual synchrony index and community synchrony index for each phenophase.

Statistical analysis

We used circular statistics to analyze the phenological data (Morellato et al., 2000; Morellato, Alberti, & Hudson, 2010), in which we used the monthly frequency of phenophases during two years of observation to calculate the seasonality of the communities in both precipitation and chronic human disturbance gradients. We entered with the data according to the date of occurrence of phenophases, that is, the frequency of individuals in each month of observation. Later, we applied the circular analyses including: (1) mean angle – that indicates the vector or mean month, (2) length of vector r – that indicates the frequency of the phenophases around the mean angle, (3) standard deviation and (4) Rayleigh test – that tests the uniformity of data distribution (Zar, 1999; Morellato et al., 2000). The length of mean vector varies from 0 to 1, when 0 the data are equally distributed in the circle and when 1 the data are concentrated at a single angle. So, the higher the concentration of data around an angle the greater the seasonality. If, *p value* is significant, the distribution of the data differs from a homogeneous distribution, indicating seasonality of events. We performed all the circular statistics analyzes in the Oriana® software.

We tested the flowering and fruiting events with species composition in each plot for know if there is relation between the floristic composition and reproductive frequency of the woody flora. For this, we used the Pearson’s correlation test comparing the frequency of individuals and species with the respective composition of individuals and species in each area (Zar, 1999). We performed all analysis in the computational environment R software (R Development Core Team, 2017).

To evaluate the effect of precipitation and chronic human disturbance we preformed linear models (GLM) using the isolated and interaction variables between them (Prec:GMDI), to test such effects with flowering (number of species and individuals frequency) and fruiting (number of species and individuals frequency). We performed all the models in the computational environment R (R Development Core Team, 2017).

RESULTS

The woody species community of Catimbau National Park presented a continuous flowering pattern, with floral buds and flower production throughout the year. We observed two peaks of flowering, one in May/2015 and other in February/2016, both during the rainy season (Figure 2a). The frequencies of floral buds and anthesis were seasonal due to phenophases peak (Figure 3a–b). The fruiting of the woody community also presented a continuous pattern, with fruit production along the years of observation and soft peaks in August/2015 and March/2016 (Figure 2b). The production of ripe fruits was lower than the production of unripe fruits, with higher frequency of both phenophases between August and December, corresponding to the dry season of the region (Figure 3c–d).

Frequency of flowering individuals increased with the precipitation gradient (Figure 4a–f), i.e. there were more individuals with floral bud and flower in anthesis in areas of higher precipitation. Flowering seasonality was more evident in areas with lower rainfall (Figure 4a–c). The same pattern was observed for the fruiting phenophase (Figure 4g– l), which presented a marked seasonality in the community with a higher frequency of individuals in this phenophase, mainly in areas with mean and high precipitation (Figure 4j–k).

The results of the circular statistic indicated seasonality for all reproductive phenophase due significant results in the Rayleigh (Z) test (Table 1) for, woody plant community. In addition, when the precipitation gradient was tested, flowering presented higher seasonality in low and medium precipitation areas, with non-seasonal occurrence only in two areas of high precipitation (Table 2). Fruiting presented significant seasonality in only six of the 10 studied areas (Table 2), which in turn corresponded to areas of low (66.7%), mean (66.7%) and high rainfall (50%).

Individuals' synchrony in woody community was low for flowering and fruiting, with 0.25 and 0.32 for floral buds, 0.23 and 0.26 for flowers in anthesis, 0.24 and 0.28 for unripe fruits and 0.26 and 0.25 for ripe fruits in the first and second year of observation, respectively. Individuals' synchrony was also low along the precipitation gradient (Figure 5), although individuals in low and high precipitation areas presented higher synchronization of buds and flowers in anthesis (Figure 5a–b). Greater synchronicity of unripe fruits was observed in areas of low precipitation (Figure 5c), while for the mature fruits the highest synchrony occurred in mean precipitation (Figure 5d).

The most common species in woody community, present in seven of the ten plots, were *Cnidoscolus bahianus* (Ule) Pax & K. Hoffm, *Commiphora leptophloeos* (Mart.) J.B. Gillett and *Poincianella microphylla* (Mart. ex G. Don) L.P. Queiroz (see Table S1, Supporting Information), which presented seasonality in both flowering and fruiting phenophases. Thus, confirming the seasonality patterns, the following results were found in the Rayleigh test: *C. bahianus* with $Z = 6.39$; $p = 0.001$ and $Z = 4.15$; $p = 0.011$, *C. leptophloeos* with $Z = 13.75$; $p = 2.64 \times 10^{-07}$ and $Z = 2.89$; $p = 0.04$ and *P. microphylla* with $Z = 5.46$; $p = 0.003$ and $Z = 8.95$; $p = 6.94 \times 10^{-05}$ for flowering and fruiting, respectively. These species had the highest frequency of individuals in the phenophases in distinct months, being *C. bahianus* in February and April, *C. leptophloeos* in December and February, and *P. microphylla* in June and August for flowering and fruiting, respectively.

Flowering synchrony in most common species was high in *C. leptophloeos* and *P. microphylla*, in both years of observation (Table 3). However, fruiting synchrony was higher in *C. leptophloeos* in the first year and *C. bahianus* in the second year (Table 3), with occurrence of phenophases at different times of the year between the two species.

The events of flowering and fruiting of the woody flora had significant relations with species composition in each plots for both individuals and species frequency. So, for flowering we obtained $r = 0.78$, $p = 0.008$; $r = 0.92$, $p = 0.0001$ and for fruiting $r = 0.64$, $p = 0.044$; $r = 0.87$, $p = 0.0009$ to species and individuals frequency, respectively.

Significant relations were found when analyzing the effect of gradients between phenological variables. Human disturbance and interaction between precipitation and human disturbance affected the amount of species and frequency of individuals in both flowering and fruiting. On the other hand, precipitation only showed significant effect on the frequency of individuals in both flowering and fruiting (Table 4).

DISCUSSION

Our results suggest that first, both precipitation and chronic human disturbance act on the occurrence and frequency of flowering and fruiting species. Second, human disturbance (including its interaction with precipitation) has negative effect on the frequency of species and individuals in flowering and fruiting, because decreased the frequency of reproductive individuals due to the environmental stress in disturbed areas. Third, the seasonality and synchrony of reproductive phenophases is higher, especially in areas with lower rainfall. In synthesis, our findings support the initial hypotheses that rainfall favors the events of flowering and fruiting, chronic human disturbance acts as environmental pressure limiting the reproduction of woody species and the synchrony of the reproductive events is related with hydric deficit in Caatinga.

Although the production of flowers and fruits in Caatinga community occurs along the year, the peaks of occurrence of reproductive phenophases related to the rainy season in each year of observation shows seasonality of flowering and fruiting in the study area. Seasonality of reproductive events reflects the differentiation of niche spaces in order to avoid competition by pollinators and seed dispersers that depend on the same food resources at a given time of the year (Ferraz, Artes, Mantovani, & Magalhães, 1999; Murali & Sukumar, 1994; Poole & Rathcke, 1979). In this way, flowering and fruiting in different periods of the year contribute to the maintenance of pollinators and dispersers guilds (Fortunato & Quirino, 2016), especially in periods of resources scarcity that are common in Caatinga environments (Quirino & Machado, 2014; Santana & Machado, 2010).

Intense seasonality of water resources in Caatinga forms a selective pressure that acts on the evolution of species with different phenological and physiological strategies related to water availability in the soil or water stored in plant tissues (Lima et al., 2012). Seasonality of reproductive phenophases occurring in Dry Tropical Forest species is already known, with peaks recorded in dry or rainy seasons (Barbosa et al., 2003; Griz & Machado, 2001; Machado et al., 1997; Quirino & Machado, 2014). The highest frequencies of flowering and fruiting species in the rainy season are evidenced by the dependence of water availability to trigger reproductive events in plants of semi-arid environments (Bullock & Solis-Magallanes, 1990; Lesica & Kittelson, 2010).

Higher frequency of flowering and fruiting events in areas with higher precipitation indicates the dependence of dry forest plants species on performing their reproductive processes when water is available (Barbosa et al. 1989; Nogueira, Pacheco Filho, Gallão, Bezerra, & Medeiros Filho, 2013), and it reflects the need of plants to maximize efforts in cyclic activities and reproduction during the rainy season in regions with water deficit (Lesica & Kittelson, 2010; Shen, Piao, Cong, Zhang, & Jassens, 2015). As observed in this study, more evident seasonality of flowering and fruiting in areas with lower precipitation indicates that species that compose this physiognomy depend on beginning reproduction along with the rainy season, so all species can maximize efforts to guarantee reproduction in a short period. Phenology studies point to precipitation as a triggering factor for phenological events in Caatinga plants (Amorim, Sampaio, & Araújo, 2009; Barbosa, Alves, Prazeres, & Paiva, 1989; Griz & Machado 2001; Lima et al., 2012; Machado et al., 1997), which may be related to Caatinga characteristic such as low and irregular precipitation and high evapotranspiration potential (Sampaio, 1995).

Distribution of species along the precipitation gradient may be related to their affinity with water availability. Precipitation acts as a filter of species that require greater amount of water to develop their activities (Rito et al., 2017), e.g. *Psidium oligospermum* DC., *Ruprechtia laxiflora* Meisn. and *Zanthoxylum stelligerum* Turcz. On the other hand, some species seem to need a lower amount of water available for their development and reproductive activities, which is observed exclusively in areas with low precipitation volume (e.g. *Cynophalla hastata* (Jacq.) J. Presl, *Spondias tuberosa* Arruda and *Ziziphus joazeiro* Mart). In turn, some species are well distributed along the precipitation gradient and are able to well establish themselves independent of water availability, as in the case of *Cnidoscolus bahianus*, *Commiphora leptophloeos* and *Poincianella microphylla*. This phenological diversity on dry forest shows the existence of divergent ecological strategies to deal with seasonal moisture constraints, which exhibit limits in response to extreme dry events (Lasky, Uriarte, & Muscarella, 2016).

Low synchrony in the reproduction of individuals in woody community as well as in each area with different levels of precipitation may have occurred due to the low number of individuals reproducing along the study. Depending on the time scale, phenology of plant communities can be characterized by synchronous, asynchronous and compensatory dynamics partly due to seasonal fluctuations in abiotic constraints (Lasky et al., 2016). We observed that some species and/or individuals did not reproduce in all years of the study, which may be related to the supra-annual occurrence of reproductive phenophases, in which individuals intercalate the reproductive period in the species. The supra-annual pattern occurs in rare flowering species (reproductive cycle of more than 12 months), being common in species distributed along environments with strong environmental filtration such as dry tropical forests and wet forest edges (Newstrom et al., 1994). This pattern may be an intrinsic strategy of these species, which controls the energy demand to invest in reproduction only when optimal conditions of water availability is present and thus avoiding loss of energy (Araújo, Castro, & Albuquerque, 2007).

C. leptophloeos and *P. microphylla* presented high synchronization of flowering and fruiting in the precipitation gradient. They have high seasonality in occurrence of reproductive phenophases related to the rainy season, regardless of the respective location along the precipitation gradient. The high reproductive capacity of these species can also be related to their capacity of adaptation to the water deficit, which can be well established independent of the water availability on the environment, which explains its wide distribution in the studied area. However, *C. bahianus* presented low synchrony of individuals in reproduction phase due to the continuous reproductive pattern, since this species was observed in flowering and fruiting stages in most months of the years, even at low intensity. The seasonal reproductive pattern favors high synchrony of individuals in a certain phenophase, while the continuous pattern is responsible for the low synchrony of individuals (Augspurger, 1983).

The effect of chronic disturbance on frequency of individuals and species in flowering and fruiting indicates that human activities may reduce the reproductive capacity of woody species of Caatinga, including when there is interaction with precipitation. In this way, the chronic disturbance is acting as an environmental filter limiting the reproductive development in Caatinga. Both habitat loss and human activities have a negative effect on the reproduction of plants in dry forests (Quesada et al., 2011), which are related to changes in temperature, irradiation, evapotranspiration and wind exposure (Kapos, Wandelli, Camargo, & Ganade, 1997; Laurance et al., 2002; Wright, 1996).

In summary, we can conclude that clustering and relation of the areas with precipitation and chronic disturbances indeces in Catimbau National Park were due to the influence of environmental variables associated with species composition. Thus, it is observed that both precipitation and chronic disturbances may be acting in structure and organization of woody community on Caatinga. Water availability is the most important abiotic factor of Caatinga plants development (Sampaio, 1995), while anthropic actions act modifying the natural landscape and consequently the ecosystem processes (Araújo et al., 1997). Anthropogenic activities can cause simplification and homogenization of plant communities due to habitat loss for the use of natural resources by traditional populations (Singh, 1998; Leal et al., 2013). Dry forests are important wildlife refuges due to their high diversity, high endemism and high species substitution (beta diversity) in Seasonally Dry Tropical Forests. Consequently, they require a stricter conservation policy for the maintenance of ecological interactions (Dryflor, 2016).

In this context, precipitation seems to be an essential factor for reproductive phenological development of Caatinga species, especially when water restriction is more limiting as in areas with the lowest precipitation gradient. Seasonality of the reproductive phenophases is greater in these areas, since it acts determining the trigger to reproductive processes of species. On the other hand, chronic disturbance acts as an environmental filter limiting the frequency of species reproduction. In this way, we showed that availability of precipitation favors flowering and fruiting events of woody species of Catimbau National Park, while human disturbance limits those events.

AUTHORS’ CONTRIBUTIONS

M.E.M.F., M.T. and I.C.S.M. conceived the ideas and designed methodology; M.E.M.F. and N.M.A. collected the data; M.E.M.F. and M.T. analyzed the data; M.E.M.F. and M.T. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

This study was supported by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (PELD process 403770/2012-2, Universal process 470480/2013-0). Thanks to Fundação de Amparo à Ciência e Tecnologia do Estado de Pernambuco (Facepe) for funding the scholarship to M.E.M.F. (process IBPG-0820-2.03/13). We also thank Davi Jamelli for elaborating Figure 1.

Table 1. Results of circular statistical analysis of reproductive phenophases of woody community of Catimbau National Park. Significant values that indicate seasonality of reproductive events are in bold.

	Flower buds	**Flower**	**Unripe fruit**	**Ripe fruit**
Observations (N)	617	473	406	245
Mean angle	38.17°	27.46°	150.26°	285.41°
Mean date	february	january	june	october
Angular standard deviation	102.24°	108.21°	101.19°	101.09°
Length of the mean vector (r)	0.20	0.168	0.21	0.21
Rayleigh Test (Z)	25.55	13.36	17.94	10.90
Rayleigh test (p)	$\mathbf{7.9 \times 10^{-12}}$	$\mathbf{1.6 \times 10^{-06}}$	$\mathbf{1.6 \times 10^{-08}}$	$\mathbf{1.9 \times 10^{-05}}$

Table 2. Results of circular flowering and fruiting of woody species in ten plots (P1 to P10) along the precipitation gradient in Catimbau National Park. Significant values that indicate seasonality of reproductive events are in bold. Legend: Flo = flowering and Fru = Fruiting.

	P1 510 mm		**P2 540 mm**		**P3 588 mm**		**P4 645 mm**		**P5 647 mm**		**P6 653 mm**		**P7 762 mm**		**P8 787 mm**		**P9 843 mm**		**P10 940 mm**	
	Flo	**Fru**	**Flo**	**Fru**	**Flo**	**Fru**	**Flo**	**Fru**	**Flo**	**Fru**	**Flo**	**Fru**	**Flo**	**Fru**	**Flo**	**Fru**	**Flo**	**Fru**	**Flo**	**Fru**
Observations (N)	24	11	39	22	87	31	85	68	17	16	85	76	35	22	77	82	85	37	20	8
Mean angle	13.06°	120.67°	32.02°	105.98°	16.57°	160.16°	6.025°	100.93°	295.89°	228.23°	60°	173.38°	295.48°	56.57°	84.76°	187.79°	23.92°	345.22°	139.11°	141.77°
Mean date	Jan	May	Feb	Apr	Jan	Jun	Jan	Apr	Oct	Aug	Feb	Jun	Oct	Feb	Mar	Jul	Jan	Dec	May	May
Angular standard deviation	71.73°	63.22°	74.33°	46.43°	103.29°	89.31°	101.048°	109.51°	74.43°	61.57°	85.41°	71.18°	94.11°	68.50°	95.33°	88.36°	101.69°	94.71°	94.25°	78.15°
Length of the mean vector (r)	0.46	0.54	0.43	0.72	0.20	0.30	0.21	0.16	0.43	0.56	0.33	0.46	0.26	0.49	0.25	0.31	0.21	0.26	0.26	0.39
Rayleigh Test (Z)	5.01	3.26	7.25	11.41	3.37	2.73	3.79	1.76	3.15	5.04	9.21	16.25	2.36	5.27	4.83	7.61	3.64	2.41	1.35	1.25
Rayleigh test (p)	**0.006**	**0.035**	**5.43 x 10^{-04}**	**2.06 x 10^{-06}**	**0.034**	0.06	**0.023**	0.17	**0.04**	**0.005**	**9.9 x 10^{-05}**	**8.9 x 10^{-08}**	0.094	**0.004**	**0.008**	**5.0 x 10^{-04}**	**0.026**	0.09	0.27	0.30

Table 3. Synchrony of individuals of most common species in reproductive phenophases in woody community of Catimbau National Park. Highest values of synchrony are in bold.

	Cnidoscolus bahianus		*Commiphora leptophloeos*		*Poincianella microphylla*	
	Year 1	Year 2	Year 1	Year 2	Year 1	Year 2
Bud	0,33	0,33	**0,76**	**0,78**	**0,81**	0,51
Anthesis	0,32	0,22	**0,76**	**0,78**	**0,73**	**0,72**
Unripe Fruit	0	**0,6**	**1**	0	0,41	0,42
Ripe Fruit	0	0	0	0	0,34	0,18

Table 4. Effects of precipitation and human disturbance gradients on number of species and frequency of individuals in flowering and fruiting of woody species of Caatinga.

	Estimate	SE	z	P	DE
Flowering species					
Precipitation	-1.59×10^{-03}	1.55×10^{-03}	-1.03	0.31	0.46
GMDI	-1.14×10^{-01}	5.83×10^{-02}	-1.96	**0.05**	
Precipitation:GMDI	1.72×10^{-04}	8.37×10^{-05}	2.06	**0.04**	
Flowering frequency					
Precipitation	-3.17×10^{-03}	6.35×10^{-04}	-5.00	**6.0×10^{-07}**	0.26
GMDI	-1.45×10^{-01}	2.38×10^{-02}	-6.12	**9.53×10^{-10}**	
Precipitation:GMDI	2.09×10^{-04}	3.43×10^{-05}	6.08	**1.19×10^{-09}**	
Fruiting species					
Precipitation	-1.71×10^{-03}	1.67×10^{-03}	-1.03	0.31	0.5
GMDI	-1.47×10^{-01}	6.44×10^{-02}	-2.28	**0.02**	
Precipitation:GMDI	2.12×10^{-04}	9.10×10^{-05}	2.33	**0.01**	
Fruiting frequency					
Precipitation	-5.74×10^{-03}	8.38×10^{-04}	-6.85	**7.36×10^{-12}**	0.51
GMDI	-0.31	0.03	-10.01	**$< 2 \times 10^{-16}$**	
Precipitation:GMDI	4.34×10^{-04}	4.38×10^{-05}	9.9	**$< 2 \times 10^{-16}$**	

Figure Legends

Figure 1. Location of study area in the Northeastern region of Brazil (a) and highlighting the Catimbau National Park area (rectangle) in the State of Pernambuco (b). Details of plot marking (c), in which color variation indicates the water deficit (stronger colors indicate lower precipitation) (Source: PELD Catimbau database).

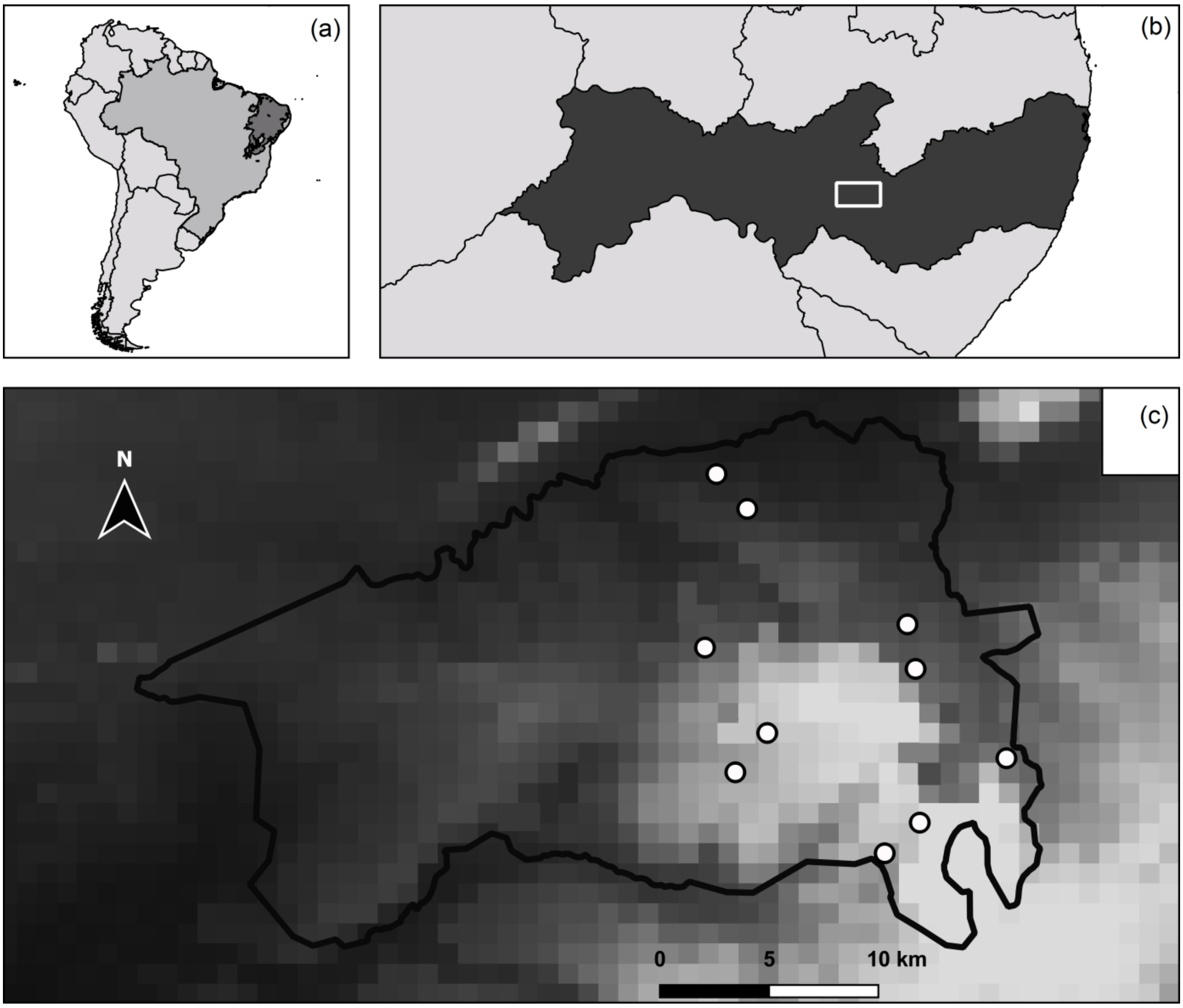
Figure 2. Phenology of flowering (a) and fruiting (b) and their respective amounts of individuals in phenophases in low, medium and high precipitation areas of Caatinga woody species of Catimbau National Park, Brazil. The rainy season in each year of study is highlighted.

Figure 3. Circular histograms of frequency of individuals in flowering and fruiting in woody community of Catimbau National Park. (a) frequency of floral buds, (b) frequency of open flowers, (c) frequency of unripe fruits and (d) frequency of ripe fruits.

Figure 4. Circular histograms of frequency of flowering individuals (a–f) and fruiting (g–l) of woody species along the precipitation gradient in the different plots analyzed (low precipitation: P1 = 510 mm and P2 = 540 mm; mean precipitation: P5 = 647mm and P6 = 653mm, high precipitation: P8 = 787mm and P9 = 843mm) of Catimbau National Park. (a–b) flowering in low precipitation, (c–d) flowering in mean precipitation, (e–f) flowering in high precipitation, (g–h) fruiting in low precipitation, (i–j) fruiting in mean precipitation, (k–l) fruiting in high precipitation.

Figure 5. Synchrony of individuals in flowering and fruiting phenophases in woody community in a precipitation gradient in Catimbau National Park. (a) synchrony of individuals in floral buds, (b) synchrony of individuals in open flowers, (c) synchrony of individuals in unripe fruits and (d) synchrony of individuals in ripe fruits.

Figure 1.



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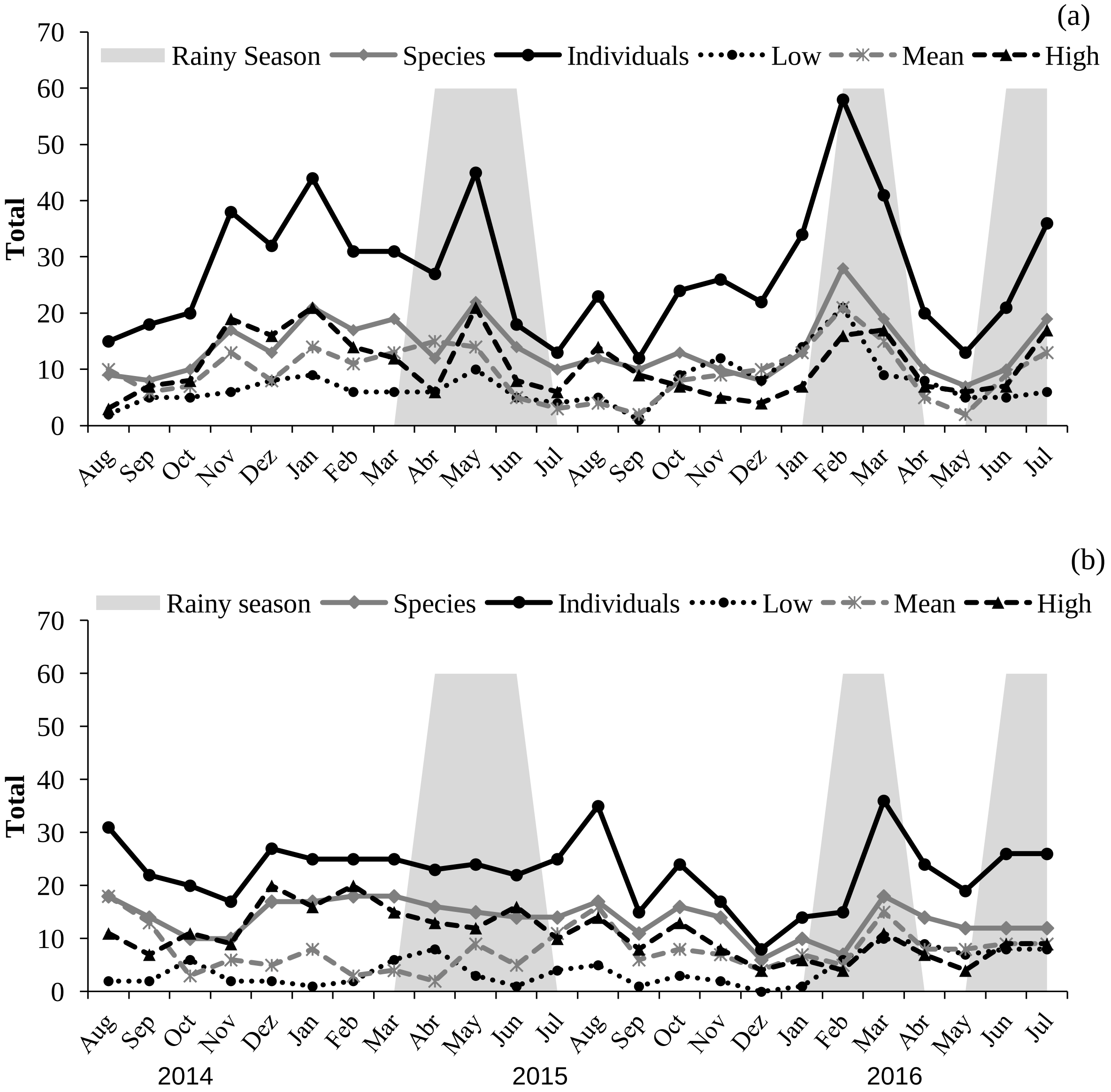
(a)
Rainy Season
Species
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Mean
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May
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(b)
Rainy season
Species
Individuals
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Figure 3.

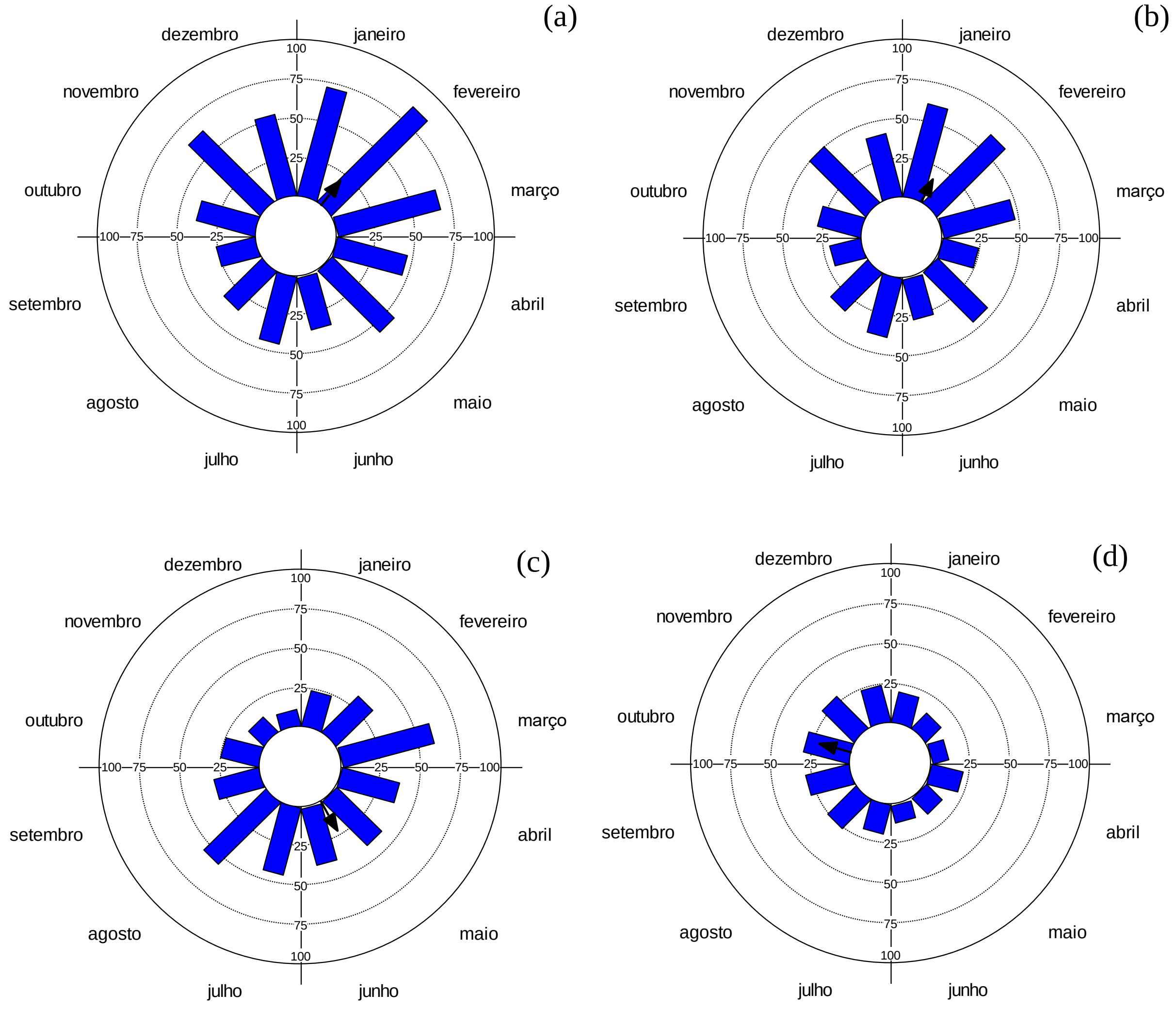
(a)
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Figure 4.

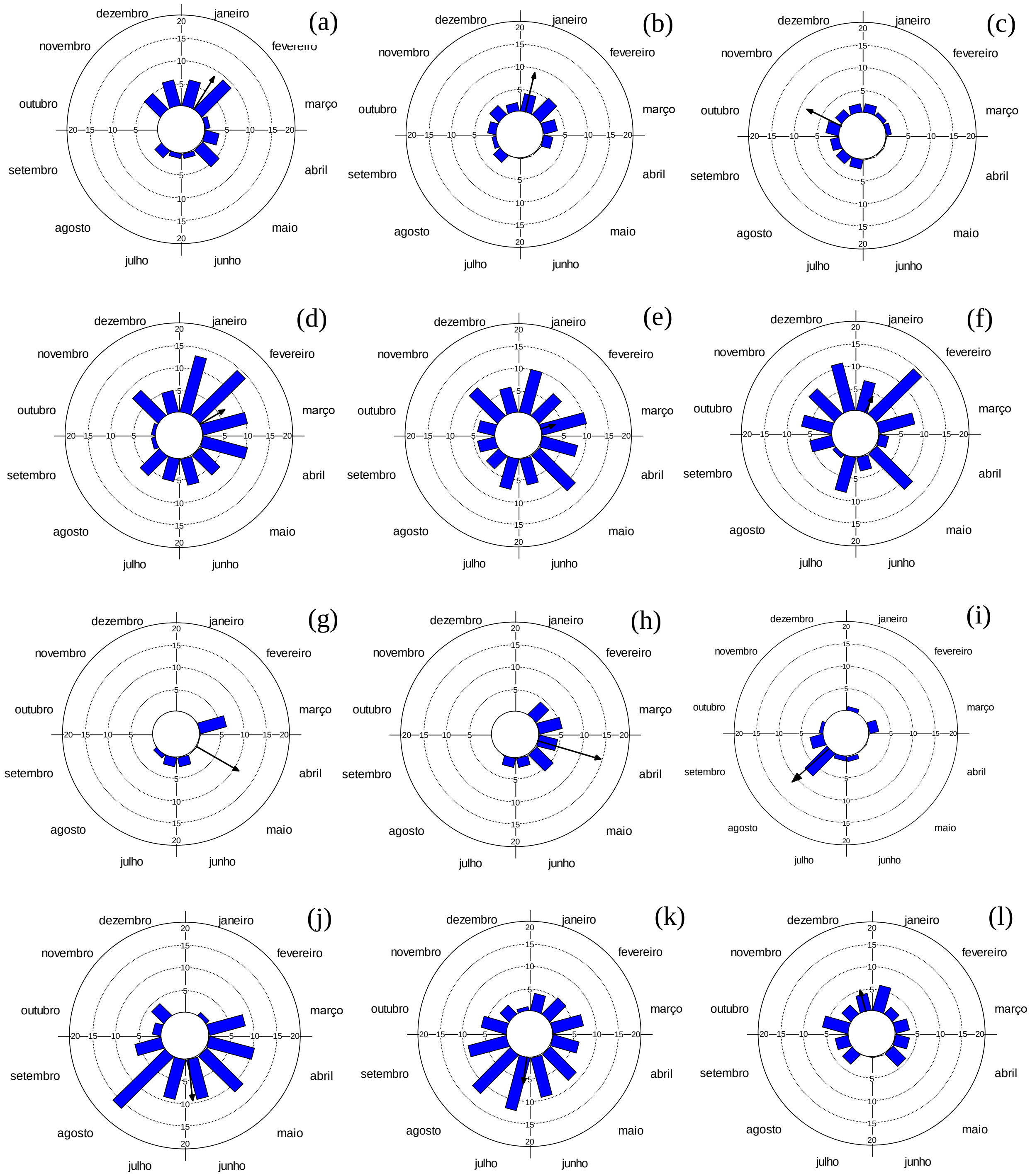
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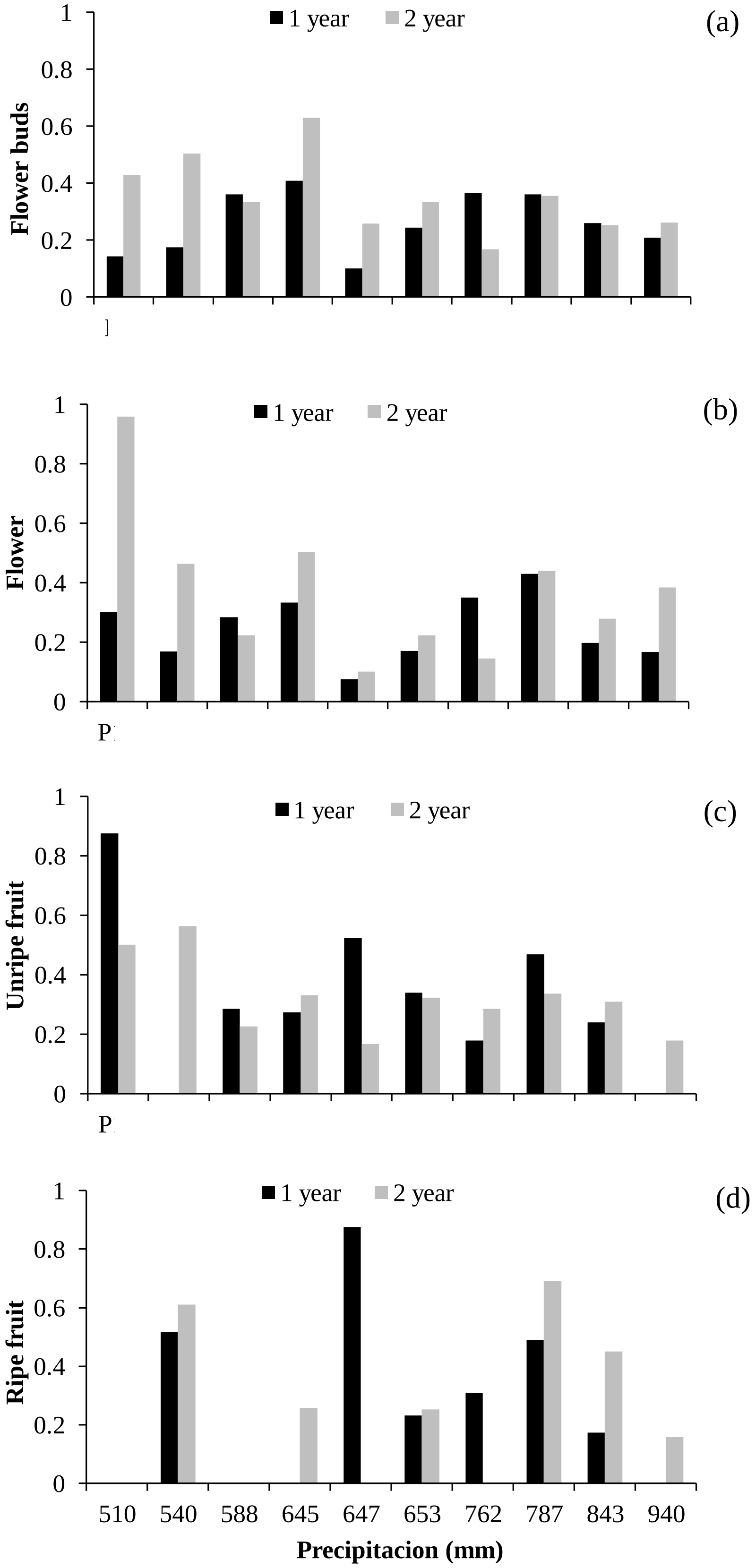
Figure 5.


(a)
Flower buds
1
0.8
0.6
0.4
0.2
0
■ 1 year
■ 2 year
(b)
Flower
(c)
Unripe fruit
(d)
Ripe fruit
510
540
588
645
647
653
762
787
843
940
Precipitacion (mm)

Supporting Information

Table S1. List of woody species studied for reproductive phenology in Caatinga in area the Catimbau National Park. Legend: Yes - occurrence of reproduction, NO - No occurrence of reproduction, Individuals - Total of individuals of the species and Plots - Total of plots of occurrence of the species.

Family	**Species**	**Reproduction**	**Individuals**	**Plots**
Anacardiaceae	sp1	Yes	1	1
	sp2	NO	1	1
	Spondias tuberosa Arruda	NO	1	1
Annonaceae	*Annona leptopetala* (R.E. Fr.) H. Rainer	Yes	7	4
Apocynaceae	*Allamanda blanchetii* A. DC.	Yes	3	2
	Aspidosperma pyrifolium Mart.	Yes	2	2
	Aspidosperma sp.	NO	2	1
Bignoniaceae	*Handroanthus impetiginosus* (Mart. ex DC.) Mattos	Yes	2	1
Boraginaceae	*Varronia leucocephala* (Moric.) J.S. Mill.	Yes	2	1
Burseraceae	*Commiphora leptophloeos* (Mart.) J.B. Gillett	Yes	12	7
Capparaceae	*Cynophalla hastata* (Jacq.) J. Presl	Yes	1	1
	Neocalyptrocalyx longifolium (Mart.) Cornejo & Iltis	Yes	9	4
Celastraceae	*Maytenus rigida* Mart.	Yes	2	1
Erythroxylaceae	*Erythroxylum revolutum* Mart.	Yes	2	1
Euphorbiaceae	*Cnidoscolus bahianus* (Ule) Pax & K. Hoffm.	Yes	14	7
	Cnidoscolus obtusifolius Pohl	Yes	2	1
	Croton argyrophyllus Kunth	Yes	10	5
	Croton heliotropiifolius Kunth	Yes	1	1
	Jatropha mutabilis Benth.	Yes	12	6
	Manihot pseudoglaziovii Pax & K. Hoffm.	NO	1	1
Fabaceae	*Bauhinia acuruana* Moric.	Yes	4	2
	Chamaecrista hispidula (Vahl) H.S. Irwin & Barneby	Yes	2	1
	Chloroleucon foliolosum (Benth.) G.P. Lewis	Yes	2	1
	Dalbergia cearensis Ducke	NO	2	1
	Hymenaea martiana Hayne	Yes	13	7
	Luetzelburgia bahiensis Yakovlev	Yes	2	1
	Mimosa tenuifolia L.	Yes	1	1
	Parapiptadenia sp.	NO	1	1
	Piptadenia stipulacea (Benth.) Ducke	Yes	8	5
	Piptadenia zehntneri Harms	NO	2	1
	Pityrocarpa moniliformis (Benth.) Luckow & R. W. Jobson	Yes	11	6
	Poincianella microphylla (Mart. ex G. Don)	Yes	14	7

	L.P. Queiroz			
	Poincianella pyramidalis (Tul.) L.P. Queiroz	Yes	4	2
	Senegalia bahiensis (Benth.) Seigler & Ebinger	Yes	4	2
	Senegalia polyphylla (DC.) Britton	Yes	5	3
	Senegalia sp1	NO	1	1
	Senegalia sp2	Yes	2	1
	Senna acuruensis (Benth.) H.S. Irwin & Barneby	Yes	2	1
	Trischidium molle (Benth.) H.E. Ireland	Yes	2	1
	Fabaceae	Yes	2	1
Malpighiaceae	*Byrsonima gardneriana* A. Juss.	Yes	2	1
	Byrsonima lancifolia A. Juss.	Yes	1	1
Malvaceae	*Waltheria brachypetala* Turcz.	Yes	2	1
Myrtaceae	*Campomanesia eugenioides* (Cambess.) D.Legrand ex Landrum	Yes	6	3
	Eugenia sonderiana O. Berg	Yes	11	2
	Myrcia sp.	NO	2	1
	Psidium oligospermum DC.	Yes	1	1
Nyctaginaceae	*Guapira noxia* (Netto) Lundell	Yes	5	3
	Guapira sp.	NO	1	1
Polygonaceae	*Ruprechtia laxiflora* Meisn.	NO	1	1
Rhamnaceae	*Ziziphus joazeiro* Mart.	Yes	1	1
Rubiaceae	*Cordiera rigida* (K. Schum.) Kuntze	Yes	1	1
Rutaceae	*Balfourodendron molle* (Miq.) Pirani	Yes	2	1
	Zanthoxylum stelligerum Turcz.	Yes	1	1
Sapindaceae	*Allophylus quercifolius* Radlk.	Yes	2	1
Verbenaceae	*Lippia origanoides* Kunth	Yes	7	5

4 MAINTENANCE OF TREE REPRODUCTIVE FUNCTIONALITY ALONG PRECIPITATION AND HUMAN-DISTURBANCE GRADIENTS IN A TROPICAL DRY FOREST

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Artigo submetido à Journal PPEES (Fator de Impacto = 6.13, Qualis = A1, esta seção segue a norma da revista, com normas em anexo B).

Highlights

- Precipitation and human disturbance can shape tree reproductive functionality
- We tested this hypothesis in the Brazilian Caatinga, a dry tropical forest
- Both predictors showed weak effect on functional diversity and structure of flowers and fruits
- There was no significant interaction effect of precipitation and disturbance

- Tree reproductive functionality seems to be resistant to current human disturbances

ABSTRACT

Climate change and chronic human disturbances are expected to reorganize tropical diversity from population to ecosystem level with potential impacts for biodiversity persistence, provision of ecological services and human well-being. However, the functional reorganization of plant assemblages has been poorly addressed in seasonally dry tropical forests. We describe tree reproductive functionality (i.e., functional diversity and structure of flowers and fruits) and pollination and dispersal syndromes, and assess how these variables respond to precipitation and chronic human disturbance in the Brazilian Caatinga – a species-rich but poorly studied dry tropical forest. We hypothesized that precipitation and chronic human disturbance limit tree reproductive functionality, particularly in wetter sites (i.e., interacting effect of precipitation and disturbance), which are predicted to show more species, more reproductive traits, and a higher frequency of specialized syndromes. We analyzed separately floral and fruit traits of 101 woody species distributed along gradients of precipitation and disturbance (20 forest sites). We used generalized linear models to assess the isolated and interaction effects of annual precipitation and a chronic disturbance index on functional diversity, four multimetric functional indices (functional richness, evenness, divergence and dispersion), and the proportion of species with different pollination and seed dispersal syndromes. All response variables in both flowers and fruits were weakly related to precipitation and human disturbance, with no significant interaction effect. These surprising findings are “good news” for biodiversity conservation in this endangered ecosystem, as they suggest that reproductive functionality and success of tree assemblages are not limited by current human disturbances, with potential benefits for the integrity of plant-animal networks.

Keywords: Caatinga; flowers; fruits; pollination; seed dispersal; woody flora.

1. Introduction

Tropical forests are experiencing increasing levels of human-imposed disturbances, including habitat loss and fragmentation, exploitation of forest products and climate change (Malhi et al., 2014). Collectively these disturbances are expected to modify biological systems (from DNA to ecosystem level), with tangible effects on biodiversity persistence, provision of ecosystem services and human well-being (Carpenter and Folke, 2006; Shaanker et al., 2004). In recent decades, however, the impact caused by continuous and frequent removal of small portions of biomass has also gained attention ("chronic disturbances", *sensu* Singh, 1998), and has been reported to cause population collapse, alteration of taxonomic and phylogenetic diversity, and disruption of ecosystem functioning (Arroyo-Rodríguez et al., 2017; Singh, 1998).

Functional diversity is a key attribute of ecological communities, directly related to ecosystem functioning and their response to environmental disturbance (Araújo, 2016; Cadotte et al., 2011; Díaz and Cabido, 2001; Tilman et al., 1997; Walker et al., 1999), making it critical for the provision of ecosystem services (Díaz et al., 2007). Plant functional diversity can be altered by chronic disturbances, since selective logging, firewood extraction, overgrazing, and similar types of chronic disturbances can extirpate or reduce the abundance of targeted species with sensitive traits, syndromes, or life-history strategies (hereafter functional attributes) (Fisher et al., 2012; Ringrose et al., 2002). By altering forest biomass and microclimate, chronic disturbance can also affect functional diversity by imposing new environmental pressures, such as water scarcity (Andrew et al., 2016). However, even under both pressures (species exploitation and environmental alteration), species with attributes adapted to these new conditions can proliferate (Gonzalez and Loreau, 2009), leading to altered patterns of functional diversity in disturbed forests (Jucker et al., 2014).

Pollination and dispersal processes can be particularly altered in human-modified landscapes due, not only to plant species extirpation (Cordeiro and Howe, 2003; Lopes et al., 2009; Quesada et al., 2011), but also to animal species extirpation (Montoya, 2008). The disruption of these processes have important consequences for plant recruitment and forest regeneration, with tangible effects on forest structure and ecosystem functioning (Arroyo-Rodríguez et al., 2017; Díaz and Cabido, 2001; Freitas et al., 2014). However, studies assessing community-level functional responses have focused on vegetative traits, particularly in the context of succession (e.g., Lohbeck et al., 2013; Pinho et al., 2018) and acute disturbances, such as habitat loss and fragmentation (Aizen et al., 2002; Girão et al., 2007; Oliveira et al., 2015; Sfair et al., 2016). Our understanding of the effects of chronic disturbances on tropical plant reproductive functionality is still highly limited, and biased towards wet forests (Araújo, 2016; Girão et al., 2007; Mayfield et al., 2006; Warring et al., 2016; but see Sobrinho et al., 2016).

The Brazilian Caatinga is a species-rich seasonally dry tropical forest (SDTF), which has been strongly altered by chronic disturbance (e.g., Araújo et al., 2007; Ribeiro et al., 2015, Silva et al. 2017), and has a marked rainfall gradient (Albuquerque et al., 2012). Thus, this SDTF is an interesting ecosystem to address potential impacts of chronic disturbance and climate change on plant reproductive functionality (i.e., functional diversity and structure of flowers and fruits) (Leal et al., 2003, Santos et al., 2014). Remaining vegetation represents a key source of forest products, from firewood to fodder for livestock, and thus, chronic disturbances threatens biodiversity maintenance (Ribeiro et al., 2015, 2016), especially in wetter sites, which are known to show more species than drier sites (Rito et al., 2017). Therefore, the reduction in rainfall predicted by global climate change scenarios (Trenberth, 2011) can amplify the impact of chronic disturbances.

Here, we examined potential responses from pollination and seed dispersal strategies and tree reproductive functionality of Caatinga vegetation to changes in precipitation and chronic human disturbance. We first describe tree reproductive functionality (i.e., functional diversity and structure of flowers and fruits) and pollination and dispersal syndromes, to then assess whether flower- and fruit-related functional traits and metrics, including five measures of functional diversity and structure at the community level, were related to annual precipitation and a chronic disturbance index. We hypothesized that precipitation and chronic human disturbances act as environmental pressures that limit tree reproductive functionality, particularly in wetter sites (i.e., interacting effect of precipitation and disturbance), which are predicted to show more species, more reproductive traits, and a higher frequency of specialized syndromes.

2. Material and methods

2.1. Study area

This study was carried out in the Catimbau National Park, northeastern Brazil (8°24’00” and 8°36’35” S; 37°0”30” and 37°1’40” W; 62000 ha; Fig. 1). The landscape is dominated by arboreal and shrubby vegetation that frequently have spines, microphilia and xerophilic characteristics (Prado, 2003; Rodal et al., 1998). The climate of the region is hot and dry (BSh, sensu Köppen, 1948), with a mean annual temperature of 26 °C, and annual rainfall between 650 and 1100 mm. The rainy season occurs between April and June (SNE, 2002; SUDENE, 1990). This region was designated a national park in 2002 despite many people still living within its borders that depend on natural resources for their livelihoods, including wood extraction and extensive livestock farming, among others chronic human disturbances (Freire et al., 2015).

2.2. Functional traits and metrics

We selected twenty 20 × 50 m permanent plots with a minimum distance of 2 km between them. Plots covered a gradient of precipitation and human disturbance, but all were located in sites with similar soil (i.e., sandy soil) and topographic (i.e., flat terrain) characteristics. From the 101 woody species recorded in the plots (Rito et al., 2016, 2017), we collected flower and fruit samples from 10 randomly collected individuals per species (one random flower/fruit per individual). We stored flowers and fleshy fruits in 70% alcohol and dried fruits at room temperature for further measures of functional traits.

We assessed floral traits according to their role in the attraction of pollinators (Machado & Lopes, 2004) to calculate the functional diversity indices as follow: (1) floral size (length and diameter); (2) type of resources (nectar, pollen or oil); (3) visible resource guides (presence or absence); and (4) visual floral coloration (yellow, white, orange, pink, purple, green or red). We also considered (5) pollination unit (i.e., individual, intermediate or collectivist), depending on the amount of flowers visited by the pollinator during each visit (Ramirez et al., 1989). Also, we classified species based on general characteristics of flower attributes (6) pollination syndromes (melittophily = bees, DSI = diverse small insects, psychophily = butterflies, phalenophily = moths and sphingidae, ornithophily = birds, and chiropterophily = bats; Faegri and Pijl, 1979), and other floral characteristics, such as (7) floral type (bell-funned, brush, chamber, disk, flag, inconspicuous and tube; Faegri & Pijl, 1979), (8) symmetry (actino- and zygomorphic), and (9) sexual system (hermaphrodite, unisexual monoicious and dioecious; Bawa, 1980; Endress, 1994). We did not include attributes (6) to (9) in the analyses of the functional diversity indices because they are not directly related to the attraction of pollinators, but are important to the floral classification. Yet, as they are important to understand variations of floral diversity and the importance of pollinators, we described them and later tested the homogeneity of the distribution of the characteristics found.

To calculate the functional diversity of fruit traits we chose those traits that play an important role in seed dispersal (Van der Pijl, 1982), including: (1) fruit size (length and diameter); (2) fresh fruit weight; (3) seed size (length and diameter); (4) number of seeds per fruit; (5) consistency of pericarp (dry or fleshy); and (6) attachments in the integument (presence or absence). We also assessed the attributes used in the general classification of fruits, such as: (7) dispersal syndromes (anemocory, autochory and zoochory), (8) fruit color (black, brown, green, yellow, orange, purple and red), and (9) fruit type (achene, berry, capsule, drupe, follicle, legume, nut, samara and schizocarp). We did not include attributes (7) to (9) in the analyses of the functional diversity indices because they are not directly related to seed dispersal, but are important to the fruit classification. These fruit attributes help us to understand the diversity of fruits, and were later used to test distribution homogeneity. Spatial occurrence of pollination and dispersal syndromes along the precipitation and human disturbance gradients were visualized from their respective percentage of occurrence in each plot, in order to understand how the syndromes are distributed spatially.

The morphometric measurements were carried out with a digital caliper. When a given species was not flowering or fruiting (52.5% of species), we obtained all attributes from herbarium specimens and the literature. When there was no information for a given species, we used mean trait values at the genus level (19% of species).

2.3. Annual precipitation and disturbance index

Following Rito et al. (2017), we used the average historical precipitation of each site which was obtained from the updated global climate data repository of WorldClim, at a 1 km spatial resolution. The precipitation gradient ranged from 510 to 940 mm. The plots were established in areas with no record of acute disturbance in the last 80 years, confirmed by aerial photographs and interviews with the local community.

Following Câmara et al. (2018), we assessed chronic human disturbances in each site with a chronic disturbance index (CDI) based on three different sub-indexes that use different sources of chronic disturbance: (1) livestock grazing, related to consumption of vegetation, trampling, and other physical damage caused by goats and cattle; (2) wood extraction, related to the extraction of dead and live wood for fuel, construction, and handicraft; and (3) miscellaneous resource use, related to the use of non-wood resources (i.e. medicinal plants) (Câmara et al., 2018). For the livestock grazing index, we used the length of goat trails (meters) and the frequency of goat and cattle dung (n/0.1 ha) combined in a PCA axis (88% of variance explanation). For the wood extraction index, we used the amount alive stems cuts (cm^2/0.1ha) and the amount of wood litter collected by families (1/Kg litter/Kg total plot biomass). For the miscellaneous resource use index, we used three indirect variables that are proxies for local anthropogenic pressure and habitat accessibility: plot proximity to the nearest house (1/x in meters), plot proximity to the nearest road (1/x in meters) and number of people living in the area that influence the plot. The geographical distances were calculated using satellite imagery and ArcGis 10.1 software. The information about the amount of wood litter collected by families and number of people living near the plots were obtained from semi-structured interviews with local communities (n = 69). We calculated the sub-indexes values using the following formula (Câmara et al., 2018):

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

where I is disturbance intensity; y_i is the observed value for a given disturbance metric in plot i; y_{min} is the minimum observed value for the disturbance metric across all plots; y_{max} is the maximum observed value for the disturbance metric across all plots; and n is the number of individual disturbance metrics incorporated in the index. This formula standardizes the metrics of different units and its value vary between 0 and 1, allowing them to be combined in the same index. The three sub-indices were not correlated between each other. We then integrated the three sub-indices using the same formula described above, in a single global chronic disturbance index. This global index varied from 0 (minimum disturbance) to 100 (maximum disturbance).

2.4. Data analysis

To describe floral and fruit attributes and pollination and dispersal syndromes in the study area, we first tested if they were homogeneously distributed among species with chi-squared tests (Zar, 1999). To test whether some groups of species benefit or not from certain precipitation and disturbance conditions, the frequency of individuals of each species in each plot were correlated separately with precipitation and disturbance (Pearson's correlation).

We calculated functional diversity (FD) and four multidimensional diversity indices based on reproductive traits: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), and functional dispersion (FDis) (Mason et al., 2005; Petchey and Gaston, 2002; Villéger et al., 2008). FD is based on the total sum length of a dendrogram's arms. This measure is related to species richness and increasing values of FD indicate losses of functional redundancy (Petchey and Gaston, 2002). FRic represents the size of the functional space occupied by a community (Villéger et al., 2008). FEve describes the equability of the distribution of abundance in the functional space (Mason et al., 2005). FDiv represents how abundance is distributed along an axis of functional traits within the space occupied by the community (Mason et al., 2005). FDis describes the mean distance in multidimensional trait space of individual species to the centroid of all species (Laliberté and Legendre, 2010). We used the "vegan" package for R (Oksanen et al., 2017) to calculate FD, and "FD" package (Laliberté et al., 2014) to calculate the multidimensional diversity indices, considering the Gower dissimilarity index for calculations of functional diversity metrics, since our traits include continuous and binary variables (Laliberté and Legendre, 2010).

We then assessed the effect of precipitation, chronic disturbance and the interaction effect of these two predictor variables on the proportion of each pollination and seed dispersal syndrome, and each functional metric (FD, FRic, FEve, FDiv, and FDis) with generalized linear models (R Development Core Team, 2017). We fixed a Gaussian error distribution for continuous response variables (i.e., all functional metrics), and a binomial error distribution for proportion response variables (i.e., pollination and dispersal syndromes) (Crawley, 2007). We then calculated the percentage of explained deviance by each model as a measure of goodness-of-fit of the models (Crawley, 2007).

3. Results

We sampled 4892 stems from 101 woody species belonging to 29 families and 74 genera. Mean (± SD) number of species per plot was 26.1 ± 7.0 species. The most abundant families were Fabaceae (2242 individuals, 45.8% of individuals sampled), Euphorbiaceae (1645 individuals, 33.6%), and Myrtaceae (69 individuals, 1.4%). Floral attributes were highly variable (Table A1 in Supplementary Material). In particular, mean flower size was 9.6 ± 10.4 mm, mainly white (47.5% of species; $\chi^2 = 145.1$, d.f. = 6, $P < 0.001$), with absent resource guides (71.3% of species; $\chi^2 = 18.3$, d.f. = 1, $P < 0.001$), offering nectar (88.1% of species; $\chi^2 = 137.4$, d.f. = 2, $P < 0.001$), and arranged as individual pollination units (61.4% of species; $\chi^2 = 35.8$, d.f. = 2, $P < 0.001$). Flowers were generally hermaphrodites (84.2% of species; $\chi^2 = 117.9$, d.f. = 2, $P < 0.001$), actinomorphs (80.2% of species; $\chi^2 = 36.8$, gl = 1, $P < 0.001$), and disk type (28.7% of species; $\chi^2 = 35.9$, d.f. = 6, $P < 0.001$). Melittophily was the most common pollination syndrome in the study plots (86.1% of species; $\chi^2 = 351.5$, d.f. = 5, $P < 0.001$) followed by chiropterophily (5%).

Fruit attributes were also highly variable (Table A.2). Mean fruit size was 133 ± 373.1 mm, and fresh weight averaged 3 ± 4.2 g. The average amount of seeds was 19.3 ± 100.5 mm. Seed size averaged 22.2 ± 89 mm, and they were mainly dehiscent (57.4% of species; $\chi^2 = 2.2$, d.f. = 1, $P < 0.14$), dry (67.3% of species; $\chi^2 = 12.1$, d.f. = 1, $P < 0.0005$), and presented attachments in the integument (54.4% of species; $\chi^2 = 0.8$, d.f. = 1, $P < 0.37$). Fruits were generally brown (53.5% of species; $\chi^2 = 136.2$, d.f. = 6, $P < 0.001$) and capsule type (28.7% of species; $\chi^2 = 90.7$, d.f. = 8, $P < 0.001$). Seed dispersal syndrome was mainly autocory (49.5% of species; $\chi^2 = 20.5$, d.f. = 2, $P < 0.001$), followed by zoocory (38.6%) and anemocory (11.9%).

No significant correlations were found between the distribution of individuals and species and precipitation and disturbance gradients (Fig. A.1). All flower and fruit syndromes were distributed along the entire precipitation and disturbance gradient (Fig. A.2 and A.3), and thus, both gradients were weakly related to the percentage of individuals and species within each pollination and seed dispersal syndrome (Table 1). Similarly, all functional indices (FD, FRic, FEve, FDiv, and FDis) for both flower (Fig. 2) and fruit traits (Fig. 3) were weakly related to precipitation and human disturbance (Tables 2 and 3).

4. Discussion

This study sheds new light on the functional diversity and structure of the Brazilian Caatinga vegetation. In particular, we show that Caatinga woody flora is composed of a reproductively simple flora mainly consisting of species bearing small and inconspicuous flowers, which are mainly pollinated by bees and diverse small insects. Seeds are primarily dispersed by abiotic factors. Both reproductive syndromes and diversity-related reproductive attributes exhibited low spatial variation, which was weakly related to annual precipitation and chronic human disturbance gradients. Thus, our novel findings are “good news” for the conservation of plant assemblages in this species-rich but endangered ecosystem, as they suggest that reproductive functionality and success of tree assemblages are not limited by current human disturbances.

Surprisingly, our findings do not support the hypothesis that the reproductive profile of plant communities respond to environmental changes (Neuschulz et al., 2016). Several studies in the tropics have documented changes in the reproductive profile of plant communities associated with forest loss and fragmentation, including changes in the frequency of pollination syndromes and reduced functional diversity

(Girão et al., 2007; Mayfield et al., 2005; Sobrinho et al., 2016; Warring et al., 2016), especially in smaller forest fragments and along forest edges (Sobrinho et al., 2016; Warring et al., 2016). The lack of strong responses to environmental changes in our study may be related to the fact that our study landscape is dominated by mellitophilous or insect-pollinated plant species, with dry fruits, which is consistent with previous studies in this and other dry forests (Griz and Machado, 2000; Machado and Lopes, 2004; Machado et al., 2006; Quesada et al., 2011; Quirino, 2006; Quirino and Machado, 2014). Floriferous plants and bees have diversified together throughout coevolution, and nowadays bees represent the most important group of pollinating insects (Ollerton et al., 2011). The Caatinga is no exception (Machado and Lopes, 2004; Quirino and Machado, 2014), as it maintains a great diversity and high degree of endemism of bees (Zanella and Martins, 2003). Regarding abiotic dispersal, it can also be facilitated in the Caatinga because anemocoric and autocoric diaspores are preferentially dispersed in the dry season (7-10 months), when both leaf fall and a very high incidence of winds can increase dispersal distances (Griz and Machado, 2001). We therefore suggest that these floral and fruit traits can confer adaptive advantages to woody species in the region, helping them cope with conditions of limited precipitation and recurrent chronic disturbance.

The low spatial variation in reproductive syndromes and diversity-related reproductive attributes may be caused by the dominance of few taxa (e.g., Fabaceae and Euphorbiceae) consisting of bee-pollinated and abiotically-dispersed species (Jara-Guerrero et al., 2011; Queiroz et al., 2017; Yamamoto et al., 2007). Many evolutionary and ecological forces are probably behind the dominance of these families (Queiroz et al., 2017). In terms of the adaptive value presented by bee-pollination and diverse small insects, it is worth mentioning that the main floral attributes related to the attraction of pollinators include (1) infrared floral signage, and (2) availability of nectar as a resource (Faegri and Pijl, 1979). Also, Fabaceae and Euphorbiaceae species in dry forests generally exhibit: (1) loss of leaves, (2) pronounced root growth, and (3) mechanisms of water storage which can also contribute to the persistent success of these families in this ecosystem (Queiroz et al., 2017).

Recent findings from Caatinga vegetation suggest that species and trait replacement are a basic response to disturbance (Ribeiro et al., 2016; Sobrinho et al., 2016). In particular, the population decline in some very rare taxa can be compensated for by proliferation of few "disturbance-adapted" species. Such a plant taxonomic replacement along gradients in the Caatinga vegetation, has been proposed to be associated with species' differential ability to deal with water and nutrient scarcity along environmental gradients (Ribeiro et al., 2016; Rito et al., 2017), which is partially associated with leaf-economy traits (Sfair et al., 2018). Although we did not explicitly address a compensatory mechanism, we found a replacement of species responding in contrasting directions along both environmental gradients. We refer to congeneric species sharing the same reproductive strategies (e.g., species from *Croton*, *Senna*, *Jatropha* genera), but probably bearing different abilities to deal with physical environmental stress (see also Sfair et al., 2018). The occurrence of reproductively equivalent species probably facilitates the maintenance of community-level reproductive functionality along precipitation and human disturbance gradients in the region.

In synthesis, some reproductive plant traits and syndromes appear to be unaffected by environmental changes (either natural or anthropogenic) operating at the landscape scale in the Caatinga vegetation. This may be caused by the dominance of a reproductively simple flora, mainly consisting of species bearing small and inconspicuous flowers, which are principally pollinated by bees and diverse small insects. Therefore, the reproductive profile of Caatinga plant assemblages seems to be highly resistant to current environmental changes in the region, with potential benefits for the integrity of plant-animal networks. Future studies should investigate the generality of these patterns across SDTFs, as recent phylogenentic analyses suggest that across the planet, tropical dry forests form a single tropical biome (Slik et al., 2018).

Acknowledgements

This study was supported by the Conselho Nacional de Desenvolvimento Científico e Tecnológico [PELD process 403770/2012-2, Universal process 470480/2013-0]. Thanks to Fundação de Amparo à Ciência e Tecnologia do Estado de Pernambuco (Facepe) for funding the scholarship of M.E.M.F. [process IBPG-0820-2.03/13] and to Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (Capes) for internship at the Instituto de Investigaciones en Ecosistemas y Sustentabilidad, UNAM, Morelia, Mexico [process PDSE- 88881.133050/2016-01]. K.F.R thanks DGAPA-UNAM for funding her postdoctoral stay. We also thank Davi Jamelli for elaborating Figure 1.

Figure Legends

Fig. 1. Location of the study area in northeastern Brazil (A) (rectangle) for the Catimbau National Park area in the State of Pernambuco (B), and location of plots marked (C). Different shades of gray indicate the water deficit, with darker gray indicating lower precipitation (Source: PELD Catimbau database).

Fig. 2. Variation of five functional metrics, Functional richness (FRic), Functional Evenness (FEve), Functional Divergence (FDiv), Functional Dispersion (FDis), and Functional Diversity (FD) of floral traits in relation to mean annual precipitation (A) and Chronic Disturbance Index (CDI) (B).

Fig. 3. Variation of five functional metrics, Functional richness (FRic), Functional Evenness (FEve), Functional Divergence (FDiv), Functional Dispersion (FDis), and Functional Diversity (FD) of fruit traits in relation to mean annual precipitation (A) and Chronic Disturbance Index (CDI) (B).

Fig. 1.

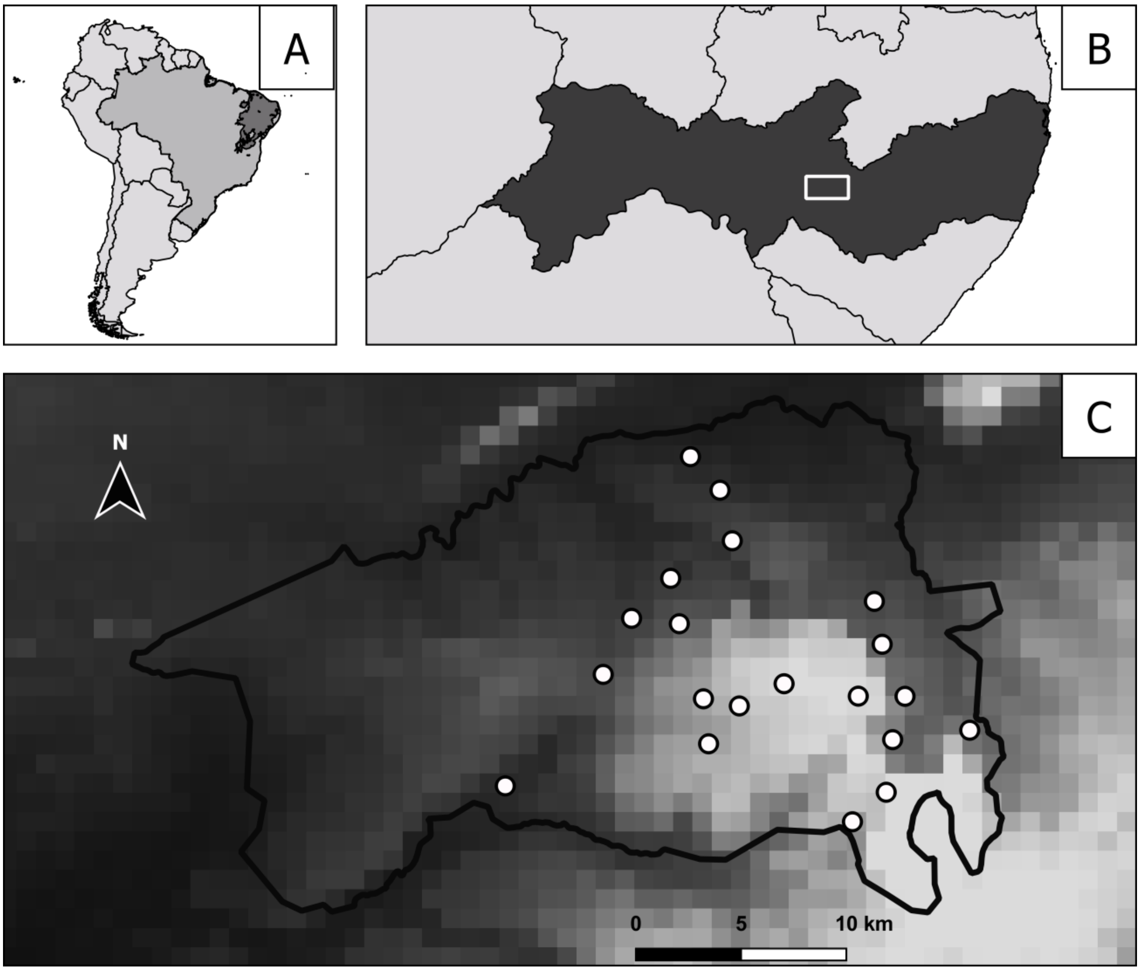
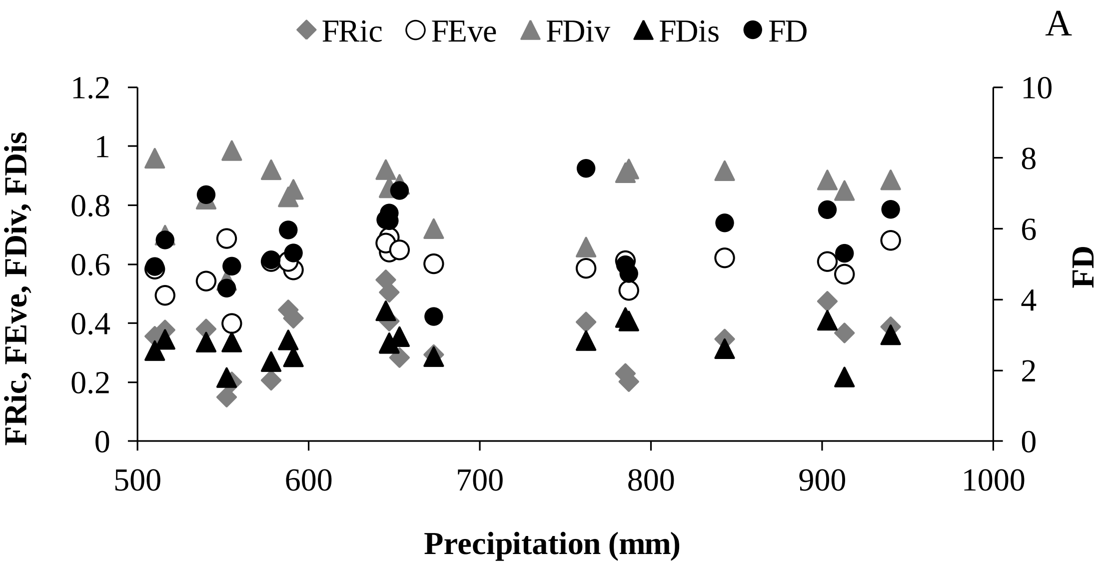


Fig. 2.


◆FRic ○FEve ▲FDiv ▲FDis ●FD
A
FRic, FEve, FDiv, FDis
1.2
1
0.8
0.6
0.4
0.2
0
FD
10
8
6
4
2
0
500
600
700
800
900
1000
Precipitation (mm)

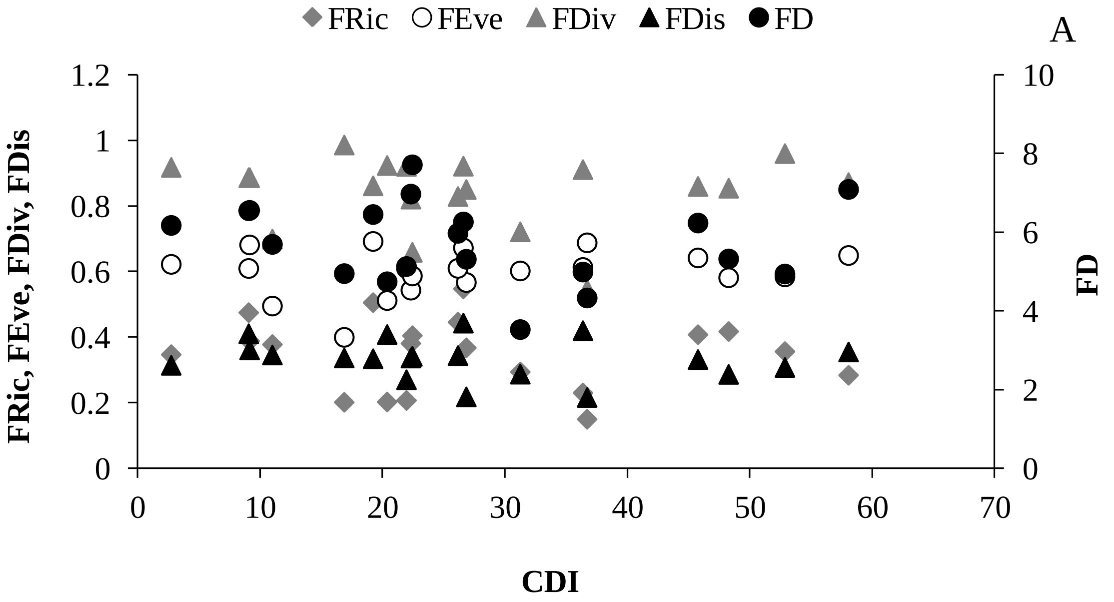

◆FRic ○FEve ▲FDiv ▲FDis ●FD
A
FRic, FEve, FDiv, FDis
1.2
1
0.8
0.6
0.4
0.2
0
FD
10
8
6
4
2
0
0
10
20
30
40
50
60
70
CDI

Fig. 3.

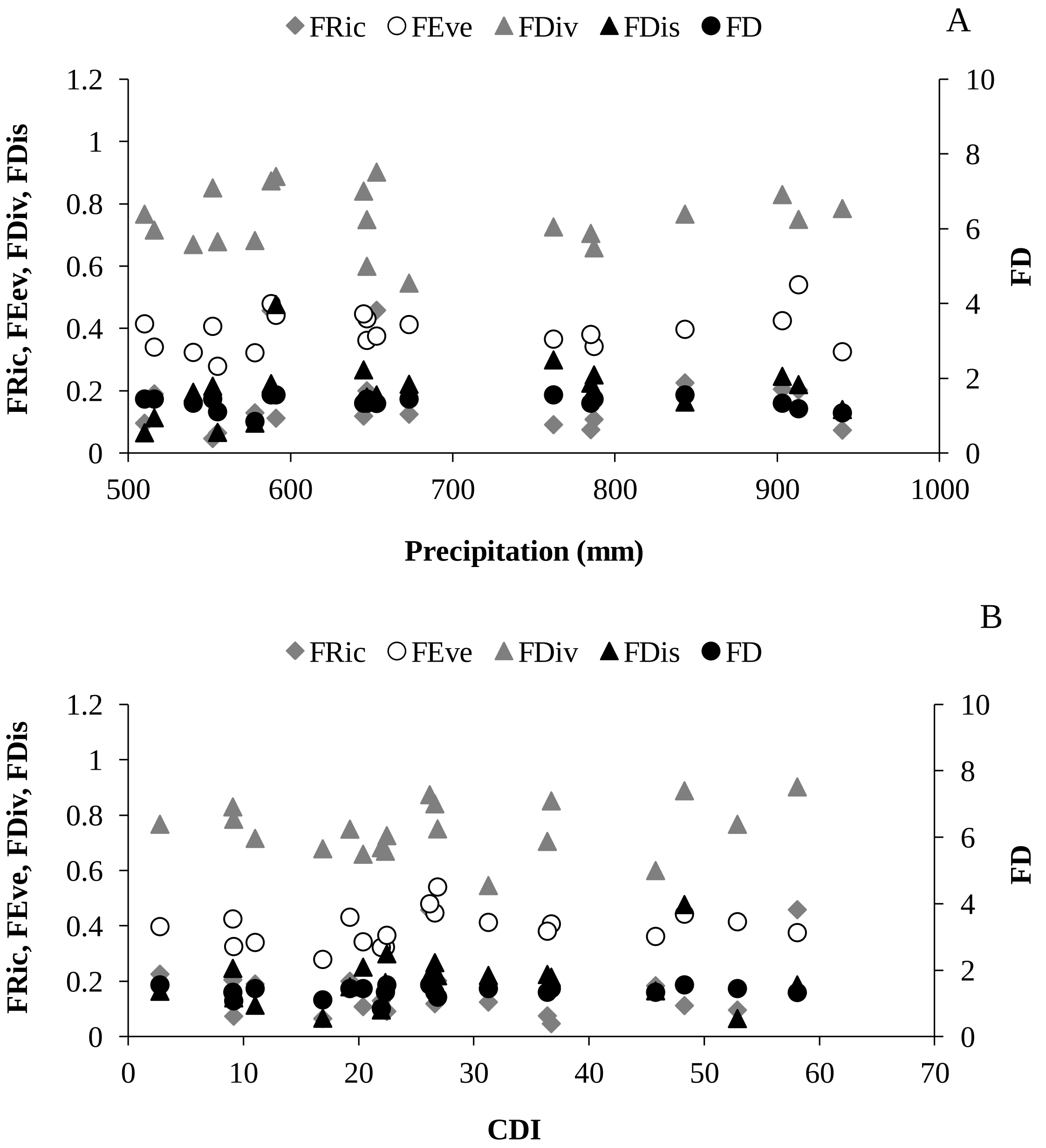

A
◆FRic ○FEve ▲FDiv ▲FDis ●FD
FRic, FEev, FDiv, FDis
1.2
1
0.8
0.6
0.4
0.2
0
FD
10
8
6
4
2
0
500
600
700
800
900
1000
Precipitation (mm)
B
◆FRic ○FEve ▲FDiv ▲FDis ●FD
FRic, FEve, FDiv, FDis
1.2
1
0.8
0.6
0.4
0.2
0
FD
10
8
6
4
2
0
0
10
20
30
40
50
60
70
CDI

Table 1. Response of pollination and dispersal syndromes of woody species to precipitation (Prec) and chronic disturbance index (CDI) in the Catimbau National Park, Brazil. The percentage of deviance explained (DE) by each generalized linear model is also included as a measure of goodness-of-fit.

	Estimate	SE	Z	P	DE
Melittophily					
Prec	-1.01 x 10^{-3}	7.91 x 10^{-3}	-0.13	0.90	0.17
CDI	-1.49 x 10^{-2}	2.37 x 10^{-1}	-0.06	0.95	
Prec:CDI	3.70 x 10^{-5}	3.13 x 10^{-4}	0.12	0.91	
Psycophily					
Prec	3.22 x 10^{-3}	1.35 x 10^{-2}	0.24	0.81	0.06
CDI	8.73 x 10^{-2}	4.03 x 10^{-1}	0.22	0.83	
Prec:CDI	-1.2 x 10^{-4}	5.35 x 10^{-4}	-0.22	0.82	
Chiropterophily					
Prec	2.04 x 10^{-4}	1.32 x 10^{-2}	0.02	0.99	0.08
CDI	-4.58 x 10^{-2}	3.91 x 10^{-1}	-0.12	0.91	
Prec:CDI	4.90 x 10^{-5}	4.94 x 10^{-4}	0.10	0.92	
DSI					
Prec	5.76 x 10^{-4}	1.57 x 10^{-2}	0.04	0.97	0.10
CDI	2.27 x 10^{-2}	5.45 x 10^{-1}	0.04	0.97	
Prec:CDI	-6.55 x 10^{-5}	7.40 x 10^{-4}	-0.09	0.93	
Phalenophily					
Prec	6.50 x 10^{-4}	2.77 x 10^{-2}	0.02	0.98	0.02
CDI	-1.88 x 10^{-2}	8.86 x 10^{-1}	-0.02	0.98	
Prec:CDI	4.29 x 10^{-6}	1.14 x 10^{-3}	0.01	0.99	
Ornitophily					
Prec	-1.17 x 10^{-3}	2.08 x 10^{-2}	-0.06	0.96	0.10
CDI	-5.03 x 10^{-3}	6.80 x 10^{-1}	-0.01	0.99	
Prec:CDI	-2.70 x 10^{-5}	9.38 x 10^{-4}	-0.03	0.98	
Autocory					
Prec	-3.57 x 10^{-3}	6.27 x 10^{-3}	-0.57	0.57	0.52
CDI	-3.61 x 10^{-2}	1.69 x 10^{-1}	-0.21	0.83	
Prec:CDI	3.81 x 10^{-5}	2.20 x 10^{-4}	0.17	0.86	
Anemocory					
Prec	2.25 x 10^{-3}	1.02 x 10^{-2}	0.22	0.83	0.04
CDI	4.94 x 10^{-2}	2.96 x 10^{-1}	0.17	0.87	
Prec:CDI	-7.01 x 10^{-5}	3.89 x 10^{-4}	-0.18	0.86	
Zoocory					
Prec	3.45 x 10^{-3}	6.67 x 10^{-3}	0.52	0.60	0.56
CDI	2.84 x 10^{-2}	1.80 x 10^{-1}	0.16	0.88	
Prec:CDI	-2.47 x 10^{-5}	2.31 x 10^{-4}	-0.11	0.92	

Table 2. Response of functional diversity of floral traits to precipitation (Prec) and chronic disturbance index (CDI) in the Catimbau National Park, Brazil. The percentage of deviance explained (DE) by each generalized linear model is also included.

	Estimate	SE	t	P	DE
Functional Richness					
Prec	-2.98×10^{-5}	4.36×10^{-4}	-0.07	0.95	0.13
CDI	-7.70×10^{-3}	1.22×10^{-2}	-0.63	0.54	
Prec:CDI	8.04×10^{-6}	1.84×10^{-5}	0.44	0.67	
Functional Evenness					
Prec	3.39×10^{-4}	1.95×10^{-4}	1.74	0.10	0.18
CDI	8.81×10^{-3}	5.46×10^{-3}	1.61	0.13	
Prec:CDI	-1.18×10^{-5}	8.22×10^{-6}	-1.44	0.17	
Functional Divergence					
Prec	3.56×10^{-4}	2.54×10^{-4}	1.40	0.18	0.17
CDI	1.27×10^{-2}	7.11×10^{-3}	1.78	0.09	
Prec:CDI	-1.82×10^{-5}	1.07×10^{-5}	-1.70	0.11	
Functional Dispersion					
Prec	-8.11×10^{-4}	2.80×10^{-3}	-0.29	0.78	0.10
CDI	-6.12×10^{-2}	7.84×10^{-2}	-0.78	0.45	
Prec:CDI	7.52×10^{-5}	1.18×10^{-4}	0.64	0.53	
Functional Diversity					
Prec	9.88×10^{-4}	3.23×10^{-3}	0.31	0.76	0.06
CDI	-1.00×10^{-2}	9.04×10^{-2}	-0.11	0.91	
Prec:CDI	-1.10×10^{-6}	1.36×10^{-4}	-0.01	0.99	

Table 3. Response of functional diversity of fruits traits to precipitation (Prec) and chronic disturbance index (CDI) in the Catimbau National Park, Brazil. The percentage of deviance explained (DE) by each generalized linear model is also included.

	Estimate	SE	t	P	DE
Functional Richness					
Prec	-8.41×10^{-5}	3.77×10^{-4}	-0.22	0.83	0.03
CDI	-2.59×10^{-3}	1.06×10^{-2}	-0.25	0.81	
Prec:CDI	5.80×10^{-6}	1.59×10^{-5}	0.37	0.72	
Functional Evenness					
Prec	1.57×10^{-4}	1.93×10^{-4}	0.82	0.43	0.16
CDI	1.23×10^{-3}	5.39×10^{-3}	0.23	0.82	
Prec:CDI	4.03×10^{-7}	8.12×10^{-6}	0.05	0.96	
Functional Divergence					
Prec	4.43×10^{-4}	3.00×10^{-4}	1.48	0.16	0.16
CDI	1.37×10^{-2}	8.39×10^{-3}	1.64	0.12	
Prec:CDI	-1.88×10^{-5}	1.26×10^{-5}	-1.49	0.16	
Functional Dispersion					
Prec	8.87×10^{-4}	2.39×10^{-3}	0.37	0.72	0.15
CDI	-1.39×10^{-2}	6.69×10^{-2}	-0.21	0.84	
Prec:CDI	4.77×10^{-5}	1.01×10^{-4}	0.47	0.64	
Functional Diversity					
Prec	2.30×10^{-4}	6.08×10^{-4}	0.38	0.71	0.05
CDI	1.19×10^{-2}	1.70×10^{-2}	0.70	0.50	
Prec:CDI	-1.57×10^{-5}	2.56×10^{-5}	-0.61	0.55	

Suplementary material

Table A.1. Floral traits of all woody species in the Catimbau National Park, in the 20 plots covering the precipitation and disturbance gradients. Legends: Floral color (Gre = Green, Yel = Yellow, Ora = Orange, Red = Red, Pur = Purple and Whi = White), Symmetry (Act = Actinomorph and Zig = Zygomorph), Resource guide (Pre = Presence and Aus = Absent), Resource (Nec = Nectar, Pol = Pollen and Oil = Oil), Floral type (Bel = Bell-funned, Bru = Brush, Cha = Chamber, Dis = Disk, Fla = flag, Inc = Inconspicuous and Tub = Tube), Pollination unit (Ind = Individual, Int = Intermediate and Col = Collectivist), Sexual system (Her = Hermaphrodite, Mon = Unisexual monoicious and Dio = Unisexual dioecious) and Pollination syndrome (Mel = Melittophily, DSI = diverse small insects, Psy = Psychophily, Pha = Phalenophily, Orn = Ornithophily and Chi = Chiropterophily).

Family/Species	Length of corolla (mm)	Diameter of corolla (mm)	Anther area (mm²)	Stigma area (mm²)	Flower color	Symmetry	Resource guide	Resource	Floral type	Pollination unit	Sexual system	Pollination syndrome
Anacardiaceae												
Anacardium occidentale L.	8	6	0.5	1.6	Pur	Act	Pre	Nec	Tub	Ind	Her	Mel
Myracrodruon urundeuva Allemão	2.5	4	0.9	1.6	Whi	Act	Abs	Nec	Dis	Ind	Her	Mel
Spondias tuberosa Arruda	1.99	6.51	0.39	8.6	Whi	Act	Abs	Nec	Dis	Col	Her	Mel
Annonaceae												
Annona leptopetala (R.E. Fr.) H. Rainer	12.38	26.11	0.14	20.63	Red	Zyg	Abs	Nec	Cha	Ind	Her	DSI
Oxandra reticulata Maas	10.2	14	1.2	1.9	Gre	Act	Abs	Nec	Bel	Ind	Her	Mel
Rollinia sp.	12.38	26.11	0.14	20.63	Whi	Act	Abs	Nec	Cha	Ind	Her	Mel
Apocynaceae												
Allamanda blanchetti A. DC.	72.67	54.84	10.2	26.21	Pur	Act	Pre	Nec	Tub	Ind	Her	Mel
Aspidosperma pyrifolium Mart.	11.62	13.55	0.43	2.86	Whi	Act	Pre	Nec	Tub	Ind	Her	Pha

Arecaceae												
Syagrus coronata (Mart.) Becc.	8.76	6.16	1.25	1.2	Yel	Act	Abs	Nec	Bel	Ind	Mon	DSI
Asteraceae												
Gochnatia oligocephala (Gardner) Cabrera	4.4	1.7	0.1	1.2	Yel	Act	Abs	Nec	Bru	Col	Her	Mel
Bignoniaceae												
Handroanthus impetiginosus (Mart. ex DC.) Mattos	38.58	21.75	1.4	19.37	Pur	Act	Pre	Nec	Tub	Ind	Her	Mel
Boraginaceae												
Cordia curassavica (Jacq.) Roem. & Schult.	4.27	3.42	0.33	1.6	Whi	Act	Pre	Nec	Bel	Int	Her	Mel
Cordia sp.	4.27	3.42	0.33	1.6	Whi	Act	Pre	Nec	Bel	Int	Her	Mel
Cordia rufescens A.DC.	55.5	36.45	0.33	1.6	Yel	Act	Pre	Nec	Bel	Ind	Her	Mel
Cordia trichotoma (Vell.) Arráb. ex Steud.	17.97	16.06	1.4	1.6	Whi	Act	Pre	Nec	Bel	Ind	Her	Mel
Varronia globosa Jacq.	16.71	7.97	2.24	20.68	Yel	Act	Pre	Nec	Bel	Ind	Her	Mel
Varronia leucocephala (Moric.) J.S. Mill.	26.21	15.83	2.24	20.68	Whi	Act	Abs	Nec	Tub	Int	Her	Mel
Burseraceae												
Commiphora leptophloeos (Mart.) J.B.Gillett	4.83	4.25	0.47	1.6	Whi	Act	Abs	Nec	Tub	Int	Dio	Mel
Capparaceae												
Cynophalla flexuosa (L.) J.Presl	19.66	12.91	1.48	76.47	Whi	Act	Abs	Nec	Bru	Ind	Her	Chi
Cynophalla hastata (Jacq.) J.Presl	19.66	12.91	1.48	76.47	Whi	Act	Abs	Nec	Bru	Ind	Her	Chi
Neocalyptrocalyx longifolium (Mart.) Cornejo & Iltis	10.62	13.33	0.97	4.2	Whi	Act	Abs	Nec	Bru	Ind	Her	Chi
Celastraceae												
Maytenus rigida Mart.	2.5	4.69	0.18	2.22	Whi	Act	Abs	Nec	Dis	Ind	Her	Mel
Combretaceae												
Combretum glaucocarpum Mart.	4.5	3.5	0.5	1.8	Yel	Act	Abs	Nec	Bru	Col	Her	Mel
Erythroxylaceae												
Erythroxylum revolutum Mart.	6.11	8.62	0.42	10.4	Yel	Act	Abs	Nec	Dis	Int	Her	Mel
Erythroxylum subrotundum A.St.-Hil.	3.87	4.74	0.31	1.7	Whi	Act	Pre	Nec	Dis	Ind	Her	Mel

Euphorbiaceae												
Acalypha brasiliensis Müll. Arg.	8	4	0.4	1.8	Red	Act	Abs	Nec	Tub	Col	Her	Mel
Cnidoscolus bahianus (Ule) Pax & K.Hoffm.	13.95	17.52	1.1	62.56	Whi	Act	Abs	Nec	Tub	Ind	Mon	Mel
Cnidoscolus pubescens Pohl	13.95	17.52	1.1	62.56	Whi	Act	Abs	Nec	Tub	Ind	Her	Mel
Croton argyrophyllus Kunth	1.26	4.92	0.59	65.25	Gre	Act	Abs	Nec	Dis	Int	Mon	Mel
Croton grewioides Baill.	1.26	4.92	0.59	65.25	Whi	Act	Abs	Nec	Dis	Ind	Mon	Mel
Croton heliotropiifolius Kunth	3.36	4.78	0.77	38.89	Yel	Act	Abs	Nec	Dis	Int	Mon	Mel
Croton nepetifolius Baill.	1.26	4.92	0.59	65.25	Whi	Act	Abs	Nec	Dis	Ind	Mon	Mel
Ditaxis desertorum (Müll.Arg.) Pax & K.Hoffm.	3.5	8.25	0.9	1.8	Whi	Act	Abs	Nec	Dis	Ind	Dio	Mel
Jatropha mollissima (Pohl) Baill.	10	12	7.16	137.54	Yel	Act	Abs	Nec	Dis	Ind	Mon	Mel
Jatropha mutabilis (Pohl) Baill.	12.15	18.78	7.16	137.54	Ora	Act	Abs	Nec	Dis	Ind	Mon	Mel
Jatropha ribifolia (Pohl) Baill.	12.15	18.78	7.16	137.54	Yel	Act	Abs	Nec	Dis	Ind	Mon	Mel
Manihot pseudoglaziovii Pax & K. Hoffm.	1.26	4.92	0.59	65.25	Yel	Act	Abs	Nec	Bel	Ind	Mon	Mel
Sapium glandulosum (L.) Morong	1.8	1.8	0.8	0.9	Red	Act	Abs	Nec	Inc	Int	Her	Mel
Stillingia trapezoidea Ule	2.29	1.28	0.51	2.2	Whi	Act	Abs	Pol	Bel	Int	Mon	Mel
Fabaceae												
Aeschynomene marginata Benth.	6	6	0.4	1.8	Yel	Zyg	Pre	Nec	Fla	Ind	Her	Mel
Amburana cearensis (Allemão) A.C. Sm.	12	11	0.64	1.2	Whi	Zyg	Pre	Nec	Fla	Ind	Her	Mel
Anadenanthera colubrina (Vell.) Brenan	4	3	0.3	0.8	Whi	Act	Abs	Nec	Bru	Col	Her	Mel
Bauhinia acuruana Moric.	29.16	17.61	9.04	54.39	Whi	Act	Abs	Nec	Tub	Ind	Her	Chi
Calliandra aeschynomenoides Benth.	9	6	0.6	1.22	Red	Act	Pre	Nec	Bru	Ind	Her	Pha
Chamaecrista hispidula (Vahl) H.S.Irwin & Barneby	21.3	24.75	5.65	3.19	Yel	Zyg	Abs	Pol	Fla	Ind	Her	Mel
Chloroleucon foliolosum (Benth.) G.P.Lewis	4.43	1.78	0.1	1.26	Yel	Act	Abs	Nec	Bru	Col	Her	Mel
Dahlstedtia araripensis (Benth.) M.J. Silva & A.M.G. Azevedo	12	6	0.9	1.8	Pur	Zyg	Pre	Nec	Fla	Ind	Her	Mel
Dalbergia cearensis Ducke	4.5	2.7	0.9	1.8	Yel	Zyg	Pre	Nec	Fla	Int	Her	Mel
Fabaceae sp.	3.43	1.12	0.03	0.63	Whi	Act	Abs	Pol	Bru	Col	Her	Mel

Libidibia ferrea (Mart. ex Tul.) L.P.Queiroz	6.5	3.75	1.9	4.2	Yel	Zyg	Pre	Nec	Fla	Ind	Her	Mel
Lonchocarpus obtusus Benth.	12	6	0.9	1.8	Pur	Zyg	Pre	Nec	Fla	Ind	Her	Mel
Luetzelburgia bahiensis Yakovlev	11.25	7.74	3.38	1.14	Whi	Zyg	Pre	Nec	Fla	Ind	Her	Mel
Mimosa lewisii Barneby	3.9	2.7	1.44	0.9	Whi	Act	Abs	Nec	Bru	Col	Her	Chi
Mimosa ophthalmocentra Mart. ex Benth.	3.9	2.7	1.44	0.9	Whi	Act	Abs	Nec	Bru	Col	Her	Mel
Mimosa tenuiflora (Willd.) Poir.	2.4	1.8	1.44	0.9	Whi	Act	Abs	Nec	Bru	Col	Her	Mel
Myroxylon peruiferum L.f.	2	2	0.5	0.9	Whi	Zyg	Pre	Nec	Fla	Ind	Her	Mel
Parapiptadenia sp.	4.75	1.53	0.04	1.15	Yel	Act	Abs	Nec	Bru	Col	Her	Mel
Peltogyne pauciflora Benth.	2.2	4.5	0.9	1.2	Whi	Act	Abs	Nec	Dis	Ind	Her	Mel
Piptadenia zehntneri Harms	3.67	1.44	0.05	0.82	Whi	Act	Abs	Nec	Bru	Col	Her	Mel
Pityrocarpa moniliformis (Benth.) Luckow & R.W.Jobson	2.22	2.47	0.2	1.19	Yel	Act	Abs	Pol	Bru	Col	Her	Mel
Poincianella microphylla (Mart. ex G. Don) L.P. Queiroz	14.06	18.95	1.91	4.25	Yel	Zyg	Pre	Nec	Fla	Ind	Her	Mel
Poincianella pyramidalis (Tul.) L.P. Queiroz	14.06	18.95	1.91	4.25	Yel	Zyg	Pre	Nec	Fla	Ind	Her	Mel
Senegalia bahiensis (Benth.) Seigler & Ebinger	4.75	1.53	0.04	1.15	Yel	Zyg	Abs	Nec	Bru	Col	Her	Mel
Senegalia piauhiensis (Benth.) Seigler & Ebinger	7.5	3.5	0.04	1.15	Whi	Act	Abs	Nec	Bru	Col	Her	Mel
Senegalia polyphylla (DC.) Britton	4.75	1.53	0.04	1.15	Whi	Act	Abs	Pol	Bru	Col	Her	Mel
Senna rizzinii H.S. Irwin & Barneby	16	8	1.8	2.2	Yel	Zyg	Abs	Pol	Fla	Ind	Her	Mel
Senna spectabilis (DC.) H.S. Irwin & Barneby	16	40	1.8	2.2	Yel	Zyg	Abs	Pol	Fla	Ind	Her	Mel
Senna splendida (Vogel) H.S. Irwin & Barneby	20	65	1.8	2.2	Yel	Zyg	Abs	Pol	Fla	Ind	Her	Mel
Senna trachypus (Mart. ex Benth.) H.S. Irwin & Barneby	20	37.5	1.8	2.2	Yel	Zyg	Abs	Pol	Fla	Ind	Her	Mel
Tamarindus indica L.	2	3.1	1.2	1.8	Whi	Zyg	Pre	Nec	Fla	Ind	Her	Mel
Trischidium molle (Benth.) H.E. Ireland	11.42	15.79	2.96	5.42	Whi	Zyg	Pre	Nec	Fla	Ind	Her	Mel
Loganiaceae												
Strychnos rubiginosa A. DC.	3	2.4	0.6	0.9	Gre	Act	Abs	Nec	Bel	Ind	Her	Mel

Malpighiaceae											
Byrsonima gardneriana A. Juss.	4.59	11.6	1.39	3.83	Yel	Act	Pre	Oil	Dis	Ind	Her	Mel
Byrsonima lancifolia A.Juss.	4.73	9.84	1.92	1.77	Whi	Act	Abs	Oil	Dis	Ind	Her	Mel
Malvaceae												
Helicteres velutina K.Schum.	23.3	8	1.5	2	Red	Act	Abs	Nec	Tub	Ind	Her	Orn
Melochia tomentosa L.	11.8	12.4	1.6	3.2	Pur	Act	Pre	Nec	Dis	Ind	Her	Mel
Waltheria brachypetala Turcz.	3.75	2.75	3.75	1.9	Yel	Act	Abs	Nec	Bel	Ind	Her	Mel
Myrtaceae												
Campomanesia eugenioides (Cambess.) D.Legrand ex Landrum	5.61	14.89	0.51	1.35	Whi	Act	Abs	Nec	Dis	Ind	Her	Mel
Eugenia brejoensis Mazine	8.7	16.1	4.4	3.2	Whi	Act	Abs	Nec	Dis	Ind	Her	Mel
Eugenia sonderiana O.Berg	8.7	16.1	4.4	3.2	Whi	Act	Abs	Nec	Dis	Ind	Her	Mel
Myrcia sp.	2.5	4	2.25	1.2	Whi	Act	Abs	Nec	Dis	Ind	Her	Mel
Psidium brownianum DC.	13.95	14.76	0.49	1.2	Whi	Act	Abs	Nec	Dis	Ind	Her	Mel
Psidium oligospermum DC.	13.95	14.76	0·49	1.2	Whi	Act	Abs	Pol	Dis	Int	Her	Mel
Psidium schenckianum Kiaersk.	13.95	14.76	0.49	1.2	Whi	Act	Abs	Nec	Dis	Ind	Her	Mel
Nyctaginaceae												
Guapira noxia (Netto) Lundell	6.2	3.2	0·5	3.2	Gre	Act	Abs	Nec	Tub	Int	Dio	Mel
Passifloraceae												
Turnera cearensis Urb.	11	0.6	0.2	0.4	Yel	Act	Pre	Nec	Bel	Ind	Her	Mel
Polygonaceae												
Ruprechtia laxiflora Meisn.	2	1.8	0.8	0.9	Pur	Act	Pre	Nec	Bel	Ind	Her	Mel
Rhamnaceae												
Ziziphus joazeiro Mart.	1.81	5.34	0.4	3.36	Yel	Act	Pre	Nec	Dis	Int	Her	Mel
Rubiaceae												
Cordiera rigida (K.Schum.) Kuntze	7.98	1.81	3.86	1.76	Yel	Act	Abs	Nec	Tub	Ind	Her	Mel
Rutaceae												
Balfourodendron molle (Miq.) Pirani	2.5	2	0.5	0.5	Whi	Act	Abs	Nec	Bru	Int	Her	Mel

Zanthoxylum stelligerum Turcz.	3	2.25	0.44	1.2	Yel	Act	Abs	Nec	Inc	Int	Mon	Mel
Salicaceae												
Casearia sylvestris Sw.	8	7	0.4	1.2	Whi	Act	Abs	Nec	Inc	Int	Her	Mel
Xylosma ciliatifolia (Clos) Eichler	1.5	1.5	0.8	1.2	Gre	Act	Abs	Nec	Bel	Ind	Mon	Mel
Sapindaceae												
Allophylus quercifolius Radlk.	0.35	0.25	0.5	0.5	Yel	Act	Abs	Nec	Inc	Int	Her	DSI
Sapotaceae												
Manilkara salzmannii (A. DC.) H.J. Lam	7.3	6.1	2.2	2.5	Yel	Act	Abs	Nec	Dis	Ind	Her	Mel
Sideroxylon obtusifolium (Humb. ex Roem. & Schult.) T.D. Penn.	6.9	4.6	0.1	0.2	Whi	Act	Abs	Nec	Dis	Int	Her	Mel
Solanaceae												
Solanum rhytidoandrum Sendtn.	5	2.8	2.28	0.8	Pur	Act	Pre	Nec	Dis	Ind	Her	Mel
Verbenaceae												
Lantana camara L.	12.15	18.78	7.16	137.54	Yel	Act	Abs	Nec	Tub	Int	Her	Psy
Lippia gracilis Schauer	5.44	3.54	0.12	1.82	Whi	Act	Abs	Nec	Tub	Int	Her	Psy
Lippia grata Schauer	5.44	3.54	0.12	1.82	Whi	Act	Pre	Nec	Tub	Int	Her	Psy
Lippia origanoides Kunth	5.44	3.54	0.12	1.82	Yel	Zyg	Abs	Nec	Tub	Col	Her	Mel

Table A.2. Fruit traits of all woody species in the Catimbau National Park, in the 20 plots covering the precipitation and disturbance gradients. Legends: Fruit type (Ach = Achene, Ber = Berry, Cap = Capsule, Dru = Drupe, Fol = Follicle, Leg = Legume, Nut = Nut, Sam = Samara and Sch = Schizocarp), Dehiscence (Deh = Dehiscente and Indeh = Indehiscente), Consistency (Dry = Dry and Fle = Fleshy), Fruits color (Blac = Black, Brow = Brown, Gre = Green, Yel = Yellow, Ora = Orange, Pur = Purple and Red = Red) and Dispersal syndrome (Ane = Anemocory, Aut = Autocoria and Zoo = Zoocoria).

Family/Species	Length of fruit (mm)	Diameter od fruit (mm)	Weight (g)	Fruit type	Seed number	Length of seed (mm)	Diameter of seed (mm)	Dehiscence	Consistency	Attachments	Fruit Color	Dispersal syndrome
Anacardiaceae												
Anacardium occidentale L.	358	187	9.39	Dru	1	335	158	Indeh	Dry	Pre	Yel	Zoo
Myracrodruon urundeuva Allemão	3.48	3.14	2	Dru	1	2.5	2	Indeh	Dry	Aus	Pur	Aut
Spondias tuberosa Arruda	338.5	302	1.61	Dru	1	18.5	15.16	Indeh	Fle	Aus	Gre	Zoo
Annonaceae												
Annona leptopetala (R.E. Fr.) H. Rainer	200	150	20	Ber	100	1.5	1	Indeh	Fle	Pre	Yel	Zoo
Oxandra reticulata Maas	13.5	10	2	Ber	2	9	5	Indeh	Fle	Pre	Pur	Zoo
Rollinia sp.	200	150	20	Ber	100	1.5	1	Indeh	Fle	Pre	Yel	Zoo
Apocynaceae												
Allamanda blanchetti A. DC.	61.71	36.85	4.17	Cap	31.44	24.1	24.16	Deh	Dry	Pre	Brow	Ane
Aspidorperma pyrifolium Mart.	85.21	46.56	18.54	Cap	8.2	44.84	39.31	Deh	Dry	Pre	Brow	Aut
Arecaceae												
Syagrus coronata (Mart.) Becc.	26.8	18.2	6.3	Dru	1	22.6	14.3	Indeh	Dry	Pre	Brow	Zoo
Asteraceae												
Gochnatia oligocephala (Gardner) Cabrera	3	3	1	Ach	1	2	2	Indeh	Dry	Aus	Brow	Aut
Bignoniaceae												

Handroanthus impetiginosus (Mart. ex DC.) Mattos	237.94	12.21	5	Cap	1000	56	25	Deh	Dry	Pre	Brow	Ane
Boraginaceae												
Cordia curassavica (Jacq.) Roem. & Schult.	17.85	9.88	1.5	Dru	1	14	8	Indeh	Fle	Pre	Red	Zoo
Cordia sp.	74.33	12.41	2	Dru	1	7.5	6	Deh	Fle	Pre	Red	Zoo
Cordia rufescens A.DC.	17.85	9.88	1.5	Dru	1	14	8	Deh	Dry	Pre	Blac	Ane
Cordia trichotoma (Vell.) Arráb. ex Steud.	10	5	1.5	Dru	1	9	5	Indeh	Fle	Pre	Yel	Zoo
Varronia globosa Jacq.	1.8	1	1	Dru	1	1.3	0.8		Dry	Aus	Brow	Aut
Varronia leucocephala (Moric.) J.S. Mill.	4.5	5.83	1	Dru	1	3	3	Deh	Dry	Pre	Blac	Ane
Burseraceae												
Commiphora leptophloeos (Mart.) J.B.Gillett	219	188	1.09	Dru	1	8.88	6.56	Deh	Fle	Pre	Gre	Zoo
Capparaceae												
Cynophalla flexuosa (L.) J.Presl	190	30	8	Cap	20	0.9	0.8	Deh	Dry	Pre	Red	Zoo
Cynophalla hastata (Jacq.) J.Presl	80	11.66	4	Cap	7.33	0.6	0.6	Deh	Fle	Pre	Red	Zoo
Neocalyptrocalyx longifolium (Mart.) Cornejo & Iltis	7.5	3.5	4	Cap	5	0.6	0.6	Deh	Fle	Pre	Gre	Zoo
Celastraceae												
Maytenus rigida Mart.	9	6	1	Cap	1	7	4	Deh	Dry	Pre	Ora	Zoo
Combretaceae												
Combretum glaucocarpum Mart.	2.6	1.9	1	Sam	1	1	1	Indeh	Dry	Pre	Brow	Ane
Erythroxylaceae												
Erythroxylum revolutum Mart.	8	4.2	0.8	Ber	1	5.2	4	Indeh	Fle	Pre	Red	Zoo
Erythroxylum subrotundum A.St.-Hil.	9.1	3.84	0.9	Ber	1	5.2	4	Indeh	Fle	Aus	Red	Zoo
Euphorbiaceae												
Acalypha brasiliensis Müll. Arg.	0.25	0.2	1	Cap	3	0.2	0.16	Deh	Dry	Aus	Brow	Aut
Cnidoscolus bahianus (Ule) Pax & K.Hoffm.	2.5	1.8	3	Cap	3	1.3	0.8	Deh	Dry	Pre	Brow	Aut
Cnidoscolus pubescens Pohl	2.5	1.8	3	Cap	3	1.3	0.8	Deh	Dry	Pre	Brow	Aut
Croton argyrophyllus Kunth	6.5	4.5	1	Cap	3	4.6	3	Deh	Dry	Aus	Gre	Aut

Croton grewioides Baill.	6.5	4.5	1	Cap	3	4.6	3	Deh	Dry	Aus	Gre	Aut
Croton heliotropiifolius Kunth	6.5	4.5	1	Cap	3	4.6	3	Deh	Dry	Aus	Gre	Aut
Croton nepetifolius Baill.	6.5	4.5	1	Cap	3	4.6	3	Deh	Dry	Aus	Gre	Aut
Ditaxis desertorum (Müll.Arg.) Pax & K.Hoffm.	4.5	5.1	0.7	Dru	3	3.2	2.4	Indeh	Fle	Aus	Yel	Zoo
Jatropha mollissima (Pohl) Baill.	240.5	259.5	0.38	Cap	3	12.91	8.35	Deh	Dry	Pre	Brow	Aut
Jatropha mutabilis (Pohl) Baill.	240.5	259.5	0.38	Cap	3	12.91	8.35	Deh	Dry	Pre	Brow	Aut
Jatropha ribifolia (Pohl) Baill.	240.5	259.5	0.38	Cap	3	12.91	8.35	Deh	Dry	Pre	Brow	Aut
Manihot pseudoglaziovii Pax & K. Hoffm.	240.5	259.5	0.38	Cap	3	12.91	8.35	Deh	Dry	Pre	Brow	Aut
Sapium glandulosum (L.) Morong	10.95	10.85	0.11	Cap	3	8.13	5.06	Deh	Dry	Aus	Brow	Aut
Stillingia trapezoidea Ule	6.22	6.4	1	Cap	3	1.8	0.8	Deh	Dry	Aus	Brow	Aut
Fabaceae												
Aeschynomene marginata Benth.	0.6	0.4	1	Leg	5	0.35	0.2	Deh	Dry	Aus	Brow	Aut
Amburana cearensis (Allemão) A.C. Sm.	623	152	0.43	Sam	1	14.09	9.7	Deh	Dry	Pre	Blac	Ane
Anadenanthera colubrina (Vell.) Brenan	2563	192	1.41	Fol	10	13.54	12.86	Deh	Dry	Aus	Brow	Aut
Bauhinia acuruana Moric.	157.5	12	3.7	Leg	9	7.73	5.6	Deh	Dry	Aus	Brow	Ane
Calliandra aeschynomenoides Benth.	60	7	13	Leg	4	12	8	Deh	Dry	Aus	Brow	Aut
Chamaecrista hispidula (Vahl) H.S.Irwin & Barneby	4	1.5	1	Leg	4	0.8	0.6	Deh	Dry	Aus	Brow	Aut
Chloroleucon foliolosum (Benth.) G.P.Lewis	110	16.5	2	Leg	5	0.7	0·6	Indeh	Dry	Aus	Brow	Aut
Dahlstedtia araripensis (Benth.) M.J. Silva & A.M.G. Azevedo	10	2	2.6	Sam	2	2	1.5	Indeh	Dry	Pre	Brow	Ane
Dalbergia cearensis Ducke	37.5	11	14.5	Sam	1	7.9	4.8	Indeh	Dry	Pre	Brow	Aut
Fabaceae sp.	826	168.5	0.44	Leg	6.5	598.5	5.99	Deh	Dry	Aus	Brow	Aut
Libidibia ferrea (Mart. ex Tul.) L.P.Queiroz	345.6	240.5	0.26	Leg	6.5	6.5	7.74	Indeh	Dry	Aus	Brow	Aut
Lonchocarpus obtusus Benth.	57.5	11	3	Leg	1.5	1.1	1	Indeh	Dry	Pre	Brow	Ane
Luetzelburgia bahiensis Yakovlev	56.25	15.63	0.25	Leg	1	13.82	9.57	Indeh	Dry	Pre	Brow	Ane
Mimosa lewisii Barneby	105	8	5	Cap	8.5	6	4	Deh	Dry	Aus	Brow	Aut
Mimosa ophthalmocentra Mart. ex Benth.	54	6	3	Cap	8.5	6	4	Deh	Dry	Aus	Brow	Aut

Mimosa tenuiflora (Willd.) Poir.	439	66.5	0.11	Leg	6	4.61	3.26	Deh	Dry	Aus	Brow	Aut
Myroxylon peruiferum L.f.	58.4	14.2	2	Leg	1	1.5	0.7	Deh	Dry	Aus	Brow	Aut
Parapiptadenia sp.	7.5	2	3	Leg	7.5	7	6	Deh	Dry	Pre	Brow	Ane
Peltogyne pauciflora Benth.	3.2	3.1	2	Leg	1	12	7	Deh	Dry	Aus	Brow	Aut
Piptadenia zehntneri Harms	826	168.5	0.44	Leg	6.5	598.5	5.99	Deh	Dry	Aus	Brow	Aut
Pityrocarpa moniliformis (Benth.) Luckow & R.W.Jobson	65	7	3	Fol	7	8	4	Deh	Dry	Aus	Brow	Aut
Poincianella microphylla (Mart. ex G. Don) L.P. Queiroz	78	17	3.98	Leg	3.9	10.59	6.67	Deh	Dry	Aus	Brow	Aut
Poincianella pyramidalis (Tul.) L.P. Queiroz	92.22	24.23	3.89	Leg	3.9	10.59	6.67	Deh	Dry	Aus	Brow	Aut
Senegalia bahiensis (Benth.) Seigler & Ebinger	84.54	14.86	0.59	Leg	8.1	7.89	5.61	Deh	Dry	Aus	Brow	Aut
Senegalia piauhiensis (Benth.) Seigler & Ebinger	97.5	18	6	Leg	12	6	4.8	Deh	Dry	Aus	Brow	Aut
Senegalia polyphylla (DC.) Britton	162.5	27.5	7	Leg	12	6	4.8	Deh	Dry	Aus	Brow	Aut
Senna rizzinii H.S. Irwin & Barneby	60	15	6	Leg	12	6	4.8	Deh	Dry	Pre	Brow	Zoo
Senna spectabilis (DC.) H.S. Irwin & Barneby	2476.5	113	0.42	Leg	50	6.79	4.58	Deh	Dry	Aus	Brow	Aut
Senna splendida (Vogel) H.S. Irwin & Barneby	195	6.5	6	Leg	12	6	4.8	Deh	Fle	Aus	Gre	Zoo
Senna trachypus (Mart. ex Benth.) H.S. Irwin & Barneby	95	13	6	Leg	12	45	6.5	Deh	Dry	Aus	Brow	Aut
Tamarindus indica L.	11	2.8	4	Leg	8	1	1	Indeh	Dry	Aus	Brow	Aut
Trischidium molle (Benth.) H.E. Ireland	12.5	9	2	Leg	1	6	4.5	Deh	Dry	Aus	Yel	Aut
Loganiaceae												
Strychnos rubiginosa A. DC.	10	10	0.7	Ber	1	7	7	Indeh	Fle	Pre	Yel	Zoo
Malpighiaceae												
Byrsonima gardneriana A. Juss.	6.15	4.8	1.5	Ber	6.15	4.8	1.5	Indeh	Fle	Pre	Yel	Zoo
Byrsonima lancifolia A.Juss.	6.15	4.8	1.5	Ber	6.15	4.8	1.5	Indeh	Fle	Pre	Yel	Zoo
Malvaceae												
Helicteres velutina K.Schum.	9.1	3.84	0.9	Cap	6	2.1	1.2	Deh	Dry	Aus	Brow	Aut

Melochia tomentosa L.	11	7	1	Cap	5	2.5	1.2	Deh	Dry	Aus	Brow	Aut
Waltheria brachypetala Turcz.	3	2.5	1	Cap	1	1.2	0.8	Deh	Dry	Aus	Brow	Aut
Myrtaceae												
Campomanesia eugenioides (Cambess.) D.Legrand ex Landrum	15	15	2	Ber	100	1	1	Indeh	Fle	Pre	Yel	Zoo
Eugenia brejoensis Mazine	11.33	8.3	3	Ber	5	10	7	Indeh	Fle	Pre	Blac	Zoo
Eugenia sonderiana O.Berg	11.33	8.3	3	Ber	5	10	7	Indeh	Fle	Pre	Yel	Zoo
Myrcia sp.	4.5	1.3	1	Dru	18	1.2	0.7	Indeh	Fle	Pre	Yel	Zoo
Psidium brownianum DC.	12	9	2	Ber	12	1.2	1	Indeh	Fle	Pre	Yel	Zoo
Psidium oligospermum DC.	12	9	2	Ber	12	1.2	1	Indeh	Fle	Pre	Yel	Zoo
Psidium schenckianum Kiaersk.	12	9	2	Ber	12	1.2	1	Indeh	Fle	Pre	Yel	Zoo
Nyctaginaceae												
Guapira noxia (Netto) Lundell	200	150	20	Ber	100	1.5	1	Indeh	Fle	Pre	Pur	Zoo
Passifloraceae												
Turnera cearensis Urb.	6	6	2	Cap	12	2.7	3	Deh	Dry	Pre	Brow	Aut
Polygonaceae												
Ruprechtia laxiflora Meisn.	5	2.8	1	Nut	1	2.8	1.3	Indeh	Dry	Pre	Brow	Ane
Rhamnaceae												
Ziziphus joazeiro Mart.	14.29	14.73	0.37	Dru	1.5	8.6	4.71		Fle	Aus	Yel	Zoo
Rubiaceae												
Cordiera rigida (K.Schum.) Kuntze	6	7.5	1.2	Ber	32.2	3.5	2.5	Indeh	Fle	Pre	Blac	Zoo
Rutaceae												
Balfourodendron molle (Miq.) Pirani	22.5	15	0.99	Sam	3	9	7	Indeh	Dry	Pre	Brow	Aut
Zanthoxylum stelligerum Turcz.	3	3	1	Fol	1	3	2	Deh	Dry	Aus	Brow	Aut
Salicaceae												
Casearia sylvestris Sw.	2	2	1	Cap	3	0.8	0.8	Deh	Dry	Pre	Red	Zoo
Xylosma ciliatifolia (Clos) Eichler	6	6	1	Ber	4	1.5	1.3		Fle	Pre	Red	Zoo
Sapindaceae												

Allophylus quercifolius Radlk.	0.55	0.35	1	Dru	1	0.5	0.3	Indeh	Fle	Pre	Yel	Zoo
Sapotaceae												
Manilkara salzmannii (A. DC.) H.J. Lam	18.5	22.8	1	Ber	3	5.2	3.1	Indeh	Fle	Pre	Brow	Zoo
Sideroxylon obtusifolium (Humb. ex Roem. & Schult.) T.D. Penn.	13.12	10.27	3	Dru	1	10	7	Indeh	Fle	Pre	Blac	Zoo
Solanaceae												
Solanum rhytidoandrum Sendtn.	20	15	2	Dru	23	4.3	3.3	Indeh	Fle	Pre	Pur	Zoo
Verbenaceae												
Lantana camara L.	7	6	0.7	Dru	1	5	4	Indeh	Fle	Pre	Pur	Zoo
Lippia gracilis Schauer	7	6	0.7	Cap	1	5	4	Deh	Dry	Aus	Blac	Aut
Lippia grata Schauer	7	6	0.7	Cap	1	5	4	Deh	Dry	Aus	Blac	Aut
Lippia origanoides Kunth	2	5	4	Sch	3	5	4	Deh	Dry	Aus	Brow	Aut

Fig. A.1. Correlation of the abundance of woody species on the precipitation (A) and human disturbance gradients (B) in the Catimbau National Park, Brazil, followed by their respective pollination and dispersal syndromes. Where: MEL = melittophily, DSI = diverse small insects, PSY = psychophily, PHA = phalenophily, ORN = ornithophily, CHI = chiropterophily, ANE = anemocory, AUT = autochory and ZOO = zoochory.

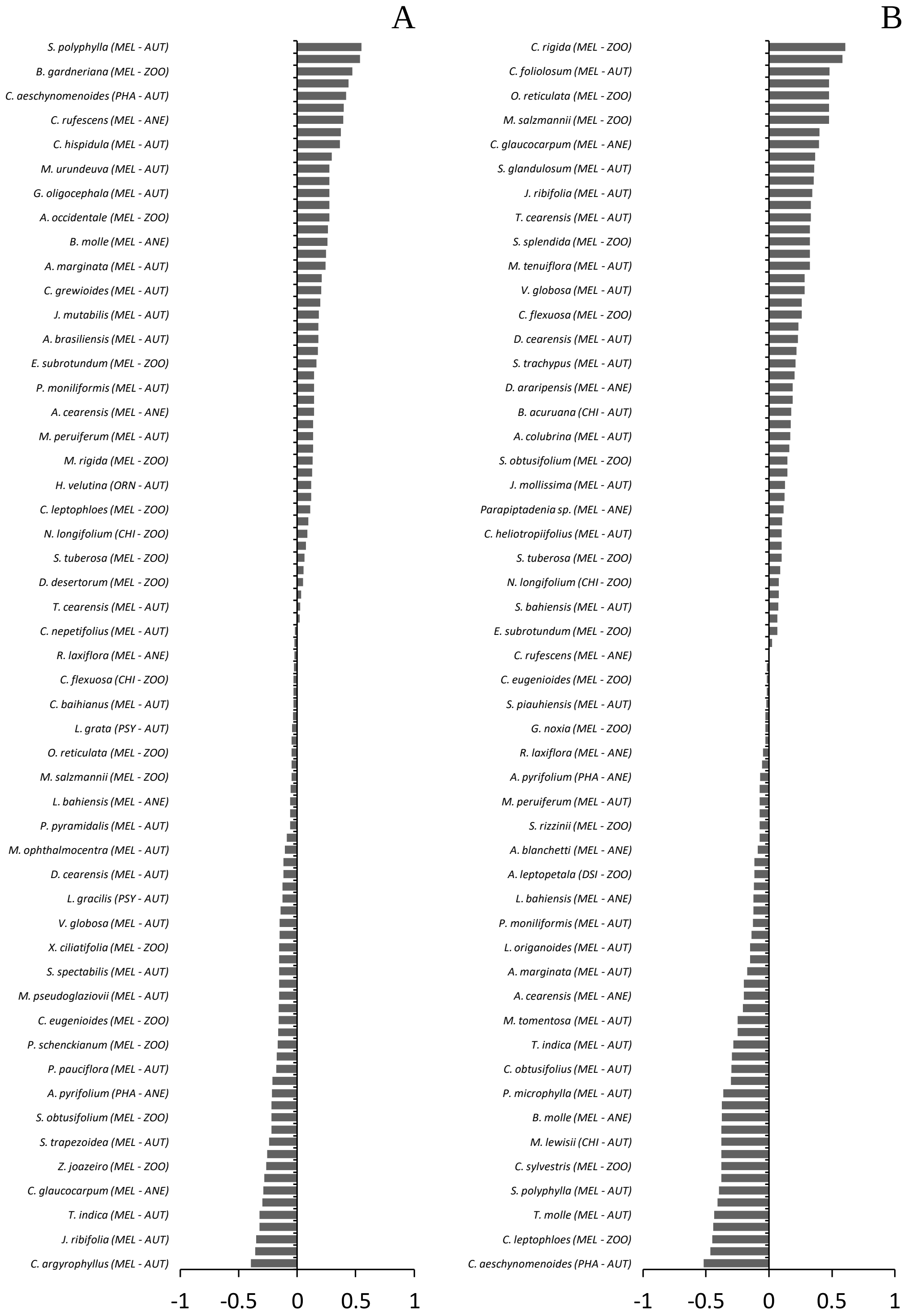


Fig. A.2. Percentage of plant species per pollination syndrome along the precipitation (A) and human disturbance gradients (B). The percentage of individuals per pollination syndrome is also indicated (C and D) in the Catimbau National Park.

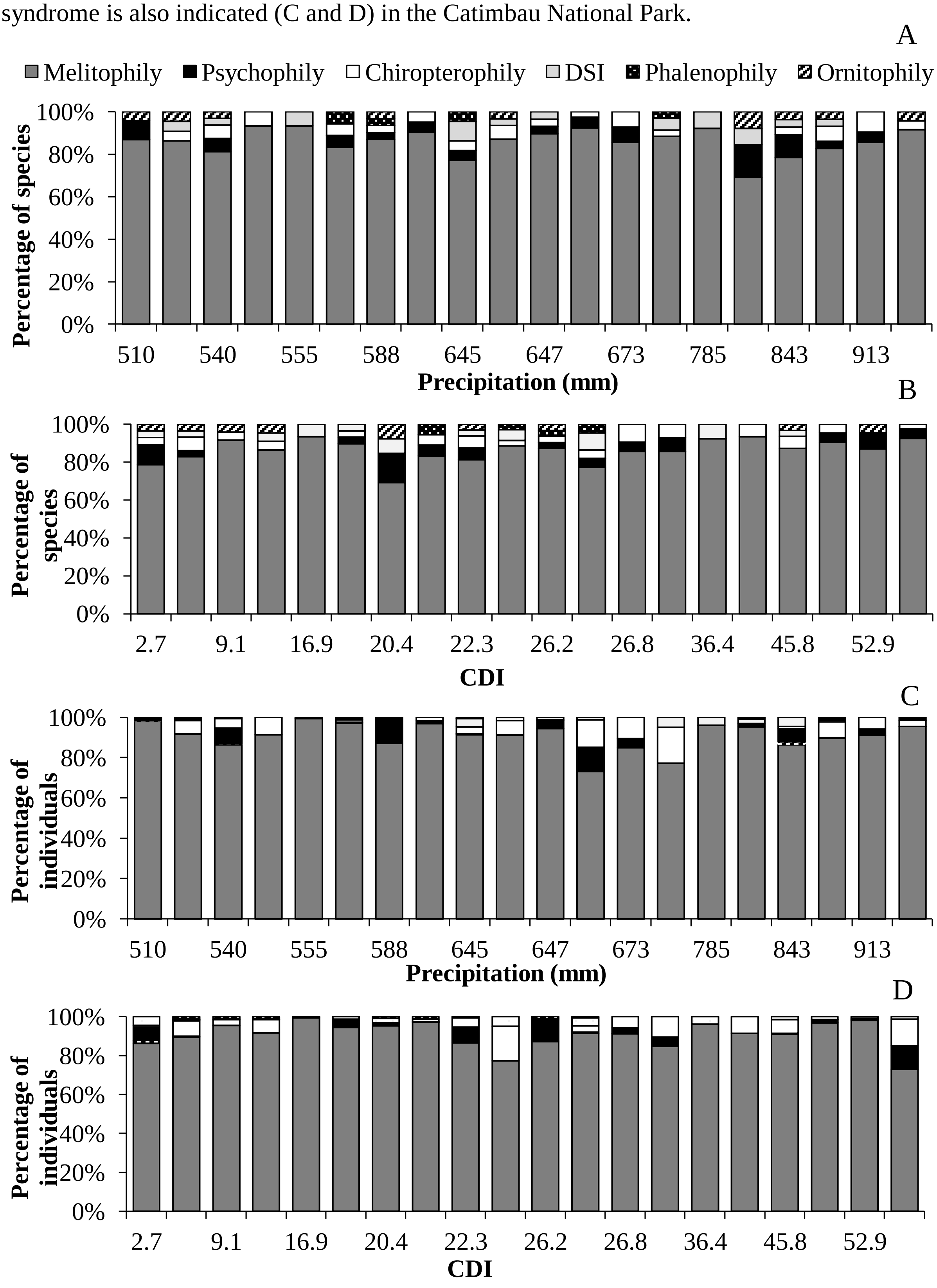
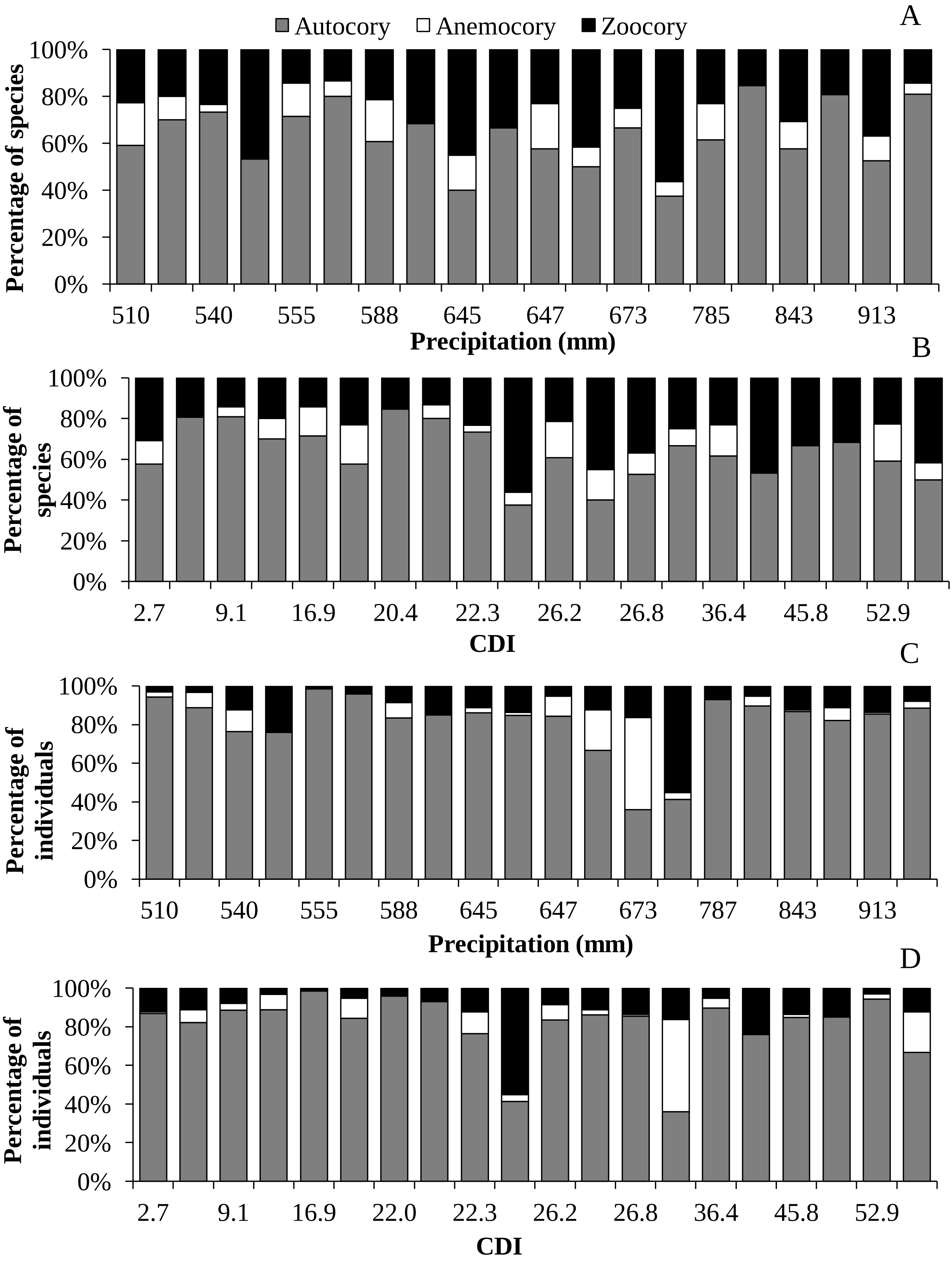


Fig. A.3. Percentage of plant species per dispersal syndrome along the precipitation (A) and human disturbance gradients (B). The percentage of individuals per pollination syndrome is also indicated (C and D) in the Catimbau National Park.



5 CONCLUSÕES

Com o desenvolvimento dessa tese chegamos às seguintes conclusões para a fenologia e diversidade funcional reprodutiva de espécies lenhosas da Caatinga:

- A comunidade de espécies lenhosas da Caatinga apresenta padrão reprodutivo contínuo de floração e frutificação, devido à produção de flores e frutos ao longo dos anos e picos reprodutivos nas estações seca e chuvosa;
- A maior frequência de espécies em floração coincide com a estação chuvosa enquanto a maior frequência de espécies em frutificação coincide com a estação seca da região;
- A baixa sincronia de indivíduos em floração e frutificação na comunidade lenhosa da Caatinga está relacionada com a ocorrência contínua das fenofases reprodutivas;
- A sincronia das espécies comuns é maior nas áreas com menor precipitação, pois o período reprodutivo está concentrado no período chuvoso da região;
- Perturbação antrópica parecer ser um fator essencial no desenvolvimento fenológico reprodutivo de espécies da Caatinga, especialmente quando a restrição hídrica é mais limitante, como nas áreas do gradiente com menor precipitação;
- A sazonalidade das fenofases reprodutivas é maior nas áreas com menor precipitação, uma vez que o período chuvoso atua determinando o desencadeamento de processos reprodutivos de espécies;
- A diversidade funcional de flores e frutos é mantida ao longo dos gradientes de precipitação e perturbação antrópica, em virtude da ampla distribuição das espécies que compartilham os mesmos atributos funcionais;
- Melitofilia e autocoria são, respectivamente, as síndromes de polinização e de dispersão mais comuns e ocorrem em todo gradiente, devido ao grande sucesso dos atributos que as classificam, nas áreas de Caatinga;
- Precipitação e perturbação antrópica crônica parecem não influenciar a ocorrência das síndromes de polinização e de dispersão de sementes nas espécies lenhosas; isto pode ser reflexo da ampla distribuição das espécies com os mesmos atributos funcionais ao longo de todo gradiente;

- A manutenção funcional de flores e frutos é uma boa notícia para as espécies lenhosas da Caatinga, visto que as espécies conseguem manter no seu conjunto a capacidade reprodutiva, mesmo com as variações do ambiente.

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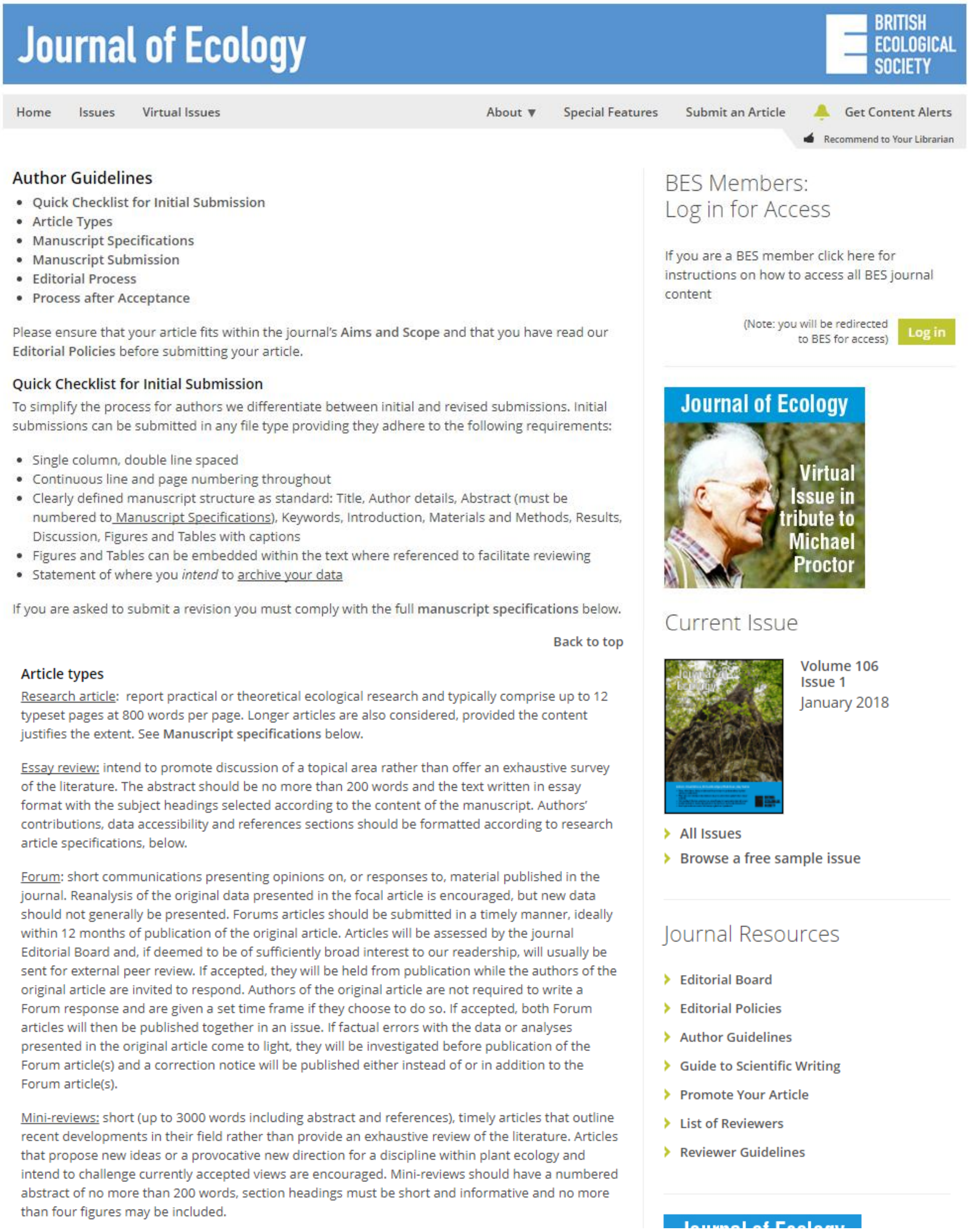
ANEXO A – NORMAS PARA SUBMISSÃO DE MANUSCRITO NA JOURNAL OF ECOLOGY



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ANEXO B – NORMAS PARA SUBMISSÃO DE MANUSCRITO NA PERSPECTIVES IN PLANT ECOLOGY, EVOLUTION AND SYSTEMATICS

PERSPECTIVES IN PLANT ECOLOGY, EVOLUTION AND SYSTEMATICS

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