KÁTIA FERNANDA RITO PEREIRA

ESTRUTURAÇÃO DE COMUNIDADES DE PLANTAS LENHOSAS DA CAATINGA: O EFEITO DOS DISTÚRBIOS ANTRÓPICOS EM UM GRADIENTE DE PRECIPITAÇÃO

Recife – PE

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Orientador: Dr. Marcelo Tabarelli

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Resumo

A expansão das populações humanas promove alterações nos ecossistemas naturais. Estas alterações ocorrem desde a perda de hábitat ao nível de paisagem e a extração de recursos a nível local até mudanças climáticas a nível regional e global. No entanto, pouco se sabe acerca das consequências que estas alterações têm à biodiversidade e estrutura das comunidades de plantas e ao empobrecimento biológico dos ecossistemas e distribuição de espécies em florestas tropicais secas. A Caatinga, um bosque seco do Brasil, possui uma grande área modificada pelas ações humanas e os modelos climáticos predizem que nos próximos anos este ecossistema vai sofrer uma importante redução na precipitação e um aumento na temperatura. Esta tese buscou compreender, em uma escala de paisagem, como ações humanas afetam a composição e estrutura da flora lenhosa da Caatinga. Foram estudadas 18 áreas dentro de 214.3 km^2 dominados por Caatinga madura exposta a diferentes tipos de distúrbio. O primeiro capítulo avaliou o efeito aditivo e multiplicativo da precipitação (gradiente de 510 a 940 mm), três preditores de distúrbio crônico (i.e. distancia para fazendas e estradas, densidade de trilhas de caprinos) e um preditor de distúrbio agudo (i.e. porcentagem de cobertura vegetal em um raio de 1 km) sobre a diversidade taxonômica, densidade de indivíduos, equabilidade, composição de espécies e biomassa de indivíduos adultos de árvores e arbustos. A precipitação anual foi o melhor preditor da composição e estrutura da vegetação, afetando positivamente a biomassa e riqueza de espécies, mas reduzindo a equabilidade das comunidades devido à perda de espécies raras em áreas com baixa precipitação. Os distúrbios agudos e crônicos tiveram fraco impacto sobre a vegetação, mas a distância para as estradas esteve negativamente relacionada com a riqueza, densidade e equabilidade das comunidades. No segundo capítulo, foi provada se a diversidade β taxonômica e a diversidade filogenética dentro e entre comunidades (α e β

– filogenética) mudam com a disponibilidade hídrica (déficit hídrico médio anual, 658–1086 mm) e com os três preditores de distúrbios crônicos. A disponibilidade hídrica foi o melhor preditor da diversidade α – filogenética e as diversidades β taxonômica e filogenética quando consideradas as espécies raras e comuns, porém não para dominantes. Os distúrbios crônicos não foram bons preditores da diversidade α nem β – filogenética. Apenas a diversidade β – taxonômica quando consideradas espécies raras foi explicada pela limitação de dispersão (i.e. distância geográfica) e distância para estradas. Os resultados desta tese mostram que (i) a disponibilidade de água e os distúrbios crônicos são importantes forças estruturadoras das comunidades de Caatinga, (ii) que a perda de espécies não é aleatória ao longo da filogenia das comunidades e que portanto, (iii) as comunidades locais de plantas não representam um subgrupo aleatório das espécies da flora regional e sim um subgrupo de espécies adaptadas ao estresse hídrico e distúrbios antrópicos.

Palavras chave: distúrbios antrópicos crônicos, distúrbios antrópicos agudos, disponibilidade hídrica, mudanças climáticas, diversidade taxonômica, diversidade filogenética, α – diversidade, β – diversidade.

Abstract

Human population growth promotes changes in natural ecosystems, ranging from landscape level by habitat loss to regional and global level by climatic changes. However, there is a lack of knowledge about the effects of habitat loss and climatic changes on community biodiversity in Seasonally Dry Tropical Forest (STDF) through changes in vegetation structure and species' distribution. The Caatinga is Brazilian SDTF threatened by climate change (future predictions estimate a decreasing in precipitation and an increasing in temperature) and by anthropogenic disturbance such as overgrazing, continuously collection of forest products and livestock production. In this study, we tested at landscape scale the impacts of precipitation and human disturbances in the composition and the structure of Caatinga wood flora. We carried out 18 0.1 ha plots across 21 430 ha of Brazilian Caatinga dominated by mature forests exposed to different disturbance types. The first chapter, we evaluated the additive and synergic effects of precipitation (510 to 940 mm gradient), plus three predictors of chronic disturbance (i.e. distance to nearest farm and road, and length of goat trails) and one predictor of acute disturbance (i.e. landscape vegetation cover) on the diversity, stem density, evenness, taxonomic composition and biomass of adult trees and shrubs. The annual mean precipitation was the best predictor of vegetation structure and composition, affecting positively the biomass and species richness, but reducing the community equability due to the rare species loss in low precipitation areas. The acute and chronic disturbance had a weaker impact on vegetation, but the distance to nearest roads was negatively related to species richness and density and community equability. In the second chapter, we prove whether taxonomic β diversity and phylogenetic diversity within and between communities (α e β – phylogenetic) change with water availability (annual average water deficit, 658–1086 mm) and with the three chronic disturbance predictors. The water availability was the best predictor of α – phylogenetic and β taxonomic and phylogenetic diversity when considered rare and common species, but not for dominant species. Chronic disturbances were not good predictors to α or β – phylogenetic diversity. Only β – taxonomic diversity, when considering rare species, was explained by dispersion limitation (i.e. geographic distance) and distance to the nearest road. In this thesis, our results show that (i) the water availability and chronic disturbances are important community assembly forces in Caatinga, (ii) the species loss is not random across the phylogeny and, therefore, (iii) the local plant communities do not represent a random subgroup of regional flora but a subgroup of human disturbance and water stress adapted species.

Key-words: chronic anthropogenic disturbance, acute anthropogenic disturbance, water availability, climate changes, taxonomic diversity, phylogenetic diversity, α – diversity, β – diversity.

SUMÁRIO

Apresentação

Existem inúmeras evidências de que a biodiversidade e por consequência os serviços ambientais providos pelas florestas tropicais são fortemente ameaçados por distúrbios humanos (GARDNER et al., 2009; SUPP & ERNEST, 2014). Em escalas locais, regionais e globais, a perda de habitat e as mudanças climáticas alteram processos ecossistêmicos e modificam a capacidade de resposta dos diferentes ambientes às mudanças ambientais (THUILLER, 2007; CHAPIN III et al., 2000). Porém, pouco se conhece ainda sobre as conseqüências destes fatores no empobrecimento biológico dos ecossistemas e na distribuição de espécies, especialmente em florestas secas tropicais (SÁNCHEZ-AZOFEIFA et al., 2005).

Em florestas tropicais secas, os efeitos negativos de distúrbios crônicos e agudos ao empobrecimento da flora são bem reconhecidos (MILES et al., 2006; BLACKIE et al., 2014). Embora se saiba que distúrbios crônicos são uma das principais ameaças a esse tipo de floresta dado seu histórico de colonização e uso de seus recursos, os efeitos de distúrbios humanos crônicos ainda são pouco estudados quando comparado aos agudos (SINGH, 1998). Mais do que isso, como estes distúrbios podem afetar as biotas frente às mudanças climáticas ainda é uma incerteza. No nordeste brasileiro, por exemplo, a Caatinga já possui grande parte de sua área modificada pelas ações humanas. Além disso, os cenários mais quentes e secos projetados por modelos climáticos para região nordeste apontam para uma possível aridização de todo o ecossistema (MARENGO, 2007).

Diante do exposto, esta tese visa compreender, em uma escala de paisagem, como os distúrbios humanos afetam a composição e estruturação da flora lenhosa da Caatinga em um gradiente de precipitação. Para isso, estudei 18 áreas dentro de 214.3 km^2 dominada por Caatinga madura exposta a distúrbios antrópicos crônicos (i.e. extração contínua de pequenas quantidades de recursos madeireiros e não madeireiros para subsistência; criação extensiva de caprinos) e agudos (i.e. perda de cobertura vegetal) distribuídas em um gradiente de precipitação de 510 a 940 mm. Esta tese está dividida em dois capítulos.

O primeiro capítulo avaliou o efeito aditivo e multiplicativo da precipitação (gradiente de 510 a 940 mm), três medidas de distúrbio crônico (i.e. distancia para fazendas e estradas, densidade de trilhas de caprinos) e uma métrica de distúrbio agudo (i.e. porcentagem de cobertura vegetal em um raio de 1 km) sobre a diversidade taxonômica, densidade de indivíduos, equabilidade, composição de espécies e biomassa de indivíduos adultos de árvores e arbustos. No segundo capítulo, foi provada se a diversidade β taxonômica e a diversidade filogenética dentro e entre comunidades (α e β – filogenética) mudam com a disponibilidade de água (déficit hídrico médio anual, 658–1086 mm) e com os preditores de distúrbios agudos.

FUNDAMENTAÇÃO TEÓRICA

A biodiversidade em florestas tropicais é influenciada por uma série de processos associados às atividades humanas que operam em diferentes escalas espaciais e temporais. Dentre elas as atividades agropecuárias, urbanização e exploração de recursos madeireiros e não madeireiros. Estas atividades geram então, impactos secundários que incluem a alteração da dinâmica natural dos ambientes (e.g. ocorrência de fogo), alterações no fluxo hidrológico, superexploração de recursos e invasão de espécies exóticas (veja GARDNER *et al.*, 2009). Estas mudanças no uso de terra têm efeitos diretos no ciclo do carbono, afetando o clima através do aumento da emissão de gases do efeito estufa, das mudanças do fluxo de radiação e de água (KALNAY & CAI, 2003).

Embora as práticas de uso de terra variem em ecossistemas do mundo todo, qualquer uma delas tem o mesmo objetivo, que é a aquisição de recursos naturais para suprir necessidades humanas imediatas (FOLEY *et al.*, 2005). Assim, estas práticas variam desde a alteração de paisagens inteiras para implantação de, por exemplo, cultivo de monoculturas (e.g. TABARELLI *et al.*, 2010), construção de barragens (e.g. FEARNSIDE, 2005) e construção de estradas (e.g. PERZ *et al.*, 2007) à práticas de agricultura e exploração de recursos para subsistência exercidas por grupos familiares. Deste modo as ações humanas, dependendo da abrangência espacial e impacto do distúrbio, podem ser classificadas como crônicas ou agudas. Distúrbios humanos agudos são aqueles que removem toda ou quase toda biomassa de uma dada área como, por exemplo, a perda de hábitat causada pela criação de pastagens (SINGH, 1998). Já os distúrbios humanos crônicos são frequentes e contínuas remoções de pequenas porções de biomassa florestal como a extração de recursos madeireiros e não madeireiros para subsistência (SINGH, 1998).

A ocorrência de distúrbios humanos crônicos está intimamente associada às áreas mais pobres do globo, em países subdesenvolvidos e regiões onde a densidade populacional é alta e os recursos florestais são ainda a base de necessidades como construção, combustível e alimentação (BARBIER, 2000; DAVIDAR *et al*., 2010; METHA *et al*., 2008; MILES *et al*., 2006; RIBEIRO et al., 2015; SINGH, 1998). Estas áreas tem grande sobreposição com os trópicos e as Florestas Tropicais Sazonalmente Secas que se estendem por países da América do Sul e Central, México, África, Índia, sudeste asiático e Austrália (MILES *et al*., 2006). De fato, as florestas secas compõem quase metade das florestas tropicais e subtropicais (SUNDERLAND *et al*., 2015) e compreendem mais de um terço da população global (MILES *et al*., 2006). Elas estão entre as florestas mais ameaçadas no mundo pelas ações humanas decorrentes de atividades como a fragmentação, fogo, conversão de áreas naturais para agricultura e pelas mudanças climáticas (MILES et al., 2006; PORTILLO-QUINTERO & SÁNCHEZ-AZOFEIFA, 2010). Além disso, cenários climáticos futuros indicam que florestas secas enfrentarão aumento da evaporação e temperatura até 2100 (BURKETT *et al*., 2014).

Os distúrbios antrópicos e a diversidade biológica

Padrões de organização biológica, desde organismos até o ecossistema, podem ser completamente alterados ou interrompidos diante das severas mudanças abióticas e bióticas observadas em ambientes perturbados por atividades humanas (MURCIA,1995; TABARELLI *et al*., 2009). Quando um ambiente passa por uma perturbação ele fica mais instável devido à perda de diversidade e funcionalidade (BRUELHEIDE & LUGINHBÜL, 2009). Isso resulta em menor capacidade de recuperação do ambiente. Por exemplo, áreas de floresta (as quais possuem, tipicamente, mais de 80% de cobertura vegetal) que tenham sua cobertura florestal reduzida a menos de 60%, tendem a se transformarem em savanas (20% de cobertura florestal) ou em vegetação arbustiva (sem cobertura vegetal) (HIROTA *et al.*, 2011). Sendo assim, a extração continuada de madeira, comum nas florestas tropicais sazonalmente secas (MURPHY & LUGO, 1986; MILES *et al.*, 2006; REID *et al.*, 2008), pode levar as áreas cobertas por este tipo de vegetação a se tornarem cada vez mais savânicas ou mesmo arbustivas.

Embora existam evidências que as Florestas Tropicais Sazonalmente Secas sejam tolerantes a secas prolongadas (MIER & PENNINGTON, 2011), existem evidências também que demonstram que a interação de fatores como duração e intensidade da seca, o aumento de temperatura e a diminuição da precipitação criam um limiar que se ultrapassado resulta em mortalidade das plantas (ALLEN *et al.*, 2009). Como por exemplo, em florestas secas da Índia, onde secas severas foram associadas com o aumento da mortalidade de várias espécies de árvores (KHAN *et al.*, 1994). Assim, é esperado que espécies de crescimento lento com estratégias de eficiência do uso de água (e.g. densidade da madeira, profundidade e arquitetura das raízes, órgãos de reserva) sejam beneficiadas em um cenário de aumento da frequência e duração das secas (MIER & PENNINGTON, 2011; CRAVEN *et al.*, 2013). Em contrapartida, estudos apontam que o aumento da emissão de CO_2 na atmosfera tem incrementado a produtividade em ambientes áridos (DONOUHE et al., 2013; LU *et al.*, 2016), uma vez que o aumento do CO_2 atmosférico implica na redução da condutância estomática e aumento da eficiência no uso de água da fotossíntese (para mais detalhes ver DONOUHE *et al.*, 2013). Desse modo, é precipitado dizer que existe um padrão de respostas da vegetação às futuras mudanças climáticas. Isso porque estas respostas dependem da intensidade das mudanças no clima e sua interação com os outros tipos de distúrbios (PULLA *et al*., 2015). Foi demonstrado em escala global que para formigas, por exemplo, a interação entre distúrbios antrópicos e clima geraram a perda de diversidade em áreas perturbadas com baixa precipitação e alta temperatura (GIBB *et al*., 2015). Isto sugere que os distúrbios antrópicos e mudanças climáticas podem interagir de modo complexo na estruturação de comunidades e que lugares quentes e áridos estão propensos a maior risco (GIBB *et al*., 2015).

As atividades humanas tem impactos negativos na composição e diversidade das comunidades, estrutura trófica, produtividade (VILLAGRA *et al*., 2009), mortalidade (MALKINSON & KADMON, 2007) e diversidade filogenética (RIBEIRO *et al*., 2016). A manutenção da diversidade em ambientes já alterados pelas ações humanas depende da substituição de espécies entre localidades (MORANTE-FILHO *et al*., 2015). Se por um lado áreas muito degradadas e simplificadas sustentam apenas poucas espécies de populações e comunidades aninhadas e espacialmente homogeneizadas (TSCHARNTKE *et al*., 2012). Por outro lado os mosaicos criados pelas perturbações criam paisagens complexamente estruturadas (com grande diversidade de habitat) e podem ter uma grande diversidade regional devido à alta beta diversidade (LOREAU *et al*., 2003) potencialmente favorecendo florestas secundárias com a chegada de alto número de espécies. Esses movimentos de espécies podem garantir resiliência uma vez que a troca de espécies entre locais permite que se levem diferentes funções ecológicas a diferentes pontos no espaço e no tempo (LUNDBERG & MOBERG, 2003). No entanto, os padrões de beta diversidade devem ser avaliados com cautela porque a retirada de espécies sensíveis ao distúrbio pode ser compensada pela proliferação de espécies adaptadas (SUPP & ERNEST, 2014), mascarando respostas ao nível de comunidade. Portanto, análises de diversidade que aliam as respostas das espécies ao nível de comunidade (i.e. diversidade alfa) e a substituição de espécies entre comunidades (i.e. diversidade beta) pode dar uma visão mais clara de como os distúrbios afetam as biotas. Enquanto a diversidade alfa provê a segurança local na manutenção de funções ecossistêmicas, uma alta beta-diversidade pode prover segurança contra mudanças ambientais sincrônicas em larga escala como as mudanças climáticas e mudanças no regime de nutrientes (PARSCHE *et al*., 2011).

Estruturação de comunidades

Predizer os fatores chave que modificam as assembleias de comunidades tem sido uma das principais questões dos ecólogos, principalmente frente às alterações nas assembleias de diversos organismos ocasionadas pelas perdas de habitat e modificações climáticas (NAEEM & WRIGHT, 2003; MCGILL *et al.*, 2006). O debate sobre quais fatores influenciam a montagem de uma comunidade envolve três perspectivas: processos relacionados ao nicho, processos neutros e fatores históricos (COYLE *et al.*, 2014). Hubbell (2001) defende a idéia de que todas as populações e comunidades estão sujeitas a mesma estocasticidade demográfica. Dessa maneira, uma comunidade estruturada aleatoriamente dependeria exclusivamente de eventos randômicos de colonização, migração e extinção (GOTELLI & MCGILL, 2006). Já em uma perspectiva de nicho, dois processos determinísticos podem estruturar comunidades: (1) exclusão competitiva, que seleciona espécies com atributos distintos (i.e. princípio da limitação de similaridade) e (2) filtros ambientais, que aumentam a similaridade (convergência), pois espécies que tem tolerâncias ecológicas similares são capazes de coexistir em determinado ambiente (GRIME, 2006).

A teoria prediz que, com o aumento da escala espacial, os fatores influenciando na montagem de comunidades variam de fatores bióticos que resultam em divergência (i.e. limitação de similaridade) a fatores abióticos que resultam em convergência (i.e. filtros ambientais) (WEIHER & KEDDY, 1995). No entanto, recentemente Mayfield & Levine (2010) propuseram que em pequenas escalas uma convergência de atributos pode ocorrer quando espécies que baixa habilidade de competição conseguem superar as outras espécies devido a diferenças sutis de nicho, aumentando assim a similaridade entre espécies coexistentes numa comunidade. Por outro lado, a divergência em escalas locais pode não apenas ser explicada pela limitação de similaridade, mas também por fatores abióticos. Isso ocorre quando em um ambiente a ocorrência de micro-habitas permite que espécies funcionalmente diferentes ocupem uma mesma área (DE BELLO *et al*., 2013).

É importante considerar que os filtros ambientais e as interações bióticas não atuam de maneira exclusiva na estruturação da comunidade, eles podem atuar em conjunto e possuindo diferentes pesos nesta estruturação. Assim, a coocorrência de espécies é um produto do acaso, de fatores históricos de especiação e migração, da dispersão, de fatores abióticos e de interações bióticas, com nenhum destes processos sendo mutuamente exclusivos (WEIHER & KEDDY, 2001). Compreender como cada um desses fatores contribui para a estruturação de uma comunidade ajuda a revelar porque as espécies são restritas a habitats específicos, porque a abundância das mesmas varia no tempo e espaço ou quais os fatores ambientais que impõem os limites primários da abundância e distribuição destas espécies (KEDDY, 1992; WEIHER & KEDDY, 2001).

O estudo da filogenia na estruturação de comunidades

De modo geral, os estudos vêm demonstrando que as ferramentas de análise filogenética tem sido bastante úteis para avaliar a relação evolucionária entre espécies. Evidências empíricas demonstram que a extinção e a vulnerabilidade à extinção são seletivas taxonomicamente (BENNETT & OWENS, 1997; VAMOSI & WILSON 2008). Assim, a perda de grupos específicos pode gerar homogeneização genética e funcional, afetando processos ecológicos e funções ecossitêmicas (D'AGATA *et al.*, 2014). Mais do que estudar se padrões de perda de diversidade taxonômica estão diretamente associados à perda de diversidade filogenética, o estudo da filogenia permite entender quais os processos estão envolvidos nestas perdas, ajudando a prever como a diversidade pode se comportar diantes de forças bióticas e abióticas específicas.

Dentre as ferramentas para avaliar os processos ecológicos que estruturam comunidades, a análise da estrutura filogenética pode ajudar a entender o papel da evolução de atributos na determinação dessa estrutura (WEBB, 2000; WEBB *et al.*, 2002; CAVENDER-BARES *et al.*, 2006). Considerando que atributos ecológicos são filogeneticamente conservados, é esperado que comunidades que estão submetidas a ambientes menos restritivos sejam compostas por mais espécies. Assim, a força estruturadora da comunidade é a competição, havendo exclusão de táxons similares (repulsão fenotípica) e resultando na dispersão filogenética das espécies (WEBB *et al.*, 2002). Por outro lado, em ambientes mais restritivos, onde poucas espécies são capazes de se estabelecer com sucesso devido às condições adversas que requerem adaptações variadas, as comunidades são estruturadas por filtros ambientais, apresentando atributos convergentes que resultam em um agrupamento filogenético de espécies (WEBB *et al.*, 2002). Em outras palavras, se a competição for a principal força atuante, a estrutura filogenética tende a ser dispersa, pois as espécies filogeneticamente mais próximas são excluídas competitivamente por repartir o mesmo nicho (princípio da exclusão competitiva). Se o filtro ambiental for a principal força atuante, a estrutura filogenética tende a ser agrupada, pois o ambiente selecionaria organismos que possuem história evolutiva semelhante (WEBB *et al.*, 2002; WEBB *et al.*, 2006).

O contrário é verdadeiro se os atributos ecológicos são filogeneticamente convergentes. A competição ou limitação de similaridade gera comunidades com padrões randômicos ou possivelmente agrupados de histórias evolutivas, pois o atributo em questão está disperso na filogenia (KRAFT *et al*., 2007). Já os filtros ambientais vão gerar comunidades com padrões uniformemente dispersos de história evolutiva, pois selecionam espécies pertencentes a varias linhagens diferentes, porém com o mesmo atributo (KRAFT *et al*., 2007).

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Manuscrito 1

Precipitation impacts the Brazilian Caatinga vegetation more strongly than chronic and acute human disturbances

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Summary

1. Seasonally dry tropical forests (SDTFs) are one of the most threatened forests worldwide. These species-rich forests not only cope with several acute (e.g. forest loss) and chronic (e.g. overgrazing and firewood extraction) human disturbances, but also with climate change (i.e. longer and more severe droughts).

2. Given the historical climatic constrictions in STDFs, environmental filters (i.e. reduced precipitation) may be relatively more important in determining patterns of vegetation diversity, composition and structure than human disturbances. Alternatively, the effects of disturbances could be mediated by precipitation (i.e. interacting effect), but to our knowledge, the isolated and combined effects of climate and acute and chronic human disturbances on SDTF vegetation have never been explored.

3. We tested these alternative hypotheses in 21 430 ha of Brazilian Caatinga – a SDTF threatened by climate change and habitat disturbances. We evaluated the isolated and combined effect (both additive and multiplicative) of precipitation, three predictors of chronic disturbance (i.e. distance to nearest farm and road, and length of goat trails) and one predictor of acute disturbance (i.e. landscape vegetation cover) on the diversity, stem density, evenness, taxonomic composition and biomass of adult trees and shrubs across 18 0.1-ha plots distributed along a disturbance and precipitation gradient.

4. We recorded 5661 stems from 132 species. Average annual precipitation alone was the best predictor of vegetation composition and structure, positively affecting forest biomass and species richness, but negatively affecting community evenness because of the loss of rare species in areas with lower precipitation. Acute and chronic disturbances showed a weak impact on vegetation, but the distance to roads was negatively related to stem density, species richness, and community evenness.

5. *Synthesis*. Our results suggest that (i) water availability and human chronic disturbances represent forces shaping plant community assembly and forest structure in the Caatinga vegetation, and (ii) local plant assemblages do not represent random subsets from the regional flora, but a particular subset of disturbance and stress-adapted species. Therefore, rapid climatic change in the region will probably have stronger effects on Caatinga vegetation than habitat disturbances.

Key-words: anthropogenic disturbance, biodiversity loss, climate change, seasonally dry tropical forest, semiarid ecosystem, woody flora.

Introduction

Anthropogenic disturbances encompass a large array of phenomena, from local habitat loss and perturbation to global climate change, and are important drivers of biodiversity loss in the tropics (Malhi *et al*. 2014). This is particularly true in the case of SDTFs, which has become one of the most threatened ecosystems in the world due to massive deforestation (Miles *et al*. 2006). Biodiversity persistence in SDTFs can also be threatened by climate change, as climate extremes impose strong environmental filters within this ecosystem (Moro *et al*. 2015). Dry forests will face an increase in evaporation and temperature by 2100 (Burkett *et al*. 2014), leading to longer and more severe droughts that can limit biodiversity persistence by (i) reducing primary net production (Zhao & Running 2010), (ii) inducing changes in the annual growth of populations (Ureta *et al*. 2012), and (iii) increasing the probability of species extinction (Araújo & Rahbek 2006). In fact, drought can limit tree recruitment and survival in dry forests, potentially leading these ecosystems to alternate stable states, such as shrublands or grasslands (Anderson-Teixeira *et al*. 2013).

In addition to climate change and acute disturbance such as habitat loss, most SDTFs historically support low-income rural populations widely dependent on forest resources for proper livelihood, such as fodder, firewood and timber (Singh 1998; Davidar *et al*. 2010; Ribeiro *et al*. 2015). Such a frequent and continuous removal of small portions of forest biomass has been referred to as “chronic anthropogenic disturbance” (Singh 1998). Yet, the impacts of chronic disturbances on biodiversity persistence and on provision of ecosystem services and livelihood have just started to be systematically addressed globally (Arroyo-Rodríguez *et al*. 2016). We refer, for instance, to decreases in plant population densities (Hernández-Oria, Chavez & Sánchez 2006), limited seedling establishment and disrupted forest regeneration (Singh, Rawat & Garkoti 1997), decreases in tree species diversity and stem abundance (Ribeiro *et al*. 2015), and changes in forest structure, species composition (Kumar & Shahabuddin 2005), and tree phylogenetic diversity and structure (Ribeiro *et al*. 2016). Furthermore, there have been increasing evidence that climate change and disturbance can have complex (sometimes synergistic) effects on biodiversity (Travis 2003; Ponce-Reyes *et al*. 2013; García-Valdés *et al*. 2015), with hot and arid environments likely to be at greatest risk (Anderson-Teixeira *et al*. 2013; Gibb *et al*. 2015). Yet, to our knowledge, the isolated and combined effects of climate and acute and chronic human disturbances on SDTF biodiversity have never been explored.

Like other SDTFs, the Brazilian Caatinga vegetation is a diverse (species endemism ranging from 10 to 50%) and threatened biota (Leal *et al*. 2005). This patch of dry forest and scrub vegetation stretches over 800 000 km^2, supporting one of the most populous semiarid regions globally (i.e. 26 inhabitants per km^2; Medeiros *et al*.

2012). Cattle-ranching, wood extraction and subsistence agriculture have imposed a continuum of degradation varying from biomass reduction to complete desertification (Leal *et al*. 2005; MMA & IBAMA 2010). Unfortunately, the region will probably face the most impressive increase in temperature among Brazilian regions (1.8 °C to 4 °C in A2 and B2 scenarios; IPCC 2001) and a reduction in rainfall of -22% by 2100 (Magrin *et al*. 2014). These climatic changes may threatens local populations due the low tolerance of agricultural cultures to climatic variations (Barbieri *et al*. 2010). Exposed to chronic anthropogenic disturbance and covering a large range of climatic variation (e.g. mean annual precipitation ranges between 240 and 1500 mm; Sampaio 1995), the Caatinga vegetation offers an interesting opportunity to examine potential effects on biodiversity emerging from relationships between local human disturbance and climate change.

To address this issue, we examined a 21 430-ha Caatinga landscape with a long history of human disturbance and naturally exposed to a rainfall gradient. In particular, we examined how precipitation and chronic and acute disturbances affect the composition and structure of woody plant assemblages (i.e. shrub and tree species). We tested the hypothesis that human disturbances may be relatively less important than variations in precipitation in determining patterns of vegetation composition and structure. Alternatively, the effects of disturbances may be mediated by precipitation (i.e. interacting effect). To test such alternative hypotheses, we evaluated the isolated and combined effect (both additive and multiplicative) of precipitation, three predictors of chronic disturbance and one predictor of acute disturbance. This study contribute to improve our understanding of the effects of human disturbances and precipitation on the structure and diversity of vegetation in STDFs, thus allowing to predict (and possibly mitigate) future changes in vegetation within this vanishing biome.

Materials and methods

STUDY AREA

The Caatinga is a mosaic of seasonally dry tropical forests and scrub vegetation (Pennington, Lavin & Oliveira-Filho 2009) that is restricted to Brazil and has suffered deforestation since the sixteenth century for extensive livestock and temporary farming (Leal *et al*. 2005; IBGE 2010). Annual temperature averages 25 °C, and average annual precipitation ranges from 240 to 1500 mm, being an important driver of plant composition and structure in the region (Sampaio 1995). The majority of rainfall is concentrated in three months per year and there is a high interannual variability in rainfall with severe droughts, which may extend for years (Sampaio 1995; Chiang & Koutavas 2004).

We studied the Caatinga vegetation of the Catimbau National Park, Pernambuco state, Brazil (8º24'00" and 8º36'35" S; 37º0'30" and 37º1'40" W). This park has an area of ca. 60 000 ha, and shows a high variation in relief and precipitation. Approximately 70% of the park is dominated by litosoils. The Catimbau National Park is occupied by low-income rural populations (IBGE 2004), which extract different forest products for medicinal purposes, animal and human food, and fuelwood. Hunting and overgrazing by stock (goats and cattle) also represent important disturbances for vegetation in the region (Ribeiro *et al*. 2015; 2016).

STUDY SITES

Based on the RapidEye satellite imagery, maps of soil, precipitation and field exploitations, we selected 18 areas to cover a wide range of disturbance and precipitation levels. We established 18 20×50-m plots with a minimum 2-km distance within a 21 430-ha area dominated by old-growth vegetation exposed to chronic disturbance. To control for the potential effects of terrain slope and soil characteristics on species responses (see Pinheiro, Rodal & Alves 2010), all plots were located in areas with the same soil type (sand soil) and similar slope (i.e. plain terrain).

PREDICTORS OF DISTURBANCES AND PRECIPITATION DATA

We adopted a landscape scale perspective to obtain a gradient of chronic disturbance intensity. Using satellite imagery in ArcGIS 10.1 software, we assessed three indicators of chronic disturbance that have been described as important drivers of human disturbance in previous tropical forests studies, including: (i) distance to nearest farms (DF) (Sagar, Raghubanshi & Singh 2003; Martorell & Peters 2005; Leal, Andersen & Leal 2014); (ii) distance to nearest roads (DR) (Sagar, Raghubanshi & Singh 2003; Leal, Andersen & Leal 2014; Ribeiro *et al*. 2015); and (iii) total length of all goats' trails within each plot (GT), all measures in meters. We also assessed landscape vegetation cover (VC, in square meters) – an important indicator of acute disturbance (Gould 2000; Fahrig 2013). DF and DR refer to the average Euclidian distance from the centre of each plot to all farms (DF) and roads (DR) within a 15-km radius, considering the relief of the terrain (i.e. cost distances). VC was assessed within a 1-km radius (buffer) from the centre of each plot. We considered this buffer size to avoid overlap among buffers, thus increasing the independence among samples (Eigenbrod, Hecnar & Fahrig 2011). VC data was obtained from a vegetation classification map. This map was performed from RapidEye satellite imagery by unsupervised classification based on clusters of statistically different sets of multiband data (radiances expressed by their radiance averaged over each spectral interval). Classification accuracy was assessed with 172 field observations points, and was very high (ca. 80% of correctly classified points). All metrics are proxies of human pressure (e.g. logging, cutting, and hunting) and overgrazing by livestock. Following previous studies (Martorell & Peters 2005; Leal, Andersen & Leal 2014; Ribeiro *et al*. 2015), we opted for these proxies because chronic disturbances are very difficult to quantify directly in the field.

The variation in precipitation is a good predictor of climate change (Houghton *et al*. 2001) and is an important driver of species performance (Weltzin *et al*. 2003). In the Caatinga ecosystem (Prado 2003) and other SDTFs (Hirota *et al*. 2011; Choat *et al*. 2012), precipitation can have a strong influence on vegetation composition and structure. Mean annual precipitation within each plot was obtained from the updated WorldClim global climate data repository (www.worldclim.org) with a 1-km resolution, using the "*maptolls*" package for R 3.1.2 (Bivand & Lewin-Koh 2015). Mean annual precipitation in the plots ranged from 510 to 940 mm.

PLANT SURVEY AND COMMUNITY STRUCTURE

We sampled all shrubs and trees with diameter at basal height (DBH) ≥ 3 cm and total height ≥ 1 m. We identified all stems, and measured the DBH and total height to calculate the stem density and total plant aboveground biomass per plot. Total biomass was calculated using an allometric equation for Caatinga vegetation ($\text{Biomass}_{\text{kg}} = 0.173\ \text{DBH}_{\text{cm}}^{2.295}$) as proposed by Amorim, Sampaio & Araújo (2005), which is based on basal area and height.

We used the coverage estimator recommended by Chao & Jost (2012) to estimate the accuracy of tree inventories:

$$\hat{C}_n = 1 - \frac{f_1}{n}\left[\frac{(n-1)f_1}{(n-1)f_1 + 2f_2}\right]$$

where f_1 and f_2 are the number of species with one individual and with two individuals in the sample, respectively, and n is the number of individuals. Sample coverage was very high in all sites (> 93% of the species recorded; Table S1), indicating that our sampling effort was adequate, and that our diversity estimates were not biased by differences in sample coverage among sites (Chao & Jost 2012; Chao *et al*. 2014). To assess changes in species diversity, we used Hill numbers of order 0 (${}^{0}D$, species richness), 1 (${}^{1}D$, exponential Shannon entropy) and 2 (${}^{2}D$, inverse Simpson concentration) (Jost 2006; 2007), calculated with the *entropart* package for R (Marcon, Zhang & Hérault 2014). ${}^{0}D$ (i.e. species richness) is not sensitive to species abundances and thus gives disproportionate weight to rare species (Jost 2006). ${}^{1}D$ weighs each species according to its abundance in the community, being interpreted as the number of 'common' or 'typical' species in the community (Jost 2006). Finally, ${}^{2}D$ favours abundant species, and is actually interpreted as the number of 'very abundant' or 'dominant' species in the community. Jost (2006) details the formulas for calculating these diversity measures. We also assessed changes in community evenness with the evenness factor (EF) proposed by Jost (2010): $EF = {}^{2}D/{}^{0}D$. We selected this index because it is based on Hill numbers, and is very easy to interpret. EF simply represents the proportion of dominant species in the community and it ranges between 1 (when the community is perfectly even) and nearly $1/{}^{0}D$ (when the community is dominated by one species; Jost 2010).

DATA ANALYSIS

We first assessed whether the study plots can be considered independent samples by correlating a matrix with the Euclidean distances between plots and a matrix showing the differences between plots in species composition (i.e. ${}^{q}D_{\beta}$, one per order q; Jost

2007). The β-diversity matrices were calculated with the *entropart* package. To correlate the distance matrix with each β-diversity matrix we used Mantel tests with the *vegan* package for R, and the *P*-values were calculated using the distribution of the *R* coefficients obtained from 10 000 permutations. Because the Mantel tests did not detect a significant spatial autocorrelation of data sets (${}^{0}D_{\beta}$: $r = 0.09$, $P = 0.18$; ${}^{1}D_{\beta}$: $r = 0.13$, $P = 0.13$; ${}^{2}D_{\beta}$: $r = 0.07$, $P = 0.28$), we considered the plots as independent samples in the following analyses.

To test the isolated and combined (both additive and multiplicative) effect of precipitation and each predictor of chronic and acute disturbances on each response variable we used generalized linear models. We fixed a Gaussian error distribution for continuous response variables (i.e. stem density, ${}^{1}D$, ${}^{2}D$, *EF*, and total biomass). As recommended for count-dependent variables, ${}^{0}D$ was assessed by fixing a Poisson error distribution (Crawley 2007). To assess the independency among predictor variables we assessed the collinearity among predictors with the Variance Inflation Factor (VIF) using the *car* package for R. All VIF values were < 2.8, suggesting independence among predictors (Jou, Huang & Cho 2014). To identify the most plausible and parsimonious models for the data, we first constructed 36 models per response variable, which represented the isolated and combined (both additive and multiplicative) effect of all predictors on each response variable (Tables S2-S7). We then compared the models using an information-theoretic approach with *bbmle* package for R (Calcagno & Mazancourt 2010). In particular, for each model, we computed the Akaike's information criterion corrected for small samples (AICc). To correct for overdispersion associated with count data, ${}^{0}D$ was assessed with qAICc instead of AICc values (Calcagno & Mazancourt 2010). Models with a difference in (q)AICc < 2 when compared to the best model [i.e. the one with lowest (q)AICc value] were considered to have similar plausibility (Burnham & Anderson 2002). We also calculated the percentage of explained deviance by each model compared with the deviance explained by the null model as a measure of goodness-of-fit of each model (Crawley 2007).

We then evaluated the relative effect of each predictor on each response variable with a multimodel inference approach (Burnham & Anderson 2002) using the *glmulti* package for R. For each response variable we constructed 32 models, representing all combinations of predictor variables. We computed the (q)AICc for each model, and obtained model-averaged parameter estimates using Akaike weights (w_i). The set of models for which Σw_i was 0.95 represents a set that has 95% probability of containing the true best model (Burnham & Anderson 2002). A given spatial attribute was considered an important explanatory variable for a given response variable if: (i) it showed a high Σw_i (i.e. considering each candidate model in which it appeared); and (ii) the model-averaged parameter estimate did not include zero (i.e. the unconditional variance was lower than the model-averaged parameter estimate). Finally, we performed a Canonical Correspondence Analysis (CCA) to identify the predictor variables with highest impact on species composition. In this case, we excluded rare species (i.e. those with <5 stems) to prevent spurious effects caused by the distribution of rare species and to minimize risk of type II statistical error. The CCA analysis was carried out with the *vegan* package for R.

Results

We recorded 5661 stems belonging to 132 species (24.5 ± 9.1 species per plot; mean ± SD) and 31 families. The most representative family was Fabaceae (28% of species), followed by Euphorbiaceae (14%) and Myrtaceae (8%). The stem density per plot varied from 120 to 440 stems/1000 m^2 (272 ± 89 stems/1000 m^2), and total biomass per plot varied from 3794 to 96 067 kg (12 360 ± 7407 kg).

The best models predicting the species richness (^{0}D) were those including the interaction (multiplicative) effect between precipitation and distance to nearest roads, and precipitation and length of goats' trails (see Table S2 in Supporting Information). In particular, precipitation showed a positive effect on ^{0}D when the communities were far from roads, and when they showed longer goat´s trails (Fig. S1). Yet, without considering multiplicative effects (i.e. when considering isolated and additive effects of predictors), precipitation was the best predictor of ^{0}D, with a very strong positive effect (Fig. 1). The rest of response variables were better predicted by models including isolated variables (Table S3-S7). In particular, precipitation was the best predictor of the number of common species (^{1}D) and biomass, with a positive effect on both cases, and a negative effect on community evenness (Fig. 1; Tables S3, S5 and S7). Because ^{2}D was weakly related to precipitation ($\Sigma w_i = 0.20$; Fig. 1), the positive relationship between ^{0}D and precipitation was associated with a higher number of rare species in plots with higher precipitation (Fig. 2), which in turn reduced community evenness (*EF*) in these sites (Fig. 1d). The number of dominant species (^{2}D) was more strongly related (negatively) to vegetation cover (Fig. 1; Table S4), whereas stem density was more strongly associated (negatively) with the distance to the nearest roads (Fig. 1; Table S6). Therefore, the predictor variables with the strongest impact on plant assemblages were annual precipitation (included in the set of best models for 4 out of 6 response variables) and distance to nearest roads (included in the set of best models for 3 out of 6 response variables) (see black bars in Fig. 1). The rest of disturbance predictors showed a weaker effect on plant assemblages, with the length of goats' trails and distance to the nearest farms being only included in one set of best models (Fig. 1). In particular, the distance to the nearest farms was positively related to ${}^{0}D$, whereas the length of goats' trails was negatively related to ${}^{1}D$. Also, the length of goats' trails tended to be negatively associated with ${}^{0}D$, ${}^{2}D$, and *EF*, whereas stem density tended to increase in plots with higher length of goats' trails (i.e. the model-averaged parameter estimates did not include zero for these response variables; Fig. 1).

When assessing variations in species abundances associated with each environmental predictor, the first and second CCA axes explained 31% and 25% of the variation in species composition, respectively (Fig. 3). In particular, the predictor variables with a significant impact on species composition were annual precipitation ($\chi^2 = 0.41$, $P = 0.03$) and distance to nearest farms ($\chi^2 = 0.40$, $P = 0.03$), with both factors showing opposite effects on plant assemblages (Fig. 3). The CCA thus identified a group of species that are particularly abundant in sites with relatively high precipitation and low disturbance (e.g. *Senegalia piauhiensis, S. bahiensis, Lipia grata*, *Maytenus rigida*, *Guapira* sp., *Colycodendron yco*, *Handroanthus impetiginosus*, *Croton argyrophylloides* and *Libidibia ferrea*), and a group of species particularly abundant in sites with relatively lower precipitation and higher disturbance level (e.g. *Commiphora leptophloeos, Poincianela pyramidalis, Croton heliotropiifolius, Cnidoscolus obtusifolius*, *Piptadenia stipulacea* and *Byrsonima gardneriana*). The CCA also identifies a group of generalist species, widely distributed in the plots (e.g. *Pityrocarpa moniliformis*, *Annona leptopetala*, *Croton nepetifolius* and *Jatropha mutabilis*) (Fig. 3). Although the effect of the length of goats' trails on species stem density was not significant, the CCA analysis detected a group of shrub species related to sites surrounded by higher length of goats' trails (e.g. *Varronia leucocephala* and *Dahlstedtia araripensis*), whereas other species seems to be positively associated with sites surrounded by higher vegetation cover (e.g. *Senna trachypus*, Fig. 3).

Discussion

Our study suggests that woody plant assemblages in the Brazilian Caatinga vegetation are affected by a combination of forces, especially by annual precipitation and distance to nearest roads. Although all community-level attributes respond to such forces, species richness was the most sensitive attribute. In particular, precipitation positively affects species richness, since our sites with higher precipitation show a higher number of rare species and lower community evenness. Moreover, distance to nearest roads and length of goats' trails also affect species richness, but such effects are apparently mediated by precipitation (interacting effects). Interestingly, distance to roads and distance to farms (i.e. variables that determine people access to forest resources) were relatively more important than grazing pressure (as inferred from goat trails) and landscape vegetation cover. In other words, chronic disturbance is more important than habitat loss (i.e. acute disturbance). Regarding species composition, in general, our findings support the notion that assemblages inhabiting the extremes of the environmental gradient (i.e. the driest sites and exposed to more intense chronic disturbances) are dominated by a set of stress and disturbance-adapted species (e.g. *Croton blanchetianus*, *Croton argyrophylloides*, *Commiphora leptophloeos*), while many rare species (e.g. *Anadenanthera colubrina*, *Lonchocarpus obtusus*) and some common species (e.g. *Senegalia bahiensis* and *S. piauhiensis*) in the region are particularly abundant in plots with higher precipitation and lower disturbance. In synthesis, water availability and human chronic disturbances emerge as forces shaping plant community assembly and forest structure in the Caatinga vegetation.

The importance of direct or indirect measures of water availability for plant species, such as average annual rainfall, is well known, particularly in SDTFs. Briefly, decreasing water availability results in increased level of physiological stress, and consequently, reduction in biomass production and fitness, potentially leading to the death of stress-sensitive individuals (Santos *et al*. 2014; Figueiredo *et al*. 2015). In the Caatinga vegetation, decreasing precipitation leads to lower aboveground biomass, tree abundance and species richness, and can also result in changes in the functional composition of plant assemblages, such as a lower abundance of woody plant species bearing fleshy fruits (Tabarelli, Vicente & Barbosa 2003). Wood density, for example, is an attribute related to cavitation, where high wood density confers less resistance to drought (Hacke *et al*. 2001). In fact, in our study, all species but one (*Guapira* sp.: 0.6 g/cm^3) from areas with high precipitation have a high wood density (> 0.7 g/cm^3: Michalski, Nishi & Peres 2007). As argued for other SDTFs (Grime, Hodgson & Hunt 1988; Prentice *et al*. 1992), it is highly probable that reduced water availability represents a strong environmental filter for water-demanding species in the Caatinga vegetation, particularly influencing colonization, establishment, reproductive success, and consequently, species spatial distribution. Plant dominance and evenness patterns can actually change with different environmental filters (e.g. precipitation, CO_2, air temperature; Kardol *et al*. 2010). Phytomass (O'Connor, Haines & Snyman 2001) and plant phylogenetic structure (Moro *et al*. 2015) are also related to changes in precipitation. However, we still lack a comprehensive knowledge on how reduced water availability influences different plant life stages in the Caatinga vegetation, such as seedling recruitment, plant growth and reproduction. Thus, the mechanisms that lead to the establishment of impoverished communities are not well understood.

In addition to precipitation (the best predictor), chronic human disturbances are also affecting the composition and structure of woody plant assemblages in the Caatinga vegetation, as already proposed in previous studies (Ribeiro *et al*. 2015; 2016).

Exploitation of forest products, nutrient exportation via shifting cultivation, and overgrazing by livestock have been demonstrated to affect tropical plants at population and community levels in SDTFs (Shahabuddin & Prasad 2004; Martorell 2007, Ribeiro *et al*. 2015; 2016; Arroyo-Rodríguez *et al*. 2016). As distance to roads and distance to farms favours the access and exploitation of forest resources (Laurance, Goosem & Laurance 2009), it is not surprisingly that these two predictors were relatively more important than length of goats' trails in determining patterns of plant assemblages. Distance to roads and human settlements are known to be related to changes in soil properties (Müllerová, Vítková & Vítek 2011), plant population and community attributes (Ribeiro *et al*. 2015), and ecosystem functioning and services (Laurance *et al*. 2014; Leal, Andersen & Leal 2014). Precisely, collection of forest products directly alters vegetation structure, creating more open, light and desiccated habitats (Kumar & Shahabuddin 2006; Mehta *et al*. 2008). Moreover, targeted plant populations experience decline or even local/regional extirpation (Shahabuddin & Prazad 2004). Collectively, these processes tend to disfavour disturbance-sensitive species, while enhancing the proliferation of those disturbance-adapted species, including both exotic and native plant species, such as some short-living shrubs from the Euphorbiaceae family in the Caatinga vegetation (Ribeiro *et al*. 2016).

In the Caatinga region, rural human populations are dependent from forest products for livelihood (Leal *et al*. 2005; Ribeiro *et al*. 2015). It includes the nutrients stored in forest biomass to support subsistence agriculture via slash-and-burn practices, foliage as fodder, firewood, timber and a myriad of non-timber products, including fruits/seeds, medicinal plants and bushmeat (Lucena *et al*. 2007; de Albuquerque *et al*. 2012). Farmers tend to target more humid sites because they are more suitable for agriculture and livestock and support more developed vegetation patches near roads

(Santos & Tabarelli 2002). Additionally, goat herds prefer to browse in secondary forest patches and fallow vegetation instead of in old-growth forest stands (D. Jameli, unpublished data). Such a spatial concentration of disturbances forces may explain our uncovered patterns, including increased stem density in plots near roads and the presence of relatively hardwood species (e.g. *Maytenus rigida*, *Handroanthus impetiginosus* and *Libidibia ferrea*) in less disturbed plots. In fact, we shall highlight the fact that chronic disturbances are relatively more important than acute disturbances (landscape forest loss) in our focal landscape. Two possible explanations are: (i) forest loss is usually related to negative edge effects in the tropics (e.g. Laurance *et al*. 2002), but edge effects have a relatively lower impact on vegetation in SDTFs; and (ii) chronic disturbances accumulate through time, and the region has a long history of chronic disturbances.

In synthesis, many SDTF biotas, such as the Caatinga vegetation, are currently exposed to a "package" of human disturbances across different spatial and temporal scales, from local habitat loss and disturbance to regional and global climate change (Blackie *et al*. 2004). Yet, the relative impact of all these kinds of disturbances on the biology, ecology and conservation of natural communities remains uncertain. Our findings support the idea that woody plant assemblages are sensitive to variations in both precipitation levels and chronic human disturbances, although precipitation seems to impact the Brazilian Caatinga vegetation more strongly than chronic and acute human disturbances. As observed in other ecological contexts exposed to intense human disturbances or/and physical stress, local plant assemblages do not represent random subsets from the regional flora, but a particular subset of disturbance and stress-adapted species (i.e. deterministic view of species assembly) probably due to increased environmental filtering, disruption of species interactions and overexploitation of natural resources (Singh 1998, Laurance *et al*. 2006; Tabarelli, Lopes & Peres 2008). Although we are not able to explicitly exam the basic mechanisms leading to community-level responses, it is reasonable to expect that future precipitation declines (as already proposed) will have stronger effects on the Caatinga vegetation, which can be amplified by chronic disturbances. Given the spatiotemporal association among disturbance drivers, controlled experiments are required to disentangle the myriad of mechanisms that are leading to community-level responses. We explicitly refer to those related to environmental filtering imposed by reduced water availability, collection of forest products, and perhaps, overgrazing by domestic livestock, which are apparently able to reorganize plant assemblages.

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Figure legends

Figure 1. Predictor variables included in the ΔAICc < 2 set of models (black bars) and 95% set of models (gray bars) for species diversity (Hill numbers of order 0, 1, and 2), community evenness, stem density and biomass of woody plant assemblages of Caatinga vegetation in the Catimbau National Park, Brazil. The importance of each predictor is shown by the sum of Akaike weights (Σw_i, panels in the left side). Panels in the right side indicate the values of model-averaged parameter estimates (β) and unconditional variance of information-theory-based model selection and multimodel inference. We tested separately the impact of distance to nearest farm (DF), distance to nearest road (DR), total length of all goats' trails within each plot (GT), vegetation cover (VC) and precipitation (PREC). The sign (+/-) of parameter estimates represents a positive or negative effect of the predictor on the response variable. We also indicate, in parentheses, the goodness-of-fit of each complete model (i.e. the percentage of deviance explained by each complete model).

Figure 2. Relative abundance of wood plant species in different precipitation levels in the Catimbau National Park, Brazil. Precipitation levels were ordered from the lowest to the highest and then pooled in groups of three (triplets). Each curve represents the woody plant assemblage in a triplet. The dashed line indicates the number of species

representing < 5% of individuals sampled in each triplet. We also indicate the identity of dominant species within each triplet: Abr=*Acalypha brasiliensis*, Cyco=*Colicodendron yco,* Carg=*Croton argyrophylloides,* Che=*Croton heliotropiifolius,* Cne=*Croton nepetifolius,* Jmu=*jatropha mutabilis,* Melto=*Melochia tomentosa*, Ppau=*Peltogyne pauciflora*, Psti=*Piptadenia stipulacea*, Pmon=*Pityrocarpa moniliformis*, Pmi=*Poincianela microphylla*, Sba=*Senegalia bahiensis*, Spia=*Senegalia piauhiensis*, Tpal=*Tacinga palmadora*.

Figure 3. Canonical Correspondence Analysis showing the shrub and tree species recorded in the Catimbau National Park, Brazil and its association with annual precipitation and indicators of human-induced acute (i.e. VC = vegetation cover) and chronic disturbances (i.e. DF = distance to nearest farms; DR= distance to nearest roads; GT= total length of goat's trails). Plant species: Abr= *Acalypha brasiliensis,* Ala= *Anemopaegma laeve,* Alep= *Annona leptopetala,* Bmol= *Balfourodendron molle,* Bacu= *Bauhinia acuruana,* Bgar= *Bbyrsonima gardneriana,* Ceug= *Campomanesia eugenioides,* Csil= *Casearia silvestris,* Czyg= *Chamaecrista zygophylloides,* Chfo= *Chloroleucon foliolosum,* Cnba= *Cnidoscolus bahianus,* Cnob= *Cnidoscolus obtusifolius,* Cyco= *Colicodendron yco,* Clep= *Commiphor leptophloeos,* Ctric=*Cordia trichotoma,* Carg= *Croton argyrophylloides,* Cbla= *Croton blanchetianus,* Che= *Croton heliotropiifolius,* Cnep= *Croton nepetifolius,* Cgre= *Croton grewioides,* Cyfle= *Cynophalla flexuosa,* Dara= *Dahlstedtia araripensis,* Erev= *Erythroxylum revolutum,* Esp1= *Eugenia* sp1, Esp2= *Eugenia* sp2, Estic= *Eugenia stictopetala,* Elin= *Evolvulus linoides,* Guasp= *Guapira* sp., Himp= *Gandroanthus impetiginosus,* Jmu= *Jatropha mutabilis,* Lca=*Lantana camara,* Lfe=*Libidibia ferrea,* Lipgc=*Lippia gracilis,* Lipgt=*Lippia grata,* Mpse= *Manihot cf pseudoglaziovii,* Mari= *Maytenus rigida,*

Melto=*Melochia tomentosa,* Sp3= *Sp3,* Ppau= *Peltogyne pauciflora,* Pigou= *Pilosocereus gounellei,* Pipach=*Pilosocereus pachycladus,* Psti= *Piptadenia stipulacea,* Pmo= *Pityrocarpa moniliformis,* Pmi= *Poincianela microphylla,* Ppy= *Poincianella pyramidalis,* Psbr= *Psidium brownianum,* Psoli= *Psidium oligospermum,* Pssc= *Psidium schenckianum,* Sba=*Senegalia bahiensis,* Spo= *Senegalia polyphylla,* Spia=*Senegalia piauhiensis,*Ssp=*Senegalia* sp., Snriz= *Senna rizzinii,* Sntr= *Senna trachypus,* Sp 1= *Sp 1,* Sp 2= *Sp 2,* Stitr= *Stillingia trapezoidea,* Stru= *Strychnos rubiginosa,* Tpal= *Tacinga palmadora,* Trmol= *Trischidium molle,* Vglo= *Varronia globosa,* Vleu= *Varronia leucocephala,* Wbra= *Waltheria brachypetala,* Zjoa= *Ziziphus joazeiro*.

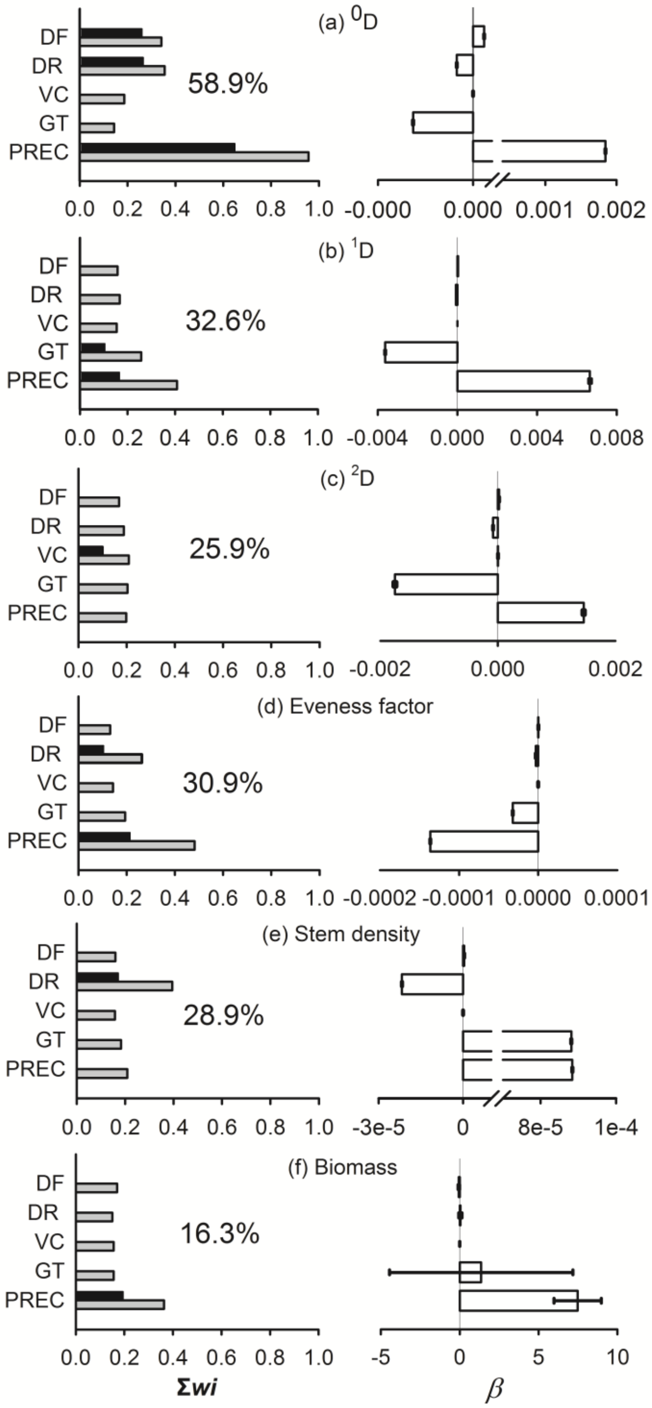
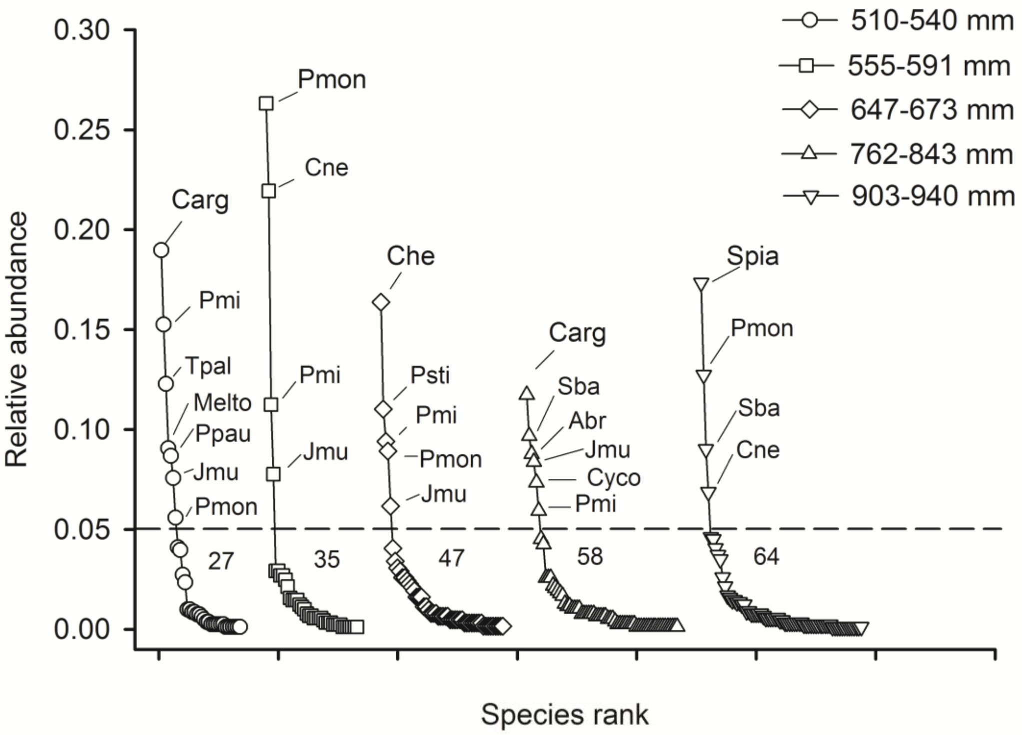

(a) ^{0}D
DF
DR
VC
GT
PREC
58.9%
0.0 0.2 0.4 0.6 0.8 1.0
-0.000 0.000 0.001 0.002
(b) ^{1}D
32.6%
-0.004 0.000 0.004 0.008
(c) ^{2}D
25.9%
-0.002 0.000 0.002
(d) Eveness factor
30.9%
-0.0002 -0.0001 0.0000 0.0001
(e) Stem density
28.9%
-3e-5 0 8e-5 1e-4
(f) Biomass
16.3%
-5 0 5 10
Σwi
β

Fig. 1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0.25
0.20
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0.10
0.05
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Relative abundance
Species rank
510-540 mm
555-591 mm
647-673 mm
762-843 mm
903-940 mm
Carg
Pmi
Tpal
Melto
Ppau
Jmu
Pmon
Pmon
Cne
Pmi
Jmu
Che
Psti
Pmi
Pmon
Jmu
Carg
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27
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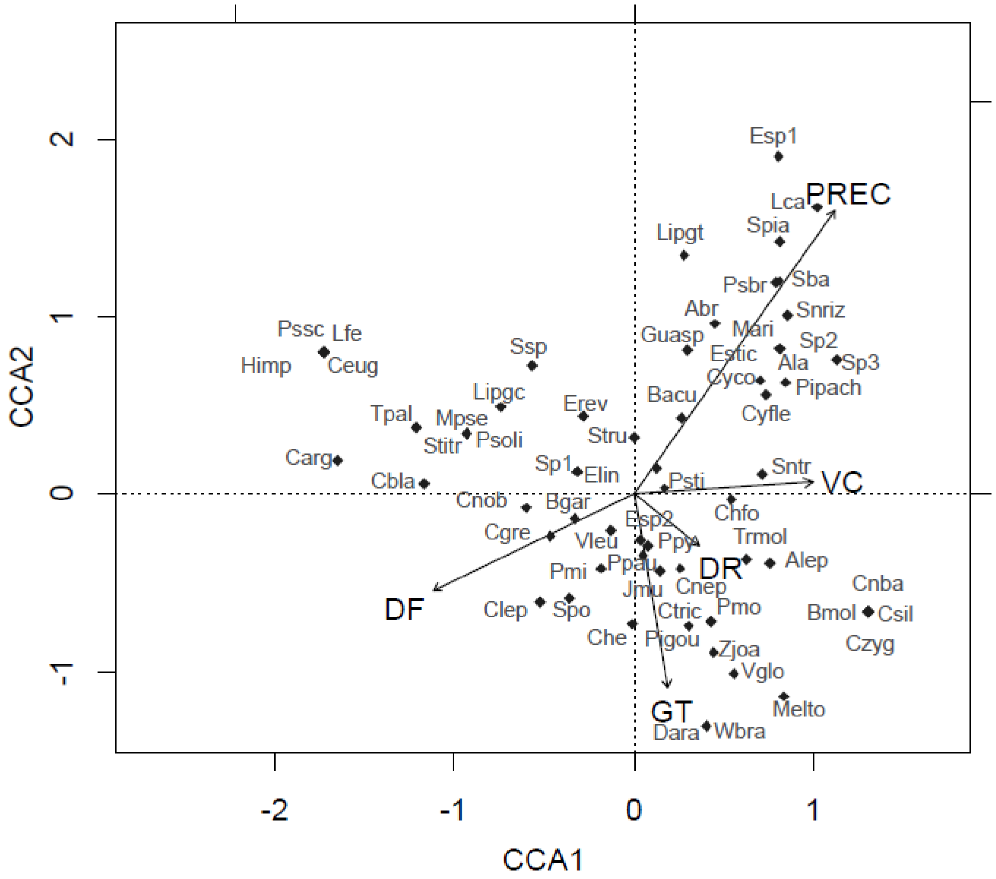
64

Fig. 2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2
1
0
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CCA1
-2
-1
0
1
PREC
VC
DR
DF
GT
Esp1
Lca
Spia
Lipgt
Psbr
Sba
Abr
Snriz
Guasp
Mari
Sp2
Estic
Ala
Sp3
Cyco
Pipach
Bacu
Cyfle
Pssc
Lfe
Himp
Ceug
Ssp
Lipgc
Erev
Tpal
Mpse
Stitr
Psoli
Stru
Carg
Sp1
Elin
Sntr
Cbla
Psti
Cnob
Bgar
Chfo
Esp2
Cgre
Vleu
Ppy
Trmol
Ppau
Alep
Pmi
Jmu
Cnep
Cnba
Clep
Spo
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Che
Pigou
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Czyg
Vglo
Melto
Dara
Wbra

Fig. 3

Supplementary material

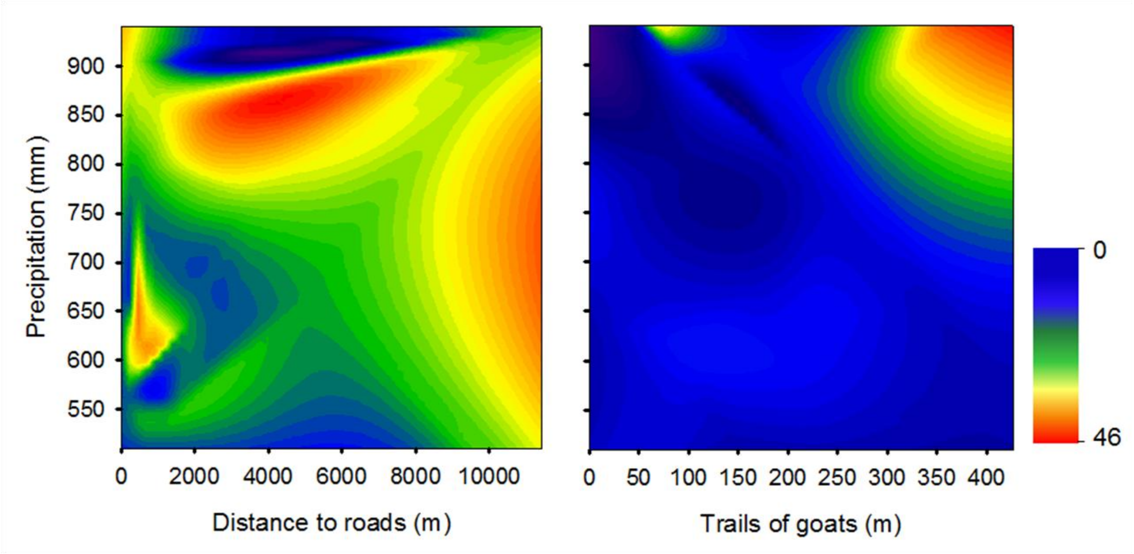

Figure S1. Contour plots showing model predictions for the interaction effect of precipitation and two chronic anthropogenic disturbance metrics (i.e., distance to roads and length of all goats' trails) on plant species richness (${}^{0}D$) in the Catimbau National Park, Brazil. The colors correspond to species number.

Table S1. Species diversity (Hill numbers of order 0, 1, and 2), evenness factor, stem density (stem/0.1ha) and sample coverage ($\hat{C}_{\mathrm{n}}$) of plant assemblages in 18 plots with different precipitation located within the Catimbau National Park, Brazil. $\hat{C}_{\mathrm{n}}$ represents the percentage of the total number of individuals in an assemblage that belong to the species represented in the sample.

Plots	Precipitation (mm)	^{0}D	^{1}D	^{2}D	Eveness factor	Stem density	$\hat{C}_{\mathrm{n}}$(%)
P1	591	33	19.7	14.9	0.5	355	98.0
P2	516	16	5.0	3.4	0.2	363	98.0
P3	578	15	3.9	2.9	0.2	337	98.0
P4	647	18	5.9	3.0	0.2	198	97.0
P5	673	21	9.7	5.2	0.2	139	96.0
P6	540	22	10.3	7.7	0.4	353	98.0
P7	510	13	5.8	4.2	0.3	174	97.0
P8	555	14	7.8	5.9	0.4	284	99.0
P9	940	29	10.6	5.3	0.2	231	96.0
P10	653	30	17.4	12.3	0.4	310	99.0
P11	843	46	21.6	13.7	0.3	388	95.0
P12	552	22	12.0	8.0	0.4	205	98.0
P13	588	30	11.7	6.6	0.2	323	97.0
P14	645	15	6.9	4.2	0.3	120	93.0
P15	903	25	8.2	4.7	0.2	393	99.0
P16	787	20	6.1	3.9	0.2	152	93.0
P17	762	30	13.6	7.1	0.2	283	98.0
P18	913	43	19.3	11.4	0.3	290	95.0

Table S2. Additive and multiplicative models assessing the effects of precipitation (PREC) and anthropogenic disturbance predictors on plant species richness (^{0}D). Disturbance predictors included chronic disturbances (DF, distance to nearest farm; DR, distance to nearest road, and GT, total length of all goats' trails within each plot) and one acute disturbance (VC, vegetation cover within a 1-km radius from the centre of each plot).

Model	qAICc	ΔqAICc	% deviance explained
d0 ~ 1+ PREC*DR	65.2	0.0	43.3
d0 ~ 1 + PREC*GT	67.1	1.9	46.3
d0 ~ 1 + PREC	67.5	2.3	38.3
d0 ~ 1 + DR + DF + PREC	68.8	3.5	55.1
d0 ~ 1 + DR + PREC	69.1	3.8	57.0
d0 ~ 1 + DF + PREC	69.2	3.9	42.7
d0 ~ 1 + VEG + PREC	69.9	4.7	40.1
d0 ~ 1+ PREC*DF	69.9	4.7	50.2
d0 ~ 1 + GT + PREC	70.2	5.0	39.2
d0 ~ 1+ PREC*VEG	70.4	5.1	51.4
d0 ~ 1 + VEG + DR + DF + PREC	71.6	6.3	58.9
d0 ~ 1 + DR + GT + PREC	72.1	6.8	44.2
d0 ~ 1 + VEG + DR + PREC	72.2	6.9	43.8
d0 ~ 1 + DF + GT + PREC	72.4	7.1	43.2
d0 ~ 1 + VEG + DF + PREC	72.5	7.2	42.8
d0 ~ 1 + DR + DF + GT + PREC	72.5	7.3	55.8
d0 ~ 1 + VEG + GT + PREC	72.8	7.6	41.5
d0 ~ 1 + VEG + DR + GT + PREC	75.6	10.3	45.5
d0 ~ 1 + VEG + DR + DF + GT + PREC	76.2	11.0	58.9
d0 ~ 1 + VEG + DF + GT + PREC	76.2	11.0	43.5
d0 ~ 1	76.5	11.3	0.0
d0 ~ 1 + GT	76.9	11.7	7.1
d0 ~ 1 + VEG	78.3	13.1	2.5
d0 ~ 1 + VEG + GT	78.7	13.5	10.8
d0 ~ 1 + DF	78.9	13.7	0.5
d0 ~ 1 + DR	78.9	13.7	0.4
d0 ~ 1 + DF + GT	79.7	14.4	7.7
d0 ~ 1 + DR + GT	79.8	14.6	7.1
d0 ~ 1 + VEG + DF	80.4	15.1	5.3
d0 ~ 1 + VEG + DF + GT	80.9	15.7	14.6
d0 ~ 1 + VEG + DR	81.0	15.8	3.1
d0 ~ 1 + DR + DF	81.6	16.4	1.0
d0 ~ 1 + VEG + DR + GT	82.1	16.8	10.9
d0 ~ 1 + DR + DF + GT	83.0	17.8	7.7
d0 ~ 1 + VEG + DR + DF	83.2	18.0	7.0

d0 ~ 1 + VEG + DR + DF + GT	84.7	19.5	15.2

Table S3. Additive and multiplicative models assessing the effects of precipitation (PREC) and chronic and acute anthropogenic disturbance predictors on the number of common species (Hill number of order 1, ^1D). Disturbance predictors included chronic disturbances (DF, distance to nearest farm; DR, distance to nearest road, and GT, total length of all goats' trails within each plot) and one acute disturbance (VC, vegetation cover within a 1-km radius from the centre of each plot).

Model	AICc	ΔAICc	% deviance explained
d1 ~ 1	115.9	0.0	0.0
d1 ~ 1 + PREC	116.3	0.3	8.9
d1 ~ 1 + GT	117.2	1.2	2.3
d1 ~ 1 + VEG	118.4	2.5	18.1
d1 ~ 1 + DR + PREC	118.6	2.7	17.5
d1 ~ 1 + DF + PREC	118.7	2.8	17.4
d1 ~ 1 + GT + PREC	118.8	2.8	0.2
d1 ~ 1 + DF	118.8	2.9	0.1
d1 ~ 1 + DR	118.8	2.9	15.3
d1 ~ 1 + VEG + PREC	119.2	3.3	12.6
d1 ~ 1 + VEG + GT	119.8	3.9	27.9
d1 ~ 1 + PREC*VEG	120.0	4.1	28.9
d1 ~ 1 + DR + DF + PREC	120.2	4.3	10.1
d1 ~ 1 + DR + GT	120.3	4.4	9.0
d1 ~ 1 + DF + GT	120.5	4.6	23.5
d1 ~ 1 + PREC*GT	120.7	4.8	26.0
d1 ~ 1 + DR + GT + PREC	121.3	5.4	2.4
d1 ~ 1 + VEG + DF	121.8	5.8	2.3
d1 ~ 1 + VEG + DR	121.8	5.9	20.4
d1 ~ 1 + PREC*DF	121.9	5.9	21.1
d1 ~ 1 + DF + GT + PREC	122.0	6.1	20.4
d1 ~ 1 + VEG + GT + PREC	122.0	6.1	20.4
d1 ~ 1 + DR + DF	122.1	6.2	0.4
d1 ~ 1 + VEG + DR + PREC	122.3	6.4	19.2
d1 ~ 1 + PREC*DR	122.5	6.6	18.1
d1 ~ 1 + VEG + DF + PREC	122.6	6.7	17.7
d1 ~ 1 + VEG + DR + GT	123.5	7.6	13.4
d1 ~ 1 + VEG + DF + GT	123.6	7.7	13.1
d1 ~ 1 + DR + DF + GT + PREC	123.9	8.0	31.8
d1 ~ 1 + DR + DF + GT	124.2	8.2	10.3
d1 ~ 1 + VEG + DR + DF + PREC	124.4	8.4	29.9

d1 ~ 1 + VEG + DR + GT + PREC	125.5	9.6	25.4
d1 ~ 1 + VEG + DR + DF	125.7	9.8	2.4
d1 ~ 1 + VEG + DF + GT + PREC	126.5	10.5	21.2
d1 ~ 1 + VEG + DR + DF + GT	128.1	12.2	13.7
d1 ~ 1 + VEG + DR + DF + GT + PREC	129.2	13.3	32.6

Table S4. Additive and multiplicative models assessing the effects of precipitation (PREC) and chronic and acute anthropogenic disturbance predictors on the number of dominant species (Hill number of order 2, ${}^{2}D$). Disturbance predictors included chronic disturbances (DF, distance to nearest farm; DR, distance to nearest road, and GT, total length of all goats' trails within each plot) and one acute disturbance (VC, vegetation cover within a 1-km radius from the centre of each plot).

Model	AICc	ΔAICc	% deviance explained
d2 ~ 1	102.5	0.0	0.0
d2 ~ 1 + VEG	104.4	1.9	5.4
d2 ~ 1 + GT	104.6	2.1	4.6
d2 ~ 1 + DR	104.8	2.3	3.3
d2 ~ 1 + PREC	104.8	2.3	3.2
d2 ~ 1 + DF	105.2	2.7	1.2
d2 ~ 1 + VEG + GT	106.6	4.1	11.6
d2 ~ 1 + DR + PREC	106.6	4.1	11.6
d2 ~ 1 + DR + GT	106.8	4.3	10.4
d2 ~ 1 + VEG + PREC	107.2	4.7	8.4
d2 ~ 1 + VEG + DR	107.3	4.8	7.7
d2 ~ 1 + DF + PREC	107.5	5.0	7.1
d2 ~ 1 + GT + PREC	107.7	5.1	6.1
d2 ~ 1 + DF + GT	107.7	5.2	5.7
d2 ~ 1 + VEG + DF	107.8	5.3	5.5
d2 ~ 1 + DR + DF	107.8	5.3	5.2
d2 ~ 1 + DR + DF + PREC	108.0	5.5	22.9
d2 ~ 1 + PREC*VEG	108.5	6.0	20.8
d2 ~ 1 + PREC*GT	109.4	6.9	16.6
d2 ~ 1 + VEG + DR + GT	109.5	7.0	16.2
d2 ~ 1 + DR + GT + PREC	109.6	7.1	16.1
d2 ~ 1 + VEG + DR + PREC	109.8	7.3	14.9
d2 ~ 1 + VEG + GT + PREC	110.3	7.8	12.7
d2 ~ 1 + PREC*DR	110.3	7.8	12.6
d2 ~ 1 + DR + DF + GT	110.3	7.8	12.4
d2 ~ 1 + VEG + DF + GT	110.5	8.0	11.7
d2 ~ 1 + PREC*DF	110.8	8.3	10.1
d2 ~ 1 + VEG + DF + PREC	111.0	8.5	9.2
d2 ~ 1 + DF + GT + PREC	111.0	8.5	9.1
d2 ~ 1 + VEG + DR + DF	111.2	8.7	7.9
d2 ~ 1 +DR + DF + GT + PREC	112.0	9.5	25.9
d2 ~ 1 + VEG + DR + DF + PREC	112.6	10.1	23.2

d2 ~ 1 + VEG + DR + GT + PREC	113.2	10.7		20.5
d2 ~ 1 +VEG + DR + DF + GT	114.2	11.7		16.2
d2 ~ 1 + VEG + DF + GT + PREC	114.9	12.4		12.8
d2 ~ 1 + VEG +DR + DF + GT + PREC	117.5	15.0		25.9

Table S5. Additive and multiplicative models assessing the effects of precipitation (PREC) and chronic and acute anthropogenic disturbance predictors on community evenness (EF, evenness factor). Disturbance predictors included chronic disturbances (DF, distance to nearest farm; DR, distance to nearest road, and GT, total length of all goats' trails within each plot) and one acute disturbance (VC, vegetation cover within a 1-km radius from the centre of each plot).

Model	AICc	ΔAICc	% deviance explained
EF ~ 1 + PREC	-32.5	0.0	18.3
EF ~ 1	-31.7	0.7	0.0
EF ~ 1 + DR	-31.0	1.4	11.5
EF ~ 1 + GT + PREC	-30.2	2.2	23.3
EF ~ 1 + DR + PREC	-29.8	2.7	21.2
EF ~ 1 + VEG + PREC	-29.5	2.9	20.2
EF ~ 1 + DF	-29.2	3.2	2.2
EF ~ 1 + VEG	-29.1	3.3	1.6
EF ~ 1 + DF + PREC	-29.1	3.3	18.3
EF ~ 1 + GT	-29.0	3.5	2.9
EF ~ 1 + DR + DF	-28.5	4.0	15.5
EF ~ 1 + DR + GT	-28.3	4.1	14.7
EF ~ 1 + VEG + DR	-27.8	4.7	12.2
EF ~ 1 + PREC*VEG	-27.5	5.0	28.2
EF ~ 1 + DR + GT + PREC	-27.3	5.2	27.3
EF ~ 1 + VEG + GT + PREC	-27.0	5.4	26.3
EF~ 1 + PREC*GT	-27.0	5.5	26.1
EF ~ 1 + DF + GT + PREC	-26.4	6.1	23.7
EF~ 1 + PREC*DR	-26.3	6.2	23.2
EF ~ 1 + VEG + DR + PREC	-26.1	6.4	22.4
EF ~ 1 + DF + GT	-26.0	6.5	2.9
EF ~ 1 + VEG + GT	-26.0	6.5	2.8
EF ~ 1 + VEG + DF	-25.9	6.5	2.6
EF ~ 1 + VEG + DF + PREC	-25.9	6.5	21.6
EF ~ 1 + DR + DF + PREC	-25.9	6.6	21.4
EF ~ 1 + DR + DF + GT	-25.3	7.2	18.7
EF~ 1 + PREC*DF	-25.3	7.2	18.6
EF ~ 1 + VEG + DR + GT	-24.6	7.8	15.7
EF ~ 1 + VEG + DR + DF	-24.6	7.9	15.6
EF ~ 1 + VEG + DF + GT + PREC	-23.4	9.0	30.3
EF ~ 1 + VEG + DR + GT + PREC	-23.2	9.3	29.4
EF ~ 1 + DR + DF + GT + PREC	-22.7	9.8	27.4

EF ~ 1 + VEG + DF + GT	-22.2	10.3	3.6
EF ~ 1 + VEG + DR + DF + PREC	-21.5	11.0	22.6
EF ~ 1 + VEG + DR + DF + GT	-20.6	11.8	18.7
EF ~ 1 + VEG + DR + DF + GT + PREC	-18.0	14.5	30.9

Table S6. Additive and multiplicative models assessing the effects of precipitation (PREC) and chronic and acute anthropogenic disturbance predictors on stem density (StemD). Disturbance predictors included chronic disturbances (DF, distance to nearest farm; DR, distance to nearest road, and GT, total length of all goats' trails within each plot) and one acute disturbance (VC, vegetation cover within a 1-km radius from the centre of each plot).

Model	qAICc	ΔqAICc	% deviance explained
StemD ~ 1	24.0	0.0	0.0
StemD ~ 1 + DR	24.5	0.4	12.3
StemD ~ 1 + GT	26.1	2.1	2.6
StemD ~ 1 + PREC	26.5	2.5	0.4
StemD ~ 1 + DR + PREC	26.5	2.5	17.0
StemD ~ 1 + VEG	26.6	2.5	0.2
StemD ~ 1 + DF	26.6	2.5	0.0
StemD ~ 1 + DR + GT	27.3	3.2	12.9
StemD ~ 1 + DR + DF	27.3	3.3	12.4
StemD ~ 1 + VEG + DR	27.4	3.3	12.3
StemD ~ 1 + GT + PREC	28.8	4.8	3.9
StemD ~ 1 + VEG + GT	29.0	5.0	2.7
StemD ~ 1 + DF + GT	29.1	5.0	2.6
StemD ~ 1 + DR + DF + PREC	29.4	5.3	20.1
StemD ~ 1 + VEG + PREC	29.4	5.4	0.6
StemD ~ 1 + VEG + DF	29.4	5.4	0.5
StemD ~ 1 + DF + PREC	29.4	5.4	0.4
StemD ~ 1 + DR + GT + PREC	29.6	5.6	18.8
StemD ~ 1 + VEG + DR + PREC	29.9	5.8	17.2
StemD ~ 1 + DR + DF + GT	30.6	6.6	13.0
StemD ~ 1 + VEG + DR + GT	30.6	6.6	12.9
StemD ~ 1 + VEG + DR + DF	30.7	6.7	12.5
StemD ~ 1 + DF + GT + PREC	32.2	8.1	4.0
StemD ~ 1 + VEG + GT + PREC	32.2	8.1	3.9
StemD ~ 1 + VEG + DF + GT	32.4	8.3	2.8
StemD ~ 1 + VEG + DR + DF + PREC	32.6	8.6	24.0
StemD ~ 1 + VEG + DF + PREC	32.8	8.7	0.6
StemD ~ 1 + DR + DF + GT + PREC	32.9	8.8	22.6
StemD ~ 1 + PREC*GT	33.3	9.2	8.3
StemD ~ 1 + VEG + DR + GT + PREC	33.5	9.4	19.0
StemD ~ 1 + PREC*VEG	33.9	9.8	0.7
StemD ~ 1 + PREC*DF	34.2	10.2	16.4

StemD ~ 1 + VEG + DR + DF + GT	34.5	10.5	13.1
StemD ~ 1 + PREC*DR	35.8	11.8	36.8
StemD ~ 1 + VEG + DF + GT + PREC	36.1	12.1	4.0
StemD ~ 1 + VEG + DR + DF + GT + PREC	36.4	12.3	29.0

Table S7. Additive and multiplicative models assessing the effects of precipitation (PREC) and chronic and acute anthropogenic disturbance predictors on plant biomass (BIO). Disturbance predictors included chronic disturbances (DF, distance to nearest farm; DR, distance to nearest road, and GT, total length of all goats' trails within each plot) and one acute disturbance (VC, vegetation cover within a 1-km radius from the centre of each plot).

Model	qAICc	ΔqAICc	% deviance explained
BIO ~ 1	375.6	0.0	0.0
BIO ~ 1 + PREC	376.0	0.4	13.0
BIO ~ 1 + DF	377.8	2.2	4.0
BIO ~ 1 + DR	378.2	2.5	2.0
BIO ~ 1 + GT	378.5	2.8	0.4
BIO ~ 1 + VEG	378.5	2.9	0.0
BIO ~ 1 + GT + PREC	378.7	3.1	16.1
BIO ~ 1 + DF + PREC	379.3	3.7	13.4
BIO ~ 1 + VEG + PREC	379.4	3.8	13.0
BIO ~ 1 + DR + PREC	379.4	3.8	13.0
BIO ~ 1 + DR + DF	380.6	5.0	7.1
BIO ~ 1 + VEG + DF	381.0	5.4	4.9
BIO ~ 1 + DF + GT	381.1	5.5	4.4
BIO ~ 1 + DR + GT	381.3	5.7	3.1
BIO ~ 1+ PREC*GT	381.4	5.8	21.8
BIO ~ 1 + VEG + DR	381.5	5.9	2.0
BIO ~ 1 + VEG + GT	381.8	6.2	0.5
BIO ~ 1 + PREC*DR	381.8	6.2	19.9
BIO ~ 1 + PREC*VEG	382.5	6.9	16.8
BIO ~ 1 + VEG + GT + PREC	382.6	7.0	16.3
BIO ~ 1 + DF + GT + PREC	382.6	7.0	16.2
BIO ~ 1 + DR + GT + PREC	382.7	7.0	16.1
BIO ~ 1 + PREC*DF	383.2	7.6	13.7
BIO ~ 1 + VEG + DF + PREC	383.2	7.6	13.4
BIO ~ 1 + DR + DF + PREC	383.2	7.6	13.4
BIO ~ 1 + VEG + DR + PREC	383.3	7.7	13.1
BIO ~ 1 + VEG + DR + DF	384.1	8.5	9.0
BIO ~ 1 + DR + DF + GT	384.3	8.7	8.1
BIO ~ 1 + VEG + DF + GT	384.9	9.3	5.1
BIO ~ 1 + VEG + DR + GT	385.3	9.6	3.1
BIO ~ 1 + VEG + DF + GT + PREC	387.2	11.6	16.3
BIO ~ 1 + VEG + DR + GT + PREC	387.2	11.6	16.3

BIO ~ 1 + DR + DF + GT + PREC	387.3	11.6	16.2
BIO ~ 1 + VEG + DR + DF + PREC	387.9	12.2	13.4
BIO ~ 1 + VEG + DR + DF + GT	388.6	13.0	13.4
BIO ~ 1 + VEG + DR + DF + GT + PREC	392.8	17.2	16.3

Manuscrito 2

Water availability drives α and β phylogenetic diversity in plant communities in a Brazilian seasonally dry forest

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Running title: Water deficit shapes phylogenetic diversity

Abstract

Human activities modify natural environments provoking habitat loss and climatic changes. These factors act shaping local species assemblages by filtering species from the regional species pool to local communities causing the nonrandom extinction of species. We evaluated how chronic disturbances predictors (i.e., distance to the nearest farms and roads and goat trails density) may affect the taxonomic and phylogenetic diversity of woody plant community in different water deficit levels. We studied 18 0.1 ha plots in 214.3 km^2 of STDF landscape with a long history of chronic anthropogenic disturbance and with a high variation in water availability (average annual climatic water deficit, 658mm -1086 mm) in Caatinga ecosystem, Brazil. We assessed 3777 stems belonging to 109 species and 31 families and tested whether human disturbance and environmental distance are strongest predictors of phylogenetic α – diversity and taxonomic and phylogenetic β – diversity. It is we expected that the extended drought and the increase of anthropogenic disturbances results in low phylogenetic α-diversity and which communities in sites with similar degrees of disturbance and drought will present lower levels of both taxonomic and phylogenetic β-diversity. Overall, the major force structuring wood plant communities in Caatinga is the water availability. The increase of water deficit implies in a loss of lineages at local scales. There is a high total and between plots turnover of species and lineages when considered rare and common species. However, for the dominant species, none of predictors influence local phylogenetic diversity or turnover of species and lineages. Dominant species were, generally, restrict to Euphorbiaceae and Fabaceae families and different species belongs to these families dominated local floras along the water availability and disturbance gradient. Only distance to roads was important to determine changes in the flora increasing the taxonomic β-diversity. Our results demonstrate that the communities are structured by environmental filters at landscape and between plots scale and there is a non-randon species loss. At finest scale (i.e. within communities) the competition between confamiliar and congeneric species shapes changes in the dominant flora. The rare species loss in dry areas reinforce that there is a imminent need to protect representative areas of diferent fisionomies in Caatinga and STDF in general to avoiding the flora homogenization as outcome of future aridization.

Keywords: chronic human disturbance, climatic changes, phylogenetic alfa diversity, taxonomic beta diversity, phylogenetic beta diversity, Seasonally Dry Tropical Forests.

INTRODUCTION

Changes in biodiversity due to human activities were more rapid in the past 50 years causing a contemporary biodiversity crisis (Millennium Ecosystem Assessment 2005). Habitat degradation, fragmentation and destruction, overexploitation and climatic changes are the main drivers of biodiversity loss, leading to not only changes in species composition but also in ecosystem services (Pereira et al. 2010). These anthropogenic-induced disturbances can influence directly in community assembly, by creating strong environmental filters, creating local communities composed by species sharing similar traits (Bello et al. 2013). It results in a nonrandom extinction of species by generate changes in environmental characteristics influencing niche structure and biological interactions at local scale and limiting dispersion and colonization at larger spatiotemporal scales (Myers et al. 2013).

In the past decades, many studies in human-disturbed landscapes have focused in taxonomic diversity, ignoring the traits or the relatedness between species, what is a strong tool to understand the mechanisms of community assembly. The study of phylogenetic diversity links ecology and evolutionary history, predicts biological and ecological processes (Turcker et al. 2016), and it allow to predict the responses of biodiversity, stability (Cadotte et al. 2012) and productivity (Cadotte 2013) in face to these global change drivers. Moreover, studies addressing phylogenetic similarity between communities in a given landscape (i.e. phylogenetic β-diversity) may allow connecting local to regional processes (Graham and Fine 2008).

At the same time, comparisons of taxonomic diversity with phylogenetic (alpha and beta) diversity can provide insights about to what extent community assembly is driven by deterministic or stochastic processes (Purshke et al. 2013), once dynamics do not act on the number of species, but rather on ecological differences among species (e.g., Swenson 2011). More than this, when combined with traditional measures of beta diversity and environmental gradient analyses, phylogenetic beta diversity can provide significant and novel insights into the mechanisms underlying current patterns of biological diversity (Graham et al. 2008).While beta diversity effectively captures the amount of overlap in species composition between sites (habitats, geographic regions), it does not provide information about how deep in evolutionary time these lineages have been separated, which can provide very different insights about the ecological, historical and evolutionary processes that structure communities (Chave et al. 2007, Hardy and Senterre 2007), once is possible simultaneously detect a high species turnover and a low turnover of lineages due to the presence of many congeneric species.

Seasonal Tropical Dry Forests (STDFs) are one of most threatened ecosystem in the world (Portillo-Quintero and Sánchez-Azofeifa 2010, Miles et al. 2006), given that up to a third of global population live in these regions (Miles et al. 2006) and extracts a myriad of timber and non-timber forest products and fodder resources (Sunderland et al. 2015), specially in times of agricultural scarcity (Rowland et al. 2015). Brazilian Caatinga is the largest and most species-rich dry forest in Latin America (Sunderland et al. 2015), occupying 17% of Brazilian territory (Portillo-Quintero and Sánchez-Azofeifa 2010). This ecosystem has been explored by human populations since the mid-sixteenth century and it is estimated that more than 50% of all Caatinga territory are degraded by human activities (MMA and IBAMA 2011). The Caatinga historic of occupation and exploration in part is due to in the occupancy of low-income rural populations that are largely dependent on a resource extraction-based economy (Barbier 2000, Davidar et al. 2010, Metha et al. 2008, Ribeiro et al. 2015, Singh 1998), which leads chronic anthropogenic disturbances (i.e. overgrazing, selective logging and extraction of firewood and non-timber forest products) (Singh et al. 1984, Gunderson 2000). Evidence from disturbed Caatinga indicates that the phylogenetic diversity and structure of trees in different ontogenetic stages are negatively affected by chronic disturbances and suggests that the loss of evolutionary history may limit the ecological resilience of this ecosystem to disturbance and climatic changes (Ribeiro et al. 2016). However, Brazilian Caatinga biodiversity also may be threatened by climate changes as the Intergovernmental Panel on Climatic Change forecasted an increase of 1.8 °C to 4 °C of temperature and a reduction of 22% in rainfall by 2100 in this region (IPCC 2001, Magrin et al. 2014). Therefore, studies addressing not only chronic disturbance but also environmental variables related to aridity can help to understand the rules of community assembly and also to predict future scenarios of biodiversity maintenance in Brazilian Caatinga.

The responses of phylogenetic diversity to human disturbances and drought on Caatinga will depend on to what extent the traits that are possible filtered by these factors are conserved conserved along phylogeny. If these traits are conserved (i.e. they are restricted to some clades), disturbance and drought-mediated environmental filtering can exclude entire clades, resulting in a low phylogenetic diversity in more disturbed drought sites (Webb et al. 2002). On the other hand, if the traits are not conserved and can be found in many clades of the phylogenetic tree, entire clades will not be affected by disturbance and drought-mediated environmental filtering, which can result in no changes in phylogenetic diversity. Using this same reasoning for phylogenetic beta diversity, if the traits associated with vulnerability are conserved, disturbance and drought-mediated environmental filter tend to reduce phylogenetic beta diversity between sites with similar degree of disturbance and drought, but in this case, the geographic distance between two sites can limit the phylogenetic similarity.

Here, we assessed different components of phylogenetic diversity of plant communities in a Caatinga landscape that presents a long history of anthropogenic disturbance and a large variation in water availability (average annual climatic water deficit, 658 mm -1086 mm) to answer how these factors influences in community assembly in STDF. We hypothesized that chronicle disturbances and drought act as environmental filters, assembling more related species in Brazilian Caatinga. Thus, we expected that the extended drought and the increase of anthropogenic disturbances results in low phylogenetic α-diversity and which communities in sites with similar degrees of disturbance and drought will present lower levels of both taxonomic and phylogenetic β-diversity. Briefly, we first assessed phylogenetic α and β-diversity and taxonomic β-diversity in 18 communities and evaluated the impact of human disturbance and drought on these metrics. Second, we compare phylogenetic and taxonomic β-diversity. Finally, we discuss about the mechanisms that structure plant community in Caatinga and we make some projections about the potential of these landscapes to maintain biodiversity in face to anthropogenic activities and climatic changes.

METHODS

Study area

The Caatinga ecosystem is a mosaic of seasonally tropical dry forests and scrub vegetation (Pennington et al. 2009) that covers 826,411 km² restricted to Brazilian territory. It is an ecosystem with high annual and interannual seasonality of precipitation with the majority of rainfall is concentrated in three months per year and with severe droughts which may extend for years (Sampaio 1995, Chiang and Koutavas 2004). The average annual precipitation in Caatinga ranges from 450 to 1100 mm and the annual temperature averages 25 °C.

We developed this study in the Caatinga vegetation of the Catimbau National Park, Pernambuco State, Brazil (8º24'00" and 8º36'35" S; 37º0'30" and 37º1'40" W). This park has an area of ca. 60,000 ha and approximately 70% of the area is dominated by sand quartzolic soils. In the Park, there is high variation in precipitation (510 mm to 1100 mm). The Catimbau National Park is occupied by low-income rural populations (IBGE 2004) that extract forest products to animal and human food and fuelwood. Additionally to deforestation to agriculture and livestock, the extensive grazing by stock (goats and cattle) represent important human-caused disturbances to vegetation in the region.

Study sites

We selected 18 areas to cover a wide range of disturbance and precipitation levels based on the RapidEye satellite imagery, maps of soil and field exploitations. We established 18 20×50-m plots with a minimum 2-km distance within a 214.3 km^2 area dominated by old-growth vegetation exposed to chronic disturbance. All plots were located on areas with the same soil type (sand soil) and similar slope.

Chronic disturbances measures

To characterize the chronic anthropogenic disturbance in the 18 plots, we assessed three indicators of disturbance that have been described as important drivers of human disturbance in tropical forests studies (Table S1). Using satellite imagery we measure (1) distance to nearest farms (Sagar et al. 2003, Martorell and Peters 2005, Leal et al. 2014); (2) distance to nearest roads (Sagar et al. 2003, Leal et al. 2014); and (3) density of goats trails within each plot (GT; i.e. length of goat trails per area; Leal et al. 2014, Ribeiro et al. 2015). Distance to nearest farms and distance to nearest roads refer to the average distance from the centre of each plot to all farms and roads within a 15-km radius, considering the relief of the terrain (i.e., cost distances). These metrics are proxies of human pressure (e.g. logging, cutting and hunting) and overgrazing. We opted for these proxies because chronic disturbances are very difficult to quantify directly in the field (Martorell and Peters 2005, Leal et al. 2014, Ribeiro et al. 2015).

Annual climatic water deficit data

The annual water amount is an important driver of plant composition and structure in Caatinga (Prado 2003) and tropical dry forests in general (Hirota et al. 2011, Choat et al. 2012). To represent the water stress suffer by Caatinga vegetation, we used the average annual climatic water deficit (D, Table S1). D represents the potential additional evaporative demand not met by available water based on energy input and precipitation (Stephenson 1998, Lutz et al. 2010). It was calculated based in 30-arc-seconds (1km) resolution maps of long-term average annual potential evapotranspiration (PET) and actual evapotranspiration (AET) [CGIAR-CSI’s Global Aridity and PET Database and Global

High-Resolution Soil-Water Balance database, (Trabucco and Zomer 2009, 2010)]. These maps are generated using temperature and precipitation data from WorldClim global climate data repository (www.worldclim.org). For each plot was calculated the difference between PET and AET to obtain D values. All measures were performed with ArcGIS 10.0 (ESRI 2011). Average annual water deficit ranged from 658 mm to 1086 mm.

Plant survey and phylogeny construction

We sampled all shrubs and trees with diameter at basal height (DBH) ≥ 3 cm and total height ≥ 1 m in the 18 0.1-ha plots. We identified all stems and produced a species list based on the APG III (Bremer et al. 2009) classification. We searched GenBank (http://www.ncbi.nlm.nih.gov/genbank/) for four genes sequence used in published angiosperm phylogenies: ribulose-bisphosphate carboxylase gene (*rbc*L), maturase K (*mat*K), 5.8S ribosomal RNA gene, and *trn*L-*trn*F intergenic spacer (*trn*L-F) (Table S2). Based in these four DNA regions we estimated continuous phylogenetic distance among the focal specie present in the plots and its conspecific, congener, confamilial or distant relative using a Bayesian phylogeny. When the gene sequences were not available for specie, we used a randomly chosen alternative gene sequences from a congeneric relative to estimate the relatedness to that genus (Table S2). The effect on branch length of using these substitute species is expected to be minimal given the breadth of phylogenetic sampling (Cadotte et al. 2008). We also included two representatives of early diverging angiosperm lineages as outgroup species to root the tree (*Amborella* and *Magnolia*) and to increase the depth of taxon sampling, following the work of Burns and Strauss (2011). Sequences were aligned for each region independently using MUSCLE (Edgar 2004) and combined into a single supermatrix using Geneious version 7.1.4 (http://www.geneious.com, Kearse et al.

2012). The Bayesian inference search was performed using Mr. Bayes v3.1.2 (Ronquist and Huelsenbeck 2003), allowing the general time reversible (GTR) + γ model to be estimated, and using the default settings; multiple runs were performed to ensure that the resulting phylogeny was not stuck in a local optimum. We then created a time-calibrated phylogeny (chronogram) using fossil calibration points derived from Wikström et al. (2001) using BEAST (Drummond et al. 2012). Simultaneous divergence-time and phylogenetic analyses were conducted using Markov chain Monte Carlo (MCMC) methods implemented in BEAST employs a lognormal relaxed-clock model to estimate divergence times. We then added branch lengths between taxa to estimate the phylogenetic distance between them in approximate millions of years (Fig. S1, Webb et al. 2002).

Data analysis

We evaluated the accuracy of plant inventories with the coverage estimator ($\hat{C}n$) recommended by Chao and Jost (2012) using the entropart package in R (Marcon and Herault 2013). This estimator calculates the proportion of the total number of individuals in an assemblage that belong to the species represented in the sample. Sample coverage was very high in all sites (> 93% of the species recorded), indicating that our sampling effort was adequate, and that our diversity estimates were not biased by differences in sample coverage among sites (Chao and Jost 2012, Chao et al. 2014).

We measure phylogenetic α and β – diversity and taxonomic β – diversity based on Hill numbers as described by Chao et al. (2010), Jost (2007) and Chiu et al. (2014). Hill numbers represent the true diversity because they obey the principle of replication (Jost 2007). Also, once diversity based on Hill numbers are expressed in an effective number of species, this measure allows comparing phylogenetic and taxonomic β – diversity in the same graph. Phylogenetic α – diversity [${}^{q}\bar{D}_{\alpha}(T)$] gives the mean phylogenetic diversity for the interval [-T,0] or mean effective number of species over T years. It incorporates information about the pattern of phylogenetic tree branches, the relative branch length and the relative abundance in each branch segment in the present day. For the calculation of ${}^{q}\overline{D}_{\alpha}(T)$, the phylogenetic tree is sliced in intervals of time and in each interval we can find the number of species end their abundances (by summing the abundance of their descendent in the present day). We calculate ${}^{q}\overline{D}_{\alpha}(T)$ for the order q= 0, 1 and 2. When $q = 0$, the analysis do not consider the species abundance and the results can be interpreted as the effective number of species in T years and gives greater weight to rare species. When $q = 1$, the analysis weigh each species according their abundance and the result can be interpreted as the mean effective number of common species in over T years. Finally, when $q = 2$, very abundant species are favoured and the results can be interpreted as the mean effective number of these species over T years. High values of ${}^{q}\overline{D}_{\alpha}(T)$ refers to phylogenies with deep branches well represented in the present day, while low values of ${}^{q}\overline{D}_{\alpha}(T)$ refers to phylogenies with recently emerged branches or with low representation of old branches.

To compute phylogenetic β – diversity (${}^{q}\overline{D}_{\beta}(T)$) we first assess alpha [${}^{q}\overline{D}_{\alpha}(T)$] and gamma [${}^{q}\overline{D}_{\gamma}(T)$] components of diversity and then, using the multiplicative diversity partition, we calculates phylogenetic β – diversity by the formula: ${}^{q}\overline{D}_{\beta}(T) = {}^{q}\overline{D}_{\gamma}(T)/\,{}^{q}\overline{D}_{\alpha}(T)$. As we adopt for ${}^{q}\overline{D}_{\alpha}(T)$, ${}^{q}\overline{D}_{\beta}(T)$ also was computed in three orders of q, i.e. q = 0, 1 and 2. ${}^{q}\overline{D}_{\beta}(T)$ gives the effective number of completely phylogenetic distinct communities. If all communities are similar in species composition and abundance, ${}^{q}\overline{D}_{\beta}(T)$ will be equal to 1, but if they are totally distinct in terms of phylogeny, ${}^{q}\overline{D}_{\beta}(T)$ will be equal to the number of communities. For details about the formula to calculate all the components of phylogenetic diversity based on hill numbers see Chiu et al. (2014).

Finally, taxonomic β – diversity (${}^{q}D_{\beta}$) was computed in a similar way that phylogenetic one, but without taking into account the evolutionary relationship between species. For this measurement, we also computed alpha (${}^{q}D_{\alpha}$) and gamma (${}^{q}D_{\gamma}$) components of diversity and use the multiplicative diversity partition. So ${}^{q}D_{\beta} = {}^{q}D_{\gamma} / {}^{q}D_{\alpha}$. ${}^{q}D_{\beta}$ gives the effective number of distinct communities. If all communities are identical, ${}^{q}D_{\beta}$ will be equal to 1, but if they are totally distinct, ${}^{q}D_{\beta}$ will be equal to the number of communities. We also computed ${}^{q}D_{\beta}$ when q=0, 1 and 2, what emphasizes rare, common and dominant species, respectively. For more details about how to calculate ${}^{q}D_{\beta}$ see Jost (2007). All diversity measures reported here were calculated with the package entropart in R (Marcon and Herault 2013).

To test whether patterns of α – phylogenetic diversity is influenced by water deficit and chronic disturbance predictors we used generalized linear models. We used Mantel tests to assess whether the matrices of β – taxonomic and phylogenetic diversity among plots were correlated to plot location (i.e. with the matrix of the geographical distances among sites), water availability (i.e. average annual water deficit) and/or chronic disturbance predictors (i.e. distance to roads, distance to farms and goat trails density). These analyses were carried out with R software, using the vegan package (Oksanen et al. 2013).

RESULTS

We assessed 3777 stems belonging to 109 species (23.3 ± 8.5 species per plot; mean ± SD) and 31 families. The most representative families were Fabaceae (29.4% of species), Euphorbiaceae (14.7%) and Myrtaceae (7.3%). The mean effective of distinct lineages was 10.2 (±2.9) considering species richness [${}^{0}\overline{D}_{\alpha}(T)$], 3.9 (±1.2) of common species [${}^{1}\overline{D}_{\alpha}(T)$] and 2.5 (±0.6) of dominant species [${}^{2}\overline{D}_{\alpha}(T)$]. Only the number of lineages considering species richness $[{}^{0}\bar{D}_{\alpha}\ (T)]$ was influenced by average water deficit decreasing the phylogenetic diversity in dry areas (GLM, t=-3.62, d.f.=13, p<0.01; Table 1, Fig. 1). No chronic disturbance predictors were important to predict changes in α – phylogenetic diversity for any order *q* (Table 1).

The taxonomic β – diversity was higher than phylogenetic β – diversity for any order *q* at the landscape scale (Fig. 2A). The same occurred for the β – diversity between pairs of plots (Fig. 2B). Yet, while the taxonomic β – diversity does not change among *q* orders between plots, at landscape scale the turnover was high when considering rare species $({}^{0}D_{\beta\ \mathrm{plot}} = 4.5)$ than when considering common $({}^{1}D_{\beta\ \mathrm{plot}} = 3.8)$ and dominant $({}^{2}D_{\beta\ \mathrm{plot}} = 4.1)$ species (Fig 2A). The phylogenetic β – diversity at the landscape was relatively higher when considering rare species $[{}^{0}\bar{D}_{\beta}\ (T)_{\mathrm{land}} = 2.8]$, than when considering common $[{}^{1}\bar{D}_{\beta}\ (T)_{\mathrm{land}} = 1.6]$ and dominant $[{}^{2}\bar{D}_{\beta}\ (T)_{\mathrm{land}} = 1.3]$ species (Fig 2A). The same occurred for average phylogenetic β – diversity between plots when considering rare species $[{}^{0}\bar{D}_{\beta}\ (T)_{\mathrm{plot}} = 1.4]$, than when considering common $[{}^{1}\bar{D}_{\beta}\ (T)_{\mathrm{plot}} = 1.2]$ and dominant $[{}^{2}\bar{D}_{\beta}\ (T)_{\mathrm{plot}} = 1.1]$ species (Fig 2B).

The results of the Mantel tests show that taxonomic and phylogenetic β – diversity was generally more correlated with differences in water deficit rather than chronic disturbance predictors to 0 and 1 *q* orders (Table 2). Phylogenetic β – diversity between plots increased with increasing interplots differences in water deficit (Table 2). For taxonomic β – diversity, the geographic distance and the distance to roads were important to predict the turnover when considering rare species (Table 2). Higher phylogenetic β – diversity values were found among plots more isolated from each other and when increased interplots differences in distance to roads (Table 2).

Given the absence of patterns when considered dominant species, we construct a table of dominant species distribution in the water deficit rank to the 18 plots. We construct this table with an aim of observing distribution patterns of dominant species across the water availability gradient and identify the species identity. We considered as dominant those species with 13% or more of abundance in each plots, because when we observed the most abundant in each plot, the less relative abundant presented 13%. Interestingly, of the 16 species observed as dominant in the 18 plots, only four do not belong to Euphorbiaceae and Fabaceae families. Yet, when considered these dominant species distribution in the average water deficit rank, almost was not observed species overlap among plots. A maximum of four dominant species in one plot and three dominant species in two plots was founded (Table 3). The overlap of dominant species to the Fabaceae occurred only for three plots and for two plots considering only Euphorbiaceae (Table 3).

DISCUSSION

Our study suggests that the major force structuring communities in Caatinga is the water availability. Regions with high water availability hold a high number of rare species belonging to distinct lineages, i.e. with an increased phylogenetic diversity at local scale and turnover of species and lineages in the landscape. Thus, both deterministic and stochastic process seems to operate on the community assembly when observed the turnover of rare species. If on one hand the environmental filters (i.e. water availability and selective logging) are contributing to the occurrence of rare species, on the other hand, the dispersal limitation (i.e geographic distance) seems to be an important determinant of community assembly to rare species too. Yet, the high common species taxonomic turnover is associated with water availability and there is a tendency that it reflects in turnover of lineages. So, the species strategies to avoiding desiccation seem to be phylogenetically grouped for rare and common species. Dominant species appearing mostly associated with the families Euphorbiaceae and Fabaceae. This may indicates that avoiding desiccation strategies are dispersed in the group and that they possess high plasticity within groups to tolerate wide range of precipitation. So, the competition among confamiliar and congeneric species seems the major community assembly driver for dominant species because almost there is no overlap among species of the same family.

Natural communities are not only assembled by stochastic events and dispersion. Studies have shown that community trait composition is often influenced by different environmental factors (Swenson and Enquist 2009, Mason et al. 2011). Environmental drivers select hierarchically species best adapted to local conditions from the regional pool according to sets of functional traits (de Bello et al. 2013). The first environmental driver acts by large-scale environmental factors (e.g. climate) and then more fine-scale environmental factors (e.g. chronic disturbances) and finally, biotic interactions determine the relative abundances of species (de Bello et al. 2013, Gross et al. 2013). In our study, the prevalent environmental driver is the water availability that changes through the landscape, filtering species based in characteristics related to water efficiency use. So, probably these characteristics are conserved over phylogeny (see Kraft et al. 2007) and the consequence is the loss of lineages of rare and common species in driest areas at local scale, causing changes in the taxonomic and phylogenetic β – diversity patterns.

Dominant species in a disturbed landscape generally belongs to groups of related species adapted to stress with a large range of capacity adaptation to environmental changes (Olden et al. 2004, Santos et al. 2010). In our landscape the dominant groups are Euphorbiaceae and Fabaceae, which are frequently reported as pioneers plants in Caatinga. When attributes are conserved across phylogenies, competitive exclusion will cause closely related species to co-occur less frequently than expected by chance (Webb et al 2002, Cavender –Bares et al 2009). The more functionality clustering among confamiliar and congeneric Euphorbiaceae and Fabaceae groups of species results in the finest scale promotes competition avoiding overlap. This result support theoretical predictions about competition role in community assembly, where competition limits correlated species to coexist (Cavender –Bares et al. 2009) particularly at finest spatial scales because species compete for the same local resources (de Bello et al. 2013). This reinforces the idea that coexisting species are typically more functionally clustered than expected (Swenson and Enquist 2009) and why in our areas the lineages remains but the taxonomic diversity changes.

The negative effect of people access (i.e. small distance to farms) in phylogenetic β –diversity of rare species can be related to selective logging, once the households in general use high quality wood to firewood (Ramos et al. 2008). Besides the water availability, the selective logging is an important filter to turnover of rare species, but it seems the traits related to wood quality are not conserved across the lineages causing no resemblance in phylogenetic terms. This result is contrary to a recent study realized in Caatinga vegetation, which indicates that chronic disturbance are promoting phylogenetic impoverishment of woody flora, specially seedlings and saplings (Ribeiro et al. *in press*). We have strong evidences that the evaluation of only chronic disturbance predictors to infer phylogenetic loss in STDF is not sufficient because the high seasonality of rain and high temperatures in this ecossystems imposes a environmental filtering more strong than chronic anthropogenic disturbances.

Predicting key factors that change community assembly has been an issue for ecologists, mainly due to changes in community diversity of various organisms caused by habitat loss and climatic changes (Naeem and Wright 2003, McGill et al. 2006). Climatic changes consequences tend to be perceived in a time scale much bigger than those generated by changes in land use (Thuiller 2007). However, in a near future, climatic changes may affect the biodiversity more severely than habitat loss, because climatic change effects occur in larger scales, affecting entire biotas. Thus, to be able to predict ecosystem responses to future disturbance events is necessary to understand the processes that govern community assembly. Our study represents, to the best of our knowledge, the first demonstration of how climatic factors and human disturbances influence the phylogenetic diversity and assembly of plant communities on Caatinga flora. In the actual context, where anthropogenic disturbance encompass since habitat loss to climatic changes, phylogenetic community structure and diversity holds promise for predicting processes and impacts of global change. Quantify the phylogenetic structure of communities help us to discuss community assembly processes and how it affects present-day species coexistence in local communities and identify the idiosyncrasies of habitats permits evaluate the potential biodiversity retention and help in management plans of areas in risk. The rare species loss in dry areas reinforce that there is a imminent need to protect representative areas of diferent fisionomies in Caatinga and STDF under all range of precipitation emcompassing the variety of communities and lineages that represent them, foment the biodiversity manutention and stability to keep ecossistem functions.

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Figure legends

Figure 1. Relation between mean phylogenetic α – diversity [$^{q}\overline{D}_{\alpha}$ (T)] for the three orders q (0, 1 and 2) and average annual water deficit (mm).

Figure 2. Plant β-diversity in 18 0.1 ha plots with different water deficit level and exposed to chronic anthropogenic disturbance located within the Catimbau National Park, Brazil. A= total taxonomic and phylogenetic β – diversity (i.e. for the landscape). B= taxonomic and phylogenetic β – diversity between pairs of plots. Error bars correspond to standard deviation.

Table 1. Relations between taxonomic α diversity, average water deficits and three chronic human disturbances predictors in 18 plots located within the Catimbau National Park, Brazil. Phylogenetic α – diversity [${}^{q}\overline{D}_{\alpha}$ (T)] was calculated considering three orders q (0, 1 and 2), which determine the sensitivity of each α diversity component to the relative abundances (see methods).

Variables	${}^{0}\overline{D}_{\alpha}(T)$		${}^{1}\overline{D}_{\alpha}(T)$		${}^{2}\overline{D}_{\alpha}(T)$	
	t	p	t	P	t	P
Water déficit (mm)	**-3.62**	**0.003**	-2.069	0.059	-1.417	0.179
Distance to road (m)	-1.062	0.307	-0.748	0.467	-0.913	0.377
Distance to farm (m)	1.518	0.153	0.918	0.375	0.552	0.590
Goat trails density (m/0.1ha)	-0.134	0.896	-0.937	0.366	-1.349	0.200

Table 2. Correlations between taxonomic and phylogenetic β diversity and different average water deficits and chronic human disturbances 18 plots located within the Catimbau National Park, Brazil.

Variables	Taxonomic β diversity						Phylogenetic β diversity					
	q0		q1		q2		q0		q1		q2	
	R	*P*	*R*	*P*	*R*	*P*	*R*	*P*	*R*	*P*	*R*	*P*
Geographic distance	**0.22**	**0.036**	0.13	0.136	0.07	0.265	0.15	0.083	0.10	0.179	0.00	0.449
Water deficit	**0.41**	**0.002**	**0.24**	**0.028**	0.09	0.216	**0.35**	**0.001**	**0.21**	**0.050**	0.01	0.416
Distance to roads	**0.30**	**0.029**	0.20	0.149	0.09	0.289	0.15	0.129	0.21	0.133	0.11	0.205
Distance to farms	-0.06	0.734	-0.08	0.796	-0.08	0.822	-0.10	0.878	-0.09	0.837	-0.04	0.628
Goat trails	0.14	0.153	0.09	0.248	0.07	0.276	0.14	0.097	0.11	0.176	0.15	0.166

We indicate the correlation coefficients calculated with Mantel tests. Significant coefficients are indicated in bold. Taxonomic β-diversity ($^{q}D_{\beta}$) and phylogenetic β-diversity [$^{q}\bar{D}_{\beta}(T)$] were calculated considering three orders q (0, 1 and 2), which determine the sensitivity of each β-diversity component to the relative abundances (see methods).

Table 3. Dominant species distribution in a water deficit rank of 18 plots located within the Catimbau National Park, Brazil. We considered as dominant those species with 13% or more of abundance in each plots, because when we observed the most abundant in each plot, the less relative abundant presented 13%.

Family	**Species**	**Plots (water deficit rank) →**																		**Total of plots**
Boraginaceae	*Varronia leucocephala*										■									1
Cactaceae	*Tacinga palmadora*																	■		1
Capparaceae	*Neocalyptrocalyx longifolium*				■															1
Euphorbiaceae	*Acalypha brasiliensis*				■															1
Euphorbiaceae	*Croton heliotropiifolius*							■											■	2
Euphorbiaceae	*Jatropha molissima*					■											■		■	3
Euphorbiaceae	*Croton nepetifolius*			■										■	■		■			4
Euphorbiaceae	*Croton tricolor*						■						■					■		3
Fabaceae	*Poincianella microphylla*										■									1
Fabaceae	*Peltogyne pauciflora*															■				1
Fabaceae	*Piptadenia stipulacea*								■											1
Fabaceae	*Senegalia piauhiensis*		■																	1
Fabaceae	*Senegalia bahiensis*		■			■														2
Fabaceae	*Poincianella pyramidalis*									■		■			■		■		■	5
Fabaceae	*Pityrocarpa moniliformis*	■												■	■		■			4
Malvaceae	*Melochia tomentosa*															■				1
Total of species		1	2	1	2	2	1	1	1	1	2	1	1	2	3	2	4	2	3	

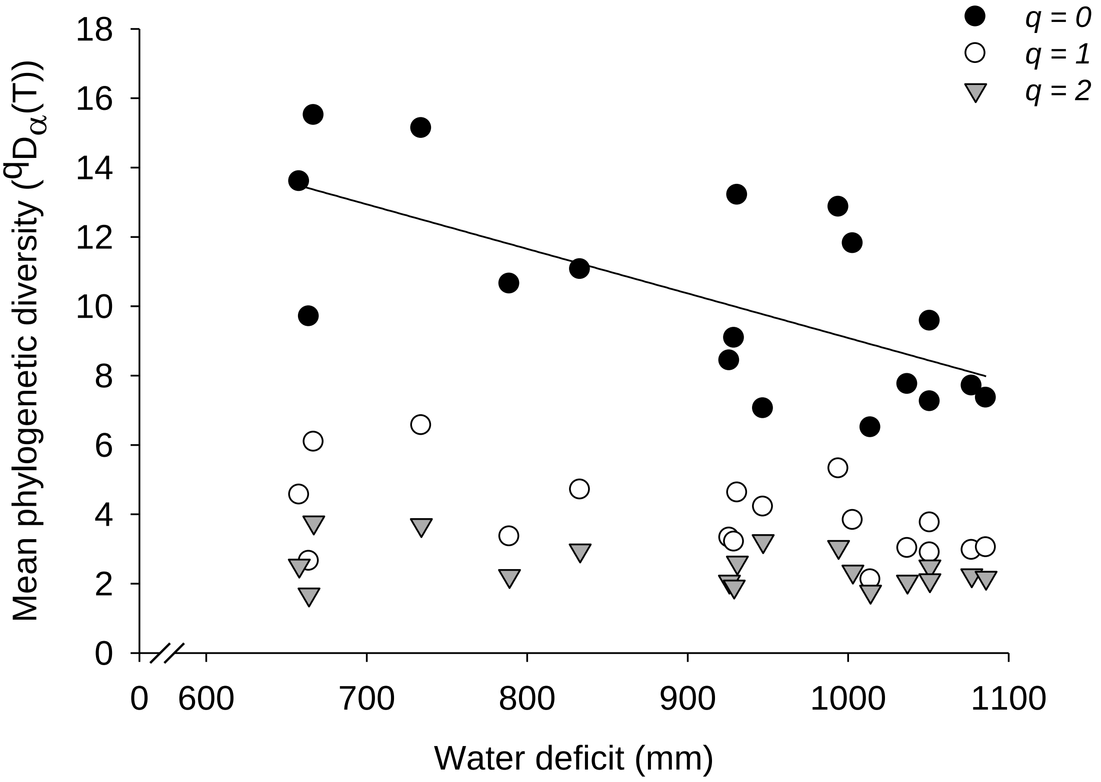
q = 0
q = 1
q = 2
Mean phylogenetic diversity (qDα(T))
0
2
4
6
8
10
12
14
16
18
0
600
700
800
900
1000
1100
Water deficit (mm)

Fig. 1

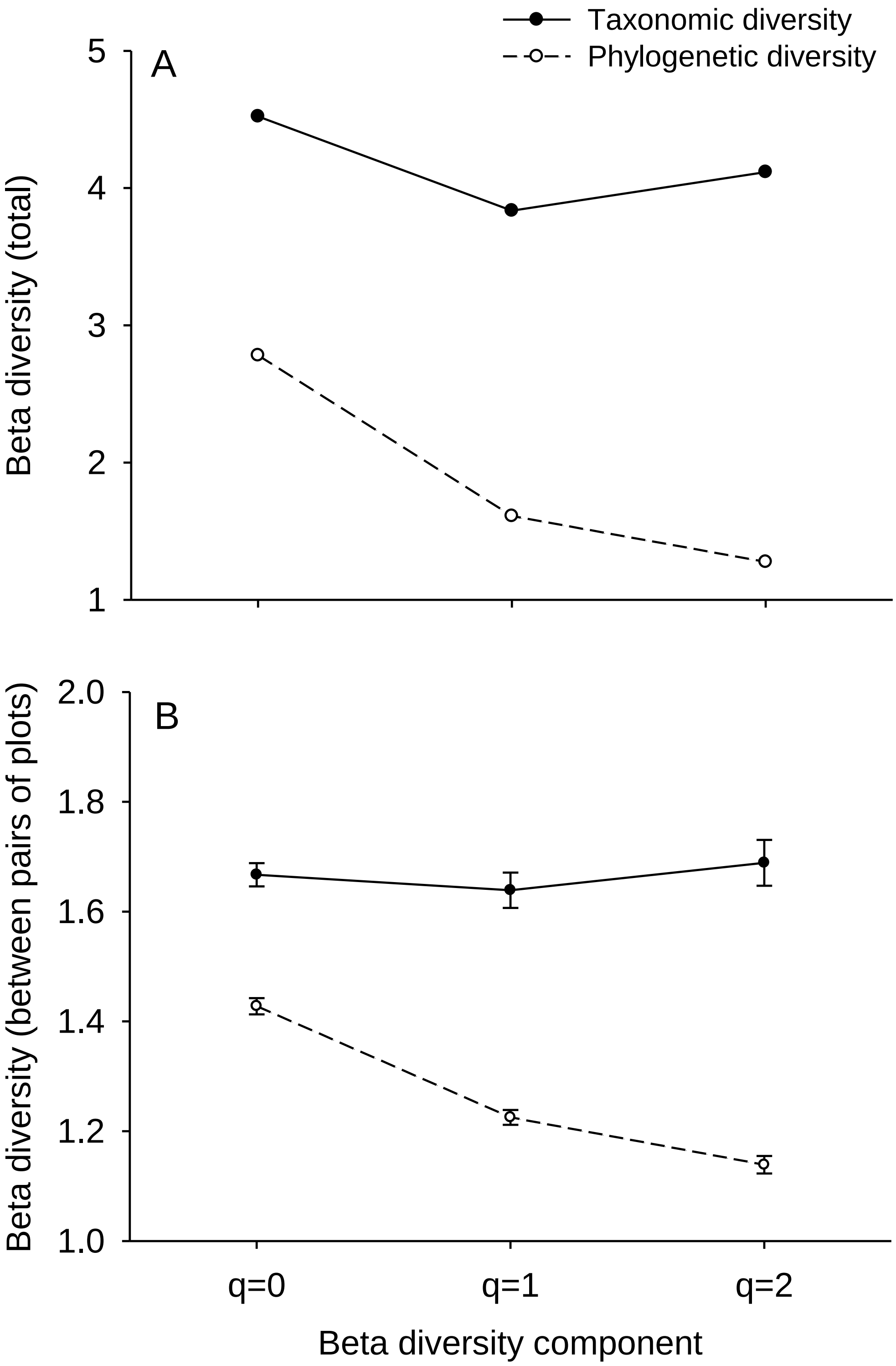
Taxonomic diversity
Phylogenetic diversity
A
B
Beta diversity (total)
5
4
3
2
1
Beta diversity (between pairs of plots)
2.0
1.8
1.6
1.4
1.2
1.0
q=0
q=1
q=2
Beta diversity component

Fig. 2

Supplementary material

Figure S1. Bayesian tree for plant species founded in 18 plots located within the Catimbau National Park, Brazil. The Bayesian tree was estimated based in four DNA regions: maturase K (*mat*K), 5.8S ribosomal RNA gene (5.8S), ribulose-1,5-carboxylase/bisphosphate gene (*rbc*L), and intergenic spacer (*trn*L-*trn*F).

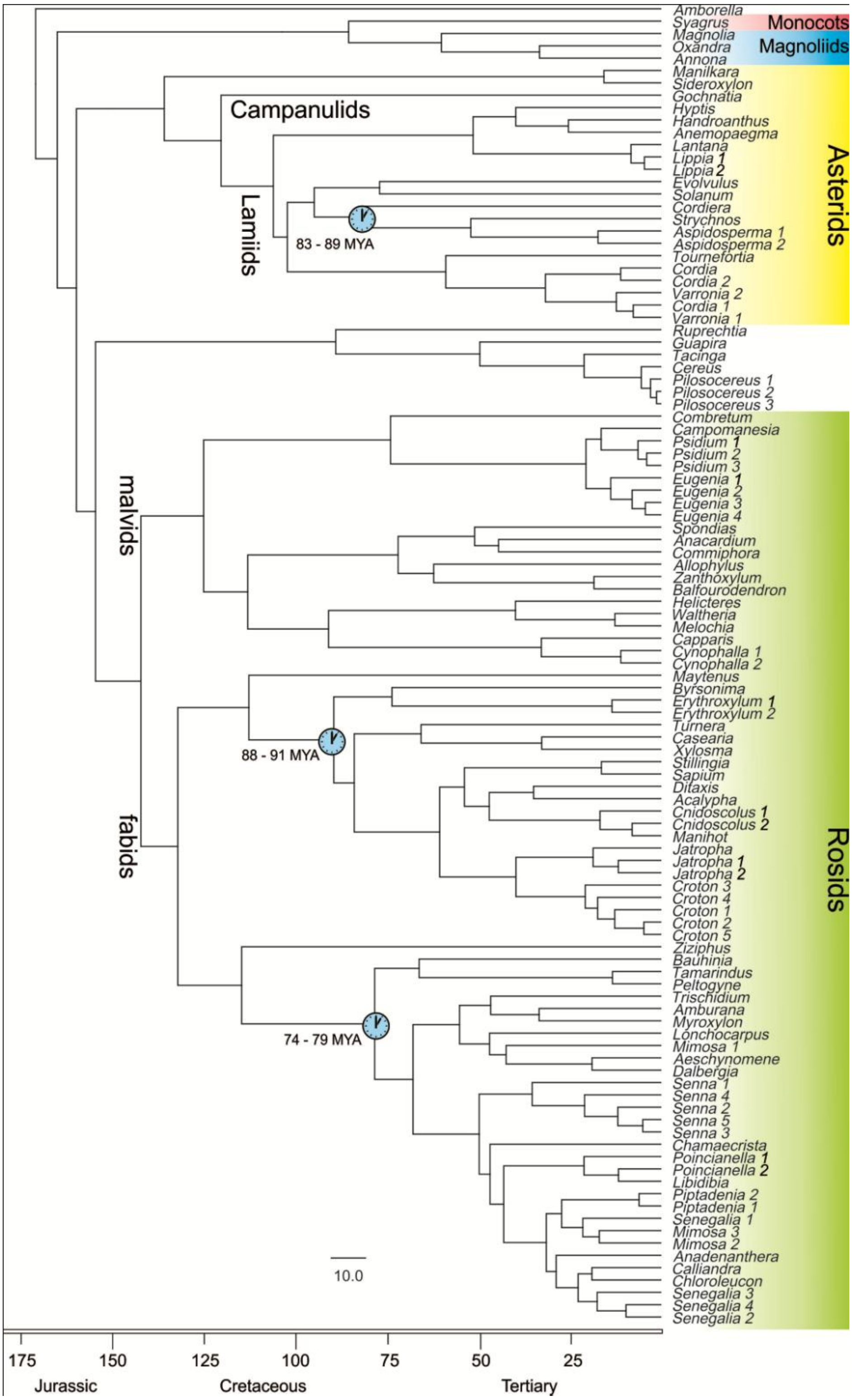

Table S1. Environmental variables data from 18 plots exposed to different average water deficits and chronic human disturbances located within the Catimbau National Park, Brazil.

Variable	**Median**	**Min**	**Max**
Geographic distance (km)	9.1	2.1	19.7
Water deficit (mm)	939.0	658.0	1086.0
Distance to road (m)	0.9	0.0	11.4
Distance to farm (m)	8.9	2.7	16.5
Goat trails density (m/0.1ha)	0.2	0.0	0.4

Table S2. Sequences used to estimate the Bayesian tree (Fig. S1) for plant species founded in 18 plots located within the Catimbau National Park, Brazil. The Bayesian tree was estimated based in four DNA regions: maturase K (*mat*K), 5.8S ribosomal RNA gene (5.8S), ribulose-1,5-carboxylase/bisphosphate gene (*rbc*L), and intergenic spacer (*trn*L-*trn*F). Data from sequences available in GenBank (http://www.ncbi.nlm.nih.gov/genbank/) and in *Amborella* Genome Database (http://amborella.huck.psu.edu/shortstack).

Species	**Species used for matK**	**matK**	**Species used for 5.8S**	**5.8S**	**Species used for rbcL**	**rbcL**	**Species used for trnL-trnF**	**trnL-trnF**
Amborella trichocarpa	*Amborella trichocarpa*	AF543721	*Amborella trichocarpa*	AmTr_v1.0_scaffold03396	*Amborella trichocarpa*	L12628	*Amborella trichocarpa*	AY14532
Acalypha brasiliensis	*Acalypha californica*	EF135499	*Acalypha rhomboidea*	DQ006003	*Acalypha californica*	AY380341	*Acalypha californica*	AY794776
Aeschynomene marginata	*Aeschynomene indica*	AF272084	*Aeschynomene indica*	KC899206	*Aeschynomene indica*	AF308701	*Aeschynomene indica*	AF208927
Allophylus quercifolius	*Allophylus bullatus*	JN191101	*Allophylus bullatus*	JN190966	*Allophylus bullatus*	JN191137	*Allophylus longipes*	AY207572
Amburana cearensis	*Amburana cearensis*	JX846614	*Amburana cearensis*	KJ813615	NA	NA	*Amburana cearenses*	EF466144
Anacardium occidentale	*Anacardium occidentale*	AY594459	*Anacardium occidentale*	KF664192	*Anacardium occidentale*	AY462008	*Anacardium occidentale*	AY594497
Anadenanthera colubrina	*Anadenanthera colubrina*	EU812064	*Anadenanthera colubrina*	JQ910930	*Anadenanthera peregrina*	KJ082119	*Anadenanthera peregrina*	EU811875
Anemopaegma laeve	*Anemopaegma orbiculatum*	JQ586982	NA	NA	*Anemopaegma orbiculatum*	KJ594098	*Anemopaegma parkeri*	FJ870015
Annona	*Annona*	GQ139718	*Annona*	GQ139686	*Annona*	AY841597	*Annona*	GQ139892

leptopetala	*sclerophylla*		*sclerophylla*		*senegalensis*		*sclerophylla*	
Aspidosperma pyrifolium	*Aspidosperma pyrifolium*	JX850029	*Aspidosperma marcgravianum*	FJ037794	*Aspidosperma cylindrocarpon*	DQ660633	*Aspidosperma quebracho-blanco*	AF214165
Aspidosperma sp1	*Aspidosperma cruentum*	JQ626476	*Aspidosperma cruentum*	FJ037792	*Aspidosperma cruentum*	JQ626066	*Aspidosperma cuspa*	AF214315
Balfourodendron molle	*Balfourodendron riedelianum*	FJ716747	*Balfourodendron riedelianum*	KC502921	*NA*	NA	*Balfourodendron riedelianum*	EU853779
Bauhinia acuruana	*Bauhinia tomentosa*	AY386893	*Bauhinia cheilantha*	DQ787410	*Bauhinia guianensis*	JQ626034	*Bauhinia forficata subsp. pruinosa*	FJ801053
Byrsonima gardneriana	*Byrsonima crassifolia*	JX661932	*Byrsonima gardneriana*	DQ787385	*Byrsonima crassifolia*	JX664036	*Byrsonima crassifolia*	AF350945
Calliandra aeschynomenoides	*Calliandra rhodocephala*	JQ587534	*Calliandra depauperata*	JX870682	*Calliandra vaupesiana*	KR082842	*Calliandra ulei*	JX870815
Campomanesia eugenioides	*Campomanesia guazumifolia*	AY521532	*Campomanesia guazumifolia*	AM234076	NA	NA	NA	NA
Casearia sylvestris	*Casearia velutina*	KP093517	*Casearia velutina*	KP092978	*Casearia sylvestris*	JQ625967	*Casearia javitensis*	AY935782
Cereus jamacaru	*Cereus alacriportanus*	AY015313	*Cereus alacriportanus*	AY064344	*Cereus fernambucensis*	AY875240	*Cereus aethiops*	JQ779665
Chamaecrista zygophylloides	*Chamaecrista diphylla*	JQ587555	*Chamaecrista diphylla*	FJ009868	*Chamaecrista diphylla*	JQ591641	*Chamaecrista diphylla*	FJ009922
Chloroleucon foliolosum	*Chloroleucon mangense*	AY386921	*Chloroleucon mangense*	EF638183	*NA*	NA	*Chloroleucon mangense*	AF278517
Cnidoscolus bahianus	*Cnidoscolus aconitifolius*	AB268041	NA	NA	*Cnidoscolus aconitifolius*	AB267937	*Cnidoscolus tubulosus*	EU518895
Cnidoscolus obtusifolius	*Cochlospermum vitifolium*	JQ587264	NA	NA	*Cochlospermum vitifolium*	JQ591114	NA	NA

Neocalyptrocalyx longifolium	*Capparis spinosa*	AY491650	*Capparis spinosa*	KF454307	*Capparis spinosa*	AY167985	*Capparis spinosa*	AY122422
Combretum glaucocarpum	*Combretum elaeagnoides*	KC130317	*Combretum fragrans*	FJ381754	*Combretum apiculatum subsp. apiculatum*	KC158546	*Combretum paniculatum*	AY905455
Commiphora leptophloeos	*Commiphora schlechteri*	KF147383	*Commiphora schimperi*	JN882702	*Commiphora falcata*	GU246030	*Commiphora leptophloeos*	KM516816
Cordia curassavica	*Cordia curassavica*	KJ012548	*Cordia curassavica*	JF332114	*Cordia curassavica*	KJ082238	*Cordia curassavica*	EU861998
Cordia rufescens	*Cordia nevillii*	HQ384571	*Cordia rufescens*	JF332086	*Cordia nevillii*	HQ384923	*Cordia decandra*	EF688851
Cordia trichotoma	*Cordia torrei*	JX517572	*Cordia revoluta*	HM443775	*Cordia trichotoma*	EU599827	*Cordia lutea*	KF158215
Cordiera rigida	*Alibertia myrciifolia*	KF981358	*Gardenia hansemannii*	HM443775	*Alibertia myrciifolia*	KF981281	*Alibertia edulis*	AF201029
Croton tricolor	*NA*	NA	*Croton tricolor*	EF421752	*Croton tricolor*	EF405854	*Croton tricolor*	EF408125
Croton sonderianus	*Croton menyharthii*	JF270729	*Croton cupulifer*	EU478063	*Croton setiger*	EF405853	*NA*	NA
Croton grewioides	*Croton laevifolius*	KJ708871	*Croton dichogamus*	KR734257	*Croton maestrense*	EF405857	*Croton dichogamus*	KP878421
Croton heliotropiifolius	*Croton heliotropiifolius*	AY794695	*Croton tenuilobus*	HM071963	*Croton yucatanensis*	EF405855	*Croton heliotropiifolius*	AY794695
Croton nepetifolius	*Croton glandulosus*	KJ772691	*Croton glandulosus*	AY971211	*Croton glandulosus*	KJ773418	*Croton glandulosus*	EU497713
Cynophalla flexuosa	*Cynophalla flexuosa*	KJ012556	NA	NA	*Cynophalla flexuosa*	KJ082258	*Cynophalla flexuosa*	AY122418
Cynophalla hastata	*Cynophalla hastata*	KJ012557	*Capparis acutifolia*	KP092569	*Cynophalla hastata*	KJ082259	NA	NA
Dahlstedtia sp	*Lonchocarpus muehlbergianus*	JX506615	*Dahlstedtia muehlbergiana*	KJ411648	*Lonchocarpus heptaphyllus*	KJ082389	*Lonchocarpus muehlbergianus*	JX506502
Dalbergia	*Dalbergia*	KJ593846	*Dalbergia*	EF451070	*Dalbergia*	U74236	*Dalbergia*	KP338261

cearensis	*monetaria*		*miscolobium*		*hupeana*		*hupeana*	
Ditaxis desertorum	*Ditaxis montevidensis*	AB233761	*Ditaxis guatemalensis*	DQ997792	*Ditaxis montevidensis*	AB233865	*Ditaxis simoniana*	AY794742
Erythroxylum revolutum	*Erythroxylum areolatum*	JX661939	*Erythroxylum argentinum*	AF130316	*Erythroxylum confusum*	L13183	*Erythroxylum argentinum*	AF127731
Erythroxylum suberosum	*Erythroxylum sinense*	KP094049	*Erythroxylum sinense*	KP092916	*rythroxylum novocaledonicum*	AB233930	*Erythroxylum argentinum*	AF127731
Eugenia brejoensis	*Eugenia uniflora*	GU135006	*Eugenia uniflora*	KM064994	*Eugenia uniflora*	AF294255	*Eugenia uniflora*	KP722326
Eugenia sp1	*Eugenia pacifica*	KM495179	*Eugenia pacifica*	KM495178	*Eugenia tetramera*	JQ626289	NA	NA
Eugenia sp2	*Eugenia pseudopsidium*	KJ012595	*Eugenia foetida*	AY487298	*Eugenia foetida*	KJ773495	NA	NA
Eugenia stictopetala	*Eugenia oerstediana*	JQ588485	*Eugenia beaurepairiana*	KJ187609	*Eugenia oerstediana*	JQ592955	NA	NA
Evolvulus linoides	*Evolvulus nuttallianus*	KT176618	*Evolvulus nuttallianus*	DQ219869	*Evolvulus nuttallianus*	KT178137	*Evolvulus glomeratus*	AY101121
Gochnatia oligocephala	*Gochnatia hypoleuca*	EU385357	*Gochnatia hypoleuca*	KF989565	*Gochnatia hypoleuca*	EU384978	*Gochnatia hypoleuca*	KF989674
Guapira graciliflora	*Guapira fragrans*	KJ012616	*Guapira fragrans*	JX844233	*Guapira fragrans*	KJ082334	*NA*	NA
Handroanthus impetiginosus	*Handroanthus albus*	KF981308	*Handroanthus impetiginosus*	JX856460	*Handroanthus albus*	KF981207	*Handroanthus guayacan*	EF105094
Helicteres velutina	*Helicteres baruensis*	JQ589303	*Helicteres guazumifolia*	AF233300	*Helicteres angustifolia*	AY082356	*NA*	NA
Hyptis suaveolens	*Hyptis suaveolens*	JF357872	*Hyptis suaveolens*	KC878602	*Hyptis mutabilis*	KJ773582	*Hyptis suaveolens*	AJ505453
Jatropha mollissima	*Jatropha curcas*	KJ663789	*Jatropha gossypiifolia*	KF551972	*Jatropha curcas*	JX571853	*Jatropha integerrima*	AY794685
Jatropha mutabilis	*Jatropha integerrima*	AB233775	*Jatropha integerrima*	EU340795	*Jatropha integerrima*	AY794902	NA	NA

Jatropha ribifolia	*Jatropha podagrica*	KJ150223	*Jatropha curcas*	EU700455	*Jatropha zeyheri*	JQ025058	NA	NA
Lantana camara	*Lantana camara*	HM853859	*Lantana camara*	AF477784	*Lantana camara*	HM850104	*Lantana camara*	HM216633
Libidibia ferrea	*Libidibia ferrea*	EU361901	*Libidibia coriaria*	KP003691	*Libidibia coriaria*	KJ082382	*Libidibia coriaria*	AY899692
Lippia gracilis	*Lippia javanica*	JX517480	*Lippia alba*	EU761078	*Lippia javanica*	JX572735		
Lippia grata	*Lippia integrifolia*	HM853860	*Lippia salsa*	FJ867399	*Lippia javanica*	JX572735	*Lippia sidoides*	AY945838
Manihot pseudoglaziovii	*Manihot esculenta*	JQ587466	*Manihot esculenta*	GU214953	*Manihot esculenta*	AB233880	*Manihot tristis*	EU518925
Manilkara salzmannii	*Manilkara salzmannii*	JQ413908	*Manilkara salzmannii*	JQ434149	*Manilkara salzmannii*	KM036004	*Manilkara zapota*	DQ924309
Maytenus rigida	*Maytenus oblongata*	FJ514623	*Maytenus rigida*	HQ267190	*Maytenus oblongata*	JQ626259	*Maytenus sp.*	JQ812688
Melochia tomentosa	*Melochia tomentosa*	JQ589306	*NA*	NA	*Melochia tomentosa*	JQ594216	*NA*	NA
Mimosa lewisii	*Mimosa pudica*	AY177668	*Mimosa pudica*	KC952022	*Mimosa pudica*	KJ008941	*Mimosa pudica*	LM643810
Mimosa ophthalmocentra	*Mimosa revoluta*	DQ790607	*Mimosa guatemalensis*	AF458784	*Mimosa strigillosa*	KJ773686	*Mimosa revoluta*	DQ784650
Mimosa tenuiflora	*Mimosa tenuiflora*	JX850057	*Mimosa guatemalensis*	AF458784	*Mimosa strigillosa*	KJ773686	*Mimosa quitensis*	AF278514
Myroxylon peruiferum	*Myroxylon peruiferum*	JX295911	*Myroxylon balsamum*	JF491257	*Myroxylon balsamum*	U74208	*Myroxylon balsamum*	JF491285
Oxandra reticulata	*Oxandra espintana*	DQ018260	*NA*	NA	*Oxandra espintana*	AY319066	*Oxandra espintana*	AY319180
Peltogyne pauciflora	*Peltogyne confertiflora*	EU362021	*Peltogyne pauciflora*	AY955799	*Peltogyne confertiflora*	AF308718	*Peltogyne paniculata*	AY958524
Pilosocereus gounellei	*Pilosocereus rosae*	JX683850	*NA*	NA	*NA*	NA	*Pilosocereus chrysacanthus*	HM041340
Pilosocereus	*Pilosocereus*	JX683847	*NA*	NA	*NA*	NA	*Pilosocereus*	JN035566

pachycladus	*floccosus*						*aureispinus*	
Pilosocereus tuberculatus	*Pilosocereus alensis*	FN997213	*NA*	NA	*NA*	NA	*Pilosocereus chrysacanthus*	HM041340
Piptadenia stipulacea	*Piptadenia flava*	JQ587930	*NA*	NA	*Piptadenia flava*	JQ592113	*Piptadenia moniliformis*	AF278496
Pityrocarpa moniliformis	*Piptadenia flava*	JQ587930	*NA*	NA	*Piptadenia flava*	JQ592113	*Piptadenia flava*	AY574110
Poincianela microphylla	*Caesalpinia coriaria*	JQ587523	*Poincianella pluviosa*	KP003693	*Poincianella mexicana*	JX856662	*Poincianella eriostachys*	EF177389
Poincianella pyramidalis	*Poincianella pyramidalis*	JX850053	*Poincianella gaumeri*	KP003692	*Caesalpinia calycina*	AM234236	*Poincianella caladenia*	EF177383
Psidium brownianum	*Psidium cattleyanum*	AB354959	*Psidium cattleyanum*	KM064916	*Psidium cattleyanum*	HM850290	*NA*	NA
Psidium oligospermum	*Psidium guajava*	AB354958	*Psidium guajava*	AY781099	*Psidium guajava*	GU135250	*NA*	NA
Psidium schenckianum	*Psidium amplexicaule*	KJ012735	*Psidium cinereum*	AM234079	*Psidium amplexicaule*	KJ082521	*NA*	NA
Ruprechtia laxiflora	*Ruprechtia obovata*	HQ693208	*Ruprechtia laxiflora*	AY256535	*Ruprechtia laxiflora*	EF437987	*NA*	NA
Sapium glandulosum	*Sapium glandulosum*	JQ589779	*Sapium sebiferum*	AF537586	*Sapium glandulosum*	AY794841	*Sapium glandulosum*	AY794626
Senegalia bahiensis	*Senegalia mellifera*	KR734988	*Senegalia mellifera*	KR734204	*Senegalia catechu*	KF532043	*NA*	NA
Senegalia polyphylla	*Senegalia tenuifolia*	KJ593761	*Senegalia caffra*	JQ265905	*Senegalia tenuifolia*	KJ594092	*Senegalia berlandieri*	HM020797
Senegalia piauhiensis	*Senegalia tenuifolia*	JQ587888	*Senegalia senegal*	EF638213	*Senegalia tenuifolia*	KJ594092	*NA*	NA
Senegalia sp.	*Senegalia nigrescens*	JX518103	*Senegalia nigrescens*	JQ265858	*Senegalia nigrescens*	JX572216	*NA*	NA
Senna rizzinii	*Senna rizzinii*	AM086615	*Senna gardneri*	FJ009822	*NA*	NA	*Senna gardneri*	FJ009877

Senna spectabilis	*Senna spectabilis*	JQ301876	*Senna obtusifolia*	KR082773	*NA*	NA	*Senna pleurocarpa*	AF367007
Senna splendida	*Senna splendida*	AM086617	*Senna alata*	HQ833041	*NA*	NA	*Senna alata*	AY232769
Senna trachypus	*Senna candolleana*	AY386848	*Senna hirsuta*	KT279733	*NA*	NA	*NA*	NA
Senna velutina	*Senna italica*	JQ024997	*Senna italica*	KT279732	*NA*	NA	*NA*	NA
Sideroxylon obtusifolium	*Sideroxylon obovatum*	KJ012774	*Sideroxylon obtusifolium*	AM408087	*NA*	NA	*NA*	NA
Solanum rhytidoandrum	*Solanum aethiopicum*	KC535801	*Solanum rhytidoandrum*	GU591089	*NA*	NA	*Solanum rhytidoandrum*	GU591039
Spondias tuberosa	*Spondias mombin*	AY594480	*Spondias mombin*	AF445882	*Spondias tuberosa*	KP774626	*Spondias tuberosa*	GU943750
Stillingia trapezoidea	*Stillingia sylvatica*	KJ773185	*Stillingia sylvatica*	JN250101	*Stillingia sylvatica*	AY794843	*Stillingia sylvatica*	AY794631
Strychnos rubiginosa	*Strychnos nux-vomica*	AB636281	*Strychnos rubiginosa*	JF938032	*Strychnos nux-vomica*	JX856772	*Strychnos nux-vomica*	HQ412966
Syagrus coronata	*Syagrus smithii*	HQ265572	*NA*	NA	*Syagrus smithii*	AJ404827	*Syagrus smithii*	AJ241310
Tacinga palmadora	*Tacinga palmadora*	JF786872	*Tacinga palmadora*	JF787028	*Tacinga saxatilis*	JF787308	*Tacinga funalis*	HM041364
Tamarindus indica	*Tamarindus indica*	EU362056	*Tamarindus indica*	KF055236	*Tamarindus indica*	AB378732	*Tamarindus indica*	KF794199
Tournefortia rubriflora	*Tournefortia cuspidata*	KJ594072	*Tournefortia hirsutissima*	HQ286128	*Tournefortia hirsutissima*	KF158146	*Tournefortia hirsutissima*	KC542474
Trischidium molle	*Trischidium molle*	JX295868	*Trischidium molle*	GU220017	*Trischidium molle*	EF466252	*Trischidium molle*	EF527583
Turnera cearensis	*Turnera ulmifolia*	EF135599	*Turnera cearensis*	AY973377	*Turnera ulmifolia*	JX664074	*Turnera ulmifolia*	JQ723405
Varronia globosa	*Varronia linnaei*	JQ587112	*Varronia globosa*	JF332121	*Varronia bullata*	KF158132	*Varronia bullata*	KF158211
Varronia leucocephala	*Varronia guanacastensis*	JQ589896	*Varronia revoluta*	HM443774	*Varronia bullata*	KF158132	*Varronia bullata*	KF158211

Waltheria brachypetala	*Waltheria indica*	JQ589310	*Waltheria indica*	GQ478115	*Waltheria indica*	JQ594226	*Waltheria indica*	KR738059
Xylosma ciliatifolia	*Xylosma congesta*	AB233834	*Xylosma congesta*	DQ521290	*Xylosma congesta*	AB233938	*Xylosma congesta*	JF950896
Zanthoxylum stelligerum	*Zanthoxylum americanum*	EF489101	*Zanthoxylum americanum*	HM851470	*Zanthoxylum americanum*	KT695513	*Zanthoxylum americanum*	EF489249
Ziziphus joazeiro	*Ziziphus rignonii*	KJ012831	*Ziziphus lloydii*	JN900312	*Ziziphus nummularia*	JX856807	*Ziziphus glabrata*	AJ225799

Considerações finais e conclusões

A disponibilidade hídrica é o principal fator determinando a flora da Caatinga. Áreas com maior disponibilidade hídrica possuem maior biomassa e são menos equáveis, além de terem maior diversidade de espécies. Além disso, a disponibilidade hídrica é o principal fator influenciando a diversidade filogenética local e a substituição de espécies e linhagens entre comunidades. Áreas mais úmidas tem maior ocorrência de espécies raras e esse grupo de espécies é o principal responsável pelas diferenças na diversidade e composição de espécies e diversidade filogenética. Em contrapartida, as espécies dominantes de todas as parcelas estudadas pertencem a grupos de espécies filogeneticamente aparentadas que provavelmente compartilham os mesmos atributos funcionais relacionados à eficiência do uso de água. Estas espécies estão agrupadas em duas principais famílias: Euphorbiaceae e Fabaceae.

Os distúrbios humanos por sua vez, também possuem influencia na estruturação das comunidades de lenhosas na paisagem estudada. Distúrbios crônicos relacionados ao acesso de pessoas (distância para fazendas e estradas) são principal fator determinando a estrutura das comunidades. A exploração direta de recursos madeireiros diminui a cobertura vegetal e influencia a composição e a substituição de espécies entre as comunidades por afetar diretamente a ocorrência de espécies raras. Além disso, os distúrbios crônicos (distância para estradas) afetam negativamente a riqueza de espécies quando avaliadas suas interações com a precipitação, demonstrando que áreas mais secas são mais afetadas pela perturbação. No entanto, a perda de espécies em decorrência dos distúrbios antrópicos dentro e entre comunidades não ocorre através de linhagens inteiras indicando que as espécies que compartilham atributos relacionados ao distúrbio não são agrupadas filogeneticamente.

Assim, nossos achados suportam a ideia que as assembleias de plantas lenhosas da Caatinga são sensíveis tanto a variações na precipitação e disponibilidade hídrica quanto aos distúrbios humanos. As assembleias que estão expostas a maior perturbação e menor disponibilidade hídrica são dominadas por espécies adaptadas ao estresse e distúrbio, não sendo um subgrupo aleatório do grupo regional de espécies. Além disso, nossos achados indicam que tanto processos determinísticos quanto estocásticos conduzem a montagem de comunidades em Caatinga, não sendo mutuamente excludentes. A limitação de dispersão e filtros ambientais (disponibilidade hídrica e pressão de corte) atua principalmente na substituição de espécies raras entre as comunidades, enquanto a competição entre espécies congenéricas e confamiliares define quais espécies dominam as comunidades.

Embora os distúrbios antrópicos crônicos apresentem menor influencia sobre a flora quando comparados à disponibilidade hídrica, eles ainda representam uma força importante na manutenção da diversidade em florestas secas. Um entendimento claro das respostas da flora de florestas secas às mudanças nos fatores ambientais é critico para dar suporte a estratégias de conservação. Para isso, é necessário concentrar esforços para alcançar medidas mais diretas e acuradas de distúrbios crônicos e investigar mais profundamente seus efeitos sobre estas biotas. Além disso, é necessário promover projetos que façam introdução de técnicas de manejo aliada ao conhecimento tradicional a fim de empoderar as famílias que vivem nas áreas para que mantenham sua subsistência diminuindo a pressão de exploração sobre áreas naturais.

A perda de espécies raras em áreas mais secas e perturbadas reforça também a ideia de que há uma necessidade urgente de proteger uma porção representativa das diferentes fisionomias existentes na Caatinga, englobando assim, as diferentes comunidades e linhagens que representam cada um destes ambientes. Isso ajudaria a garantir a sobrevivência das espécies e, por consequência, a manutenção da estabilidade ecológica e das funções ecossistêmicas providas por elas. Além de prover segurança contra mudanças ambientais sincrônicas em larga escala como as mudanças climáticas.