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ELÂINE MARIA DOS SANTOS RIBEIRO

EFEITO DE PERTURBAÇÕES ANTRÓPICAS CRÔNICAS SOBRE A DIVERSIDADE DA FLORA LENHOSA DA CAATINGA

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Tese apresentada ao Programa de Pós-Graduação em Biologia Vegetal da Universidade Federal de Pernambuco como um dos requisitos necessários para obtenção do título de Doutor em Biologia Vegetal.

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"EFEITO DE PERTURBAÇÕES ANTRÓPICAS CRÔNICAS SOBRE A DIVERSIDADE DA FLORA LENHOSA DA CAATINGA"

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À minha avó Generina,
Que além do amor, me ensinou a andar no
mato pra pegar vassoura e casca de mutamba.
E sem querer, despertou em mim uma vocação,
a de querer entender a natureza e as
consequências desse nosso uso.

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RESUMO

Este estudo teve como objetivo investigar quais os efeitos de perturbações antrópicas crônicas (*e.g.* coleta de madeira e de produtos florestais não madeireiros, pastoreio extensivo, caça e danos causados à vegetação pela introdução de espécies exóticas que ocorrem em áreas remanescentes de floresta) sobre a diversidade taxonômica e filogenética da flora lenhosa da Caatinga. Inicialmente, investigamos como se dá a questão da perturbação crônica da flora e seus efeitos sobre a biodiversidade através da revisão de 51 artigos que tratam do tema. Verificamos que estes estudos, em sua maioria, foram realizados em países em desenvolvimento, cujas populações humanas utilizam a floresta para subsistência e comércio. Os efeitos da perturbação foram acessados principalmente ao nível de populações e comunidades, sendo a coleta de produtos florestais não madeireiros a fonte de impacto mais analisada. Os efeitos sobre a biodiversidade foram em geral negativos, mas efeitos neutros e positivos também foram registrados. O segundo capítulo traz um estudo de caso que verifica a influência das perturbações humanas crônicas sobre a diversidade e composição taxonômica da flora lenhosa da Caatinga, realizado em várias propriedades privadas na cidade de Parnamirim-PE, Brasil. Neste estudo foram amostradas comunidades lenhosas de adultos, jovens e plântulas, e como preditores da perturbação crônica utilizaram-se a densidade de pessoas e animais domésticos (caprinos e bovinos), além de indicadores de acessibilidade às áreas, como a distância ao centro urbano mais próximo, à estrada mais próxima e à propriedade rural mais próxima às parcelas amostradas. Esses preditores tiveram em geral efeitos negativos sobre a diversidade taxonômica independente do estágio ontogenético, sendo a densidade de pessoas e de animais os preditores mais importantes desses efeitos. Verificou-se ainda que a composição das espécies nas áreas perturbadas foi distinta, sendo pouco representada pela abundância de espécies de madeira densa nas áreas mais perturbadas. O terceiro e último capítulo verificou como as comunidades lenhosas de adultos, jovens e plântulas da Caatinga, amostradas no capítulo anterior, são afetadas pela perturbação crônica do ponto de vista de diversidade e estrutura filogenética. Neste capítulo, utilizaram-se os mesmos preditores da perturbação citados anteriormente, porém agora combinados em um índice de perturbação crônica. A diversidade de famílias esperadas para história evolutiva da região e a distância média entre os indivíduos dessas comunidades, medida em anos, foi reduzida em ambientes mais perturbados e para todos os estágios ontogenéticos. As comunidades de jovens e de plântulas apresentaram maior grau de parentesco em áreas mais perturbadas, sendo os táxons Euphorbiaceae e *Cnidoscolus* responsáveis por esse aumento de parentesco. Os resultados desta tese demonstram que as perturbações antrópicas crônicas na Caatinga não podem ser negligenciadas, pois conferem efeitos negativos importantes à diversidade taxonômica e filogenética da flora lenhosa. Dessa forma, estratégias de manejo que conciliem o uso dessas florestas e a manutenção da biodiversidade da Caatinga são urgentes.

Palavras-chave: diversidade e estrutura taxonômica e filogenética, comunidades vegetais, florestas tropicais secas, coleta de madeira, criação extensiva de animais, produtos florestais não madeireiros.

ABSTRACT

The aim of this study was to investigate the effect of chronic anthropogenic disturbances (e.g. harvesting of timber and non-timber forest products, hunting, livestock, and damage to vegetation caused by exotic species that occur in natural remnant forests) on the taxonomic and phylogenetic diversity of wood flora from Brazilian Caatinga. Initially, 51 scientific papers were revised in order to investigate how chronic anthropogenic disturbances affect the flora of natural ecosystems. Most studies were conducted at developing countries, where human populations use forest resources for subsistence and commerce. Chronic disturbance effects were accessed mainly at population and community levels, and harvesting of non-timber forest products was the disturbance source more frequently analyzed in those papers. Effects of the chronic disturbances were in general negative, however positive and neutral effects were also documented. The second chapter brings a case study that evaluates the influence of chronic disturbances on the taxonomic diversity and composition of Caatinga wood flora from private propreties at the municipality of Parnamirim-PE, Brazil. Adult, sapling and seedling of wood plant communities were sampled, and the density of people and livestock (goats and catle) near the plot were used as predictors of chronic disturbance, as well as the distances to the nearest urban centre, road and rural property. In general, these disturbance predictors showed negative effects on taxonomic diversity irrespective to ontogenetic stage. Moreover, the density of people and livestock near the plot were the main predictors of these negative effects. Species composition differed between plots with low and high level of disturbance, especially in relation to hard wood species, which were rare in the plots highly disturbed. The third and last chapter analyzed how the adult, sapling and seedling communities, surveyed previously, were affected by chronic disturbances from the viewpoint of the phylogenetic diversity and structure. In this chapter the chronic disturbance predictors described above were combined into a chronic disturbance index. The diversity of families expected to the local evolutionary history and the mean phylogenetic distance between the individuals were reduced in plots with higher level of disturbance for all ontogenetic stages. Sapling and seeedling communities had higher degree of relatedness in most disturbed sites, being Euphorbiaceas and *Cinidoscolus* taxa responsible for this increasing in the relatedness degree. Overall, this thesis demonstrates that chronic anthropogenic disturbance at Caatinga could not continue to be neglected, as it imposes deleterious effects to the taxonomic and phylogenetic diversity of wood plant assemblages. Management strategies conciliating forest use and the maintenance of Caatinga biodiversity are urgent.

Key-words: taxonomic and phylogenetic diversity and structure, plant communities, tropical dry forests, timber harvesting, extensive livestock, non-timber forest products.

ÍNDICE

APRESENTAÇÃO

As mudanças no uso da terra decorrentes das atividades humanas tem reduzido drasticamente a cobertura florestal em escala global. Essas mudanças, em geral, ocorrem a partir da transformação aguda dos ecossistemas causada pelo desmatamento, que pode implicar na redução do habitat e na consequente perda direta de espécies. Além das transformações agudas, os fragmentos florestais remanescentes podem ser submetidos a impactos humanos em pequena escala conhecidos como perturbações crônicas, que se caracterizam pela remoção contínua e frequente de biomassa da floresta a partir de diversas atividades (ex. criação extensiva de animais, extração de lenha e outros produtos florestais não madeireiros, caça e danos causados à vegetação pela introdução de espécies exóticas). Como essas perturbações crônicas são contínuas e frequentes, elas são consideradas igualmente deletérias às agudas, ameaçando a manutenção da biodiversidade e dos serviços ecossistêmicos.

Visando contribuir com o conhecimento sobre os efeitos das perturbações crônicas nas florestas tropicais secas, esta tese avaliou como essas perturbações afetam a diversidade taxonômica e filogenética de comunidades de plantas lenhosas da Caatinga em distintos estágios ontogenéticos. A tese consiste em duas partes, a primeira é a fundamentação teórica que aborda os temas montagem de comunidades vegetais e reorganização de comunidades vegetais após perturbação humana. A abordagem desses temas teve por objetivo fundamentar a hipótese diante da questão geral da tese, a saber: Quais os efeitos da perturbação crônica sobre a flora lenhosa da Caatinga? A hipótese de trabalho é que as perturbações crônicas predizem o empobrecimento da diversidade taxonômica e filogenética, uma vez que esses impactos ocorrem de forma gradual e contínua, comprometendo a resiliência da comunidade e permitindo a persistência apenas de espécies tolerantes a esse tipo de distúrbio.

A segunda parte da tese é composta por três capítulos. O primeiro deles é um artigo de revisão que surgiu da necessidade de entender melhor o fenômeno da perturbação crônica relacionada à flora sob o ponto de vista socioeconômico, suas fontes e seus preditores de impacto, bem como as consequências desses impactos sobre a biodiversidade. No segundo capítulo, o objetivo foi entender como as perturbações crônicas afetam componentes da diversidade taxonômica (riqueza, abundância, equitabilidade e composição) das assembleias de plantas lenhosas da Caatinga em diferentes estágios ontogenéticos (adultos, jovens e plântulas). Por fim, o terceiro capítulo analisa como a perturbação crônica afeta a diversidade e estrutura filogenética das assembleias adulta, jovem e de plântulas em áreas de Caatinga.

FUNDAMENTAÇÃO TEÓRICA

Montagem das comunidades vegetais

Um dos mais antigos desafios da ecologia de comunidades é: “elucidar os processos que são responsáveis por padrões de montagem das comunidades” (PAVOINE; BONSSAL, 2011). De fato, esta sentença será ainda muito utilizada, já que dia após dia as comunidades biológicas se rearranjam no espaço e tempo, permitindo a proposição de hipóteses que apoiem ou neguem as teorias já existentes. As primeiras e principais teorias que discursaram sobre conceitos e natureza das comunidades vegetais, propostas por Frederich Clements e Henry Gleason no início do século XX, identificavam os possíveis processos responsáveis pela montagem dessas comunidades (GUREVICH; SCHEINER; FOX, 2009). Para Clements (1916) comunidades eram superorganismos ou unidades discretas, onde fatores abióticos (ex. clima e solo), bióticos (ex. interações como competição, mutualismo e predação) e história local eram importantes para formação das mesmas. Por outro lado, Gleason (1926) defendia que as comunidades vegetais eram determinadas por mudanças graduais, não discretas, mediadas por eventos históricos e eventos ao acaso, e pelas interações entre espécies individuais e o meio ambiente (fatores bióticos e abióticos). Segundo Gleason, as comunidades eram formadas por espécies que possuem tolerância similar a estes fatores, não constituindo um superorganismo como defendido por Clements.

Embora os conceitos de comunidades vegetais entre esses autores divergissem, fica clara a convergência entre os principais fatores responsáveis pela estrutura das comunidades vegetais, o que contribuiu para que, na atualidade, ecólogos, em geral, aderissem a uma posição intermediária entre as ideias desses dois autores. E a esses fatores responsáveis pela inclusão e coexistência das espécies nas comunidades (*i.e.* o arranjo das espécies na comunidade) se deu o nome de regras de montagem (GÖTZENBERGER *et al.*, 2012). Essas regras de montagem podem ser ecológicas quando abrangem filtros ecológicos como a dispersão, o ambiente abiótico e as interações bióticas, e podem ser também filogenéticas quando considera as relações filogenéticas existentes na comunidade (WEBB, 2000).

Uma das propostas sumarizadas lançadas para entender como são as regras montagem ecológicas de comunidades se baseou em dois modelos determinísticos chave que agrupam muitos dos fatores estruturadores descritos acima. O primeiro modelo é chamado de paradigma de ilhas, pois trata dos processos que ocorrem entre continente e ilhas, como a imigração/extinção, dispersão, competição e coexistência (Figura 1, WEIHER; KEDDY 1995, 2004). Neste caso, as comunidades são organizadas pelas interações entre organismos, e a coocorrência das espécies depende da baixa similaridade entre elas (sobredispersão dos atributos). O outro modelo, o paradigma atributos/ambiente, foi baseado no conjunto de atributos das espécies que podem ser modelados pelo ambiente, neste caso o habitat é considerado como um filtro que pode levar a convergência/similaridade de suas características (subdispersão dos atributos) (Figura 1, WEIHER; KEDDY 1995, 2004). A capacidade de determinar a influência desses paradigmas na montagem da comunidade depende ainda da escala (WEIHER *et al.*, 2011). Quando consideramos o paradigma de ilhas, os efeitos deste tipo de modelo serão observados principalmente em escala local, uma vez que a interação entre os organismos pode ocorrer numa escala de centímetros a milímetros (WEIHER; KEDDY 1995; GÖTZENBERGER *et al.*, 2012). Já o paradigma atributos/ambiente, em geral, supõe que a subdispersão dos atributos é geralmente observada quando se consideram maiores ecalas (WEIHER; KEDDY 1995, CHASE 2014; GARZON-LOPEZ et al. 2014).

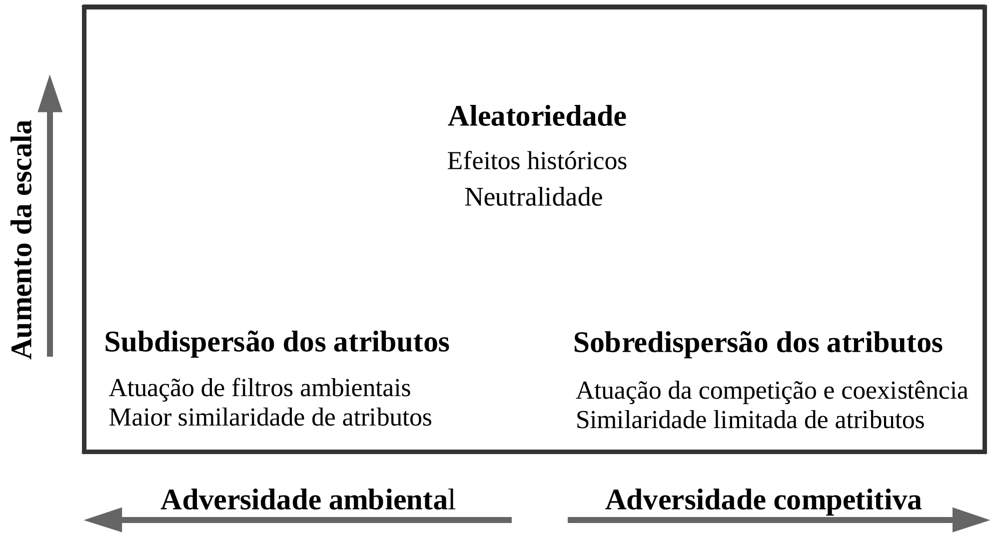

Figura 1. Ilustração adaptada que demonstra como podem ser as regras de montagem de comunidades biológicas (WEIHER; KEDDY, 1995). Segundo os autores, o primeiro passo para entender as regras de montagem é buscar padrões na comunidade. Os modelos baseados no paradigma de ilhas prevêm que com o aumento da adversidade competitiva (à direita) encontram-se padrões relacionados à sobredispersão. Por outro lado, os modelos que se baseiam no paradigma da adversidade ambiental (à esquerda) têm foco na subdispersão dos atributos da comunidade. Entre os dois paradigmas, existe uma zona de aleatoriedade na qual

atuam forças estocásticas históricas na montagem da comunidade. A seta no eixo y representa a escala de estudo, que também pode definir de esses modelos serão ou não encontrados.

Quando os paradigmas determinísticos (ilhas e atributos/ambiente) contribuem pouco para a montagem da comunidade, como resultado, se observa maior influência dos processos estocásticos (neutralidade e efeitos históricos) (WEIHER; KEDDY, 1995). O resultado de comunidades organizadas por processos estocásticos é a ausência de regras biológicas determinando a coocorrência das espécies (WEIHER *et al*., 2011). Quando se considera que a comunidade é organizada por processos estocásticos, assume-se que espécies com diferentes atributos biológicos tem igual probabilidade de imigrar/dispersar e se extinguir (local ou globalmente) caso tenham abundâncias iguais (HUBBELL, 2001). Assim, a probabilidade de uma determinada espécie se manter na comunidade local é proporcional à abundância de seus indivíduos na comunidade local, ou na metacomunidade. Em relação à escala de aplicação desta teoria, alguns autores reportam que ela atua principalmente em pequenas escalas (CHASE 2014; GARZON-LOPEZ *et al*., 2014), embora a teoria neutra incorpore eventos que ocorrem em grandes escalas como a especiação e a deriva ecológica (MAUER; MCGILL 2004). Os efeitos históricos dizem respeito à ordem (tempo) em que as espécies chegam a uma comunidade o que também pode determinar a sua organização (CHASE, 2003). Esse efeito histórico sobre a montagem da comunidade é observado, por exemplo, quando em uma região com as mesmas adversidades competitivas e ambientais, observam-se sítios cujas comunidades locais possuem estrutura e composição distintas, sendo atribuída esta distinção às diferentes ordens de colonização da região pelas espécies (FUKAMI; NAKAJIMA, 2011; CHASE, 2003).

Além dos aspectos ecológicos, as relações filogenéticas entre as espécies da comunidade podem estar relacionadas à estruturação da mesma (WEBB, 2000). A distribuição agregada por táxons aparentados numa comunidade pode representar a existência de atração filogenética, indicando que o tipo de uso do habitat é uma característica conservada dentro do conjunto de espécies da comunidade (WEBB *et al*., 2002). Um exemplo são as comunidades que se desenvolvem em condições ambientais restritivas (*i.e.* secas severas e inundações), e por isso possuem estratégias de sobrevivência exclusivas de alguns táxons aparentados (VELLEND *et al*., 2010). Mais recentemente, algumas evidências têm apontado que a distribuição agregada dos táxons na comunidade pode também ser efeito da competição entre as espécies na comunidade (MAYFIELD; LEVINE, 2010; HILLELISLAMBERS *et al.*, 2012). Essas evidências se apoiam na idéia que, considerando mesmas condições ambientais, a competição pode levar a dominância de uma espécie com desempenho competitivo superior, e, como consequência, pode ocorrer a exclusão dos competidores inferiores e a permanência apenas dos táxons mais aparentados que possuem o desempenho que garante a vantagem competitiva (MAYFIELD; LEVINE, 2010). A competição também pode levar à sobredispersão dos táxons na comunidade, devido à exclusão competitiva de espécies com nichos similares e mesmo desempenho competitivo, ou pode, ainda, ocorrer sobredispersão, quando táxons pouco aparentados convergiram para um uso similar do nicho (WEBB *et al.*, 2002). No caso da sobredispersão dos táxons, ele pode ser resultado da forte competição entre as espécies da comunidade que faz com que os táxons sejam distantes filogeneticamente, ou resultado de convergência adaptativa (VELLEND *et al.*, 2010).

Em síntese, podemos afirmar que a montagem das comunidades biológicas é um processo interativo, tendo o determinismo e a estocasticidade sua parcela de contribuição (TILMAN, 2004) e as relações filogenéticas fazendo parte deste processo (GÖTZENBERGER *et al.*, 2012). Imaginemos que um propágulo chega a um determinado sítio num tempo (t), ele pode ou não germinar e estabelecer-se (neutralidade). Se este propágulo consegue estabelecer-se, reproduzir-se e formar uma população na área, os indivíduos desta população podem influenciar a disponibidade de recursos para outras espécies (adversidade competitiva e sobredispersão). Já se o mesmo propágulo chegar ao sítio no tempo (t) e não encontrar condições ideais de umidade para estabelecimento (alta adversidade ambiental e atração filogenética ou convergência adaptativa), não se estabelecerá e não formará uma população que influencie a disponibilidade de recurso para outras espécies predecessoras. Como se observa, tanto fatores determinísticos quanto os estocásticos atuam na montagem das comunidades biológicas, as relações filogenéticas também fazem parte da estruturação das mesmas e nos dão pistas sobre a montagem ecológica das comunidades.

Paisagens modificadas pelo homem e a reorganização das comunidades vegetais

Como as atividades humanas têm provocado enormes mudanças em todos os ecossistemas, acessar as consequências da perturbação gerada por estas atividades sobre a estruturação da comunidade é uma questão indispensável e desafiadora (CHAZDON, 2008; SUNDING *et al.*, 2008). Ecossistemas que são modelados pelas atividades humanas geralmente têm em comum características como homogeineização da paisagem e alta entrada de nutrientes e energia e cadeias alimentares simplificadas (WESTERN, 2001; ALMEIDA; WIRTH; LEAL, 2008; LÔBO *et al.*, 2011). O desmatamento é uma das principais atividades antrópicas agudas que comprometem os ecossistemas terrestres, sendo reportadas taxas da ordem de 64.000 km²/ano, por exemplo, para as florestas tropicais (WRIGHT, 2010). Quando um bloco florestal contínuo é deflorestado o que resta são pequenos fragmentos imersos em matrizes agrícolas e urbanas (RIBEIRO *et al.*, 2009). Esses fragmentos, por sua vez, resguardam apenas uma pequena parcela do habitat original, sendo agora um conjunto de manchas de floresta pequenas e isoladas (FAHRIG 2003). Como consequência da fragmentação, comunidades remanescentes das bordas florestais enfrentam novos regimes microclimáticos e efeitos bióticos diretos e indiretos (MURCIA, 1995). A regeneração natural das áreas deflorestadas próximo ao fragmento pode ocorrer, mas geralmente essas áreas são utilizadas para agricultura e criação de animais (RIBEIRO *et al.*, 2009; Santos *et al.*, 2010), o que impede o avanço natural da regeneração.

Além dos efeitos decorrentes da fragmentação, as áreas remanecentes de floresta nativa podem sofrer distúrbios antrópicos crônicos que não alteram drasticamente a estrutura dos mesmos, no entanto há a remoção contínua e gradual de pequenas quantidades de biomassa que pode empobrecer e simplificar ainda mais essas áreas fragmentadas (SINGH, 1998). A perturbação do tipo crônica pode ser exemplificada por atividades como a extração seletiva de madeira, criação extensiva de rebanhos na floresta, coleta de produtos não madeireiros (*e.g.* sementes, raízes, folhagem, cascas etc.) e caça, que aos poucos, transformam uma região natural em um mosaico de áreas com diferentes graus de perturbação (SINGH, 1998; MARTORELL; PETERS, 2005).

A redução na riqueza de espécies é em geral a principal consequência descrita da ação antrópica intensa (desmatamento, fragmentação, fertilização etc) nos ecossistemas (SILVA; TABARELLI, 2000; MORRIS, 2010; GERSTNER *et al.*, 2014). No entanto, a riqueza por si só pouco informa como a comunidade está se estruturando após a perturbação. Em geral, as consequências da perturbação humana são bem mais amplas afetando também funcionamento dos ecossistemas e história evolutiva das comunidades biológicas (MORIS, 2010; SANTOS *et al.*, 2010), e acessar essas consequências requer a abordagem de distintos níveis de diversidade (PAVOINE; BONSALL 2010). O processo de extinção das espécies é direcionado e não aleatório, e, em geral, as espécies vegetais vulneráveis possuem um conjunto de atributos (epífitas e árvores, distribuição restrita, pequena densidade local, sem banco de sementes, grande biomassa etc) (MCKINNEY; LOCKWOOD, 1999; FRÉVILLE *et al*., 2007; LEÃO *et al*., 2014). Se abordarmos do ponto de vista das características/atributos que conferem a vulnerabilidade ou aptidão de espécies em coexistir num determinado ambiente, estamos tratando da questão funcional que pode ser representada pela diversidade, frequência e divergência de atributos na comunidade (PLA *et al*., 2012).

Medidas de diversidade funcional vêm sendo amplamente aprimoradas e utilizadas para entender qual o papel de gradientes naturais e artificiais na organização funcional de comunidades (ver DÍAZ *et al*., 2007; MOUCHET *et al*., 2010; VILLÉGER *et al*., 2010; VIOLLE *et al*., 2011). Estudos baseados em estágios sucessionais, por exemplo, mostraram que espécies de uma mesma sere geralmente apresentam um conjunto de atributos relacionados ao ambiente em que ocorrem (e.g. sucessão inicial: espécies fixadoras de N, de folhas compostas com pequenos folíolos) (LEBRIJA-TREJOS *et al*., 2010). Comunidades abandonadas por uma década, após regime intenso de silvicultura, apresentam menor contribuição de espécies com madeira densa, maior contribuição de espécies que investem menos nitrogênio e massa por unidade de área da folha, resultando em incremento da produtividade primária e ciclagem de nutrientes em curto prazo, o que é típico de espécies de crescimento rápido (CARREÑO-ROCABADO *et al*., 2012). E sob diferentes fontes de perturbação em áreas fragmentadas, é observada menor frequência de atributos funcionais como: espécies tolerantes à sombra (OLIVEIRA *et al*., 2004, SANTOS *et al*., 2008), do estrato emergente (OLIVEIRA *et al*., 2004), polinizadas por vertebrados (GIRÃO *et al*., 2007); com sementes grandes e dispersas por vertebrados (MELO *et al*., 2006, SANTOS *et al*., 2008).

Como se pode observar, os achados citados que tratam da influencia da perturbação antrópica sobre a diversidade funcional tem mostrado que as comunidades se reorganizam mantendo maior contribuição de atributos relacionados à tolerância às novas condições ambientais criadas, bem como a estratégias que requerem pouco investimento estrutural e reprodutivo. Neste sentido, as perturbações humanas parecem atuar na montagem da comunidade como um filtro ambiental, fazendo com que apenas alguns grupos coexistam, ou neste caso se encaixa ainda a hipótese que trata do desempenho competitivo superior que pode manter espécies aparentadas que possuem vantagens competitivas superiores (MAYFIELD; LEVINE 2010; HILLELISLAMBERS *et al*., 2014).

Além da abordagem funcional, o entendimento da estruturação da comunidade após perturbação pode ser obtido a partir da estrutura filogenética das mesmas (WEBB *et al.*, 2002; SANTOS *et al.*, 2010). A análise da estrutura filogenética de uma comunidade também nos fornece pistas sobre os processos ecológicos que estão organizando comunidade, tais como os filtros ambientais e competição (WEBB, 2000; WEBB *et al.*, 2002). Se os atributos relacionados à vulnerabilidade à perturbação antrópica são exclusivos em algumas linhagens (conservatismo filogenético dos atributos segundo CAVENDER-BARES *et al.* 2004), a extinção de um clado com esses atributos pode resultar em agrupamento filogenético (DING *et al.*, 2012). Por outro lado, se os atributos relacionados à extinção são presentes em distintas linhagens da comunidade, não são esperadas mudanças significativas na estrutura e diversidade funcional/filogenética de comunidades que sofreram perturbação (ARROYO-RODRÍGUEZ *et al.* 2012). Assim, as mudanças observadas na estrutura funcional e filogenética da comunidade devido à perturbação humana vão depender das características originais da comunidade que pode ter os atributos agrupados ou dispersos filogeneticamente.

Recentemente, Zhang *et al.* (2014) analisando estudos publicados que avaliavam as relações entre a perturbação e o agrupamento/dispersão filogenética em comunidades biológicas (árvores, arbustos, lianas, ervas e aves) naturais e urbanas, concluíram que não é claro o efeito da perturbação humana sobre a estrutura filogenética. Foram levantados por Zhang *et al.* (2014) onze estudos que contemplam a flora de ecossistemas naturais (árvores, arbustos, lianas e ervas), 5 verificaram que a perturbação tornou as comunidades originais mais agrupadas filogeneticamente do que o esperado ao acaso, enquanto que 6 estudos restantes verificaram que a perturbação diminuiu a dispersão filogenética, ou houve pouca ou nenhuma mudança na estrutura filogenética. A ausência de um efeito padrão da perturbação humana sobre a estrutura filogenética é justificado pela influência de fatores como o tipo de distúrbio, forma de vida e a distribuição original dos atributos nos clados antes da perturbação (HILLERISLAMBERS *et al.*, 2012; SWENSON 2013; ZHANG *et al.*, 2014).

Para ilustrar como esses fatores afetam a estrutura filogenética de comunidades de árvores e arbustos lenhosos, que são objeto de estudo desta tese, foram reunidos os estudos que tratam exclusivamente dessas formas de vida em ecossistemas naturais (Tabela 1). Para o fator distribuição original dos atributos, não foi possível obter informações exatas para comparação nos estudos analisados. Em relação aos tipos de perturbação, os estudos listados tratam principalmente de áreas que sofreram perturbações agudas como queimadas e desmatamento, que, após o uso para agricultura, pasto ou simples abandono após o distúrbio, iniciaram a regeneração naturalmente (Tabela 1). Os estudos foram realizados principalmente em florestas tropicais, com dois casos em floresta temperada. Dentre os estudos em floresta tropical, apenas um deles avaliou as florestas tropicais secas. Em relação ao efeito da perturbação na estrutura filogenética de árvores e plantas lenhosas, este foi difuso. Dos 13 estudos que contemplam árvores e arbustos lenhosos, quatro deles encontraram maior agrupamento, em outros quatro, o padrão foi disperso, no entanto, em menor grau quando comparado às áreas não perturbadas. Os cinco estudos restantes verificaram pouco ou nenhum efeito da perturbação (Tabela 1).

Tabela 1. Relação de estudos que verificaram a influência de perturbações antrópicas sobre a estrutura filogenética de comunidades de árvores e de arbustos lenhosos.

Tipo de perturbação	Ecossistema/Habitat	Estrutura filogenética após a perturbação	Fonte
-Alta e baixa ocorrência de fogo	Floresta Tropical/Mediterâneo	Agrupada e dispersa nas áreas com mais e menos fogo, respectivamente.	Verdú; Pausas 2007
-Queima seguida de regeneração natural	Floresta Tropical/Mediterâneo	Nos estágios iniciais aleatória. Nos estágios intermediários dispersão. Nos estágios tardios aleatória.	Verdu et al., 2009
-Fragmentação (bordas, pequenos fragmentos <80ha e fragmentos em regeneração)	Floresta Tropical/Floresta Atlântica Nordestina	Redução de 11% distância média filogenética em comunidades nas bordas de pequenos fragmentos. Não houve evidência de dispersão ou agrupamento.	Santos et al.; 2010
-Áreas que passaram por agricultura e estão em regeneração natural	Floresta Tropical/Floresta úmida de terras baixas	Padrão disperso, e com o avanço da sucessão observou-se que a comunidade tende a aumentar o grau de dispersão.	Letcher 2010
-Florestas maduras com exploração de madeira <40 anos - Florestas secundárias após abandono (30 a 55 anos) de agricultura intinerante	Floresta Tropical/ Florestas tropicais de terras baixa e montana	Agrupada nas áreas mais perturbadas, aumento da dispersão nas áreas menos perturbadas, sendo o maior grau de dispersão nas florestas maduras.	Ding et al., 2011
-Desmatamento da paisagem (cobertura vegetal reduzida de 96% a 76%)	Floresta Tropical/ Floresta tropical úmida	Não verificou mudança na estrutura filogenética devido ao grau de deflorestamento.	Arroyo-Rodríguez et al., 2012
-Áreas em regeneração natural após abandono (2.5 a 45 anos) de atividades de agicultura ou pasto	Floresta Tropical/Florestas úmidas do México, Brasil e Costa Rica	Padrão disperso, principalmente para os indivíduos mais jovens da comunidade. Com o avanço da regeneração o grau de dispersão aumenta.	Letcher et al., 2012
-Áreas em regeneração natural (5 a 45 anos) após	FlorestaTropical/	Aumento da dispersão com o avanço da sucessão. As espécies pioneiras	Norden et al.,

abandono da atividade de pastagem	Floresta Atlântica Nordestina	estão agrupadas em clados aparentados. As espécies especialistas de floresta madura apresentaram menor parentesco. Houve aumento da dispersão com o avanço da sucessão.	2012
-Áreas em regeneração após (10 a 55 anos) de agricultura de subsistência	Floresta Tropical/Floresta úmida de terras baixas	Agrupada nas áreas em regeneração e dispersa nas áreas controle (florestas maduras).	Whitfield et al., 2012
Queima frequente durante 40 anos	Floresta Temperada/Floresta de carvalhos	Agrupada e com ocorrência de espécies aparentadas nas áreas queimadas com maior frequência.	Cavender-Bares; Reich 2012
-Regeneração natural (20 a 120 anos) após abandono -Perturbação temporária (coleta de madeira, linhas de corte para realização de obras) -Perturbação perpétua (áreas urbanizadas, pastos, campos de agricultura e com superfícies pavimentadas)	Floresta Temperada/Floresta Boreal	Não foram encontradas mudanças na estrutura filogenética relacionadas ao grau de perturbação.	Zhang et al., 2014
- Florestas em regeneração após (20 a 50 anos) da ocorrência de corte raso	Floresta Subtropical/ Floresta perene latifoliada	Com o avanço da sucessão diminuiu o agrupamento, considerando-se somente as angiospermas. Considerando angiospermas e giminospermas, verificou-se dispersão nas áreas perturbadas. Quando considerou somente as angiospermas verificou diminuição da dispersão com aumento da perturbação.	Feng et al., 2014
- Bordas de fragmentos com as seguintes matrizes: pasto com gado, pasto sem gado e vegetação perturbada com gado.	Floresta Tropical/Floresta seca	Não verificou influência dos tipos de matrizes sobre a estrutura filogenética da comunidade arbórea, em todos os tratamentos a estrutura filogenética foi aleatória.	Benítez-Malvido et al 2014.

Como se observa, entender como as comunidades vegetais estão se reestruturando após a perturbação humana, envolve a abordagem de distintos níveis de diversidade (taxonômicos, funcionais, filogenéticos etc.), diferente tipos de distúrbio, diferentes tipos de ecossistema e dos não mencionados anteriormente, mas também importantes, contextos econômico e sócio cultural. Do ponto de vista da influência das perturbações antrópicas sobre a diversidade taxonômica e filogenética de árvores e arbustos lenhosos, que são o foco desta tese, os efeitos negativos sobre a diversidade taxonômica devido a perturbações intensas parece ser um consenso. Por outro lado, a redução na diversidade filogenética devido a perturbações intensas não ocorre sempre, pois depende de fatores como a distribuição original dos atributos na comunidade, do tipo de habitat, da escala espacial avaliada, da quantidade e qualidade dos dados (HILLERISLAMBERS *et al*., 2012; SWENSON 2013; ZHANG *et al*., 2014). Pouca atenção tem sido dada às consequências da perturbação crônica sobre a estrutura filogenética das comunidades, ainda que já se tenha registrado efeitos deletérios à estrutura e diversidade taxonômica (SAGAR *et al*., 2003; MAREN *et al*.,2013). Dos estudos listados na Tabela 1, apenas dois deles trataram dessas perturbações e não encontraram influência sobre a estrutura filogenética da comunidade. Diante das exposições, esta tese se dedicou especificamente a entender como as perturbações caracterizadas como crônicas tem reorganizado a diversidade taxonômica e filogenética da flora lenhosa da Caatinga, uma floresta tropical seca ainda não investigada sob essa perspectiva.

Perturbações antrópicas e a flora da Caatinga

A Caatinga é um mosaico de florestas tropicais sazonalmente secas e arbusto esclerofíticos espinhentos que compreende um polígono de 826,411 km² do nordeste brasileiro (11% do território nacional) (VELOSO *et al*., 2002;). A distribuição da Caatinga é sobreposta à região de clima tropical semi-arido, que é caracterizado pela baixa precipitação (250-1000 mm; concentrada em 3-5 meses) e temperaturas médias entre 23° e 27° (REDDY, 1983; SAMPAIO, 1995). Esta severidade climática é considerada como a principal força que controla os padrões de crescimento e reprodução dos organismos, tornando as florestas tropicais secas ecossistemas naturalmente resilientes a esses pulsos climáticos (MURPHY; LUGO, 1986). A vegetação da Caatinga é predominantemente decídua, poucas espécies mantém suas folhas na estação seca (*e.g. Cynophalla hastata* (Jacq.) J. Presl, *Erythroxylum pungens* O.E. Schulz e *Ziziphus joazeiro* Mart.) (ANDRADE-LIMA 1981). A produção de flores e folhas ocorre geralmente no fim da estação seca ou durante a estação chuvosa, e existem ainda algumas poucas espécies produzem flores na durante estação seca (LIMA *et al*., 2012). As espécies vegetais da Caatinga geralmente possuem adaptações ao clima semiárido que incluem suculencia (*e.g.*família Cactaceae e gênero *Euphorbia*), ceras epicuticulares e tricomas (*e.g.* gêneros *Aspidosperma* e *Croton*), e o armazenamento de água nas raízes ou no caule (*e.g. Spondias tuberosa* Arruda *e Ceiba glaziovii* (Kuntze) K. Schum.), (ANDRADE-LIMA 1981; OLIVEIRA *et al*., 2003; BARROS; SOARES 2013). Embora a Caatinga seja descrita historicamente como um ecossistema pobre em espécies e endemismos, a diversidade de plantas vasculares chega a 932 espécies sendo cerca de 34% delas endêmicas (GIULIETTI *et al*., 2004; LEAL *et al* 2005).

Apesar da severidade climática, a região semi-árida do nordeste do Brasil é uma das regiões áridas mais populosas do mundo com 26 habitantes/km² (INSA 2012). E o desmatamento para implantação de diversas atividades humanas fez com que atualmente exista 45,6% da vegetação original representada por florestas primárias ou secundárias que provavelmente enfrentam perturbações agudas e crônicas (MMA; IBAMA 2011). Da mesma forma que outras florestas tropicais secas, a Caatinga foi historicamente utilizada para instalação de campos de agricultura e pastagem, estabelecidos primeiro nos locais mais úmidos, enquanto as áreas mais secas foram utilizadas para a agricultura itinerante (SAMPAIO 2010). Na atualidade, o sistema agropastoril ainda considerado como a fonte principal de perturbações nos remanescentes de Caatinga (MMA; IBAMA, 2011). Os rebanhos comumente pastam em áreas de vegetação natural e consomem plântulas, ramos frescos e secos de espécies do estrato herbáceo, arbustivo e arbóreo (LEAL *et al*., 2003;. SAMPAIO 2010). A demanda energética é outro fator de perturbação na Caatinga, que começou com a ocupação humana do Nordeste do Brasil (RIEGELHAUPT; PAREYN 2010). Inicialmente, a lenha foi um subproduto da agricultura itinerante, mas, posteriormente, tornou-se a principal fonte energética para os setores domiciliar, industrial e comercial (RIEGELHAUPT; PAREYN 2010). Por conseguinte, esta grande demanda de lenha está sendo responsável, ainda, pela devastação de grandes áreas remanescentes, como podemos observar na região do polo gesseiro do Araripe que tem menos de 40% de sua cobertura vegetal nativa (PERNAMBUCO 2007). Além desses distúrbios relacionados ao uso agropastoril e da lenha como matriz energética, a Caatinga vem sofrendo recentemente transformações agudas causadas por grandes obras como a transposição do Rio São Francisco e Ferrovia Transnordestina. Essas grandes obras suprimiram grandes áreas de Caatinga e também facilitaram o acesso a outras áreas que ainda apresentam alta diversidade biológica.

Algumas consequências das perturbações humanas agudas (*e.g.* corte seguido de queima, regeneração após abandono da atividade agropastoril) sobre as comunidades de plantas de Caatinga já estão sendo acessadas (*e.g.* SAMPAIO *et al*., 1998, PEREIRA *et al*., 2001; ALVES *et al*., 2010). Em geral, após a perturbação aguda, as florestas secundárias (c.a. 35 anos de regeneração) possuem altura e área basal dos indivíduos reduzida, menor abundância de indivíduos, menor riqueza e diversidade de espécies, e apresentam apenas um subconjunto de espécies que são encontradas nas áreas mais conservadas (SAMPAIO *et al*., 1998, PEREIRA *et al*., 2001; ALVES *et al*., 2010). Apenas um estudo testou experimentalmente efeitos agricultura de corte e queima sobre a regeneração da vegetação de Caatinga (SAMPAIO *et al*., 1998). Sampaio *et al*., (1998) verificaram experimentalmente que dois meses após corte de árvores e arbustos, 94% dos indivíduos rebrotam. Por outro lado, em regime de corte e queima, a rebrota representou a regeneração de apenas 10% dos indivíduos (SAMPAIO *et al*., 1998). Após dois anos, os autores observaram que os dois tratamentos, corte e corte segudo de queima, apresentaram densidade de indivíduos semelhante, mas no tratamento de corte e queima houve maior contribuição do recrutamento de novas plantas, enquanto no corte houve maior contribuição da rebrota dos ramos. Além disso, os autores demonstraram que, nessas áreas em que ocorreu corte e queima da vegetação, o retorno à biomassa e à estrutura da vegetação original, pode se prolongar por mais de seis anos (SAMPAIO *et al*.,1998). Nesse mesmo estudo, *Croton sonderianus* Müll.Arg. manteve suas populações com abundâncias similares antes e depois do regime de corte e queima, enquanto as juremas (*Mimosa* spp.) tornaram-se dominantes após o distúrbio, apresentando os maiores valores de abundância, biomassa e área basal. No entanto, os autores ressaltam que a regeneração deve ser mais lenta porque na prática da agricultura, os ramos que rebrotam são parcialmente ou totalmente eliminados.

É comum que as áreas de Caatinga destinadas à agricultura e pastagem passem, primeiro, pelo corte e queima da vegetação (SAMPAIO *et al*., 1998). Nesse processo, algumas espécies são poupadas, como, por exemplo, aquelas com valor medicinal (e.g. *Ziziphus joazeiro* e *Sideroxylon obtusifolium* Humb. ex Roem. & Schult.), nutricional (*e.g. Spondias tuberosa* e *Cereus jamacaru* DC.) ou protegidas por lei (*e.g. Myracrodruon urundeuva* Allemão e *Schinopsis brasiliensis* Engl.), as quais são mantidas em campos de cultivo e pasto. Quando essas áreas estão em sucessão secundária (cerca de 35 anos após a sua utilização na agricultura com pastejo) espécies como *Croton sonderianus* mantem suas abundâncias nos diferentes estágios de sucessão (PEREIRA *et al.*, 2001;. ALVES *et al.*, 2010). Além desta espécie, outras menos abundantes em locais conservados como *Mimosa tenuiflora* (Willd.) Poir. aumentam suas populações no início de sucessão, devido a sua capacidade de rebrota e resistência ao fogo (SAMPAIO *et al.*, 1993; PEREIRA *et al.*, 2003). Nesses estágios sucessionais, a representatividade de outras espécies é muito baixa, sendo encontrados indivíduos jovens de poucas espécies (PEREIRA *et al.*, 2003). Após os 35 anos desde o abandono, não são encontrados estudos que descrevam a regeneração da Caatinga, e, portanto, não se sabe que espécies são capazes de se estabelecer nesta etapa da regeneração.

Até agora, abordamos os distúrbios agudos, no entanto, a pastagem extensiva, exploração seletiva de madeira e caça são comuns em áreas de Caatinga e são tipos de atividades humanas que levam a perturbações crônicas. Além dos filtros criados por distúrbios agudos acima descritos, as perturbações crônicas devem agir atrasando a regeneração natural nessas áreas. Estes distúrbios crônicos ocorrem também em locais preservados e as análises de suas conseqüências são recentes, especialmente na Caatinga. No entanto, eles merecem uma atenção especial uma vez que as comunidades humanas da Caatinga utilizam os recursos florestais de múltiplas maneiras e desta forma crônica (PAUPITZ 2010). Alguns estudos preliminares já apontam que distúrbios crônicos podem reduzir a riqueza de espécies arbustivas e arbóreas da Caatinga (RIBEIRO-NETO 2013). No entanto, a maioria dos estudos que tratam da dependência humana dos produtos florestais na Caatinga tem focado especificamente na identificação de espécies, ativos farmabotânicos, potencial alimentício etc (ALBUQUERQUE *et al*., 2012), sem abordar as consequências sobre a diversidade e quais as práticas de manejo que podem conciliar o uso e manutenção da biodiversidade. Nesta tese, buscamos preencher algumas lacunas do conhecimento relacionado às consequências da perturbação crônica sobre a biodiversidade da Caatinga, tratando especificamente dos efeitos dessas perturbações sobre a flora lenhosa em distintos estágios ontogenéticos (adultos, jovens e plântulas).

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CAPÍTULO 1

Chronic antropogenic disturbances on natural plant communities: a review of causes and consequences

MANUSCRITO A SER SUBMETIDO AO PERIÓDICO

TRENDS IN ECOLOGY & EVOLUTION

Review – Trends in Ecology & Evolution

CHRONIC ANTROPOGENIC DISTURBANCES ON NATURAL PLANT COMMUNITIES: A REVIEW OF CAUSES AND CONSEQUENCES

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ABSTRACT

Chronic anthropogenic disturbances (CAD) refer to small but frequent disturbances which remove forest biomass in small quantities leaving the false notion that the forest is intact. Although CAD is considered a principal cause of degradation in developing countries it has received less attention as compared to acute disturbances as habitat loss and fragmentation. In order to provide an overview of CAD effects to biodiversity, in this essay we analyzed CAD socioeconomic scenarios, sources and predictors through the review of studies published in scientific journals from 1960 to 2014. We found 51 published studies which confirmed that CAD occurs predominantly in developing countries from Asia/Oceania, Africa and Central/Latin America. These countries were located mainly at tropical region with humid and semi arid climate, and forest use was destined to subsistence and commerce. The principal source of CAD investigated in the studies was the harvesting of non-timber forest products (NTFP), but the frequency of combined impact sources as NTFP, timber harvesting and livestock also occurred. CAD effects were most accessed in population and community levels and was used a large number of CAD predictors from direct metrics to indirect proxies. CAD effects on biodiversity were mainly negative for all diversity levels accessed, but neutral and positive effects were also registered. These neutral and positive effects were attributed to species traits as clonal regeneration and fast growing, besides the sustainable harvest management. Important steps were done in order to understand the effects of CAD on biodiversity, however conciliate forest human use and biodiversity requires more efforts to access its effects from genes to ecosystems. Additionally, the maintenance and use of these chronic disturbed forests will depend on the application of sustainable harvest rates and other alternatives as *ex situ* conservation strategies that increase forest products availability.

INTRODUCTION

Natural ecosystems can experience physical and biological natural disturbances which are key factors on community dynamics, increasing the spatial heterogeneity and shaping the evolution of life histories (Sousa 1984, Seidl et al. 2011). Natural disturbances such as treefall gaps, hurricanes, erosion and floods are conceptualized as events that cause changes on ecological properties of populations, communities and the entire ecosystem (Creed 2006). Distinct from the natural disturbances, human disturbances caused by diverse land use changes are recognized as the main driver of the current global crisis of biodiversity (Morris 2010; Laurance et al. 2014).

The comprehension of human disturbance effects on biodiversity involves an analysis of the disturbance regime, i.e. the combination of type, intensity and frequency of disturbance (Gerstner et al., 2014). Analogous to diseases in medicine, human disturbances in ecology can be classified into acute or chronic (Figure 1). Acute anthropogenic disturbances can be defined as drastic, sudden transformations with large biomass loss that preclude forest regeneration or lead regenerating forest stands to initial secondary succession stages (Singh 1998). Examples of acute disturbances are deforestation for agriculture, mining or other activities that require complete forest removal. The use of fire, common in slash-and-burn agricultural practices, increases the intensity of this type of acute disturbance. In 1998, Singh also launched the term chronic anthropogenic disturbance (CAD) to refer to a kind of disturbance less noticeable, but characterized by frequent transformations that imply in lower biomass losses generally as firewood, or in the form of fodder, leaf litter and other non-timber forest products. Because of their low intensity, CAD does not suddenly change the forest cover and geographic boundaries of the site, leaving the false notion that the ecosystem is being unaffected (Álvarez-Yépiz et al. 2008, Martorell & Peters 2009).

The number of studies that accessed the effects of human disturbance is vast, but a large proportion of it deals with acute (as opposed to chronic) forms of disturbance (Martorell and Peters 2005). However, the actual biodiversity crisis and human population growth projections points a major necessity of a widespread view of these CAD ecological implications on remnant forests (Laurance et al., 2012; 2014), in order to conciliate their relict biodiversity and the multiple forest uses. In this review we analyzed socioeconomic scenarios, sources, predictors and effects on biodiversity of chronic disturbances related to plant assemblages through the review of studies published in scientific journals from 1960 to 2014.

To accomplish our proposal, we analyzed three main questions: (i) in which continent, climatic zone, type of forest use, and human development level these studies are most frequent? (ii) what are the sources and predictors of CAD evaluated in the studies? (iii) what are the main CAD effects on biodiversity?

METHODS

Initially, we performed a literature search of scientific published articles in the database Thomson Reuters' Web of Science for all databases available (http:// webofknowledge.com/; accessed 15 Nov 2014). We limited the search for the period of 1960 to 2014 and used the keywords: chronic anthropogenic disturbance*forest impacts, non-timber forest products*impacts, forest subsistence*impacts, and firewood collection*impacts. Latter, we analyzed all articles' abstracts in order to evaluate if they really address to the chronic disturbance concept (i.e. subtle but permanent removal of small fractions of forest biomass *sensu* Singh 1998), if the disturbance was related to vegetal biomass removal (*e.g.* non-timber and timber forest products) and measured some ecological effect of CAD to biodiversity. After this step, we conducted systematic analyses of the papers in order to identify the following variables socioeconomical aspects, CAD sources and predictors, ecological level assessed, and effects on biodiversity according the ecological level (Table 1). After analyze the selected variables in each paper, we calculated the number and percentages of studies (N, %) by category.

RESULTS AND DISCUSSION

General and socioeconomic aspects

The literature search provided 635 scientific papers whose abstracts were analyzed. From these studies we selected 51 that approach chronic anthropogenic disturbance concept related to vegetal biomass removal, and also some implication on biodiversity. The first important result of this review is that the volume of publications is growing from 1996 to 2014 (Fig. 2). Second, most studies were done at developing countries from Asia/Oceania (N= 19; 37.2%), Africa (N= 14; 27.5%) and Central/South America (N= 12; 23.5%) continents. We also registered six studies from North America (11.8%) and there was no record from Europe. Most studies were developed in tropical areas (N= 44; 86.3%), and just (N= 7; 13,7%) in temperate. Whitin these tropical areas, the studies were developed mainly at wet (rainy) and humid regions, followed by semi-arid (Fig 3). These results are in concordance with estimations that points Asia/Oceania, Africa and Central/South America as regions with high forest dependence (Forest Peoples Programme 2012), and in which regions humid and dry climates are predominant (Kottek et al. 2006).

The use of forest products for subsistence was predominant in the analyzed studies (N= 26; 51%), but the commercialization of forest products in small markets (N= 8; 15.7%), and the commercial use associated to subsistence (N= 17; 33.3%) were also verified. Both subsistence and commercial forest uses are pointed as menaces to numerous wild species (Huai et al. 2013; Rakotoarinivo et al. 2014). If we compare the impact of subsistence and commercial use, it is probably that commercial use imply in more intense and frequent disturbance regimes to supply the demand, and consequently may bring more impacts on biodiversity. The human development index of the countries was distributed in the five categories: very high (N=1; 1.9%), high (N= 18; 35.3%), medium (N= 17; 33.4%) and low (N= 15; 29.4%). As we can observe the major part of the studies were realized at developing countries reinforcing the notion of their dependence on forest resources (Singh 1998; FAO 2012).

CAD sources and predictors

The main source of chronic anthropogenic disturbance analyzed was related to the harvesting of non-timber forest products (Fig. 4, Table S1). However papers also surveyed forest sites that experienced cumulative disturbances as the harvesting of timber plus non-timber forest products plus livestock (Fig. 4). The existence of more than one impact source is a characteristic of chronic disturbed habitats, which turn in to a complex mosaic of differently disturbed patches (Singh 1998; Martorell & Peters 2005).

We found in the examined papers a large number of measures and proxies used as predictors of chronic anthropogenic disturbance (Table S1).Chronic anthropogenic disturbance effects were evaluated using the predictors as single variables and predictors combined in disturbance indexes (see; Murali et al 1996; Shankar et al. 1998; Sagar et al. 2003; Martorell & Peters 2005). When used as single predictors were common categorical predictors as harvested/unhanrvested sites, harvesting intensity, harvesting techniques land cover type/use etc (Table S1). Continuous variables were also used as single CAD predictors as the distance from the settlement, number of trails, number of stumps in the plot, livestock density etc (Table S1). These single variables were also used combined in chronic disturbance indexes obtained through the simple sum of their relative impact per site (Sagrar et al. 2003; Leal et al .2014), or by multivariate analyses as principal component analyses (Martorell & Peters 2005; 2009).

CAD effects on biodiversity

The major part of studies examined the effects of CAD at population (N=23; 45%) and community level (N=18; 35.3%), followed by individual level (N=7; 13.7%) and studies that analyzed a combination of both individual and population parameters (N=3; 6%). We did not found studies that related CAD effects on ecosystem level, emphasizing the need of studies on multiple ecological levels (Ticktin 2004). In relation of the effects of CAD predictors on biodiversity, we observed that the negative effects were predominant considering all ecological levels, however we also verified neutral and positive effects related to CAD (Fig. 5).Considering the individual level, CAD negative effects were related at the reduction of individuals' reproductive success (e.g. fruit and seed sets, Sinha & Bawa 2001; Van Lent et al 2014), patterns and rates of individuals' growth and reproduction (Gaoue & Ticktin 2007; Jimenez-Valdes et al. 2010), increase in the number scatter-hoarded seeds per parental individual (Lermyte & Forget 2009), and increase of nutrient and leaf mass per area in leaves of harvested individuals (Gaoue et al. 2011). We just registered two neutral effect of CAD from individual level, one describing that the harvesting of the bryophyte *Sphagnum sp*. did not change growth and height of individuals cover (Rancura et al. 2010). Other neutral effect was related to the herb *Anemone altaica* Fisch. ex C.A. Mey., which rhizomes harvesting do not affect its production, furthermore increased flowers size, stem length, leaf length (Huai et al. 2013).

At the population level effects of CAD were related to populations' size, populations' relative stability, proportion of seedlings of a species in its total population and mortality rates (Table S1). Harvesting of timber and non-timber products and overgrazing by livestock caused decrease in populations size (Tabuti 2007; Ndangalasia et al. 2007) and were responsible for tree populations decline due the decrease in populations' relative stability ($\lambda < 1$) (Soehartono & Newton 2001; Endress et al. 2004; Venter & Witkowski 2013). CAD also affects negatively the proportion of seedlings on tree species populations (Sagar & Singh 2004) and overgrazing by livestock is usually cited as the cause of seedlings and saplings mortality (Singh 1997; Endress et al. 2004; Stewart 2009), thus not allow seedlings and saplings progress to up tree size (Singh 1997). Intensive harvesting of non-timber forest products as resin stems and barks also increase populations' mortality rates (Nakazono et al. 2004; Varghese & Ticktin 2008; Stewart 2009). We also verified cases of CAD neutral effects on plant populations' size and growth rates related to sustainable harvesting and techniques (Fedele et al. 2011; Schmidt & Ticktin 2012), and species attributes as clonal regeneration and fast growing that allowed populations persistence (Schumann et al. 2012). Intermediate degree of CAD promoted increase in populations' size of cacti species as *Mammillaria pectinifera* (Martorell & Peters 2005), and increased population growth rate of *Mammillaria hernandezii* (Ureta & Martorell 2009). However intense levels of CAD can reduce population size and growth rate, respectively (Martorell & Peters 2005; Ureta & Martorell 2009).

The effects of CAD related to forest communities were associated to taxonomic diversity and composition of distinct biological groups as fungi, plants, birds, and mammals (see Table S1). In relation to tree species, chronic disturbances as collection of timber and non-timber products and overgrazing by livestock caused negative effects as reduction in diversity components as species richness, abundance and evenness (Sagar et al. 2003; Widayati & Carlisle 2012; Maren et al. 2013). Negative effects on community structure and taxonomic composition were represented by the decrease in basal area, canopy height and cover (Metha et al. 2008; Maren et al. 2013), dominance of small wood species (Shankar et al. 1998) and convertion of mature communities to to early successional stands (Souza et al. 2012). Neutral effects of CAD on tree communities were represented by the absence of changes in sapling and seedling regeneration in harvested sites and maintenance of adults' abundance (Walters 2005; Buffum et al. 2008). These neutral effects were justified by the forest management of CAD with selective cutting (Buffum et al. 2008) and by the fact that open areas formed by disturbance are good sites for regeneration of some species groups (Walters 2005).

For the understory plant community we registered few occurrences of CAD negative effects (Table S1), which included reduction in species richness due the proximity to human settlement (Murali et al. 1996) and decrease in understory vegetation cover, diameter at breast height, stem density and Fisher's index related to harvest of understory non-timber forest products (Widayati & Carlisle 2012). Neutral and positive effects of CAD on understory community promoted maintenance or increase in taxonomic diversity, stem density, and individuals' height (Kumar & Shahabuddin 2005; Metha et al. 2008). These neutral and positive effects on plant understory were justified by the new soil and microclimate conditions created by disturbances as the removal of tree species that favors the dominance of small wood and thorny species (Metha et al. 2008) and by the fact that shrubs tend to flourish with some opening of the canopy (Kumar & Shahabuddin 2005).

Other CAD effects on community level were linked to biological interactions. The collection of timber from dead wood caused the decrease in polypore fungi richness, whose are specialists in wood decomposition (Christensen et al. 2009). CAD as harvesting of NTFP (fruits) caused decrease in the taxonomic diversity, richness of specialist species and abundance of frugivorous birds, and also reduced the species richness of fruit-eating mammals (Moegenburg & Levey 2002; 2003; Borghesio 2008). Leal et al. (2014) recorded that myrmecochorous euphorbs with large seeds had lower removal rates and shorter dispersal distance by high quality seed dispersers in chronic disturbed sites as compared to undisturbed areas. Those authors also registered positive effects of CAD as the increase in seed removal by *Ectatomma muticum* ant at sites with intermediate level of disturbance (Leal et al. 2014).

CONCLUSION

This review demonstrates that CAD is a phenomena strictly related to developing countries from tropical umid and semi-arid regions whose subsistence and cash income depend in some extent of forest products. Ecological effects of CAD were mainly studied at population and community levels, and were predominantly negative. However, neutral and positive effects were recorded, supporting the possibility of reconciliation of forest use and biodiversity maintenance. More research effort on CAD effects on ecosystem level and approach of distinct diversity components (e.g. functional, genetic, and phylogenetic) will enhance our decision capacity when planning and carrying out conservationist strategies. Management of the negative effects of CAD will depend also of work with local harvesters combining local ecological knowledge, ecological studies, and public policy (Schmidt & Ticktin 2012). Forests benefit 1.5 million of forest-dependent people worldwide (Forest Peoples Programme 2012), and can continue to be a source of poverty alleviation if combined to enhance income, employment options and strengthening of local institutions through social and conservationist policies and interventions (Belcher 2005).

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Table 1. List of variables and its categories/description analyzed in the 51 studies that approached CAD concept related to forest flora, and also some implication of CAD on biodiversity.

Variables analyzed	**Categories/description**
Socioeconomically aspects	*Continent of location* – North America, Central/South America, Africa, Asia/Oceania and Europe. *Climatic zone* – Tropical, temperate and polar. *Type of forest use* – subsistence, commercial and subsistence/commercial. *Human development index* – low, lower middle, and upper middle and high income. Developing countries are those classified as low, lower middle, and upper middle income by the World Bank (2014).
CAD sources	*Timber forest products* – firewood, timber for building and agricultural implements, charcoal and dead wood. *Non-timber forest products* - fruits, vegetables, leaves, grasses, stems, barks etc. *Livestock* - Extensive grazing on forest of goat, sheep and cattle herds. *Wildfire* – use of fire for species harvesting or some occurrence of fire.
CAD predictors	*Harvest* – measures of CAD related ho harvest (*e.g.* harvested/unharvested, harvesting techniques etc.). *Livestock* – measures of CAD related ho livestock on studied forest as animals’ density, droppings frequency etc. *Disturbance regime/history* – type or historical use of the forest (*e.g.* semi-natural, fallow etc.). *Wildfire* – fire can facilitate harvesting of forest products or accidentally occur in chronic disturbed forests. *Other indirect predictors* – canopy cover, basal area,

	number of human trails, human trails surface, number of footpaths, distance to settlements, roads etc.
Ecological level assessed	*Individuals* – rates related to individuals vegetative and reproductive growth. *Population* – population size, structure and dynamic. Individuals/population – studies that accessed both individual and population parameters. *Community* – diversity components, composition and interactions. *Ecosystem* – Energy flows, nutrient and organic matter dynamics.
Effects on biodiversity according the ecological level	*Positive, negative and neutral* – the judgment of the effect in these categories were done considering authors view about the registered effect. Each of these categories was registered once in each analyzed paper.

Legend for figures

Fig 1. Illustration of the acute and chronic human disturbances common in tropical forests (Singh 1998; Martorell & Peters 2009). We can observe the main activities that characterize these disturbances, for acute (A), slash and/or burn promote total mischaracterization of a mature forest. After land abandonment, the secondary, regenerating forest may suffer chronic disturbances and possibly never return to conditions similar to those pre-disturbance. When a mature forest is chronically disturbed (B), little changes in forest structure and composition are observed. However, if very frequent and intense chronic disturbance may lead to further biomass collapse and biotic simplification.

Fig 2. Number of scientific papers that approached chronic anthropogenic disturbances effects on biodiversity per year.

Fig 3. Number of scientific papers that addressing chronic anthropogenic disturbances (CAD) according their climatic zone.

Fig 4. Number of scientific papers according the type of chronic anthropogenic (CAD) disturbance source. Disturbance sources codes: TI – timber forest products, NT – non-timber forest products, LI – livestock and FI – wildfire. When the codes are combined by the plus sign (+) indicate that the disturbances sources occurred simultaneously.

Fig 5. Effects of chronic anthropogenic disturbances (CAD) on biodiversity according the ecological level. In each analyzed paper the presence of a positive, negative or neutral effects were registered just one time per effect type.

Fig. 1

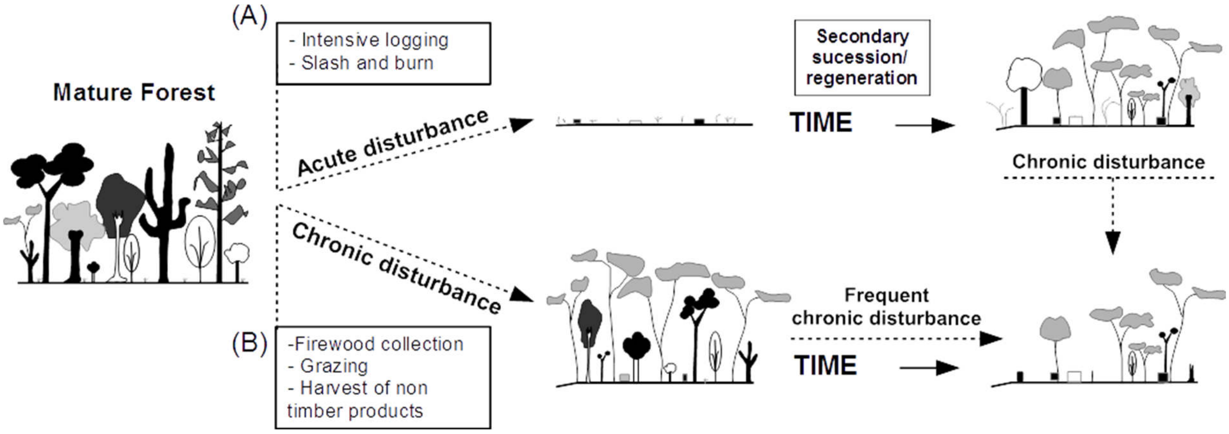
(A)
- Intensive logging
- Slash and burn
Mature Forest
Acute disturbance
Secondary sucession/ regeneration
TIME
Chronic disturbance
Chronic disturbance
Frequent chronic disturbance
TIME
(B)
-Firewood collection
- Grazing
- Harvest of non timber products

Fig. 2

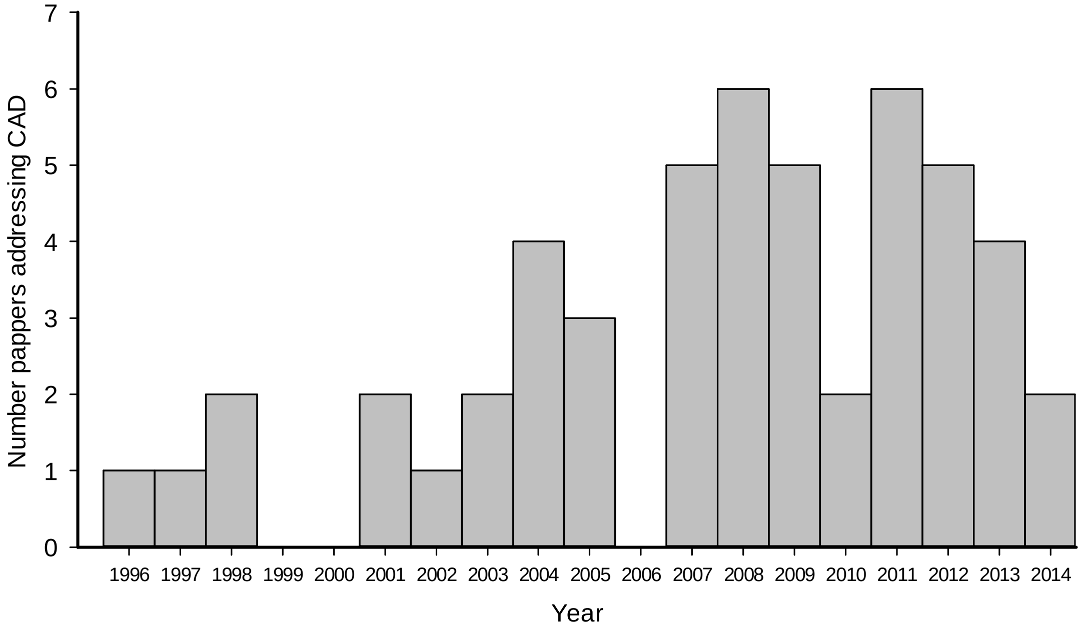
Number pappers addressing CAD
7
6
5
4
3
2
1
0
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
Year

Fig. 3

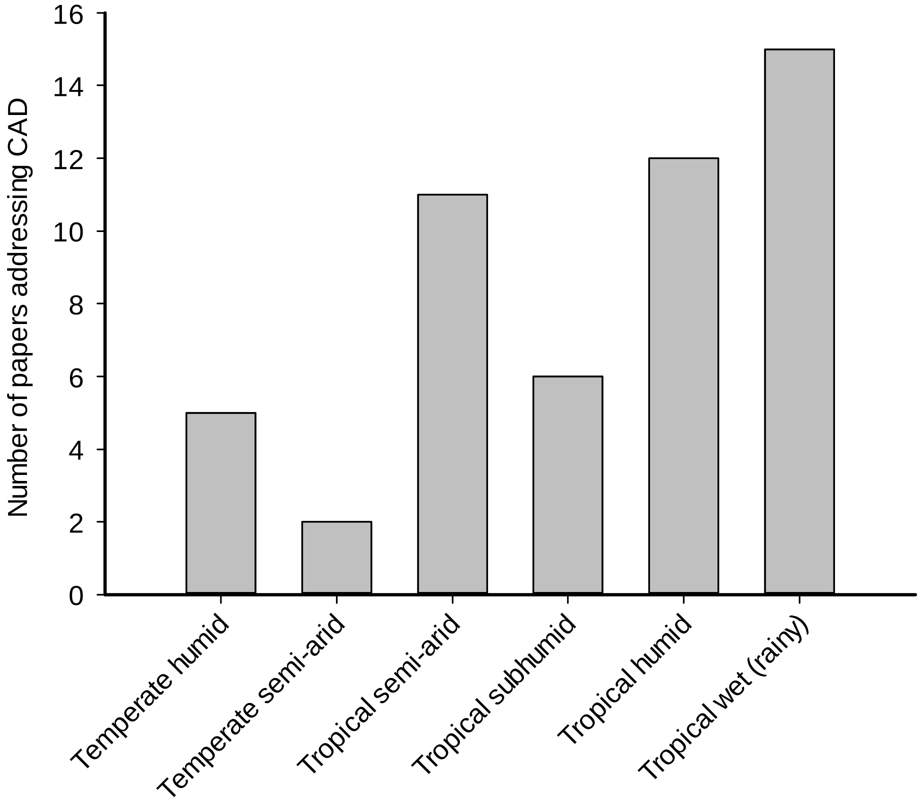
Number of papers addressing CAD
0
2
4
6
8
10
12
14
16
Temperate humid
Temperate semi-arid
Tropical semi-arid
Tropical subhumid
Tropical humid
Tropical wet (rainy)

Fig. 4

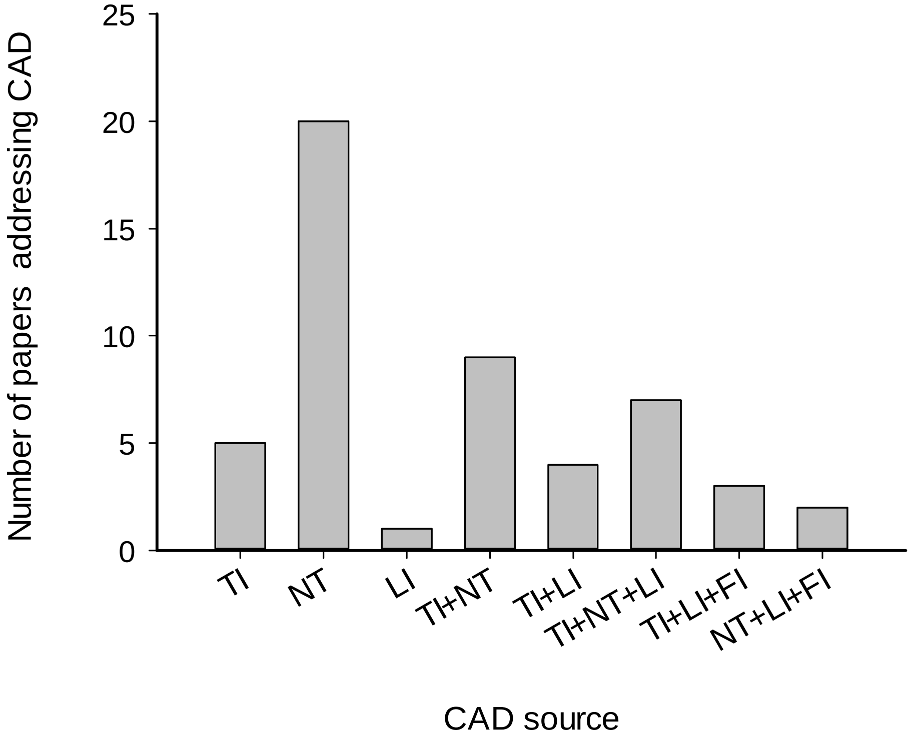
Number of papers addressing CAD
25
20
15
10
5
0
TI
NT
LI
TI+NT
TI+LI
TI+NT+LI
TI+LI+FI
NT+LI+FI
CAD source

Fig. 5

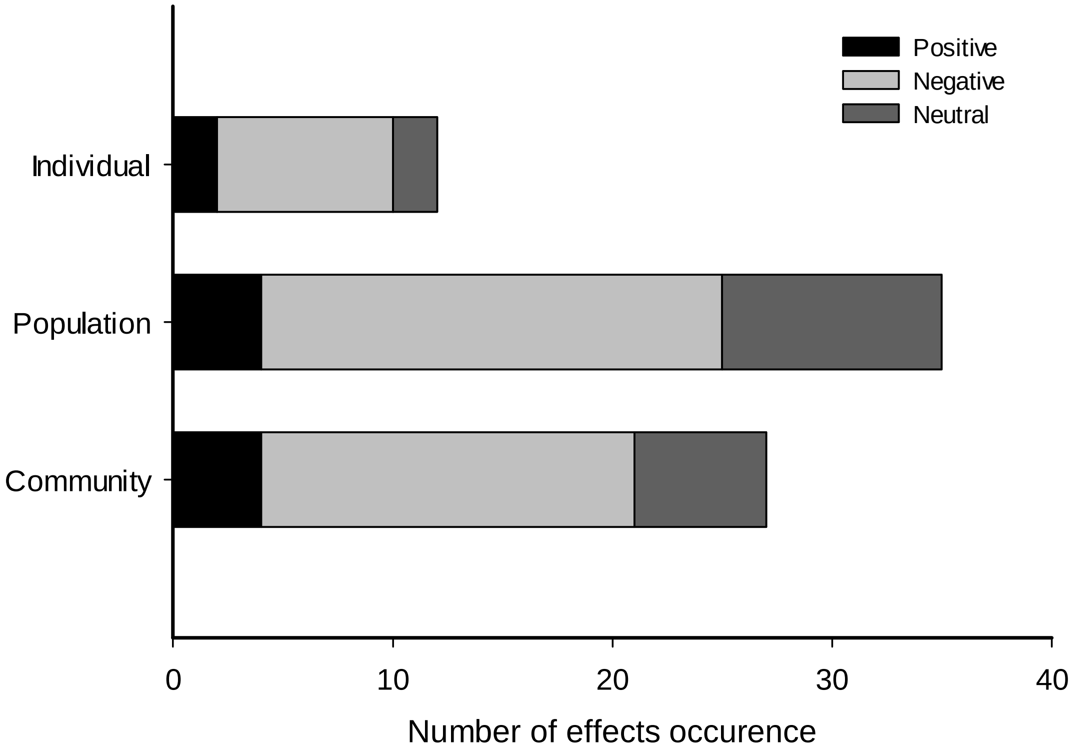
Positive
Negative
Neutral
Individual
Population
Community
0
10
20
30
40
Number of effects occurence

Table S1. List of the 51 studies that approached CAD concept and also some implication of CAD on biodiversity.

CAD source	CAD predictors	Taxon/Group effects accessed	CAD effects on biodiversity	Reference
Timber and NTFP	Distance from the settlement	Tree and understory community	Diversity, evenness and frequency of individuals at 1-10 cm height of trees were lower at proximal sites. At understory layer, richness was also lower at proximal sites.	Murali et al. (1996)
Timber, NTFP and livestock	Canopy cover and livestock presence/absence	*Quercus semecarpifolia*	Livestock promoted seedlings mortality, grazing do not allowed seedling and sapling progress to tree size.	Singh (1997)
Timber and NTFP	Distance from the settlement	Wood plant community	Stand density and basal area declined from the distant to the proximal stand, the dominance of small woody species was increased at proximal sites.	Shankar et al. (1998)
Timber and NTFP	Distance from the settlement	Tree and understory plant community	Reduction in stems number of vertebrate dispersed plant species, and increased number of stems from wind dispersed species in proximal sites. Passive dispersal mode did not exhibit any association with the disturbance index.	Ganeshaiah et al. (1998)
NTFP	Harvesting techniques	*Phyllanthus emblica and Phyllanthus indofischeri*	The harvested site had the fruit production reduced	Sinha & Bawa (2001)
Timber	Harvesting intensity	*Aquilaria malaccensis* and *Aquilaria microcarpa*	The harvesting in the study area is not sustainably, population harvesting of *Aquilaria malaccensis* individuals < 10cm dhb and *Aquilaria microcarpa* individuals < 30cm dhb can promote populations decline.	Soehartono & Newton (2001)
NTFP	Harvesting intensity	Frugivorous birds community	In the most harvested sites frugivorous diversity was reduced.	Moegenburg & Levey (2002)
NTFP	Harvesting intensity	Frugivorous birds and mammals community	Species composition changed in most harvested sites and the abundance of frugivorous birds was reduced. Fruit-eating	Moegenburg & Levey (2003)

			mammals species richness was also reduced due harvesting.	
Timber, NTFP and livestock	Distance from road, market, human habitation, intensity of cutting/lopping, grazing/browsing (basal area), impact of wild animals (saplings density) and rockiness.	Tree community	Disturbance changed species composition and spatial distribution, reduced basal area, stems density, species richness, evenness and alpha diversity.	Sagar et al. (2003)
NTFP	Harvesting intensity	*Ischnosiphon polyphyllus*	Harvest intensity of 100% caused high mortality of individuals, however in harvest treatments of < 80% mortality rates did not differ.	Nakazono et al. (2004)
NTFP	Harvesting and livestock intensity	*Chamaedorea radicalis*	Harvesting reduced fecundity and increased mortality, and projected population decline. Livestock caused seedling, juvenile and young adult mortality.	Endress et al. (2004)
Timber and livestock	Light interception, density of trees and canopy cover	Tree community	Higher species richness and diversity at intermediate disturbance. Reduction of tree density and tree basal area from the undisturbed to the highly disturbed site, changes in species composition.	Mishra et al. (2004)
Timber, NTFP and livestock	Distance from road, market, human habitation, intensity of cutting/lopping, grazing/browsing (basal area), impact of wild animals (saplings density) and rockiness.	Tree populations	34 of the 65 studied species presented populations in decline, increase in the proportion of declining species with increase in disturbance intensity.	Sagar & Singh (2004)
Timber, livestock	Looping percentage, livestock	Tree and understory plant	In the dry, Anogeissus-dominated and riparian forests the tree	Kumar &

and NTFP	dung and number of trails	community	canopy cover, basal area stems number, stems height and species richness were reduced due disturbance. In scrub forest, just stem height, canopy cover and basal area negatively affected by disturbance. The understory plant diversity and composition were not affected by disturbance.	Shahabuddin (2005)
Timber	Harvested/no harvested	Wood plant community	Affected just the relative abundance of one species, but have no effects on others species abundance and regeneration.	Walters (2005)
Timber, livestock and fire	Goat droppings frequency, cattle droppings frequency, browsing, livestock trail density, soil compactation, fuelwood extraction, human trails density, human trails surface, settlement proximity, contiguity to activities cores, land use, evidence of wildfires, erosion, presence of soil islands and Totally modified surfaces	*Mammillaria pectinifera*	Larger population density was observed at intermediate disturbance level, the complete removal of human activities from the system is likely to reduce some of the populations. Extreme disturbance may lead to extinction.	Martorell & Peters (2005)
Timber and NTFP	Harvest index	16 Wood plant populations	Reduction in tree the population’s size.	Tabuti (2007)
Timber and NTFP	Disturbed/undisturbed	*Cyathea manniana,Bridelia micrantha, Cassipourea gummiflua, Cassipourea malosana, Syzygium guineense, Aphloia theiformis,*	Reduce the population abundance in most disturbed sites.	Ndangalasia et al. (2007)

		Zanthoxylum sp. and Strombosia *scheffleri*		
NTFP	Harvesting techniques	*Garcinia lucida*	Ring-barking and felling strongly reduced the stock of harvestable trees.	Guedje et al. (2007)
NTFP	Harvesting intensity	*Euterpe edulis*	In non-disturbed sites regeneration, survival and growth was usually reduced.	Fantini & Guries (2007)
NTFP	Past logging, fire frequency, official protection status and species population distance to farms.	*Khaya senegalensis*	High harvest populations had lower densities of seedlings and saplings.	Gaoue & Ticktin (2007)
Timber, NTFP and livestock	Grazed area, distance to forest edge and wood collection intensity	Bird communities	Reduction in the abundance of bird specialist species.	Borghesio (2008)
NTFP	Harvesting history	*Bertholletia excels*	Did not verified differences in regeneration due exploitation history, all populations' structure presented by a reverse-J.	Wadt et al. (2008)
NTFP	Pruning and debark intensity	*Khaya senegalensis*	Did not found significant effects of debarking or combined debarking and pruning on reproductive performance, but heavy foliage harvest can decrease rates and patterns of reproduction.	Gaoue & Ticktin (2008)
NTFP	Harvesting techniques	*Canarium strictum*	Resin collection with and without fire increased the mortality.	Varghese & Ticktin (2008)
Timber	Harvesting intensity and distance to village	Wood plant community	Did not verified effects of cutting intensity on regeneration of seedling and saplings of preferred species, tree genera diversity and percentage of favorable trees.	Buffum et al. (2008)

Timber and livestock	Trails of cattle and jeep, cut and/or broken stems, livestock dung, people and fire	Tree and understory community	In the most disturbed sites tree density, canopy height, canopy cover and tree density were reduced. Understory height and shrub density did not change due disturbance. Most disturbed sites had greater presence and density of small woody tree species, and greater numbers of understory species.	Mehta et al. 2008
Timber	Polypore diversity	Polypore community	Reduction of polypore richness.	Christensen et al. (2009)
Timber and NTFP	Land cover use (silviculture, protected area, heavily hunted area)	*Carapa surinamensis*	In the heavily harvested plots verified seed dispersal failure and insect predation.	Lermyte & Forget (2009)
NTFP	Proximity to houses, dwellings, farms and cattle grower.	*Pentadesma butyracea*	In the most harvested sites the density of seedlings and saplings were lower, no changes in adults density. No difference when considering the density of individuals generated from root suckers.	Avocèvou-Ayisso et al. (2009)
NTFP, livestock and fire	Harvesting history	*Prunus africana*	Harvested areas had reduced fruit production and seedling survival, increase in mortality and the population structure was modified.	Stewart (2009)
Timber, livestock and fire	Goat droppings frequency, cattle droppings frequency, browsing, livestock trail density, soil compactation, fuelwood extraction, human trails density, human trails surface, settlement proximity, contiguity to	*Mammillaria hernandezii* and *Mammillaria dixanthocentron*	*Mammillaria hernandezii* had higher growth rate in intermediate disturbed sites and *Mammillaria dixanthocentron* had lower population growth rate in more disturbed sites.	Ureta & Martorell (2009)

	activities cores, land use, evidence of wildfires, erosion, presence of soil islands and totally modified surfaces			
NTFP	Harvesting techniques	*Sphagnum sp.*	Do not affect growth and height when compared to initial conditions.	Rancura et al. (2010)
NTFP	Harvested/no harvested	*Agave marmorata*	Decrease in the individual growth and fecundity in the harvested population.	JimenezValdes et al. (2010)
Timber	Local people appreciation of decreasing in plant abundance, regeneration capacity of plants, impact of root harvesting and quality of firewood	Wood tree and shrub community	Disturbance caused decline in the density of firewood species.	Thomas et al. (2011)
Timber and NTFP	Distance to nearest village, number of foot patches, canopy cover and number of stumps.	Tree and treelet communities	The abundance and basal area of useful species were reduced in the most disturbed sites.	Hoang et al. (2011)
NTFP	Pruning intensity	*Khaya senegalensis*	Harvest increased leaf nutrient concentration in large trees, water use efficiency and fruit production in dry areas.	Gaoue et al. (2011)
Timber, livestock and fire	Goat droppings frequency, cattle droppings frequency, browsing, livestock trail density, soil compactation, fuelwood extraction, human trails density, human trails surface, settlement	*Coryphantha werdermannii*	Decrease in population growth rates in the most disturbed sites, livestock reduced growth rate in intermediate disturbed sites, land degradation reduced growth rates in the most disturbed sites.	Portilla-Alonso & Martorell (2011)

	proximity, contiguity to activities cores, land use, evidence of wildfires, erosion, presence of soil islands and Totally modified surfaces			
NTFP	Distance of plant populations to the village	*Pandanus guillaumetii*	Harvesting did not affect population density of surveyed populations.	Fedele et al. (2011)
NTFP	Harvesting intensity	*Ceroxylon echinulatum*	In the most harvested sites the number of leaves after two years was smaller than the control site.	Duarte & Montúfar (2012)
Timber and NTFP	Land cover type/use (Protected area, fallow and cropland)	*Anogeissus leiocarpa*	Did not verify a declining population in studied sites due species traits as clonal regeneration and fast growing.	Schumann et al. (2012)
NTFP	Harvesting intensity, plot location and harvested plant abundance	Trees and understory community	Understory vegetation cover, stem average dbh, Fisher's index and stem density are significantly lower in harvested areas.	Widayati & Carlisle (2012)
NTFP	Harvested/no harvested	*Syngonanthus nitens*	Traditional management practices had no impact population dynamics, but earlier harvest of golden-grass leads to population decline due plant uproot.	Schmidt & Ticktin (2012)
Timber and livestock	Harvesting history	Tree plant communites	Chronic disturbed sites had a vegetation of early successional stages.	Souza et al. (2012)
Timber, NTFP and livestock	Land cover type/use (fallows, semi natural, non-arable)	30 Tree and shrub populations	Verified that land cover type modified size-class structure of the major part of species, but did not affect populations' structure.	Jurisch et al. (2012)
Livestock	Livestock density	*Adansonia digitata*	High livestock numbers caused population decline.	Venter &

				Witkowski (2013)
Timber, NTFP and livestock	Canopy cover, distance to settlements, lopping and cutting visual estimation	Wood tree community	Disturbance caused decline species richness.	Maren et al. (2013)
Timber, NTFP and livestock	Land cover type/use (fallows, semi natural, non-arable)	Wood plant community	Survival and growth of woody species seedlings and saplings are strongly related to land use. Most part of species developed better in the communal area, but other species developed better in non-arable and fallows.	Jurisch et al. (2013)
NTFP	Harvesting intensity	*Anemone altaica*	In high harvest treatments flowers were larger, stem length and leaf length were significantly higher. Moreover, in intensively harvested populations individuals' coverage and the number of individuals per unit area increased.	Huai et al. (2013)
Timber, NTFP and livestock	Distance to road, distance to houses, distance to urban center, livestock and people density	Ant-plant interactions	Seed removal by *Ectatomma muticum* was highest at intermediate disturbance level. Plant species with large elaiosome had smaller removal rates in most disturbed sites, but removal rates were not affected for plant species with small elaiosome. Mean dispersal distance was four times higher at sites experiencing low disturbance.	Leal et al. (2014)
NTFP	Defoliation intensity	*Chamaedorea ernesti-augustii*	High defoliation intensity reduced seed production and seedling recruitment rate.	Van Lent et al. (2014)

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CAPÍTULO 2

Chronic anthropogenic disturbance drives the the biological impoverishment of the Brazilian Caatinga vegetation

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Chronic anthropogenic disturbance drives the biological impoverishment of the Brazilian Caatinga vegetation

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Summary

1. In addition to acute transformations of ecosystems caused by deforestation, old-growth forests world-wide are being increasingly altered by low-intensity but chronic human disturbance. Overgrazing and the continuous extraction of forest products are important drivers of chronic disturbance, which can lead to the gradual local extinction of species and the alteration of vegetation structure.

2. We tested this hypothesis in the Brazilian Caatinga vegetation, one of the most species-rich and populated semi-arid regions of the world. Using a multimodel averaging approach, we examined the impact of five recognized indicators of chronic disturbance (i.e. proximity to urban centre, houses, roads, density of people and livestock) on the diversity, abundance and evenness of 30 woody plant communities. We separately tested the response of seedlings, saplings and adults to identify the ontogenetic stages that are most susceptible to chronic disturbance.

3. We recorded over 11 000 individuals belonging to 51 plant species. As expected, most indicators of chronic disturbance were negatively related to species diversity and stem abundance, with a variable effect on community evenness. The density of people and density of livestock were the main factors driving changes in plant communities, with a stronger negative impact on seedling and sapling diversities. Species composition also varied significantly with disturbance indicators, irrespective of ontogeny.

4. Our results show the potential negative impact that chronic disturbance can have on Caatinga plant assemblages and highlight the fact that disturbance resulting from an extractivism-based and subsistence economy are probably driving old-growth forest stands towards shrub-dominated secondary stands.

5. *Synthesis and applications*. These findings indicate that chronic disturbance should not continue to be neglected and we argue for: (i) research and rural programmes able to support better practices in terms of land use and sustainable exploitation of forest resources, (ii) improved governance and law enforcement to shift extractivism towards sustainable standards, and (iii) expanding the coverage and effective implementation of strictly protected areas.

Key-words: biodiversity crisis, chronic human disturbance, multi-model inference approach, plant assemblages, seasonally dry tropical forests, semi-arid vegetation, species diversity

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Introduction

Changes in land use have drastically decreased forest cover world-wide, with research emphasizing habitat loss and fragmentation as the main threats to tropical biodiversity and services provided by this irreplaceable ecosystem (Laurance, Sayer & Cassman 2014). However, old-growth and secondary forest patches are experiencing increasing levels of human-related disturbance that do not result in habitat loss and fragmentation, but also have negative impacts on the biological integrity of tropical biota (Singh 1998; Laurance & Peres 2006). We refer, for example, to continuous poaching, extraction of firewood and non-timber forest products, as well as the damage caused by livestock, which overall result in a subtle but permanent removal of small fractions of forest biomass (Martorell & Peters 2005; May-Tobin 2011). In contrast to large-scale habitat loss and fragmentation, chronic disturbance is (i) usually diffuse, more frequent and operate at a small spatial scale, (ii) not detected via traditional resources such as satellite imagery (Laurance & Peres 2006), and (iii) not expected to cease even in those countries where habitat loss is now regulated.

Chronic regimes in fact represent a global pervasive source of disturbance that operates as complementary sources of habitat degradation and species erosion in human-modified landscapes (Mahiri & Howorth 2001; FAO 2011). Reductions in stem density, basal area, species richness and community evenness and changes in plant demographic structure and proliferation of disturbance-adapted species, which all cause detrimental effects to forest-dependent and long-lived plant species, have been reported (Sagar, Raghubanshi & Singh 2003; Smart *et al.* 2006; Wiegmann & Waller 2006). Plant–animal interactions, such as seed dispersal, can also be altered in sites experiencing livestock, hunting and firewood collection (Leal, Andersen & Leal 2014), but our general understanding on the impacts that chronic disturbance may have on plant species diversity and vegetation structure is still limited (Álvarez-Yépiz *et al.* 2008).

The Caatinga vegetation of Brazil consists of broad mosaics of seasonally dry tropical forest and scrub vegetation (Veloso, Sampaio & Pareyn 2002). This semi-arid region sustains over 23 million people (11·8% of the Brazilian population) and is one of the most populated semi-arid regions globally, with 26 inhabitants km^{-1} (INSA 2012). Nearly 10 million m^3 per year of firewood and charcoal are obtained via exploitation of native vegetation (Gariglio *et al.* 2010), and historically goat herds can exceed 16 million animals (IBGE 2010a). Collectively, slash-and-burn agriculture, overgrazing by livestock and firewood collection impose a continuum of degradation varying from reduced biomass to complete desertification (Leal *et al.* 2005). Despite this alarming scenario, the role played by chronic disturbance on plant community structure in the Caatinga has been poorly examined (Leal *et al.* 2005; Santos *et al.* 2011). The Caatinga vegetation thus offers an interesting opportunity to address how seasonally dry tropical forest and semi-arid biotas respond to small-scale land use (as opposed to commercial land use) in order to provide conservation guidelines and better practices.

We assessed how Caatinga plant assemblages are affected by small-scale but frequent disturbance, such as extensive browsing by livestock, selective tree removal, firewood collection and hunting. Because human disturbance usually favours a small group of disturbance-tolerant species that ultimately become locally dominant (Smart *et al.* 2006; Wiegmann & Waller 2006), we expected that all indicators of chronic disturbance would be negatively related to stem abundance, species diversity and community evenness. These relationships, however, were expected to be stronger in seedling and sapling assemblages, as these ontogenetic stages are often more vulnerable to chronic disturbance (Singh, Rawat & Garkoti 1997).

Materials and methods

STUDY AREA

The Caatinga encompasses 826 411 km^2 of seasonally dry tropical forests and scrub vegetation restricted to Brazil (MMA & IBAMA 2011). The studied area is located in the Parnamirim municipality, Pernambuco state, north-east Brazil (8°5′26″S; 39°34′41″W; Fig. 1). The climate is semi-arid, with an average temperature of 26 °C and most of the 431 mm mean annual rainfall is received between January and May (IBGE 1985; CPRM 2005). Soils are predominantly non-calcic brown soils (clay soil), regosols and planosols (sandy soils) (IBGE 1985). The Caatinga vegetation has undergone deforestation since the sixteenth century for extensive livestock and temporary farming (Leal *et al.* 2005; IBGE 2010b). Parnamirim municipality has approximately 55% of the original Caatinga forest cover. Forest products extracted for medicinal purposes, animal and human food, and wood collection are also common within the forest remnants.

STUDY SITES

We established 30 50 × 20 m plots (Fig. 1) within a 220 km^2 landscape dominated by old-growth vegetation exposed to chronic disturbance. We considered old-growth vegetation to be forest stands not exposed to slash-and-burn agriculture in the last 50 years (Leal, Andersen & Leal 2014). Because the response of tree species to chronic disturbance may be affected by soil characteristics (Pinheiro, Rodal & Alves 2010), we located 15 plots on brown non-calcic soils and 15 on regosols. We adopted a landscape scale perspective to obtain a gradient of chronic disturbance intensity. We used five indicators of chronic disturbance that have been described as important drivers of human disturbance in tropical forests studies. They are (i) proximity to the nearest house (Proximity to house) (Sagar, Raghubanshi & Singh 2003; Martorell & Peters 2005; Leal, Andersen & Leal 2014), (ii) proximity to the nearest road (Proximity to road) (Sagar, Raghubanshi & Singh 2003; Leal, Andersen & Leal 2014), (iii) proximity to Parnamirim city (Proximity to city) (Sagar, Raghubanshi &

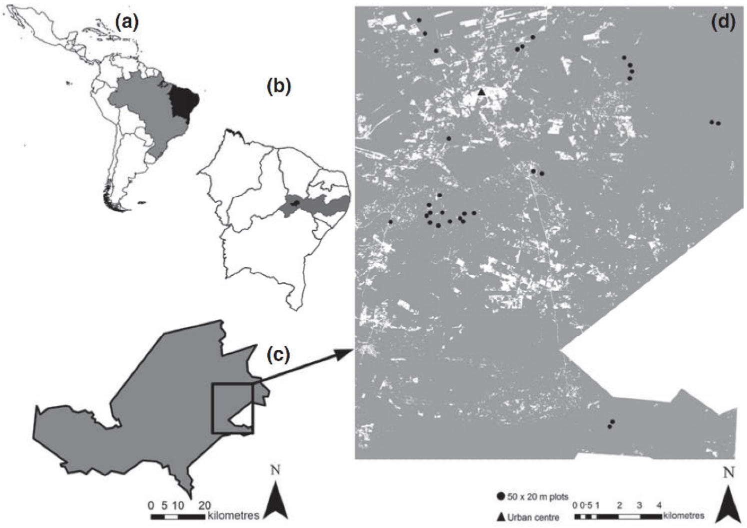

Fig. 1. (a) Study area in north-eastern Brazil, (b) the Parnamirim municipality (in black) within the Pernambuco state (in grey), (c) the study landscape in which we located 30 50 × 20 m plots and (d) the urban centre of Parnamirim (black triangle) (the white areas in (d) represent deforested areas).

Singh 2003; Leal, Andersen & Leal 2014), (iv) density of people living near the plot (People) (Leal, Andersen & Leal 2014), and (v) density of livestock (Livestock) (Leal, Andersen & Leal 2014). We opted for proxies instead of direct measures of logging, hunting, cutting and overgrazing because disturbance is not easily quantified at the landscape scale (Acharya & Dangi 2009). Thus, plots covered a wide range of disturbance level (see Table S1 in Supporting Information).

We used satellite imagery from the Advanced Land Observing Satellite (ALOS) to estimate the indicators 'Proximity to house', 'Proximity to road' and 'Proximity to city' as the reciprocal distance from the centre of each plot. To estimate 'People' and 'Livestock', we first identified all occupied dwellings near the plots. Through 40 interviews, we collected information on the number of people living in, and the number of stock managed by, each dwelling. We later used the ALOS satellite imagery to localize all dwellings in a 2-km buffer area from the centre of each plot and then estimated 'People' and 'Livestock' in terms of density taking into account the interview data and an area of 1256 ha. We selected this buffer size because local people reported that the maximum dispersal distance of herd animals is 2 km.

SURVEY OF PLANT COMMUNITIES

We sampled plant assemblages in each plot during the rainy seasons of 2012 and 2013. We considered three stages (adults, saplings and seedlings) to identify the ontogenetic stages that are most susceptible to chronic disturbance, as well as to predict compositional change in plant communities. Adults were defined as individuals with diameter at soil height (DAS) >3 cm and height >1·5 m; saplings were individuals with DAS <3 cm and height between 1 and 1·5 m; and seedlings were defined as individuals with height <1 m (Rodal, Sampaio & Figueiredo 1992; Felfili, Carvalho & Haidar 2005). We recorded all adults found in each 50 × 20 m plot. Saplings were sampled in three 5 × 5 m subplots located in the centre of each 50 × 20 m plot and separated by 10 m. Seedling communities were sampled in 2 × 2 m subplots located in the centre of each 5 × 5 m subplot. We identified all plants at species level by comparing the sampled species with samples from the Federal University of Pernambuco herbarium and the botanical nomenclature followed APG III (2009).

STRUCTURE OF PLANT COMMUNITIES

We first calculated the inventory completeness for each site and ontogenetic class using the coverage estimator recommended by Chao & Shen (2010), which is a less biased estimator of sample completeness:

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

where f_1 and f_2 are the number of species represented by one (singletons) and two (doubletons) individuals, respectively, and n is the total number of individuals in each sample.

Because sample coverage was variable among plots and ontogenetic classes (ranging from 20% to 99%), our estimates of species richness could be biased by differences in sample completeness (Chao & Jost 2012), particularly because species richness is sensitive to variations in the number of singletons and doubletons (Jost 2006). Thus, following Chao & Jost (2012), we estimated the species richness of adults, saplings and seedlings in each plot using coverage-based extrapolations with the iNEXT software (Hsieh, Ma & Chao 2013). In particular, we considered 99% completeness as a reliable estimator of richness for all plots (Chao & Jost 2012).

In addition to estimating species richness (or ${}^{0}D$), we estimated the inverse Simpson concentration (or ${}^{2}D$) (Jost 2006). Both ${}^{0}D$ and ${}^{2}D$ are in the same units and satisfy the replication principle (Jost 2006), which is required in biodiversity assessments as it considers the uniqueness of each species that compose an assemblage (Gotelli & Chao 2013). The formulas of ${}^{0}D$ and ${}^{2}D$ are detailed elsewhere (Jost 2006). ${}^{0}D$ is not sensitive to species abundances and so gives disproportionate weight to rare species (Jost 2006). In contrast, ${}^{2}D$ favours abundant species and can be interpreted as the number of 'very abundant' or 'dominant' species in the community (Jost 2006).

To assess changes in community structure, we also considered stem abundance in each plot and the evenness factor (*EF*) proposed by Jost (2010). *EF* represents the proportion of dominant species in the community, and it is derived from the measures of effective number of species ($EF = {}^{2}D/{}^{0}D$) (Jost 2010). *EF* ranges between 1 (when the community is perfectly even) and nearly

$1/{}^0D$ (when the community is dominated by one species; Jost 2010).

DATA ANALYSES

First, we ran a Mantel test to check for spatial independence of our samples before testing our hypothesis (see Appendix S1, Supporting information). Then, for each ontogenetic class (i.e. adults, saplings and seedlings) and each response variable (i.e. ${}^0D$, ${}^2D$, abundance and *EF*), we built generalized linear models including five continuous explanatory variables ('Proximity to house', 'Proximity to road', 'Proximity to city', 'People' and 'Livestock'). To avoid multicollinearity problems between the predictor variables, we first estimated the variance inflation factor (VIF) of each predictor using the *car* package for R version 3.0.1 (R Core Team 2013). All VIF values found were lower than 3·1, indicating that none of our predictors were collinear (Neter, Wasserman & Kutner 1990), allowing us to include all of them in generalized linear models.

To test (and control for) the effect of soil type on each response variable, we included this categorical factor in the models as a fixed factor, as variations in continuous covariables were independent from variations in soil type. Then, using a multimodel inference approach (Burnham & Anderson 2002), we identified the subset of models with stronger empirical support. We ranked the models from the best to the worst based on the Akaike's information criterion corrected for small samples (AICc). The set of models with a difference in AICc (i.e. ΔAICc) <2 was considered to have strong empirical support and similar plausibility, explaining most of the variation in the response variable (Burnham & Anderson 2002).

To evaluate the importance of each predictor and produce model-averaged parameter estimates, we used Akaike weights (w_i), which represent the probability that a particular model is the best model for the data. Thus, we summed w_i of ranked models until the total was >0·95 (Whittingham *et al.* 2005). The set of models for which Σw_i was 0·95 represents the models for which we have 95% confidence that the set contains the best approximating model to the true model (Burnham & Anderson 2002; Whittingham *et al.* 2005). The relative importance of each predictor was assessed based on the sum of Akaike weights (Σw_i) of each candidate model in which the predictor appeared (Burnham & Anderson 2002).

As recommended for count response variables, when analysing stem abundance, we constructed generalized linear models with a Poisson error and a log-link function (Crawley 2007). To correct for overdispersion associated with models with Poisson errors (Crawley 2007), we used QAICc values instead of AICc in such models (Calcagno & Mazancourt 2010). Models for ${}^0D$, ${}^2D$ and *EF* were tested using a Gaussian error structure, after testing that they showed a Gaussian distribution (Shapiro–Wilk test). All models were built using the package *glmulti* for R version 3.0.1 (Calcagno & Mazancourt 2010). We also estimated the goodness-of-fit of the models by estimating the percentage of deviance explained by the complete model compared with the null model (Crawley 2007).

To assess how species composition in each ontogenetic stage was related to disturbance indicators, we used a partial canonical correspondence analysis (CCA), controlling for the effect of soil type. To prevent spurious effects caused by low species abundance and to minimize the risk of type II statistical errors, CCA was performed excluding rare species (those with <5 individuals) with the package *vegan* for R version 3.0.1 (R Core Team 2013). We used a two-way ANOVA to test for CCA model and axes significance.

Results

We recorded 10 862 adult plants (362 ± 92·1 stems per plot; mean ± SD) belonging to 51 species (18·5 ± 3·6). For the sapling assemblage, we recorded 732 stems (11·6 ± 6·5) from 40 species (6·7 ± 2·2). In the seedling community, we recorded 314 stems (10·6 ± 3·5) from 34 species (5·1 ± 1·8). Among the three ontogenetic classes, the most representative families were Euphorbiaceae and Fabaceae, with 10–13 species per ontogenetic class.

In all model sets, the single best model received limited support relative to alternative models (see Table S2, Supporting information). In general, the associations between explanatory and response variables were notably stronger in the adult (21–38% of explained deviance; Fig. 2) and

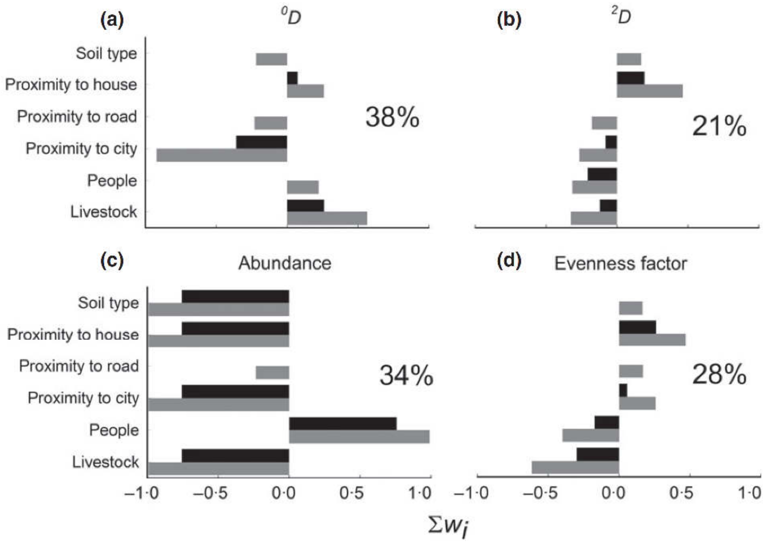

Fig. 2. Predictor variables included in the ΔAICc <2 set of models (black bars) and 95% set of models (grey bars) for (a) the species richness ${}^0D$, (b) inverse Simpson concentration ${}^2D$, (c) stem abundance and (d) community evenness of adult plant communities in the Caatinga forest, Brazil. The importance of each variable is shown by the sum of Akaike weights (axis *x*). The sign (±) of Akaike weights represents the effect (positive or negative) of each predictor on each response variable based on the model-averaged parameters shown in Table 1. We also indicate the percentage of explained deviance within each panel.

sapling communities (24–32%; Fig. 3) than in the seedling communities, in which models explained less than 24% of total deviance (Fig. 4). In most cases, the indicators of chronic disturbance showed negative associations with ^0D, ^2D and stem abundance (Table 1). In fact, considering only the cases in which the explanatory variables appeared in at least one model of the set of best models (i.e. those with a ΔAICc <2 indicated with † and ‡ in Table 1, see also Table S2), most associations (16 out of 22, 73%) were negative. This pattern was consistent in all ontogenetic classes. The few positive, but strong associations were found when evaluating the evenness factor, particularly within the adult and sapling assemblages (Table 1).

The indicators of chronic disturbance that best predicted changes in diversity, abundance and evenness of plant communities were ‘People’ (included in 20 out of 56 best models, 36%), ‘Livestock’ (36%) and ‘Proximity to house’ (34%) (see Table S3, Supporting information). The high sum of Akaike weights for these three variables further demonstrated their importance to plant communities (Figs 2–4). Yet, the predictive power of each explanatory variable varied across response variables, particularly when considering different ontogenetic classes (Figs 2–4).

In particular, ‘People’ and ‘Livestock’ showed similar impacts on the diversity and evenness of plant communities (Table 1). They were both strongly and negatively related to the number of dominant species (^2D) in the adult (Fig. 2), sapling (Fig. 3) and seedling (Fig. 4) communities. When considering adults, they were both positively related to species richness (^0D, Table 1), and as a consequence, these two factors were negatively related to community evenness (Fig. 2). However, when assessing the seedling community, both factors were negatively

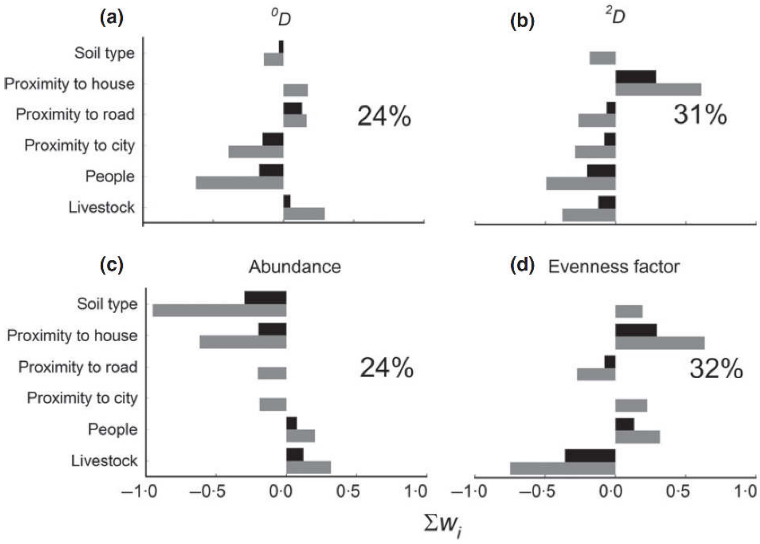

Fig. 3. Predictor variables included in the ΔAICc <2 set of models (black bars) and 95% set of models (grey bars) for (a) the species richness ^0D, (b) inverse Simpson concentration ^2D, (c) stem abundance and (d) community evenness of sapling communities in the Caatinga forest, Brazil. The importance of each variable is shown by the sum of Akaike weights (axis *x*). The sign (±) of Akaike weights represents the effect (positive or negative) of each predictor on each response variable based on the model-averaged parameters showed in Table 1. We also indicate the percentage of explained deviance within each panel.

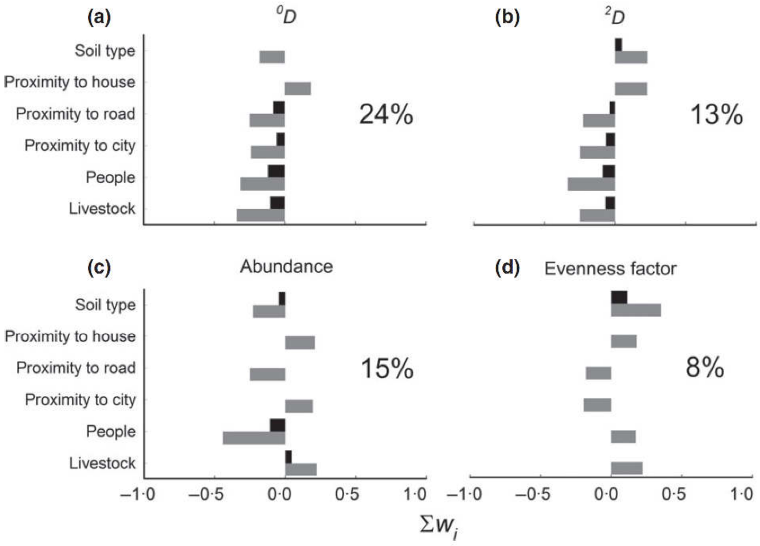

Fig. 4. Predictor variables included in the ΔAICc <2 set of models (black bars) and 95% set of models (grey bars) for (a) the species richness ^0D, (b) inverse Simpson concentration ^2D, (c) stem abundance and (d) community evenness of seedling plant communities in the Caatinga forest, Brazil. The importance of each variable is shown by the sum of Akaike weights (axis *x*). The sign (±) of Akaike weights represents the effect (positive or negative) of each predictor on each response variable based on the model-averaged parameters shown in Table 1. We also indicate the percentage of explained deviance within each panel.

Table 1. Values of model-averaged parameter estimates (β) and unconditional variance (UV) of information-theoretic-based model selection and multimodel inference for species richness (^0D), inverse Simpson concentration (^2D), stem abundance and community evenness for each ontogenetic plant community sampled in the Caatinga forest, Parnamirim municipality, Pernambuco, Brazil

	^0D		^2D		Abundance		Evenness factor	
Predictors	β	UV	β	UV	β	UV	β	UV
Adults								
Soil type	−0·242	0·774	0·000	0·099	−0·202	4·589	0·003	0·000*
Proximity to house	0·590	2·379	0·835	1·314	−0·207	1·300	0·032	0·002*‡
Proximity to road	−0·132	0·145	−0·010	0·017	−0·002	3·488	0·000	0·000*
Proximity to city	−27·90	159·25	−1·255	10·904	−0·569	2·608	0·045	0·017*
People	0·365	0·027*	−0·077	0·014*‡	0·020	2·305	−0·003	0·000*‡
Livestock	0·506	0·317*‡	−0·085	0·032*‡	−0·050	7·311	−0·109	0·001*‡
Saplings								
Soil type	−0·287	0·798	−0·077	−0·104	−0·281	6·447	0·009	0·001*
Proximity to house	0·015	1·153	1·062	1·255	−0·147	2·073	0·133	0·016*‡
Proximity to road	0·211	0·205*‡	−0·006	7·314	−0·004	3·162	−0·008	0·000*†
Proximity to city	−5·356	78·311	−0·844	0·027*†	−0·011	7·773	0·095	0·103
People	−0·153	0·061*‡	−0·084	0·014*‡	0·000	6·569	0·005	0·000*‡
Livestock	0·126	0·139	−0·150	0·042*‡	0·010	4·371	−0·038	0·000*‡
Seedlings								
Soil type	−0·008	0·226	0·112	0·128*	−0·189	0·004*	0·028	0·002*
Proximity to house	0·426	0·526	0·110	0·250	0·010	0·008*	0·007	0·002*
Proximity to road	−0·896	0·073*‡	−0·041	0·020*†	−0·009	0·000*	−0·001	0·000*
Proximity to city	−1·180	16·935	−0·714	5·653	0·009	0·000*	−0·028	0·041
People	−0·624	0·017*‡	−0·039	0·006*†	−0·012	0·000*	0·000	0·000*
Livestock	−0·135	0·071*†	−0·039	0·013*†	0·000	0·000*†	0·002	0·000*

*Values with an asterisk indicate cases where the unconditional variance was smaller than the model-averaged parameter estimates, suggesting safety in interpretation of β (Burnham & Anderson 2002). For each response variable and ontogenetic stage, we also indicate the explanatory variables that appeared in one (†) or more (‡) models within the set of best models (see Table S2).

related to species richness, but positively related to evenness (Table 1). This pattern of lower ^0D, lower ^2D and higher evenness was also observed when assessing the impact of 'People' on the sapling communities (Table 1, Fig. 3).

'Proximity to house' was positively associated with the evenness factor of the three ontogenetic classes, with a stronger effect on the adult (Fig. 2) and sapling (Fig. 3) assemblages. Although weaker, 'Proximity to road' was positively related to ^0D, but negatively associated with the evenness factor of sapling communities. However, when considering the seedling community, plots closer to roads showed lower ^0D and ^2D. Interestingly, stem abundance was poorly explained by these indicators of chronic disturbance, although the explained deviances of 'Proximity to house' and 'Proximity to road' were relatively high when considering adult and sapling communities (Figs 2 and 3). In these cases, the unconditional variances were greater than the model-averaged parameter estimates. This suggests caution in the interpretation of such model-averaged parameter estimates, as it indicates that parameter estimates were very spread out around the mean. Only when assessing the seedling community, we found model-averaged parameter estimates higher than the unconditional variances (Table 1).

The first two CCA axes explained 42% and 21%, respectively, of the variation in adult communities species composition under the disturbance indicators (Fig. 5a). In the sapling communities, these percentages were 36% and 31% (Fig. 5b), whereas in the seedling assemblage, they reached 40% and 32% (Fig. 5c). In all cases (adults, saplings and seedlings), species composition varied significantly with the disturbance predictors ($P < 0·05$). Species such as *Croton sonderianus* and *Jatropha mollissima* were positively related to disturbance indicators in all ontogenetic stages, whereas *Bauhinia cheilantha*, *Fraunhofera multiflora*, *Myracrodruon urundeuva* and *Senna macranthera* were negatively related to such indicators of disturbance (Fig. 5).

Discussion

As expected, the indicators of chronic disturbance evaluated in this study showed a negative impact on plant species diversity (both ^0D and ^2D) and stem abundance leading to a generalized impoverishment of plant communities across all ontogenetic classes, despite the fact that some species may respond positively to increased disturbance. Furthermore, degradation of plant communities increased with density of people and livestock within the stands of Caatinga vegetation (i.e. additive impacts), supporting a causal connection between rural human populations and the degradation of Caatinga vegetation. Although Caatinga degradation (including desertification) has been widely discussed in the literature (Leal *et al.* 2005; Santos *et al.* 2011), here we offer tangible quantitative

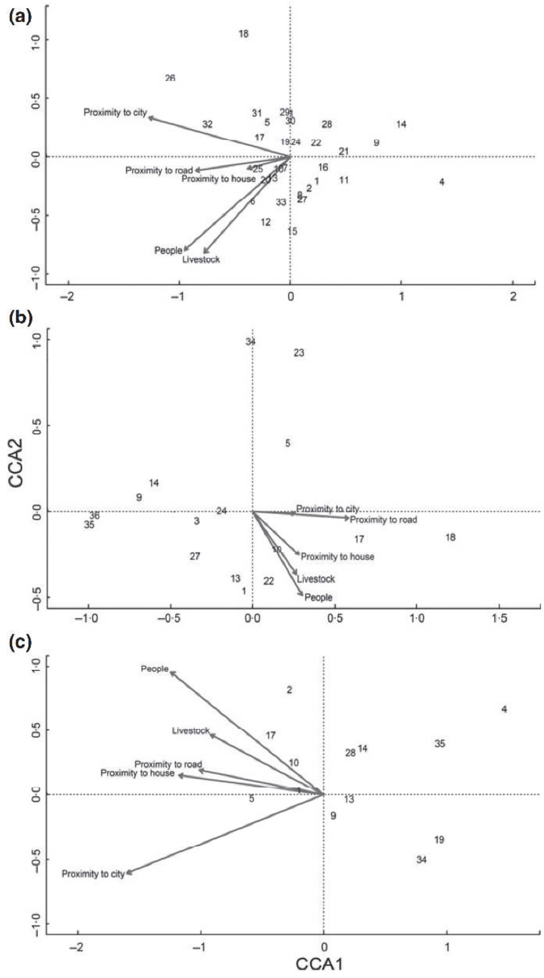

Fig. 5. CCA ordination diagrams displaying the plant–species relationships, in distinct ontogenetic stages (a – adults; b – saplings and c – seedlings), with the indicators of chronic disturbance (arrows) recorded at old-growth Caatinga forest sites in Parnamirim municipality, Pernambuco, Brazil. Each arrow points in the direction of maximum change of each disturbance indicator across the diagram, and its length is proportionate to the rate of change in this direction (i.e. disturbance indicators with longer arrows are more closely related to the pattern of species distribution shown in the ordination diagram). Plant species: 1. *Amburana cearensis* (Allemão) A.C. Sm., 2. *Anadenanthera colubrina* (Vell. Brenan), 3. *Aspidosperma pyrifolium* Mart., 4. *Bauhinia cheilantha* (Bong.) Steud., 5. *Cnidoscolus quercifolius* Pohl, 6. *Cnidoscolus vitifolius* (Mill.) Pohl, 7. *Cochlospermum vitifolium* (Willd.) Spreng., 8. *Commiphora leptophloeos* (Mart.) J.B. Gillett, 9. *Croton adamantinus* Müll. Arg., 10. *Croton sonderianus* Müll. Arg., 11. *Cynophalla hastata* (Jacq.) J. Presl, 12. *Dalbergia cearensis* Ducke, 13. *Erythroxylum pungens* O.E, Schulz, 14. *Fraunhofera multiflora* Mart., 15. *Guapira graciliflora* (Mart. ex J.A. Schmidt) Lundell, 16. *Guettarda angelica* Mart. ex Müll. Arg., 17. *Jatropha molissima* (Pohl) Baill., 18. *Jatropha ribifolia* (Pohl) Baill., 19. *Manihot pseudoglaziovii* Pax & K. Hoffm., 20. *Mimosa tenuiflora* Benth., 21. *Myracrodruon urundeuva* Allemão, 22. *Piptadenia stipulacea* (Benth.) Ducke), 23. *Poincianella microphylla* (Mart. ex G. Don) L.P. Queiroz, 24. *Poincianella pyramidalis* (Tul.) L.P. Queiroz, 25. *Sapium glandulosum* (L.) Morong, 26. *Schinopsis brasiliensis* Engl., 27. *Senegalia polyphylla* (DC.) Britton, 28. *Senna macranthera* (DC. Ex Collad) H. S. Irwin & Barbeby, 29. *Cordia trichotoma* (Vell.) Arráb. ex Steud., 30. *Ziziphus joazeiro* Mart., 31. *Cereus jamacaru* DC., 32. *Pilosocereus gounellei* (F.A.C. Weber) Byles & G.D. Rowley), 33. *Pilosocereus pachycladus* F.Ritter, 34. *Varronia leucocephala* (Moric.) J.S. Mill., 35. *Ditaxis desertorum* (Müll. Arg.) Pax & K. Hoffm., 36. *Combretum monetaria* Engl. & Diels, 37. *Jatropha mutabilis* Benth.

evidence (although indirect) for an important ecological impact that has gone unmeasured and little appreciated until now.

These findings reinforce the notions that (i) chronic disturbance can impose gradual (and hence unappreciated) but rather measurable degradation impacts on tropical forests, particularly in socio-ecological contexts marked by poverty in rural populations (Singh 1998; Sagar, Raghubanshi & Singh 2003; Martorell & Peters 2005), (ii) although human density has been considered an important driver of habitat loss in tropical countries (see Aide *et al.* 2013; Laurance, Sayer & Cassman 2014), it should be also considered a proxy of habitat degradation (Leal, Andersen & Leal 2014), and (iii) livestock is able to impose deleterious impacts on plant communities, particularly in dry forests (Carmel & Kadmon 1999; Leal, Vicente & Tabarelli 2003). Finally, as already demonstrated in the case of habitat loss and creation of forest edges in tropical forests (Lôbo *et al.* 2011; Tabarelli *et al.* 2012), few plant species benefit and may eventually proliferate in chronically disturbed habitats. This is particularly true for species with vegetative spread and high resprouting ability, such as *Croton sonderianus*.

Several processes seem to synergistically operate and underlie the simplification and homogenization of old-growth Caatinga stands under chronic disturbance. First, the potential combination of lower seed availability (Singh, Rawat & Garkoti 1997), failed seed dispersal by wild frugivores (Leal, Andersen & Leal 2014), lower germination rates and higher herbivory by livestock (Papachristou & Platis 2011; Marcora *et al.* 2013) could explain the lower diversity and simplification of seedling and sapling communities in more populated sites. In addition to bovines, goats are farmed extensively in the Caatinga, with stocking rates frequently exceeding governmental agency technical recommendations aimed at avoiding habitat degradation, as native plants (i.e. leaves, flowers, buds, fruits and bark) represent the main diet component of the goats (Pereira-Filho, Silva & Fontes 2013). Secondly, the replacement of disturbance-intolerant species, such as *B. cheilantha*, *S. macranthera*, *M. urundeuva* and *F. multiflora*, by disturbance-adapted species, such as *C. sonderianus*, *Mimosa tenuiflora* and *J. mollissima*, may permanently alter the structure and composition of plots with higher densities of people and livestock. Finally, local people have been reported to intensively collect plant resources for multiple purposes from medicine to famine alleviation (Lucena *et al.* 2008). We shall briefly discuss the collection of long-lived, hardwood species for rural fences and constructions (e.g. *M. urundeuva, F. multiflora, Anadenanthera colubrina, B. cheilantha* and *Piptadenia stipulacea*; Ramos *et al.* 2008), and vegetation harvesting for domestic and commercial firewood. In north-east Brazil, 25% of total energy demand is supplied by fuelwood and charcoal; nearly 10 million m^3 $year^{-1}$ of fuelwood and charcoal are obtained via deforestation of native vegetation (80%) and managed patches of Caatinga vegetation (1·6%), among other sources (Gariglio *et al.* 2010). Such permanent exploitation of forest resources by one of the largest human populations (in terms of density) living in a semi-arid region is likely to result in plant population collapses and the impoverishment of plant assemblages. On the other hand, disturbance-adapted but not useful species tend to proliferate and cause vegetation biomass decline due to reduced stem density.

CONSERVATION AND MANAGEMENT IMPLICATIONS

In many aspects, the Caatinga biota illustrates the multiple values and the challenges experienced by seasonally dry tropical forests and some semi-arid biotas. First, they are frequently recognized as Hotspots, Global Wilderness (Gil 2002) or important centres of endemism (Pennington, Lavin & Oliveira-Filho 2009). Secondly, they have been neglected in terms of conservation efforts and public policies devoted to sustainable development (Sanchez-Azofeifa *et al.* 2005; Santos *et al.* 2011). Most seasonally dry tropical forests still lack an effective network of protected areas (e.g. <2% of Caatinga territory is protected), with many strictly protected areas experiencing subsistence and economic activities, including low-input farming, livestock production, wood harvesting and plant collection (Leal *et al.* 2005). Thirdly, dry forests support a large density of increasing and usually poor human populations, which are heavily dependent on forest resources for their livelihoods (Blackie *et al.* 2014). Thereby, they are experiencing gradual, but persistent degradation processes, ranging from the extinction of endemic and emblematic species (e.g. the Spix's macaw in the Caatinga region) to alarming rates of desertification (Leal *et al.* 2005; MMA & IBAMA 2011). Finally, this fragile ecosystem is expected to confront drastic shifts in patterns of rainfall in response to global warming, thus scaling-up poverty-driven degradation (IPCC 2007; Blackie *et al.* 2014).

This research demonstrates the potential negative impacts caused by human-imposed chronic disturbance on Caatinga vegetation and reinforces the notion that disturbance resulting from an extractivism-based and subsistence economy is probably driving old-growth forest stands towards shrub-dominated secondary stands (Leal *et al.* 2005). These chronic, small-scale human disturbances might accumulate into major ecological impacts, ranging from biological impoverishment, as suggested here, to desertification. This possibility requires further investigation as it poses drastic challenges to reconcile human needs, biological conservation and provision of ecosystem services considering the current socio-ecological context experienced by tropical biotas. In many situations, the taxonomic impoverishment of tropical plant assemblages is associated with extirpation of key ecological plant groups (e.g. old-growth flora), reduced functional diversity and collapse of ecosystem services (Tabarelli, Lopes & Peres 2008).

Assuming increasing pressure on forest resources worldwide (Laurance, Sayer & Cassman 2014), chronic disturbance should not continue to be neglected across initiatives devoted to biodiversity conservation and rural development. Basically, we argue for (i) research and rural programmes able to support better practices in terms of land use and sustainable collection of forest resources, particularly in terms of livestock management and wood collection (i.e. improved land sharing via adaptive and mitigative approaches), (ii) improving governance and law enforcement in order to move forest extractivism towards sustainable standards, and (iii) expanding the coverage and effective implementation of strictly protected areas, that is the elimination of livestock and collection of forest products inside protected areas. Such commitment appears to be feasible in the face of increasing local and global concerns relative to the socio-ecological problems (see Melo *et al.* 2014). Unless issues of land sharing and land sparing are appropriately addressed in the Caatinga, human exploitation and habitat degradation will unavoidably lead to desertification and loss of this irreplaceable biome.

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Data accessibility

Data are available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.m7d8m (Ribeiro *et al.* 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Detailed Mantel test results description.

Table S1. Predictors of chronic disturbance measured and their range.

Table S2. Complete results of information-theoretic-based model selection and multimodel inference.

Table S3. Frequency of occurrence of each explanatory variable within the set of best models.

Appendix S1. Results of the Mantel test applied to test the sampled plots independency for each ontogenetic stage (adults, saplings and seedlings).

We applied a Mantel test with the package *vegan* for R version 3.0.1 (R Core Team 2013) to test for a significant correlation between the compositional similarity among plots (Bray-Curtis index) and the inter-plot distance matrix (one test per ontogenetic class). The Mantel test did not reveal a significant spatial autocorrelation in any of our datasets (adults: r =0·18, P=0·09; saplings: r =0·04, P = 0·29; seedlings: r =0·08, P =0·15), thus, we can consider the plots as independent samples.

Table S1. Proximate predictors of chronic disturbance measured in 30 plots at Caatinga old-growth forests in Parnamirim municipality, Pernambuco, Brazil.

Chronic disturbance predictors*	Mean (±SD)	Min	Max
Proximity to nearest house (km)	1·480	0·530	2·901
Proximity to nearest road (km)	0·356	0·003	1·423
Proximity to Parnamirim city (km)	6·494	2·498	16·530
Density of people leaving near the site (2 km)†	6·26	0	12
Density of livestock (2 km)‡	117·6	0	600

*A satellite image by the Advanced Land Observing Satellite (ALOS) was used to estimate the following indicators: proximity to nearest house, proximity to nearest road, and proximity to city as the reciprocal of distance from the center of each plot (km). The information about the density of people leaving near the site and density of livestock was obtained from interviews with 40 occupied-dwellings near studied plots.

†Corresponds to the number of persons registered in a buffer area of 2 km of radius from the center of each studied 50 m × 20 m plot.

‡Represents the density of livestock found in a buffer area of 2km of radius from the center of each studied 50 m × 20 m plot.

Table S2. Results of information-theoretic-based model selection and multimodel inference for species diversity (^{0}D, ^{2}D, abundance and *EF*) of plant communities considering three ontogenetic classes in the Caatinga forest, Parnamirim municipality, Brazil. We detailed the ΔAICc < 2 set of models. "X" indicates variable inclusion in each individual model.

Response variable*/ Ontogenetic class/ Models	Soil type	Proximity to house	Proximity to road	Proximity to city	People	Livestock	AIC$_c^f$	ΔAIC$_c^g$	w_i
^{0}D (species richness)									
Adults									
1				X		X	170·65	0·00	0·187
2				X			172·03	1·38	0·093
3		X		X		X	172·46	1·81	0·075
Saplings									
1					X		168·71	0·00	0·086
2							168·9	0·19	0·078
3				X			169·22	0·51	0·066
4			X	X			169·6	0·89	0·055
5					X	X	169·67	0·96	0·053
6			X				170·13	1·42	0·042
7			X		X		170·47	1·76	0·035
8	X			X			170·54	1·83	0·034
Seedlings									
1							149·84	0·00	0·106

2					X	149·86	0·02	0·105
3				X		150·19	0·35	0·080
4			X			150·99	1·15	0·059
5		X				151·64	1·80	0·043
6		X		X		151·76	1·92	0·040
^2D (abundant species)								
Adults								
1	X			X		124·98	0·00	0·106
2						125·68	0·70	0·075
3					X	125·73	0·75	0·073
4				X		126·07	1·09	0·061
5	X				X	126·54	1·56	0·048
6			X			126·89	1·91	0·041
7	X		X	X		126·97	1·99	0·039
Saplings								
1	X			X		116·10	0·00	0·098
2	X				X	116·42	0·32	0·084
3			X			116·48	0·38	0·081
4	X	X		X		116·91	0·81	0·065
5	X			X	X	117·89	1·79	0·040
Seedlings								
1						116·14	0·00	0·127

2					X		116·91	0·77	0·086
3						X	117·42	1·28	0·067
4				X			117·47	1·33	0·065
5	X						117·99	1·85	0·050
6			X				118·11	1·97	0·036
Abundance									
Adults	X	X		X	X	X	768·78	0·00	0·756
1									
Saplings									
1	X	X					226·65	0·00	0·170
2	X	X				X	227·32	0·67	0·122
3	X						227·70	1·05	0·100
4	X	X			X		228·25	1·60	0·076
Seedlings									
1							159·83	0·00	0·118
2					X		159·97	0·14	0·110
3	X						161·68	1·85	0·047
4						X	161·80	1·97	0·046
Evenness factor									
Adults									
1						X	-67·36	0·00	0·105
2		X				X	-67·12	0·24	0·093

3		X			X		-67·05	0·31	0·090
4				X		X	-66·14	1·21	0·057
5		X			X	X	-65·52	1·84	0·042
6					X		-65·41	1·95	0·039
Saplings									
1		X				X	-12·63	0·00	0·151
2		X	X			X	-11·31	1·32	0·077
3		X			X	X	-11·06	1·57	0·068
4					X	X	-10·69	1·93	0·065
Seedlings									
1							-19·29	0·00	0·162
2	X						-18·60	0·69	0·115

*Response variables: (^{0}D) species richness, (^{2}D) inverse Simpson concentration, stem abundance and the community evenness·

Table S3. Frequency of occurrence (numerator) of each explanatory variable within the set of best models*.

Response variable per ontogenetic class†	Explanatory variables					
	Soil type	Proximity to house	Proximity to road	Proximity to city	People	Livestock
^{0}D adults	0/3 (0 %)	1/3 (33 %)	0/3 (0 %)	3/3 (100 %)	0/3 (0 %)	2/3 (66 %)
^{0}D saplings	1/8 (13 %)	1/8 (13 %)	3/8 (38 %)	3/8 (38 %)	3/8 (38 %)	1/8 (13 %)
^{0}D seedlings	0/6 (0 %)	0/6 (0 %)	2/6 (34 %)	1/6 (17 %)	2/6 (34 %)	1/6 (17 %)
^{2}D adults	0/7 (0 %)	3/7 (43 %)	0/7 (0 %)	2/7 (29 %)	3/7 (43 %)	2/7 (29 %)
^{2}D saplings	0/5 (0 %)	4/5 (80 %)	1/5 (20 %)	1/5 (20 %)	3/5 (60 %)	2/5 (40 %)
^{2}D seedlings	1/6 (17 %)	0/6 (0 %)	1/6 (17 %)	1/6 (17 %)	1/6 (17 %)	1/6 (17 %)
Abundance adults	1/1 (100 %)	1/1 (100 %)	0/1 (0 %)	1/1 (100 %)	1/1 (100 %)	1/1 (100 %)
Abundance saplings	4/4 (100 %)	3/4 (75 %)	0/4 (0 %)	0/4 (0 %)	1/4 (25 %)	1/4 (25 %)
Abundance seedlings	1/4 (25 %)	0/4 (0 %)	0/4 (0 %)	0/4 (0 %)	1/4 (25 %)	1/4 (25 %)
EF adults	0/6 (0 %)	3/6 (50 %)	0/6 (0 %)	1/6 (17 %)	3/6 (50 %)	4/6 (67 %)
EF saplings	0/4 (0 %)	3/4 (75 %)	1/4 (25 %)	0/4 (0 %)	2/4 (50 %)	4/4 (100 %)
EF seedlings	1/2 (50 %)	0/2 (0 %)	0/2 (0 %)	0/2 (0 %)	0/2 (0 %)	0/2 (0 %)
Total	9/56 (16 %)	19/56 (34 %)	8/56 (14 %)	13/56 (23 %)	20/56 (36 %)	20/56 (36 %)

*The set of best models for each response variable refers to those models with ΔAICc < 2 (see Table S2). The total number of models within each set is indicated in the denominator (percentages in parentheses).

†Response variables: species richness (^{0}D), inverse Simpson concentration (^{2}D), and community evenness (EF).

CAPÍTULO 3

Phylogenetic impoverishment of plant communities following chronic human disturbances in the Brazilian Caatinga

MANUSCRITO ACEITO PARA PUBLICAÇÃO NO PERIÓDICO ECOLOGY

Article – Ecology

Running head: Disturbance and phylogenetic diversity

Phylogenetic impoverishment of plant communities following chronic human disturbances in the Brazilian Caatinga

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Abstract

Chronic disturbances, such as selective logging, firewood extraction and extensive grazing, may lead to the taxonomic and phylogenetic impoverishment of remaining old-growth forest communities worldwide; however, the empirical evidence on this topic is limited. We tested this hypothesis in the Caatinga vegetation – a seasonally dry tropical forest restricted to northeast Brazil. We sampled 11653 individuals (adults, saplings and seedlings) from 51 species in 29 plots distributed along a gradient of chronic disturbance. The gradient was assessed using a chronic disturbance index (CDI) based on five recognized indicators of chronic disturbances: proximity to urban center, houses and roads and the density of both people and livestock. We used linear models to test if mean effective number of lineages, mean phylogenetic distance and phylogenetic dispersion decreased with CDI and if such relationships differed among ontogenetic stages. As expected, the mean effective number of lineages and the mean phylogenetic distance were negatively related to CDI, and such diversity losses occurred irrespective of ontogeny. Yet the increase in phylogenetic clustering in more disturbed plots was only evident in seedlings and saplings, mostly because clades with more descendent taxa than expected by chance (e.g., Euphorbiaceae) thrived in more disturbed plots. This novel study indicates that chronic human disturbances are promoting the phylogenetic impoverishment of the irreplaceable woody flora of the Brazilian Caatinga forest. The highest impoverishment was observed in seedlings and saplings, indicating that if current chronic disturbances remain, they will result in increasingly poorer phylogenetically forests. This loss of evolutionary history will potentially limit the capacity of this ecosystem to respond to human disturbances (i.e., lower ecological resilience) and particularly their ability to adapt to rapid climatic changes in the region.

Key words: anthropogenic disturbance; biodiversity; community assembly; environmental filtering; forest-dependent human populations; ontogenetic response; phylogenetic diversity and structure; wood plant assemblage; seasonally dry tropical forest; semiarid ecosystem.

INTRODUCTION

Chronic human disturbances, such as the frequent and continuous removal of small portions of biomass (Singh 1998), represent a geographically-widespread and effective threat to tropical biodiversity, particularly in the socioecological context marked by the presence of dense, forest-dependent human populations (see Forest Peoples Programme 2012). The livelihoods of millions of people throughout the tropics currently depend on forest products obtained in areas considered as either biodiversity hotspots or wildernesses (Singh et al.1997, Schmidt and Ticktin 2012). This is particularly the case of seasonally dry tropical forests (SDTF), which are amongst the most endangered tropical forests (Janzen 1988, Oatham and Boodram 2006). Although large tracts of SDTF are experiencing increasing levels of habitat loss and fragmentation (i.e., acute disturbances), chronic disturbances represent a subtle but pervasive source of disturbance in this ecosystem that leads to the habitat degradation and biological impoverishment of the remaining SDTF (Mahiri and Howorth 2001, Ribeiro et al. 2015, Arroyo-Rodríguez et al. 2015).

Although the available information is still scarce and there is a lack of synthesis, research during the last decades has demonstrated some important impacts of chronic disturbances on plant assemblages (Sagar et al. 2003, Shaanker et al. 2004, Ribeiro et al. 2015). Reduced recruitment, population collapse and taxonomic impoverishment of plant assemblages have been reported, in addition to the proliferation of disturbance-adapted native and exotic species (Sagar et al. 2003, Marvier et al. 2004, Ribeiro et al. 2015). Disruptions of plant-animal interactions, such as seed dispersal (Leal et al. 2014) and plant-protection against herbivores (Leal et al. 2015), have also been reported in sites experiencing overgrazing by livestock and firewood collection. Furthermore, forest stands experiencing intense fodder extraction and small-scale slash-and-burn agriculture usually experience soil degradation and biomass collapse as trees are replaced by shrubs and grasses (Tripathi and Singh 2012, Silvério et al. 2013). Nevertheless, to our knowledge, the impact that chronic disturbances may have on the phylogenetic dimension of plant diversity has never been investigated.

In this sense, the consequences of biodiversity loss can be predicted from evolutionary history by assessing the differences in the phylogenetic diversity and structure of plant assemblages in human-modified landscapes (Cardinale et al. 2012, Santos et al. 2014*a*, Munguía-Rosas et al. 2014). This information may be useful to guide conservation priorities for specific taxa (e.g., Pavoine et al. 2005). Also, this phylogenetic information may help to infer potential mechanisms of community assembly in these landscapes (Webb et al.2002, Cavender-Bares et al. 2009, Cavender-Bares and Reich 2012, Roeder et al. 2014) and estimate the impact that evolutionary relationships among species may have on ecological processes and ecosystem functioning (Webb et al. 2002, Cadotte et al 2008).

Human disturbances may affect the phylogenetic structure and diversity of local communities in contrasting ways, depending on the level of floristic drift following disturbance (see Arroyo-Rodríguez et al. 2012). If the balance between extirpation and proliferation of particular lineages results in the co-occurrence of more related taxa, communities in disturbed sites should be phylogenetically poorer and more clustered than those in undisturbed sites (Santos et al. 2010 and 2014*a*, Munguía-Rosas et al. 2014). On the other hand, if the outcome of the floristic reorganization results in the co-occurrence of distantly related taxa, communities will be phylogenetically more diverse and disperse in disturbed sites. A third possibility is that community reorganization does not result in significant changes in phylogenetic structure and diversity because proliferating taxa are as disperse across the phylogeny as decreasing taxa (Arroyo-Rodríguez et al. 2012, Benítez-Malvido et al. 2014). Besides limited and mixed, the empirical evidence available so far relies on plant phylogenetic responses to acute anthropogenic disturbances such as deforestation and forest fragmentation (Santos et al. 2010 and 2014*a*, Arroyo-Rodríguez et al. 2012, Andrade et al. 2015). Also, all but one (Benítez-Malvido et al. 2014) evaluate tropical rainforests, and with the exception of the study by Arroyo-Rodríguez et al. (2012), only assess adult trees (diameter at breast height (DBH) ≥ 10 cm), which may mask long-term responses to disturbance. Thus, further studies that include seedlings and saplings are needed to attain a comprehensive understanding of the impact that chronic disturbances may have on the phylogenetic dimension of plant assemblages in SDTF.

We investigated the phylogenetic diversity and structure of woody plant assemblages in distinct ontogenetic stages (adults, saplings and seedlings) in the Brazilian Caatinga vegetation. This SDTF sustains over 23 million people (11.8% of the Brazilian population) and is one of the most populated semi-arid regions, with 26 inhabitants km^{-1} (INSA 2012). As a consequence, about 50% of the Caatinga original forest cover is composed of secondary and old-growth forests (MMA and IBAMA 2011). The remaining forest experiences several chronic disturbances, including fuelwood collection, fodder extraction, charcoal production, overgrazing by livestock and extraction of non-timber forest products (Pereira-Filho et al. 2007, Ramos et al. 2008).

We tested whether chronic disturbance leads to the phylogenetic impoverishment of plant assemblages using a large database of Caatinga vegetation. Because it is well known that different phylogenetic indices can lead to different and even contradicting results (e.g., Roeder et al. 2014), we used four complementary indices of phylogenetic diversity and structure to achieve accurate and more confidence interpretations (Winter et al. 2013, Roeder et al. 2014). SDTFs represent stressful environments for most drought-intolerant tropical plants (Engelbrecht et al. 2007, Santos et al. 2014*b*), and it is reasonable to expect that such environmental stress increases with chronic disturbance (Ribeiro et al. 2015). Assuming that environmental filtering operates on evolutionary conserved traits and ecological interactions (Webb et al. 2002, Gómez et al. 2010), we would expect that closely related species would occur together more frequently than expected by chance (phylogenetic clustering), thus reducing plant phylogenetic diversity in sites facing higher disturbance pressure (Webb et al. 2002, Cavender-Bares et al. 2009, Vandelook et al. 2012, González-Caro et al. 2014). We also expect that such phylogenetic impoverishment would occur across all ontogenetic stages, being stronger in seedling and sapling assemblages as these ontogenetic stages are often more vulnerable to chronic disturbance (see Singh et al.1997, Van Lent et al. 2014; Ribeiro et al. 2015).

METHODS

Study area

The Caatinga is a mosaic of SDTFs and scrub vegetation that encompasses 826411 km² restricted to Brazil (MMA and IBAMA 2011). The study area is located in the Parnamirim municipality, Pernambuco state, northeast Brazil (8°5’26’’S; 39°34’41’’W; see Appendix A). The climate is semi-arid, with an average temperature of 26ºC and most of the 431 mm mean annual rainfall is received between January and May (IBGE 1985). Soils are predominantly non-calcic brown soils (clay soil), regosols and planosols (sandy soils) (IBGE 1985). Anthropogenic activities since the 16th century in the Parnamirim municipality (e.g., extensive grazing and temporary farming) have resulted in the loss of ca. 45% of the municipality forest cover, and the remaining 55% faces gradual chronic disturbances (e.g., extraction of forest products for medicinal purposes, animal and human feeding, firewood collection and extensive livestock) (Ribeiro et al. 2015).

The study was carried out in 29 50 × 20-m plots (Appendix A) established in a 220 km^2 landscape dominated by old-growth vegetation exposed to chronic disturbances. For each plot we recorded five indicators of chronic disturbance that have been described in tropical forests studies as important drivers of chronic human disturbances (Sagar et al. 2003, Martorell and Peters 2005, Leal et al. 2014, Ribeiro et al. 2015): (i) proximity to the nearest house (PH); (ii) proximity to the nearest road (PR); (iii) proximity to the urban center (PUC); (iv) density of people living near the plot (DP); and (v) density of livestock near the plot (DL). We opted for proxies instead of direct measures of logging, hunting, cutting and overgrazing because these disturbances are not easily quantified and accessed at the landscape scale (Acharya and Dangi 2009, Arroyo-Rodríguez et al. 2015).

We quantified PH, PR and PUC as the reciprocal distance from the center of each plot using satellite imagery from the Advanced Land Observing Satellite (ALOS). To estimate DP and DL we first identified in the satellite imagery all dwellings near the plots. We identified 40 dwellings and we collected information on the number of people living in, and the number of stock managed. This information was obtained through interviews done with each householder. We then used the ALOS satellite imagery to estimate DP and DL, considering the interview data in a 2-km buffer area from the center of each plot (i.e., within an area of 1256 ha). We used this buffer size because local households assumed that the maximum dispersal distance of grazing animals falls within two km.

Chronic disturbance index

Following Martorell and Peters (2005), all these disturbance indicators (i.e., PH, PR, PUC, DP and DL) were combined in a single Chronic Disturbance Index (CDI) through a principal component analysis (PCA) performed in R software (version 3.0.1, R Core Team 2013), using the package stats. Axis 1 of the PCA explained 41% of the variation of these indicators and was significantly correlated (mean correlation coefficients: $r = 0.66$, $P < 0.05$)

with DP, DL and PH (see Appendix B and C). Thus, because DP and DL seems to be the main factors driving changes in plant communities in the region, with a stronger negative impact on seedling and sapling diversities (Ribeiro et al. 2015), this index is an accurate descriptor of important chronic human disturbances in the region. The scores of PCA axis 1 were rescaled from 0 to 100, representing the least and most disturbed sites, respectively (Martorell and Peters 2005).

Plant community sampling

In this study we surveyed trees and shrubs of plant assemblages during the rainy seasons of 2012 and 2013. We sampled adults, saplings and seedlings of these life forms in each plot to do the comparisons among ontogenetic stages. We defined adults as individuals with diameter at soil height (DSH) > 3 cm and height > 1.5 m; saplings were individuals with DSH < 3 cm and height between 1 and 1.5 m; and seedlings were individuals with height < 1 m (Rodal et al. 1992, Felfili et al. 2005). We recorded all adults found in each 50 × 20-m plot. Saplings were recorded in three 5 × 5-m subplots that were located in the center of each 50 × 20-m plot and separated by 10 m. Seedlings were sampled in 2 × 2-m subplots located in the center of each sapling subplot (see Appendix D for more information regarding the outcome of the differences in plot size on sample completeness per ontogenetic stage). All plants were identified to species level by comparing the sampled species with samples from the Federal University of Pernambuco herbarium. The botanical nomenclature followed APG III (Bremer et al. 2009).

Phylogenetic diversity and structure

For each plot we measured four complementary abundance-based phylogenetic metrics (Webb et al. 2002, Webb et al. 2008, Chao et al. 2010; see Appendix E): mean phylogenetic distance (MPD), net related index (NRI), and mean phylogenetic diversity of order q through T years [i.e., ${}^{q}\overline{D}(T)$] considering orders 0 [${}^{0}\overline{D}(T)$] and 2 [${}^{2}\overline{D}(T)$], where ${}^{q}\overline{D}(T)$ quantifies the mean effective number of lineages as a function of evolutionary time, T. The parameter q refers to the value attributed to each node's relative abundance (Chao et al. 2010). When q = 0, only species richness (presence/absence) is considered, and T represents the age of the first node (Chao et al. 2010).Yet when q = 2, only dominant or very abundant species are considered, and hence, $^{2}\overline{D}(T)$ quantifies the mean effective number of very abundant lineages as a function of evolutionary time T (Chao et al. 2010). $^{q}\overline{D}(T)$ satisfies the replication principle, which is required in biodiversity assessments as it considers the uniqueness of each species found in an assemblage (Chao et al. 2010). MPD, on the other hand, measures the mean average distance (in millions of years) among two random individuals in a specific sample, considering conspecifics, and the NRI is a standardized metric of MPD and reflects whether taxa in a sample are more phylogenetically clustered or dispersed than expected by chance (Webb et al. 2002, 2008, Vamosi et al. 2009).

To obtain these phylogenetic metrics, we first produced a full species list based on the APG III (Bremer et al. 2009) classification, after identifying all species of adults, saplings and seedlings recorded across the 29 plots. We then assembled a list of 51 species belonging to 46 genera and 23 families, considering the three ontogenetic stages (see Supplement 1), and constructed a regional time-calibrated phylogeny by estimating the continuous phylogenetic distance between the sampled species using Bayesian inference and Markov chain Monte Carlo (MCMC) methods (see Appendix F and G for more details of phylogeny construction methods). Based on the time-calibrated phylogeny, we obtained $^{q}\overline{D}(T)$ for q = 0 and q = 2 using the program PhD (Chiu and Chao 2012) that runs in the software R 3.0.1 (R Core Team 2013). We also used the time-calibrated phylogeny to calculate the MPD and NRI metrics using the COMSTRUCT function of Phylocom 4.2 adopting the switch '-a' to weight phylogenetic metrics by taxa abundances. To evaluate if the phylogenetic structure within each plot differed from the phylogenetic structure expected by chance, we compared observed

MPD to the expected MPD for 999 randomly generated null communities (MPD.rnd) using null model 2 of Phylocom 4.2. This model has the advantage of maintaining the species richness and abundance structure within communities, and assumes that all species of the pool have the same chance of colonizing any given plot (Arroyo-Rodríguez et al. 2012). After computing observed and expected MPD for each sample, we calculated the NRI metric. NRI is defined as [-1 (MPD – PD.rnd)/MPD.sd)], where MPD.sd represents the standard deviation of MPD.rnd from the 999 null communities (Webb et al. 2002, 2011). Positive values of NRI indicate phylogenetic clustering, while negative values represent phylogenetic overdispersion (Vamosi et al. 2009).

Finally, we used the NODESIG function of Phylocom 4.2 to determine which clades contributed significantly to any non-random phylogenetic structure of ontogenetic stages (adults, saplings and seedlings) (see Webb et al. 2011 for more details of this function). The NODESIG procedure verifies the occurrence of nodes with significantly more or less descendent taxa than expected by chance. Nodes that present more or fewer descendent taxa than expected by chance are highlighted as ‘sigmore’ or ‘sigless’, respectively, and allow us to identify clades responsible for the non-random phylogenetic structure in a sample (Webb et al. 2011).

Data analyses

We used linear models to test whether ${}^{0}\overline{D}(T)$, ${}^{2}\overline{D}(T)$ and MPD decreased and NRI increased with CDI, and whether such relationships differed among ontogenetic stages. We included plot relative abundance as a covariable in the models to control for differences in abundance across plot sizes. These analyses were done in JMP 8 (SAS Institute Inc.) with the standard least squares personality and the Gaussian distributions for all response variable errors after checking that they followed a Normal distribution with Shapiro-Wilk tests (see Appendix H). We also assessed if the species declining in more disturbed plots were more distantly related than those species proliferating in such plots. To do this, we correlated the CDI with the abundance of each species. These analyses were carried out using the software R 3.0.1 (R Core Team 2013), using the package Hmisc.

RESULTS

We recorded 10634 adult plants (362 ± 92.1 stems per plot; mean ± SD) belonging to 51 species (18.5 ± 3.6) (see Appendix I). For the sapling assemblage, we recorded 717 stems (11.6 ± 6.5) from 40 species (6.7 ± 2.2) (Appendix I). In the seedling community, we recorded 302 stems (10.6 ± 3.5) from 34 species (5.1 ± 1.8) (Appendix I). The most representative families in the three ontogenetic classes were Euphorbiaceae and Fabaceae, with 10–13 species per ontogenetic class. When considering species richness, the mean effective number of distinct lineages expected to the height of the phylogenetic tree [${}^{0}\overline{D}(T)$] varied among ontogenetic stages, being significantly higher in adults (10 ± 1.5 lineages per plot), than in saplings (4.9 ± 1.4 lineages) and seedlings (4.3 ± 1.2 lineages) (Table 1). When considering the number of very abundant or dominant species [${}^{2}\overline{D}(T)$], all ontogenetic stages showed a similar mean effective number of lineages: 2.3 ± 0.8 lineages per plot in adults, 2.5 ± 0.7 lineages in saplings, and 2.8 ± 0.8 lineages in seedlings (Table 1). The mean phylogenetic distance (MPD) and net relatedness index (NRI) was also similar in all ontogenetic classes. MPD averaged 106.1 ± 33.3 million years in adult assemblages, 120 ± 44.5 million years in sapling assemblages, and 126.4 ± 51.7 million years in seedling assemblages, whereas NRI averaged 2.6 ± 1.0 in adults, 1.4 ± 1.6 in saplings, and 1.8 ± 1.7 in seedlings (Table 1).

As expected, MPD, ${}^{0}\overline{D}(T)$ and ${}^{2}\overline{D}(T)$ were negatively related to CDI, and such diversity losses occurred irrespective of ontogeny (Fig. 1; Table 2; Appendix J). Yet the increase in phylogenetic clustering in more disturbed plots was only evident in seedlings and saplings (Fig. 1; Table 2; Appendix J).

Adult assemblages presented significantly non-random phylogenetic structures with respect to the regional species pool in 18 out of 29 (69%) plots (see Appendix K). Within these 18 plots we identified 13 out of 104 internal nodes with more or less descendants than expected by chance (Appendix K). These nodes were composed of major clades such as Fabids, Rosids and Malvids, as well as lower clades such as order and family (e.g., Brassicales, Malvales and Fabaceae) (Appendix K). In adults, we did not find specific ‘sigless’ or ‘sigmore’ nodes exclusively related to either the most or least disturbed sites (Appendix K).

Considering sapling and seedling assemblages, we observed a significantly non-random phylogenetic structure in 14 and 15 plots, respectively (Appendix K). For these plots, saplings and seedlings had 15 and 12 out of 104 internal nodes, respectively, with more descendent taxa than expected by chance (Appendix K). In general, these nodes were evenly distributed along the disturbance gradient, with exception of the Euphorbiaceae and its descendent taxa, which occurred frequently in the most disturbed plots (CDI > 50) (Appendix K).

Additionally, we verified that some families such as Capparaceae and Celastraceae, which are represented by a few species, did not occur in the more disturbed sites, considering all ontogenetic stages (Fig. 2). When analyzing the relationships between species abundance and disturbance, distantly related taxa such as *Fraunhofera muiltiflora* (Celastraceae), *Varronia leucocephala* (Boraginaceae), *Myracrodruon urundeuva* (Anacardiaceae) and *Bauhinia cheilantha* (Fabaceae), were negatively and significantly related to CDI, whereas closely related species such as *Croton sonderianus*, *Jatropha ribfolia* and *J. mollissima* (all within the Euphorbiaceae family) were positively and significantly related to CDI (Appendix L).

Discussion

Chronic human disturbances have been increasingly considered as important drivers of habitat degradation (Singh 1998, Sagar et al. 2003, Martorell and Peters 2005, Leal et al. 2014, Arroyo-Rodríguez et al. 2015), but until now the impact that chronic disturbances might have on the phylogenetic diversity and structure of plant assemblages was unknown. As expected, our analyses indicate that the mean phylogenetic distance (MPD) and mean effective number of lineages [$^0\overline{D}(T)$ and $^2\overline{D}(T)$] were negatively related to CDI, and that such a loss of evolutionary history occurred across all ontogenetic stages. This novel finding suggests that local extirpation of plant species across the disturbance gradient (see Ribeiro et al. 2015) does not occur randomly or uniformly, but in a clustered manner throughout the phylogenetic tree. This was confirmed by the metric of phylogenetic clustering (NRI), which increased in more disturbed plots especially for sapling and seedlings.

The decrease of phylogenetic diversity and increase of phylogenetic clustering in human-modified tropical landscapes has been demonstrated in other studies, but only in response to acute disturbances, such as forest loss and fragmentation (e.g., Santos et al. 2010 and 2014*a*; Munguía-Rosas et al. 2014, Andrade et al. 2015). For example, Munguía-Rosas et al. (2014) found that phylogenetic plant diversity (i.e., individuals with DBH > 1.6 cm) is 19% greater and more overdispersed in a continuous forest when compared to an adjacent naturally fragmented forest in the Yucatan Peninsula, Mexico. Santos et al. (2014*a*) also documented the loss of tree phylogenetic diversity (DBH > 10 cm) and the reduction in phylogenetic evenness in a fragmented tropical landscape in central Amazonia. Finally, in a hyper-fragmented landscape of the Brazilian Atlantic forest, Santos et al. (2010) show that tree phylogenetic diversity (DBH > 10 cm) is 11% lower in forest edges than in old-growth forest interior areas. Overall, these phylogenetic responses may be the result of several mechanisms. For example, higher competitive exclusion between sister taxa in conserved forests may favor the co-occurrence of less related taxa in these forests (see Roeder et al. 2014). Also, environmental filtering, which may operate on traits with significant phylogenetic signals (see Willis et al. 2010), can allow closely related species to occur together more frequently than expected by chance in disturbed forests (Munguía-Rosas et al. 2014, Santos et al. 2014*a*).

As we have used proxies instead of direct measures of chronic disturbances, we cannot test which are the main proximate and underlying mechanisms that promoted the observed shifts in phylogenetic diversity and structure. However, it is well known that plant recruitment in SDTF is driven mainly by abiotic filters imposed by seasonality and frequent droughts (Ceccon et al. 2006), thus supporting niche conservatism and life-history convergence at the community level (Pennington et al. 2009). The continuous removal of plant individuals and biomass is expected to impose additional recruitment and dispersal limitations; first, because it can reduce population sizes (Endress et al. 2004) and seed production (Singh et al. 1997), and second, because such removal can alter vegetation structure (e.g., reduced stem density, greater canopy openness) and microclimatic conditions (e.g., increased habitat desiccation; Kumar et al. 2008). Although all these alterations can reduce the recruitment of many native plant species (Endress et al. 2004), some exotic and native disturbance-adapted species can proliferate in degraded sites (Marvier et al. 2004, Ribeiro et al. 2015).

In this sense, it is clear from our results that the balance between extirpation and proliferation of particular lineages resulted in the co-occurrence of more related taxa in disturbed sites. For example, complete lineages such as the Capparaceae (with 2 species) and Celastraceae (with 1 species) families disappeared in sites with a higher degree of disturbance

(Fig. 2). The loss of these families represents the loss of evolutionary history. The Celastraceae family, especially, is represented by just one species: *Fraunhofera multiflora*, whose genus is monotypic and endemic to the Brazilian Caatinga (Simmons et al. 2012). The abundance of several distantly related species such as *F. multiflora* (Celastraceae), *Myracrodruon urundeuva* (Anacardiaceae) and *Piptadenia stipulaceae* (Fabaceae) was also negatively and significantly related to the chronic disturbance index (Appendix L). These lineages are known to be vulnerable to chronic disturbances because they have high wood density (> 0.8 g/cm³) and are good biofuel species appreciated by local people as firewood, charcoal and fences (Ramos et al. 2008).

In contrast, many species within the species-rich Euphorbiaceae family, such as those within the *Croton* and *Jatropha* genera, incremented their frequency and abundance in more disturbed plots (also see Ribeiro et al. 2015). The abundance of *Croton sonderianus* and *Jatropha ribifolia* (Euphorbiaceae) was also positively related to the disturbance index (Appendix L). Euphorbiaceae is the second most common family in the Caatinga flora (103 species, Moro et al. 2014), and many species within this family (e.g., *Croton sonderianus* and *Cnidoscolus quercifolius*) are recognized as aggressive colonizers of human-disturbed habitats (Carvalho et al. 2001). The mechanisms related to these species' ability to colonize disturbed habitats are poorly explored, but are probably related to their degree of relatedness that make this species more ecologically similar and able to compete more strongly than distant relatives (Cahill et al. 2008, but see Fritschie et al. 2014).

Conclusions and implications for conservation

Chronic human disturbances can negatively affect the biological diversity of tropical biotas at the population, community and ecosystem levels (Sagar et al. 2003; Shaanker et al. 2004). In fact, there is ample anecdotal evidence in the Caatinga literature establishing causal connections between overexploitation of long-lived hardwood species, intense firewood collection, overgrazing by goats, slash-and-burning agriculture and the emergence of degraded habitats, ranging from impoverished forest assemblages to desertified areas (Leal et al. 2005, MMA and IBAMA 2011). Here we document, for the first time, that chronic disturbances also promote the phylogenetic impoverishment of the irreplaceable woody flora of the Brazilian Caatinga forest. The greatest impoverishment was observed in seedlings and saplings, thus indicating that if current chronic disturbances remain, they will result not only in taxonomically poorer plant assemblages (Ribeiro et al. 2015), but also in phylogenetically impoverished forests.

Such phylogenetic impoverishment will limit the capacity of the ecosystem to respond to human disturbances (i.e., lower ecological resilience) (Willis et al. 2008). Hence, to retain the evolutionary capital of the Caatinga, we should promote strategies that include: (i) investments in research and implementation of rural programs able to promote better practices in terms of sustainable forest resource use and livestock management; (ii) government incentives that involves programs and funds to restore disturbed sites; (iii) law enforcement with a view to move forest extractivism towards sustainable standards; and (iv) increase the coverage of strictly protected areas, considering the phylogenetic diversity, while restricted future chronic disturbances in these areas.

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Table 1. Differences in plant phylogenetic metrics among ontogenetic classes (adult trees, saplings and seedlings) sampled in 29 sites from the Brazilian Caatinga forest, Parnamirim municipality, Pernambuco, Brazil. Different letters indicate significant differences among classes after post hoc comparisons (Tukey tests).

Ontogenetic stage	Phylogenetic metric							
	$^{0}\overline{D}(\mathrm{T})$		$^{2}\overline{D}(\mathrm{T})$		MPD		NRI	
	Mean ± SD	Max – Min	Mean ± SD	Max – Min	Mean ± SD	Max – Min	Mean ± SD	Max – Min
Adults	10.0^{a} ± 1.5	13.0 – 7.1	2.3^{a} ± 0.8	5.1 – 1.3	106.1^{a} ± 33.3	184.1–50.0	2.7^{a} ± 1.1	4.7 – 0.3
Saplings	4.9^{b} ± 1.4	7.2 – 1.3	2.5^{a} ± 0.7	4.1 – 1.0	120.0^{a} ± 44.5	191.1 – 22.7	1.7^{a} ± 1.8	6.1 – (-0.8)
Seedlings	4.3^{b} ± 1.2	7.0 – 1.9	2.8^{a} ± 0.8	4.2 – 1.3	126.5^{a} ± 51.7	203.9 – 15.6	1.8^{a} ± 1.8	5.2 – (-0.85)

Table 2. Results of linear models fitted to test the effect of chronic disturbance index on phylogenetic metrics of plant assemblages (adults, saplings and seedlings) from the Brazilian Caatinga vegetation, Parnamirim municipality, Pernambuco, Brazil†. Phylogenetic metrics: ${}^{0}\overline{D}(\mathrm{T})$ - mean phylogenetic diversity of total lineages, ${}^{2}\overline{D}(\mathrm{T})$ - mean phylogenetic diversity of dominant lineages, MPD - mean phylogenetic distance and, NRI - nearest relatedness index. Model factors codes: CDI – chronic disturbance, OS - ontogenetic stage, A – stem relative abundance of the plot.

	Whole model		Model factors			
Phylogenetic metric	R^2_{adj}	*F*	CDI	OS	A	CDI × OS
${}^{0}\overline{D}(\mathrm{T})$	0.78	51.58*	6.36*	7.26*	$2.86^{\text{n.s.}}$	$0.66^{\text{n.s.}}$
${}^{2}\overline{D}(\mathrm{T})$	0.12	2.96*	5.99*	$0.29^{\text{n.s.}}$	$0.67^{\text{n.s.}}$	$0.14^{\text{n.s.}}$
MPD	0.21	4.93*	23.65*	$0.09^{\text{n.s.}}$	$0.38^{\text{n.s.}}$	$0.84^{\text{n.s.}}$
NRI	0.18	4.16*	7.33*	$1.27^{\text{n.s.}}$	$0.76^{\text{n.s.}}$	5.63*

†We indicate the *F* values and significance level ($^{\text{n.s.}}P > 0.05$;* $P < 0.05$). Degrees of freedom: whole model (6,86), CDI (1,86), OS (2,86), A (1,86) and CDI×OS (2,86).

Figure legends

FIG. 1. Relationships between each phylogenetic metric and the chronic disturbance index in old-growth Caatinga forests in Parnamirim municipality, Brazil. The ‘r’ values in each line are the Pearson’s correlation coefficient used to illustrate the strength of relationships between phylogenetic metrics by ontogenetic stage with chronic disturbance.

FIG. 2. Relationships between adults’ (A), saplings’ (B) and seedlings’(C) relative individual densities per plant family and the chronic disturbance index. Families acronyms - Ana: Anacardiaceae; Apo: Apocynaceae; Bix: Bixaceae; Bor: Boraginaceae; Bur: Burseraceae; Cac: Cactaceae; Cap: Capparaceae; Cel: Celastraceae; Com: Combretaceae; Eup: Euphorbiaceae; Ery: Erythroxylaceae; Fab; Fabaceae; Nyc: Nyctaginaceae; Mal: Malvaceae; Ola: Olacaceae; Rha; Rhaminaceae; Rub; Rubiaceae; Sal: Salicaceae;Ver: Verbenaceae.

Figure 1.

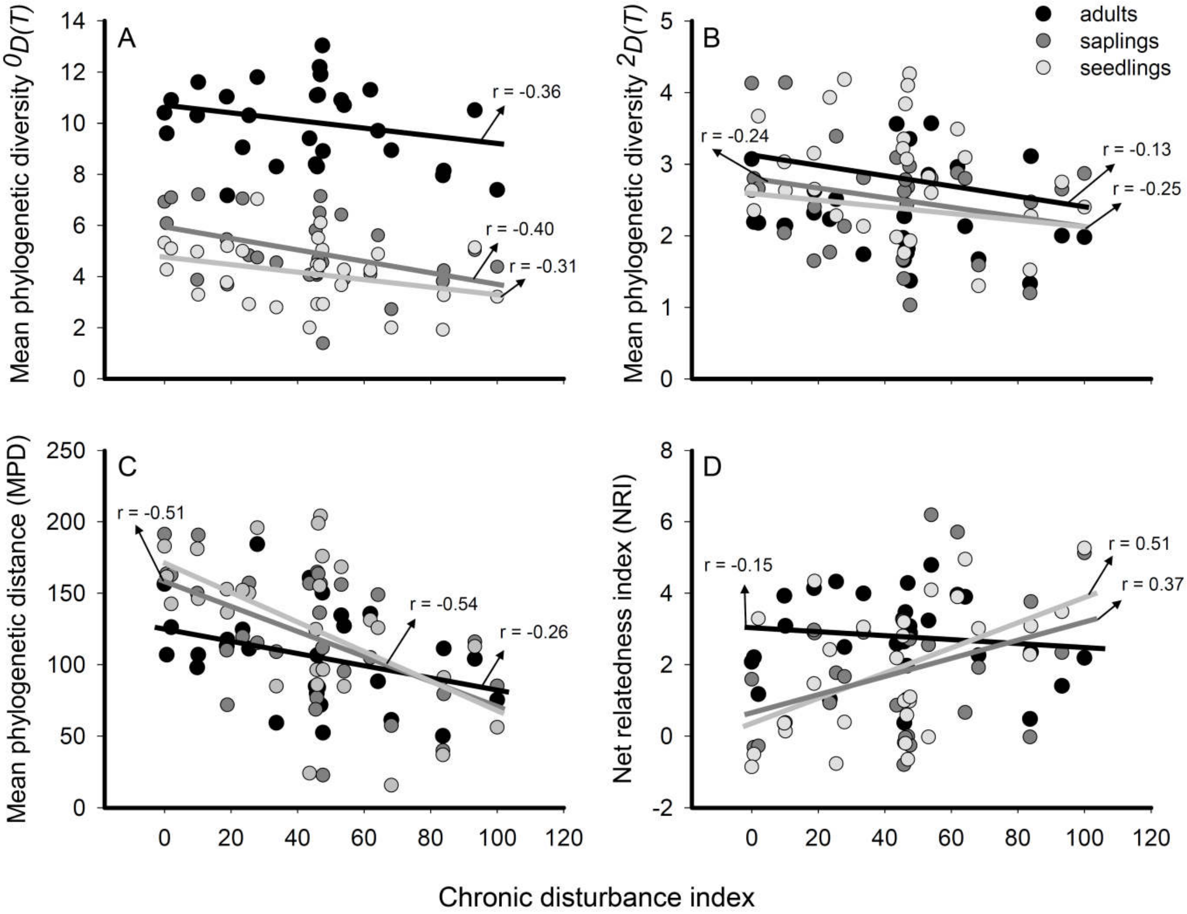
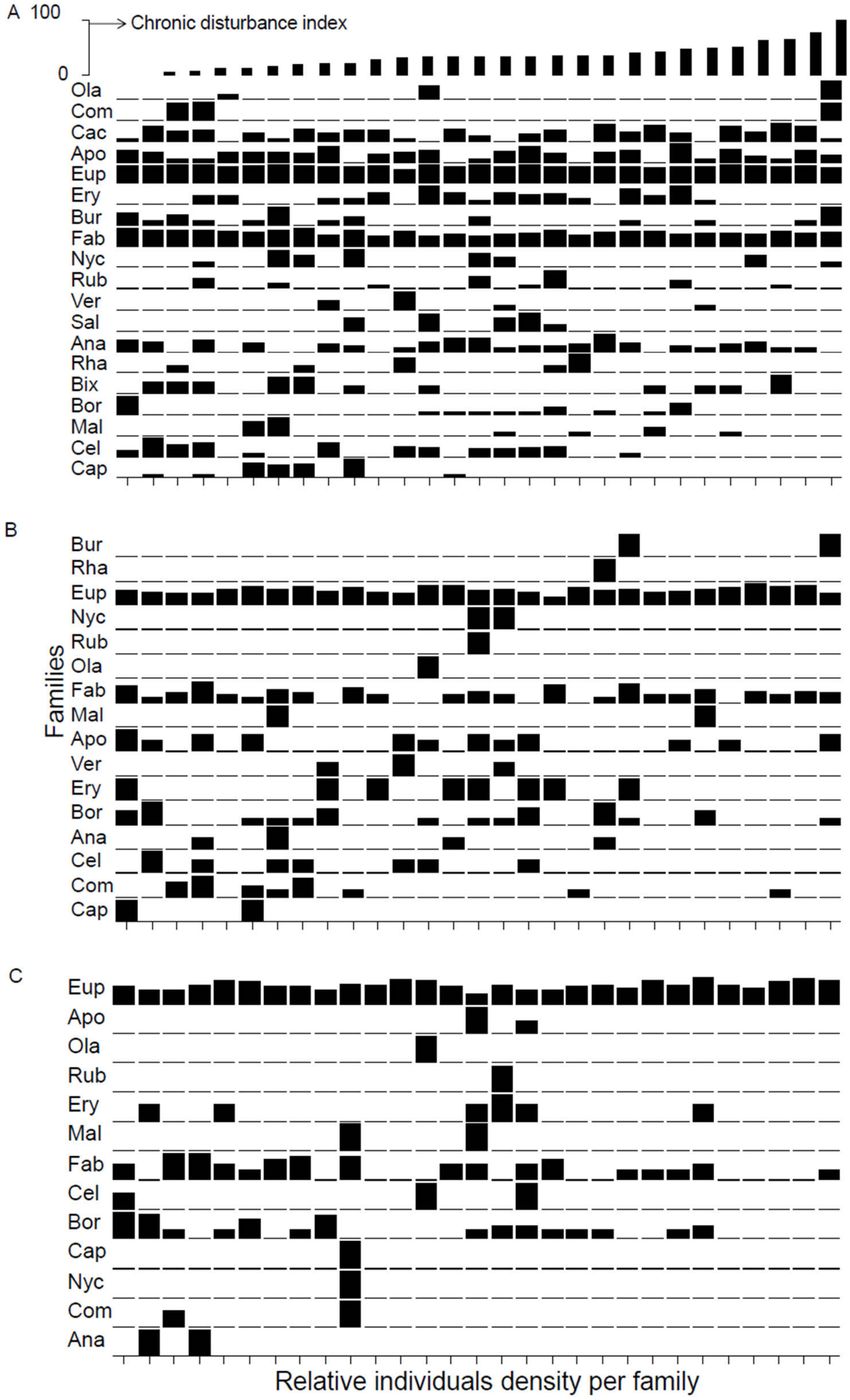

A
Mean phylogenetic diversity ⁰D(T)
r = -0.36
r = -0.40
r = -0.31
B
Mean phylogenetic diversity ²D(T)
adults
saplings
seedlings
r = -0.24
r = -0.13
r = -0.25
C
Mean phylogenetic distance (MPD)
r = -0.51
r = -0.54
r = -0.26
D
Net relatedness index (NRI)
r = -0.15
r = 0.51
r = 0.37
Chronic disturbance index

Figure 2.

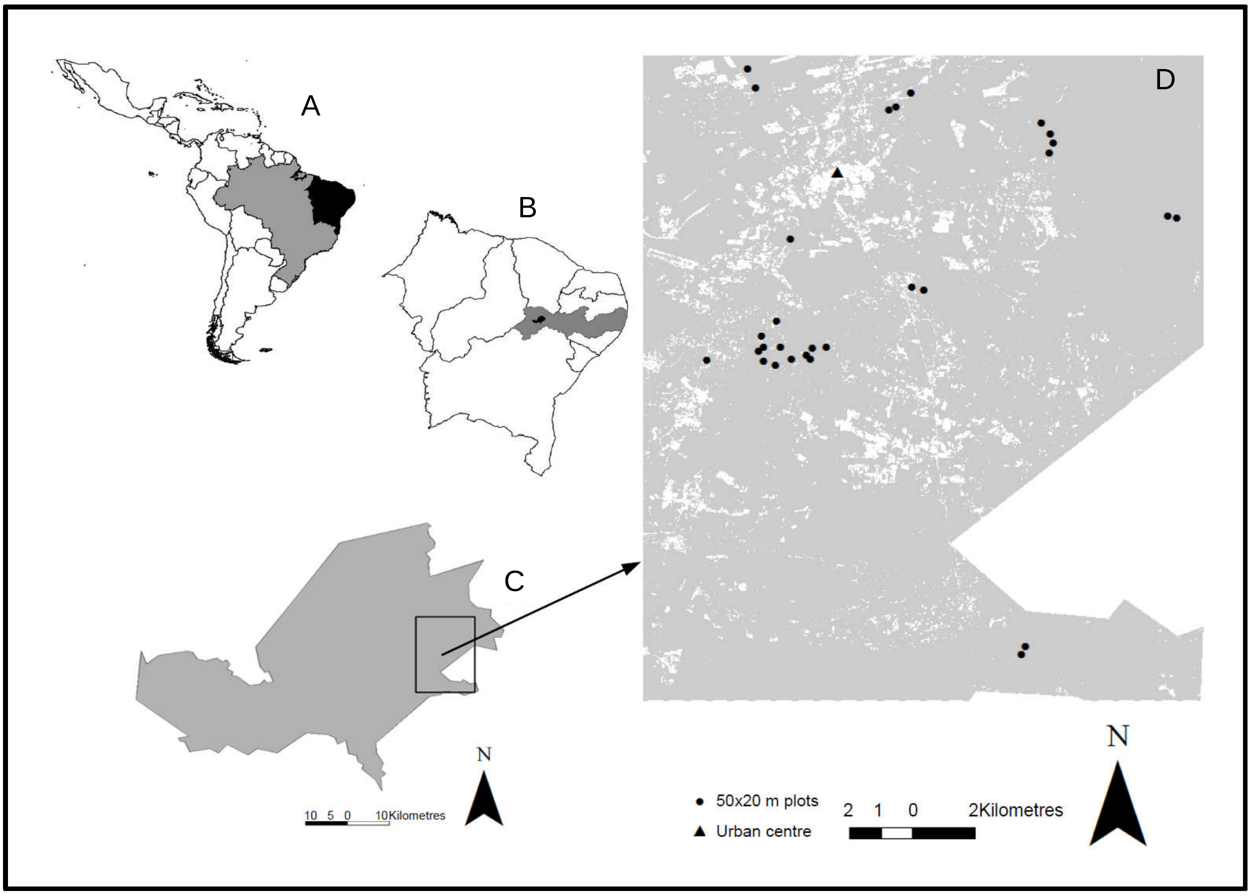

A
100
0
Chronic disturbance index
Ola
Com
Cac
Apo
Eup
Ery
Bur
Fab
Nyc
Rub
Ver
Sal
Ana
Rha
Bix
Bor
Mal
Cel
Cap
B
Families
Bur
Rha
Eup
Nyc
Rub
Ola
Fab
Mal
Apo
Ver
Ery
Bor
Ana
Cel
Com
Cap
C
Eup
Apo
Ola
Rub
Ery
Mal
Fab
Cel
Bor
Cap
Nyc
Com
Ana
Relative individuals density per family

Ecological Archives

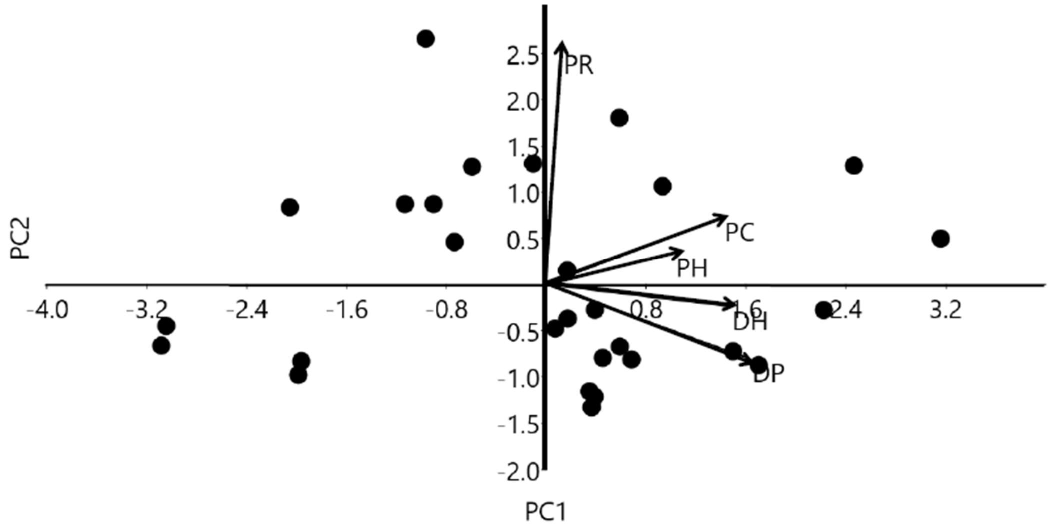
Appendices A, B, C, D, F, G, H, I, J, K, L and a Supplement are available online:

http://dx.doi.org/

Appendix A. Location of the study area in northeastern Brazil (A).We indicate the Parnamirim municipality (in black) within the Pernambuco state (in gray) (B). We also show the study landscape (C) in which we located 29 50 × 20-m plots, and the urban center of Parnamirim (black triangle) (d). The white areas in (D) represent deforested areas.



Appendix B. Principal component analysis biplot illustrating the relationship between the chronic disturbance index (PC1, which explained 41% of variation), the chronic disturbance predictors (DP: density of people; DL: density of livestock; PR: proximity to nearest road; PC: proximity to urban center; PH: proximity to the nearest house) and sample distributions (black circles). Positive values of PC1 scores represent the most chronically disturbed sites, while negative values represent the least disturbed sites.



Appendix C. Correlation matrix showing relationships between chronic disturbance index (CDI) and chronic disturbance predictors (DP: density of people; DL: density of livestock; PR: proximity to nearest road; PC: proximity to urban center; PH: proximity to the nearest house). Cell values correspond to the Pearson's correlation coefficient (below the empty diagonal) and its associated *P*-value (above the diagonal). Bold cases emphasize significant relationships (*P*<0.05).

	PR	PC	DH	DP	DL	CDI
PR		0.967	0.647	0.399	0.487	0.151
PC	-0.008		0.075	**0.014**	0.077	**0.005**
DH	-0.090	0.341		**0.019**	0.595	**0.002**
DP	-0.165	**0.456**	**0.439**		**0.011**	**0.000**
DL	-0.136	0.339	-0.104	**0.472**		**0.000**
CDI	-0.278	**0.744**	**0.553**	**0.865**	**0.610**	

Appendix D. Differences in plot size and sample completeness.

To address this potential problem, we calculated the inventory completeness for each plot and ontogenetic class using the coverage estimator recommended by Chao & Shen (2010). Sample coverage was greater in adults than saplings and seedlings, averaging 98.6% ± 1.1% for adult (mean ± SE), 87.7% ± 1.2% for saplings and 72.6% ± 3.3% for seedling plots. This suggested that our results could be biased by differences in sample completeness among ontogenetic stages (Chao & Shen 2010; Chao & Jost 2012). However, when we correlated plot sample completeness with their respective phylogenetic metrics, no pattern rose. Of the 12 correlations performed (four metrics by three ontogenetic stages), only two were statistically significant [correlations of completeness with ${}^{0}D(T)$ and MPD for saplings] and even so quite weak ($r < 0.5$). Seedling and adult assemblages, which had the lowest and greatest abundance per plot, respectively, did not show correlation between phylogenetic metrics and sample completeness. To completely discard the influence of sampling completeness, we also correlated the metrics with species richness predicted by rarefaction curves. None but one of the 12 possible correlations between predicted richness and the phylogenetic metrics was statistically significant. The only significant correlation rose between predicted richness and the adult NRI ($r = -0.456$, $p = 0.015$). Based on these analyses we conclude that differences in plot size and their effects on abundance did not significantly affect our results.

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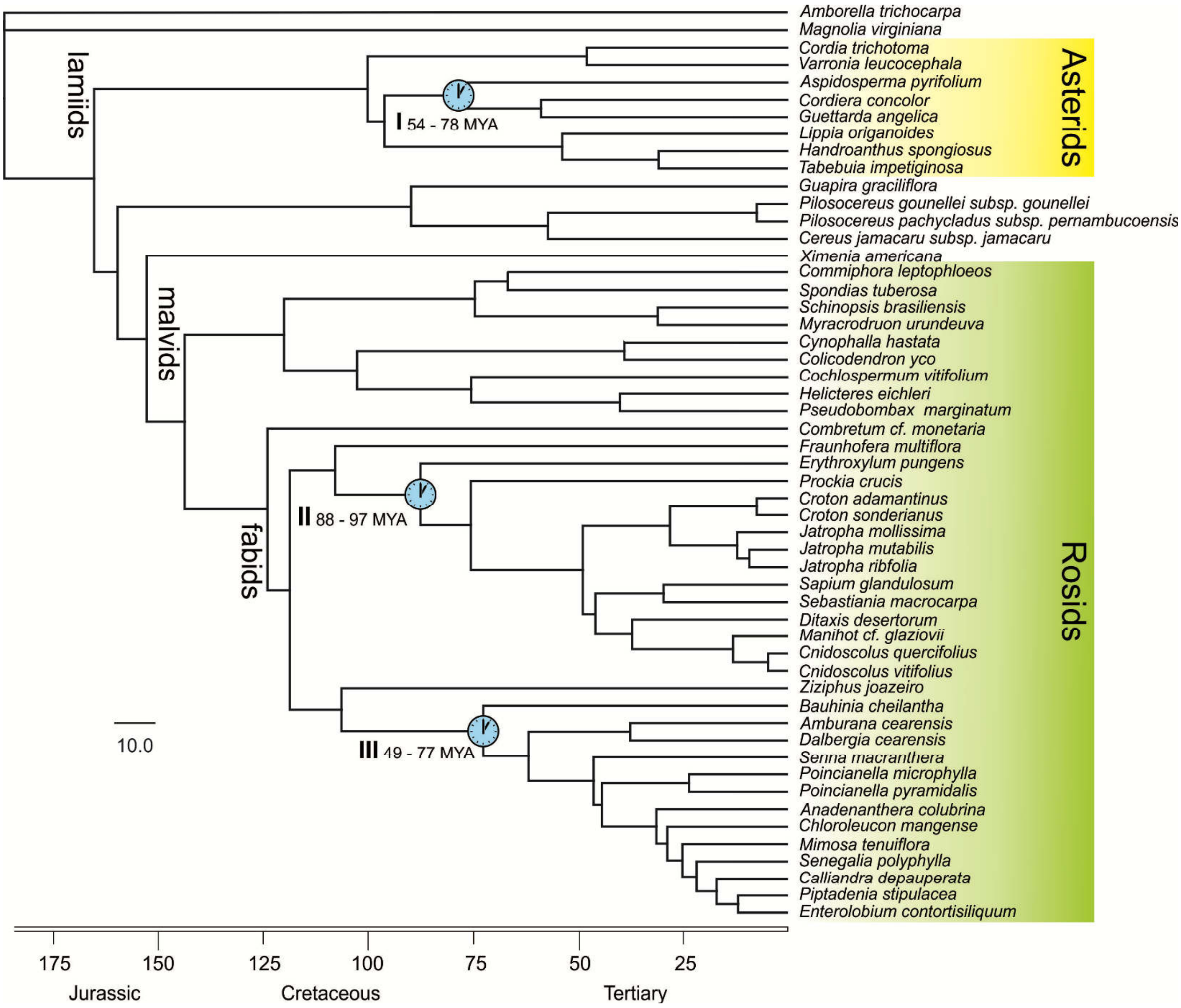
Appendix E. Correlation matrix showing relationships between phylogenetic metrics: ${}^{0}\overline{D}$(T) - mean phylogenetic diversity of total lineages, ${}^{2}\overline{D}$(T) - mean phylogenetic diversity of dominant lineages, MPD - mean phylogenetic distance and, NRI - nearest relatedness index. We can observe a weak relationship between NRI and ${}^{0}\overline{D}$(T), which indicates that the increase of lineages can result in phylogenetic clustering. Cell values correspond to the Pearson's correlation coefficient (below the empty diagonal) and its associated *P*-value (above the diagonal). Bold cases emphasize significant relationships ($P<0.05$). As NRI is a standardized measure of MPD, the increase in clustering degree result in the decrease in phylogenetic distances between the species. We can also observe that the increase in MPD values can be related to the increase of dominant lineages (${}^{2}\overline{D}$(T)).

	${}^{0}\overline{D}$(T)	${}^{2}\overline{D}$(T)	MPD	NRI
${}^{0}\overline{D}$(T)		0.500	0.258	**0.043**
${}^{2}\overline{D}$(T)	0.073		**0.000**	0.969
MPD	0.122	**0.781**		**0.000**
NRI	**0.217**	0.004	**-0.400**	

Appendix F. Methods used to build our time-calibrated phylogeny.

Initially we searched for four DNA regions [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)] from sequence data available in GenBank and in *Amborella* Genome Database (see Appendix G). When sequence data for a species were not available, we used a randomly chosen alternative species within the genus to estimate the relatedness to that genus (see Appendix F). 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, 2009). We used *Amborella trichocarpa* and *Magnolia virginiana* to root the tree and increase the depth of taxon sampling (Burns and Strauss 2011). Sequences were aligned for each region independently and later combined into a single supermatrix using Geneious version 7.1.4 (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 on a local optimum. We then created a time-calibrated phylogeny adopting fossil calibration points derived from Bell et al. (2010) using BEAST v1.8.2 (Drummond et al. 2012). Simultaneous divergence-time and phylogenetic analyses were conducted using MCMC methods implemented in BEAST v1.8.2, which employs a lognormal relaxed-clock model to estimate divergence times.

Bellow we show the time-calibrated tree which illustrates our regional phylogeny and the tree calibration points derived from Bell et al. (2010): I Gentianales (54-78 MY), (II) Malphighiales (88-97 MY) and Fabaceae (49-77 MY).



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Appendix G. Sequences used to estimate the Bayesian tree (Appendix D). We used 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 and in *Amborella* Genome Database (http://amborella.huck.psu.edu/shortstack). NA – Cases where information was absent for the species and its genera.

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_scaffold 03396	*Amborella trichocarpa*	L12628	*Amborella trichocarpa*	AY14532
Amburana cearensis	*Amburana cearensis*	JX846614	*Amburana cearensis*	KJ813615	NA	NA	*Amburana cearenses*	EF466144
Anadenanthera colubrina	*Anadenanthera colubrina*	EU812064	*Anadenanthera colubrina*	JQ910930	*Anadenanthera peregrina*	KJ082119	*Anadenanthera peregrina*	EU811875
Aspidosperma pyrifolium	*Aspidosperma pyrifolium*	JX850029	*Aspidosperma marcgravianum*	FJ037794	*Aspidosperma cylindrocarpon*	DQ660633	*Aspidosperma quebracho-blanco*	AF214165
Bauhinia cheilantha	*Bauhinia tomentosa*	AY386893	*Bauhinia cheilantha*	DQ787410	*Bauhinia guianensis*	JQ626034	*Bauhinia forficata subsp. pruinosa*	FJ801053

Calliandra depauperata	*Calliandra rhodocephala*	JQ587534	*Calliandra depauperata*	JX870682	*Calliandra vaupesiana*	KR082842	*Calliandra ulei*	JX870815
Cereus jamacaru subsp. jamacaru	*Cereus alacriportanus*	AY015313	*Cereus alacriportanus*	AY064344	*Cereus fernambucensis*	AY875240	*Cereus aethiops*	JQ779665
Chloroleucon mangense	*Chloroleucon mangense*	AY386921	*Chloroleucon mangense*	EF638183	NA	NA	*Chloroleucon mangense*	AF278517
Cnidoscolus quercifolius	*Cnidoscolus aconitifolius*	AB268041	NA	NA	*Cnidoscolus aconitifolius*	AB267937	*Cnidoscolus tubulosus*	EU518895
Cnidoscolus vitifolius	*Cnidoscolus spinosus*	KM219793	NA	NA	*Cnidoscolus urens var. stimulosus*	AY794874	*Cnidoscolus albomaculatus*	EU518894
Cochlospermum vitifolium	*Cochlospermum vitifolium*	JQ587264	NA	NA	*Cochlospermum vitifolium*	JQ591114	NA	NA
Colicodendron yco	*Capparis spinosa*	AY491650	*Capparis acutifolia*	KP092569	*Capparis spinosa*	AY167985	*Capparis spinosa*	AY122422
Combretum cf. *monetaria*	*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 trichotoma	*Cordia torrei*	JX517572	*Cordia revoluta*	HM443775	*Cordia trichotoma*	EU599827	*Cordia lutea*	KF158215
Cordiera concolor	*Alibertia myrciifolia*	KF981358	*Gardenia hansemannii*	HM443775	*Alibertia myrciifolia*	KF981281	*Alibertia edulis*	AF201029
Croton adamantinus	*Croton dichogamus*	KR735055	*Croton guildingii subsp. tiarensis*	AY971254	*Croton maestrense*	EF405857	*Croton grangerioides*	KP878425
Croton sonderianus	*Croton menyharthii*	JF270729	*Croton cupulifer*	EU478063	*Croton setiger*	EF405853	NA	NA
Cynophalla hastate	*Cynophalla hastata*	KJ012557	*Capparis acutifolia*	KP092569	*Cynophalla hastata*	KJ082259	NA	NA
Dalbergia cearensis	*Dalbergia monetaria*	KJ593846	*Dalbergia miscolobium*	EF451070	*Dalbergia hupeana*	U74236	*Dalbergia hupeana*	KP338261
Ditaxis desertorum	*Ditaxis montevidensis*	AB233761	*Ditaxis guatemalensis*	DQ997792	*Ditaxis montevidensis*	AB233865	*Ditaxis simoniana*	AY794742

Enterolobium contortisiliquum	*Enterolobium contortisiliquum*	JX495708	*Enterolobium contortisiliquum*	EF638190	*Enterolobium contortisiliquum*	JX571823	*Enterolobium timbouva*	JX870876
Erythroxylum pungens	*Erythroxylum rufum*	KJ012581	*Erythroxylum amplifolium*	DQ787423	*Erythroxylum confusum*	L13183	*Erythroxylum sp.*	KC428510
Fraunhofera multiflora	*Fraunhofera multiflora*	JF410097	NA	NA	NA	NA	*Fraunhofera multiflora*	JF410055
Guapira graciliflora	*Guapira fragrans*	KJ012616	*Guapira fragrans*	JX844233	*Guapira fragrans*	KJ082334	NA	NA
Guettarda angelica	*Guettarda scabra*	KJ012627	*Guettarda uruguensis*	DQ063692	*Guettarda acreana*	JQ626041	*Guettarda speciosa*	KJ906574
Handroanthus spongiosus	*Handroanthus albus*	KF981308	*Handroanthus impetiginosus*	JX856460	*Handroanthus albus*	KF981207	*Handroanthus guayacan*	EF105094
Helicteres eichleri	*Helicteres baruensis*	JQ589303	*Helicteres guazumifolia*	AF233300	*Helicteres angustifolia*	AY082356	NA	NA
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 ribfolia	*Jatropha podagrica*	KJ150223	*Jatropha curcas*	EU700455	*Jatropha zeyheri*	JQ025058	NA	NA
Lippia origanoides	*Lippia integrifolia*	HM853860	*Lippia salsa*	FJ867399	*Lippia javanica*	JX572735	*Lippia sidoides*	AY945838
Magnolia virginiana	*Magnolia virginiana*	GQ248153	*Magnolia virginiana*	DQ499097	*Magnolia virginiana*	GQ248639	*Magnolia virginiana*	AY145354
Manihot cf. *glaziovii*	*Manihot esculenta*	JQ587466	*Manihot esculenta*	GU214953	*Manihot esculenta*	AB233880	*Manihot tristis*	EU518925
Mimosa tenuiflora	*Mimosa tenuiflora*	JX850057	*Mimosa guatemalensis*	AF458784	*Mimosa strigillosa*	KJ773686	*Mimosa quitensis*	AF278514
Myracrodruon urundeuva	*Astronium graveolens*	JQ586471	*Myracrodruon urundeuva*	DQ787397	*Astronium ulei*	JQ625995	*Myracrodruon urundeuva*	AY594560
Pilosocereus gounellei subsp. *Gounellei*	*Pilosocereus rosae*	JX683850	NA	NA	NA	NA	*Pilosocereus chrysacanthus*	HM041340
Pilosocereus pachycladus subsp. *Pernambucoensis*	*Pilosocereus floccosus*	JX683847	NA	NA	NA	NA	*Pilosocereus aureispinus*	JN035566

Piptadenia stipulacea	*Piptadenia flava*	JQ587930	NA	NA	*Piptadenia flava*	JQ592113	*Piptadenia moniliformis*	AF278496
Poincianella 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
Prockia crucis	*Prockia crucis*	EF135588	NA	NA	*Prockia crucis*	JQ592133	*Prockia costaricensis*	AY757056
Pseudobombax marginatum	*Pseudobombax septenatum*	GQ982072	*Pseudobombax marginatum*	AF028521	*Pseudobombax septenatum*	GQ981847	*Pseudobombax croizatii*	HQ696749
Sapium glandulosum	*Sapium glandulosum*	JQ589779	*Sapium sebiferum*	AF537586	*Sapium glandulosum*	AY794841	*Sapium glandulosum*	AY794626
Schinopsis brasiliensis	*Schinopsis brasiliensis*	AY594477	*Schinopsis brasiliensis*	AY531203	NA	NA	*Schinopsis brasiliensis*	KP055559
Sebastiania macrocarpa	*NA*	NA	*Sebastiania cornuta*	AF537587	*Sebastiania klotzschiana*	AY794850	*Sebastiania hexaptera*	AY794645
Senegalia polyphylla	*Senegalia tenuifolia*	KJ593761	*Senegalia caffra*	JQ265905	*Senegalia tenuifolia*	KJ594092	*Senegalia berlandieri*	HM020797

Senna macranthera	*Senna macranthera var. nervosa*	AM086873	*Senna hirsuta*	KJ638428	*Senna macranthera var. micans*	JX856680	*Senna pleurocarpa*	AF367007
Spondias tuberosa	*Spondias mombin*	AY594480	*Spondias mombin*	AF445882	*Spondias tuberosa*	KP774626	*Spondias tuberosa*	GU943750
Tabebuia impetiginosa	*Tabebuia impetiginosa*	JQ587045	*Tabebuia impetiginosa*	JX497689	*Tabebuia impetiginosa*	JQ590850	*Tabebuia impetiginosa*	EF105097
Varronia leucocephala	*Varronia guanacastensis*	JQ589896	*Varronia revoluta*	HM443774	*Varronia bullata*	KF158132	*Varronia bullata*	KF158211
Ximenia Americana	*Ximenia americana*	KJ012821	*Ximenia americana*	DQ333869	*Ximenia americana*	DQ790149	*Ximenia americana*	DQ340620
Ziziphus joazeiro	Ziziphus rignonii	KJ012831	Ziziphus lloydii	JN900312	*Ziziphus nummularia*	JX856807	*Ziziphus glabrata*	AJ225799

Appendix H. Results of Shapiro-Wilk tests used to test the normal distribution of response variable errors. Response variables: (${}^{0}\overline{D}$(T) - mean phylogenetic diversity of total lineages, ${}^{2}\overline{D}$(T) - mean phylogenetic diversity of dominant lineages, MPD - mean phylogenetic distance and, NRI - nearest relatedness index). Model factors: CDI - chronic disturbance, OS - ontogenetic stage, A - stem abundance in the plot.

Model	*W*	*P*
${}^{0}\overline{D}$(T) = CDI + OS + A + OS×CDI	0.990	0.752
${}^{2}\overline{D}$(T) = CDI + OS + A + OS×CDI	0.973	0.07
MPD= CDI + OS + A + OS×CDI	0.986	0.506
NRI= CDI + OS + A + OS×CDI	0.987	0.558

Appendix I. Differences in species richness and stems abundance (mean ± SD) among ontogenetic stages (adults, saplings and seedlings). Different letters indicate significant differences among stages (Tukey tests).

Ontogenetic stage	Species richness	Stem abundance
Adults	$18.5^{a} \pm 3.6$	$362^{a} \pm 92.1$
Saplings	$6.7^{b} \pm 2.2$	$11.6^{b} \pm 6.5$
Seedlings	$5.1^{b} \pm 1.8$	$10.6^{b} \pm 3.5$

Appendix J. Model coefficients for each factor model included in the linear models fitted to test the effect of chronic disturbance index on phylogenetic diversity metrics of plant assemblages (adults, saplings and seedlings) from the Brazilian Caatinga, Parnamirim municipality, Pernambuco, Brazil. Model factors codes: CDI – chronic disturbance, OS – ontogenetic stage, A – individuals abundance in each plot. Significance level ($^{n.s.}P > 0.05$;* $P < 0.05$).

	Phylogenetic metrics							
	${}^{0}\overline{D}$(T)		${}^{2}\overline{D}$(T)		MPD		NRI	
Model factors	Estimate	t - ratio	Estimate	t - ratio	Estimate	t - ratio	Estimate	t - ratio
CDI	-0.014*	-2.58	-0.007*	-2.22	-0.804*	-4.98	0.001*	2.57
A	$0.005^{n.s.}$	1.69	$-0.002^{n.s.}$	-1.12	$-0.047^{n.s.}$	-0.53	$-0.004^{n.s.}$	-1.15
CDI × OS (adults)	$0.007^{n.s.}$	0.85	$-0.001^{n.s.}$	-0.07	$0.290^{n.s.}$	1.23	-0.02*	-2.99
CDI × OS (saplings)	$-0.007^{n.s.}$	-0.90	$0.000^{n.s.}$	0.11	$-0.04^{n.s.}$	-0.21	$0.00^{n.s.}$	1.08
CDI × OS (seedlings)	$-0.000^{n.s}$	-0.00	$-0.000^{n.s.}$	-0.04	$-0.244^{n.s.}$	-1.09	0.01*	2.07

Appendix K. Results of NODESIG procedure showing clades that contributed to non-random phylogenetic structure in adult, sapling and seedling communities. With this method we identified clades that contributed significantly to non-random phylogenetic structure, considering each ontogenetic stage. Based on a randomization test, NODESIG assesses whether a particular NODE in the sample has significantly more or less descendent taxa than expected by a null model (indicated as SIG in the Tables). **Abbreviations:** A = adult; Sa = sapling; Se = seedlings. **References:** Webb, C.O., Ackerly, D.D. & Kembel, S.W. (2008) Phylocom: software for the analysis of phylogenetic community structure and character evolution. Bioinformatics, **24**, 2098–2100.

Adult assemblage				**Sapling assemblage**				**Seedling assemblage**			
Plot	*Disturbance value*	*Node*	*SIG*	*Plot*	*Disturbance value*	*Node*	*SIG*	*Plot*	*Disturbance value*	*Node*	*SIG*
1	53.9	30, 50	more	1	53.9	30, 50,	more	1	53.9	30, 50, 53, 57, 58, 59	more
2	25.3	30, 50	more	2	25.3	51, 53, 57,58,59	more	2	25.3	51, 53, 57, 58, 59	more
3	53.1	28, 30, 50, 80	more	3	53.1	83	more	5	45.4	53	more
5	45.4	30, 50, 58	more	5	45.4	51, 53	more	7	61.8	53, 57, 58, 59	more
6	43.5	30, 50, 82	more	7	61.8	53, 57, 58, 59, 62	more	8	33.5	51, 53	more
7	61.8	30, 50, 78, 82	more	8	33.5	50, 51, 53	more	9	64.4	89	more
10	18.8	30, 53	more	9	64.4	89	more	10	18.8	89	more
11	47.4	30, 50, 78, 80, 82	more	10	18.8	89	more	11	47.4	88, 22	more
12	46.8	58	more	11	47.4	86, 88	more	20	46.1	59	more
15	9.8	28, 30, 50, 78, 80,	more	20	46.1	59	more	23	27.8	30	more

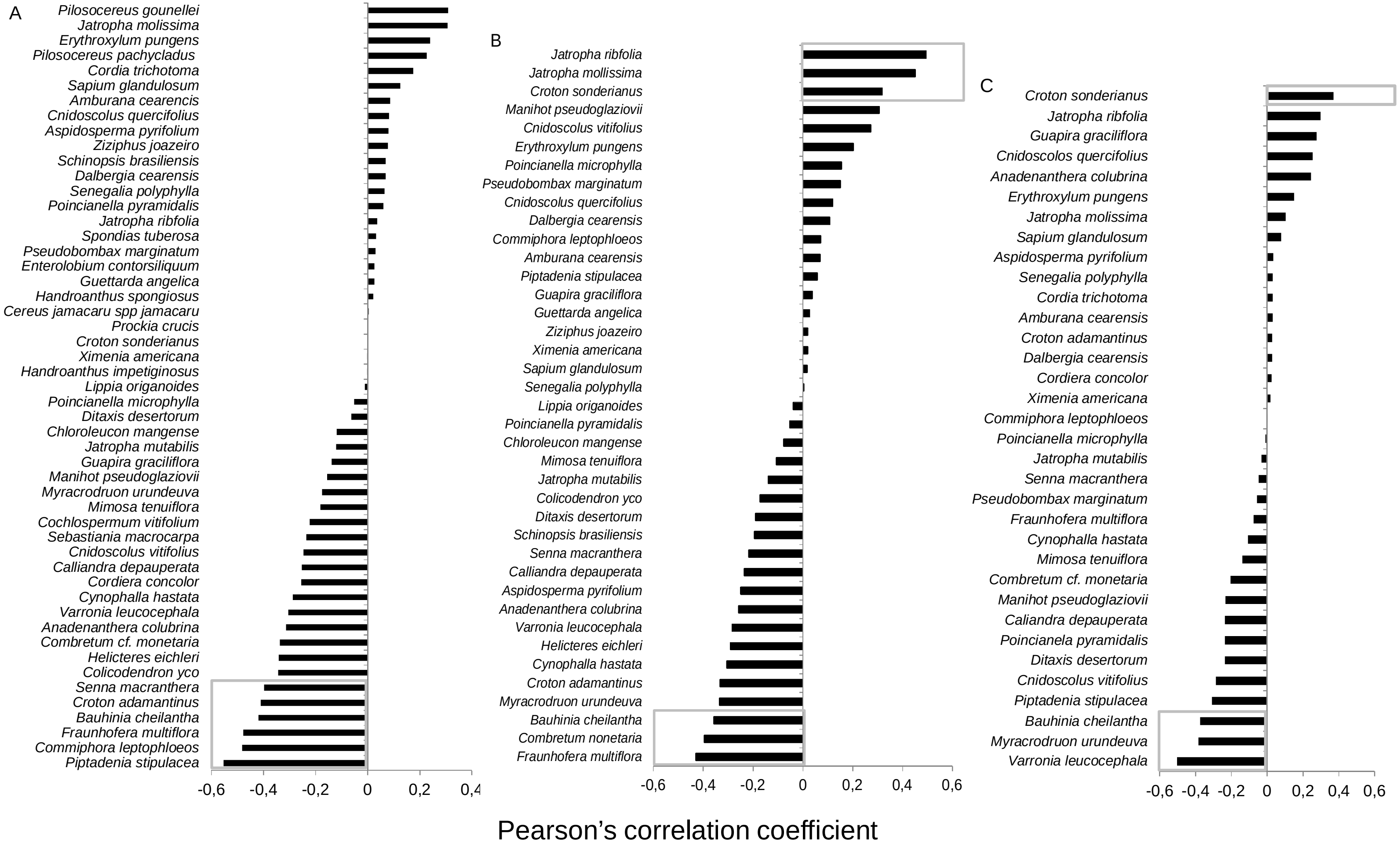
		88									
17	0.6	30	more	23	27.8	30	more	24	83.9	30, 53, 57, 75	more
19	47.5	28, 30, 50	more	24	83.9	30, 53, 57, 75	more	25	100	30, 50, 51, 53, 53,57, 58, 62	more
20	46.1	50	more	25	100	30, 50, 51, 53, 57 73	more	27	93.2	53	more
21	1.9	39	more	27	93.2	53	more	28	83.6	86, 88	more
23	27.8	28, 30	more	28	83.6	82	more	29	18.1	58, 59	more
23	27.8	7	less								
24	83.9	73	more								
26	68.1	73	more								
29	18.7	28, 30, 86	more								

Node codes

Assemblages	*Node*	*Clade*
A/	7	Lamiids (Gentianales and Lamiales)
A/	28	Core Eudicots
A/Sa/Se	30	Rosids (Fabids and Malvids)
A	39	Malvales to Brassicales
A/Sa/Se	50	Fabids (Celastrales, Malpighiales, Fabales and Rosales)
Sa/Se	51	Celastrales to Malphigiales
A/Sa/Se	53	Malphighiales
Sa/Se	57	Euphorbiaceae
A/Sa/Se	58	*Croton* to *Jathopha*
Sa/Se	59	*Croton*
Sa/Se	62	*Jatropha*
A/Sa	73	*Manihot* and *Cnidoscolus*
Sa/Se	75	*Cnidoscolus*
A	78	Fabids

A	80	Fabaceae
A/Sa/Se	82	Papilionoideae and Mimosoids
Sa	83	*Amburana* to *Dalbergia*
A/Sa/Se	86	Palpilionoideae
A/Sa/Se	88	Mimosoids
Sa/Se	89	*Poncianella*

Appendix L. Correlations between the chronic disturbance index and the abundance of each species for adult (A), sapling (B) and seedling (C) plant assemblages. Gray rectangles highlight species abundances that are significantly ($p < 0.05$) higher or lower due to chronic disturbance.



CONCLUSÕES

A literatura que aborda o efeito das perturbações humanas sobre a biodiversidade é considerada vasta, no entanto a maioria dos estudos trata da forma aguda da perturbação, pois esta forma é mais facilmente detectada. A perturbação crônica, por sua vez, ocorre de maneira silenciosa criando um mosaico de áreas com distintos graus de perturbação, sendo muitas vezes difícil mensurar todas as fontes de impacto que atuam numa determinada área. Neste trabalho buscamos contribuir para o conhecimento dos efeitos dessas perturbações crônicas sobre flora, utilizando como modelo comunidades vegetais lenhosas da Caatinga em distintos estágios ontogenéticos (adultos, jovens e plântulas). Este estudo forneceu informações importantes sobre a questão da perturbação crônica na Caatinga, e se destaca por tratar de forma integrada três estágios ontogenéticos e por utilizar conjuntamente medidas de diversidade taxonômicas e filogenéticas, que em conjunto, nos ajudaram a elucidar mais profundamente as consequências dessas perturbações.

Através de uma revisão de literatura, o primeiro capítulo desta tese demonstrou que perturbações antrópicas crônicas são comuns em países em desenvolvimento dos continentes Africano, Asiático da America do Sul/Central, cujas populações humanas pobres dependem dos recursos da floresta para subsistência e fonte de renda. A principal fonte de perturbação dos estudos analisados foi à coleta de produtos florestais não madeireiros, além da ocorrência simultânea de distintas fontes de distúrbio como a criação de animais e coleta de madeira. Os efeitos da perturbação crônica geralmente foram acessados ao nível de populações e comunidades, sendo estes efeitos em sua maioria negativos, mas ocorrendo também efeitos positivos e neutros. Os efeitos neutros e positivos da perturbação crônica estiveram associados, por exemplo, a atributos como propagação vegetativa e crescimento rápido, os quais estiveram associados à utilização dos recursos naturais de forma menos intensa e através de técnicas de manejo consideradas como sustentáveis. Ainda que o número de estudos que tratam dos efeitos da perturbação crônicas sobre a biodiversidade tenha cresido nos últimos anos, percebemos a necessidade de mais publicações que tratem dos efeitos no nível ecossistêmico, além de outros aspectos das populações (i.e. diversidade genética) e comunidades (*i.e.* processos e interações).

Os capítulos 2 e 3 se referem aos estudos de caso realizados em áreas de Caatinga do município de Parnamirim, no sertão Penambucano, os quais avaliaram o efeito de perturbações antrópicas crônicas sobre a diversidade taxonômica e filogenética, respectivamente. Demonstramos que perturbações crônicas tiveram, em geral, efeitos negativos sobre a diversidade taxonômica e composição das comunidades lenhosas adulta, de jovens e de plântulas, sendo a densidade de pessoas e de animais criados extensivamente os preditores mais importantes desses efeitos negativos. Além disso, a composição de espécies observada foi simplificada em áreas mais perturbadas, sendo raras espécies de madeira densa como *Myracrodruon urundeuva*, *Fraunhofera multiflora*, *Bauhinia cheilantha* e *Piptadenia stipulacea*. No terceiro capítulo verificou-se que os distúrbios crônicos reduziram o número de famílias esperadas para história evolutiva da região, bem como a distância filogenética (em milhões de anos) entre os indivíduos da comunidade. Além disso, constatou-se que a comunidade de jovens e de plântulas de áreas mais perturbadas apresenta maior grau de parentesco entre os indivíduos da comunidade. A perturbação crônica fez com que táxons como a família Euphorbiaceae e o gênero *Cnidoscolus*, que conseguem colonizar e são bem representados em habitats inóspitos, ocorressem com mais frequência em comunidades de plântulas e jovens. Esses resultados apontam que além do empobrecimento taxonômico, apenas grupos de espécies mais aparentados são capazes de recrutar plântulas nas áreas mais perturbadas, o que sugere que a perturbação crônica vem atuando como um filtro ambiental.

A perturbação crônica humana sobre a flora da Caatinga tem características similares a outras florestas do mundo em que as comunidades humanas dependem dos produtos florestais. O uso da floresta pelas populações humanas é considerado como uma forma de aliviar os efeitos da pobreza, mas o uso continuado e em longo prazo de seus benefícios econômicos e culturais levam ao empobrecimento da flora como apresentado em nossos resultados. Além disso, as perturbações crônicas podem se acumular e causar impactos ecolológicos maiores, indo desde o empobrecimento da flora a cenários de desertificação na Caatinga. Esta possibilidade nos traz maiores desafios cujas soluções dependem de futuras investigações que avaliem: (i) o impacto das perturbações crônicas nas comunidades ao longo do tempo, (ii) o efeito dessas perturbações sobre a viabilidade e dinâmica das populacões, (iii) como processos e interações ecológicas são afetados pela perturbação crônica, (iv) coleta de informações sobre tipos de uso, formas de extração, quantidade de recursos coletados, (v) efeitos da perturbação crônica no ecossistema etc. Considerando-se que a demanda por recursos naturais é crescente, as perturbações crônicas não podem continuar sendo negligenciadas nas iniciativas que tratam da conservação da biodiversidade e do desenvolvimento rural. Como medidas para conciliar o uso da floresta e a manutenção de sua biodiversidade nós sugerimos mais atenção e investimentos em:

1) Pesquisa e desenvolvimento de programas rurais que visem o desenvolvimento de práticas sustentáveis nas florestas remanescentes, especialmente voltadas ao manejo de rebanhos e coleta de madeira. Este manejo pode dar a partir da desintensificação dessas atividades visando conciliar a manutenção da diversidade e o uso das florestas, ao invés da imposição da conservação integral de grandes parcelas da propriedade rural. Além disto, através do incentivo a produção *ex situ* de espécies com importante valor de uso e a outras fontes de renda compatíveis com a manutenção biodiversidade da Caatinga (*e.g.* apicultura, turismo etc).

2) Melhoria na gestão governamental e aplicação das leis visando transformar o extrativismo atual em práticas de manejo sustentáveis.

3) Expansão do número de áreas protegidas de proteção integral e implementação efetiva das mesmas. Nessas áreas deverá ser evitado qualquer uso dos recursos florestais a fim de resguardar a biodiversidade no seu estado mais natural possível.

Em fim, o manejo adequado das perturbações crônicas na Caatinga requer contribuições integradas das comunidades que se utilizam dos recursos, dos conhecimentos ecológicos/multidisciplinares e das distintas esferas governamentais para que espécies e história evolutiva se mantenham neste ecossistema único.

ANEXOS

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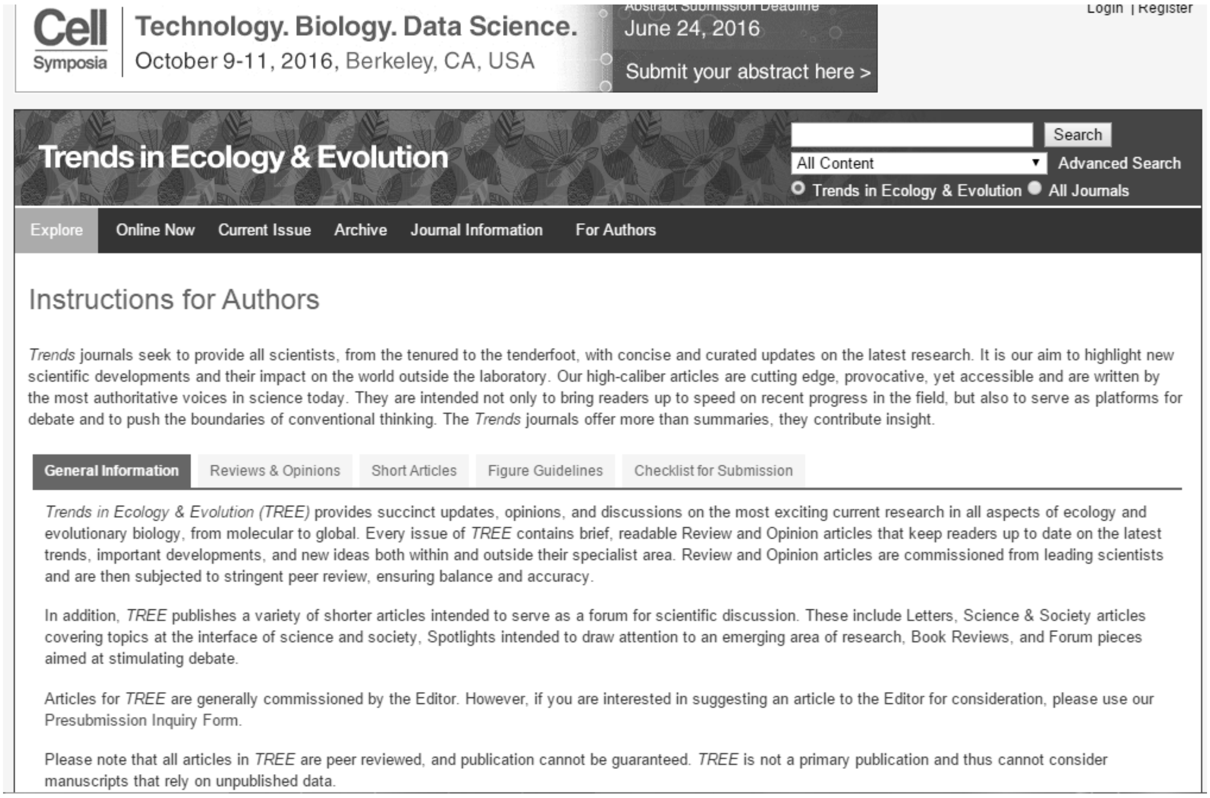

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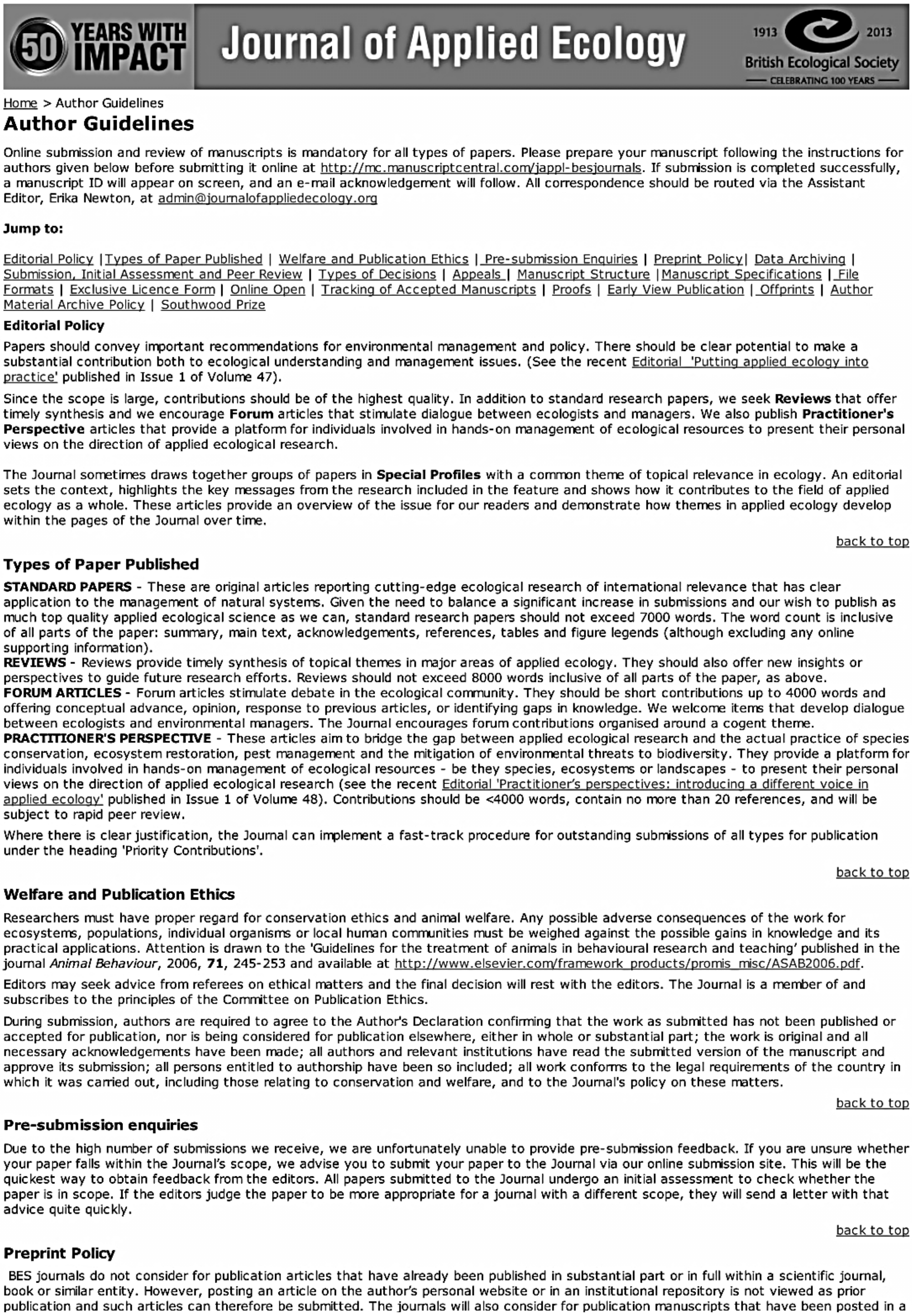

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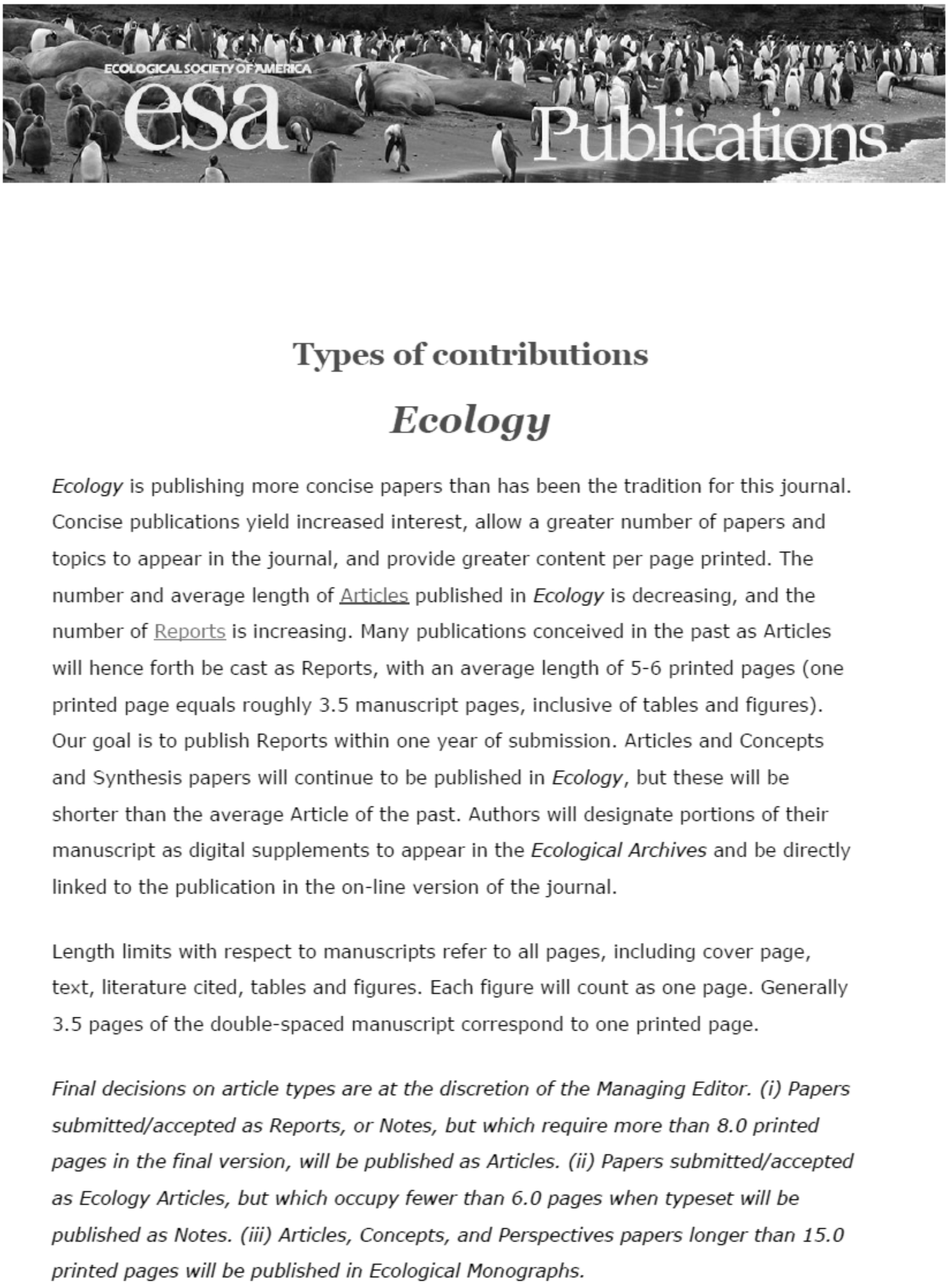

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