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AGRICULTURA DE CORTE-E-QUEIMA E A REGENERAÇÃO DA FLORESTA SECA DA CAATINGA: implicações para resiliência ecológica

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

Orientador: Dr. Marcelo Tabarelli

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RESUMO

Os ecossistemas florestais estão cada vez mais ameaçados por atividades agrícolas insustentáveis que enfraquecem seu potencial regenerativo ao limitar fontes críticas de regeneração florestal, como o banco e a chuva de sementes. Este pode ser o caso da agricultura de corte-e-queima, um método agrícola amplamente difundido em florestas secas e que pode ameaçar a resiliência dos ecossistemas florestais ao reduzir o tamanho e a diversidade das comunidades de espécies no banco e na chuva de sementes. Para testar essa hipótese e promover práticas de manejo voltadas para a melhoria da recuperação florestal, nesta tese examinei, por meio de um experimento de agricultura de corte-e-queima, como essa prática agrícola impacta o banco e a chuva de sementes de plantas lenhosas na floresta da Caatinga, uma floresta tropical seca do nordeste do Brasil. Especificamente, 1) examinei os danos e viabilidade do banco de sementes, e a estrutura (densidade e diversidade) e composição (taxonômica e funcional) das assembleias do banco de sementes antes e depois da queima, e 2) a estrutura e composição da chuva de sementes em parcelas expostas à agricultura de corte-e-queima (ou seja, parcelas queimadas) e em parcelas de controle (floresta em pé) durante um período de um ano. Encontrei uma redução significativa na frequência e proporção de sementes intactas (não danificadas) após o fogo e uma diminuição de 3,6 vezes na proporção de sementes viáveis no banco de sementes. Enquanto a densidade de sementes permaneceu constante, a diversidade de espécies caiu drasticamente após o fogo, especialmente o número de espécies raras. A dissimilaridade composicional (diversidade β) entre as parcelas também diminuiu após o fogo, particularmente seu componente de substituição, levando à homogeneização das assembleias de sementes no espaço. A composição funcional das assembleias de sementes também foi alterada, aumentando a frequência relativa de espécies arbustivas após o fogo, especialmente espécies com frutos carnosos e dispersão biótica. Em relação à chuva de sementes, a densidade de propágulos foi reduzida 15 vezes nas parcelas queimadas em comparação com as parcelas florestais. A diversidade de espécies, particularmente o número de espécies raras, diminuiu nas parcelas queimadas. Finalmente, nenhuma diferença foi observada na composição taxonômica e funcional das assembleias de espécies na chuva de sementes. Dado que esses achados revelam um drástico empobrecimento do banco e da chuva de sementes em resposta a essa prática agrícola, a regeneração da

Caatinga e provavelmente de outras florestas secas dependerá em grande parte de outras fontes de regeneração menos vulneráveis a essa prática agrícola como a rebrota de plantas - uma interessante linha de investigação para o futuro.

Palavras-chave: Potencial regenerativo; Banco de sementes; Chuva de sementes; Agricultura de subsistência; Diversidade taxonômica.

ABSTRACT

Forest ecosystems are increasingly threatened by unsustainable agricultural activities that damage their regenerative potential by disrupting critical sources of forest regeneration, such as the seed bank and seed rain. This can be the case for slash-and-burn agriculture – a farming method that is widespread in dry forests and which can threaten the resilience of forest ecosystems, largely reducing the size of the soil seed bank and seed rain species communities, while favoring regeneration based on plant resprout. To test this hypothesis and promote management practices aimed at improving forest recovery, in this thesis I examined, through a slash-and-burn agriculture experiment, how this agricultural practice impacts the seed bank and seed rain of plants woody plants in the dry tropical Caatinga forest of northeastern Brazil. Particularly, 1) I examined the damage and viability of the seed bank, and the structure (density and diversity) and composition (taxonomic and functional) of the seed bank assemblages before and after the fire, and 2) the structure and composition of the seed rain in plots exposed to slash-and-burn agriculture (i.e. burned plots) and in control plots (forest stands) over a period of one year. I found a significant reduction in the frequency and proportion of intact (undamaged) seeds after fire, and a 3.6-fold decrease in the proportion of viable seeds of the soil seed bank. While seed density remained constant, species diversity declined dramatically after the fire, especially the number of rare species. The compositional dissimilarity (β-diversity) between plots also decreased after the fire, particularly its turnover component, causing the homogenization of seed assemblages across space. The functional composition of seed assemblages was also altered, with the relative frequency of shrub species increasing after fire, especially species with fleshy fruits and biotic dispersion. Regarding to seed rain, the density of propagules was reduced by 15 times in burned plots when compared to forest plots. Species diversity, particularly the number of rare species, decreased in burned plots. Finally, no difference was observed regarding the composition and functional of the seed rain assemblages. Thus, these findings reveal a drastic impoverishment of the bank and seed rain to this common agricultural practice in dry forests, the regeneration of the Caatinga and probably other dry forests cannot rest on the seed bank and seed rain and will largely depend by other regeneration sources less vulnerable to this agricultural practice, such as plant resprout – an interesting line of research for the future. These findings have important implications

for the management and resilience potential of dry forests and for the conservation of biodiversity and provision of ecosystem services in human-modified landscapes.

Keywords: Regenerative potential; Seed bank; Seed rain; Subsistence agriculture; Taxonomic diversity.

SUMÁRIO

1 INTRODUÇÃO

O Antropoceno é marcado pelo aumento da conversão de ecossistemas florestais em terras agrícolas (MALHI, 2017). Além da perda de hábitat, tal conversão causa uma miríade de efeitos em cascata na biodiversidade, incluindo nossa própria espécie. A perda de ecossistemas florestais ao redor do mundo é principalmente associada à agricultura de larga escala. Contudo, um outro tipo de atividade agrícola que é importante em pequena escala, mas é particularmente disseminado nas florestas secas é a agricultura de corte-e-queima (CURTIS et al., 2018). Este método agrícola pode ter grandes impactos nos padrões de biodiversidade, e pode ameaçar a resiliência dos ecossistemas florestais reduzindo em grande parte o tamanho das comunidades de plantas que compreendem o banco e a chuva de sementes. Ao contrário de outros ecossistemas como o Cerrado brasileiro, as plantas lenhosas da Caatinga não apresentam adaptações ao fogo (PIVELLO et al., 2021). Logo, se é verdade que este método agrícola pode causar o empobrecimento drástico do banco e da chuva de sementes, é razoável esperar que a regeneração futura em paisagens da Caatinga expostas a agricultura de corte-e-queima terá pouca contribuição destas fontes de regeneração florestal. Portanto, se quisermos promover práticas de manejo devotadas a aumentar a resiliência dos ecossistemas florestais, entender o efeito da agricultura de corte-e-queima sobre o processo de regeneração da floresta é fundamental para promover práticas de manejo e conservação, particularmente em florestas tropicais secas, que historicamente têm sido convertidas em mosaicos sucessionais devido à agricultura de subsistência e pecuária extensiva.

Em outras palavras, é preciso promover práticas de manejo destinadas ao uso sustentável da terra, a fim de aumentar a resiliência dos ecossistemas florestais e estabelecer um compromisso ideal entre a provisão de serviços ecossistêmicos para populações humanas e a preservação da vida selvagem, e, portanto, seguir em direção a “paisagens ideais ou paisagens antrópicas amigáveis à biodiversidade” (sensu ARROYO-RODRÍGUEZ et al., 2020; MELO et al., 2013). Neste sentido, buscando entender melhor os efeitos da agricultura de corte-e-queima sobre as fontes de regeneração da floresta, particularmente no que se refere ao banco e a chuva de sementes, em esta tese avaliei por meio de experimento simulando a agricultura de corte-e-queima como este método agrícola afeta particularmente às comunidades de plantas lenhosas do banco e da chuva de sementes em uma paisagem da floresta

tropical seca da Caatinga no nordeste do Brasil. Em particular, comparei o dano e a viabilidade do banco de sementes, bem como a estrutura, especialmente no que se refere densidade e diversidade de sementes, e composição taxonômica e funcional das assembleias do banco e da chuva de sementes em resposta à agricultura de corte-e-queima.

Em dois artigos, eu demonstro que (1) florestas expostas ao fogo produzido pela agricultura de corte-e-queima apresentam bancos de sementes que suportam uma baixa proporção de sementes viáveis após o fogo; (2) existe uma diminuição drástica na diversidade de espécies após o fogo, sobretudo no que se diz respeito as espécies raras do banco de sementes; (3) a dissimilaridade composicional entre as parcelas também diminui após o fogo, o que é explicado em grande parte pela perda de espécies, causando assim a homogeneização das assembleias de espécies do banco de sementes através do espaço; (4) a composição funcional das assembleias do banco de sementes também é alterada, com a frequência relativa de espécies arbustivas aumentando após o fogo, especialmente espécies com frutos carnosos e dispersão biótica; (5) a densidade de propágulos da chuva de sementes é reduzida em 15 vezes em parcelas queimadas quando comparada a parcelas de controle; (6) a diversidade de espécies da chuva de sementes segue o mesmo padrão encontrado para o banco de sementes no que se diz respeito especialmente a redução do número de espécies raras; (7) a diversidade-β de espécies raras da chuva de sementes aumenta nas parcelas queimadas, devido ao seu componente de rotatividade de espécies; (8) no entanto, não se observa nenhuma alteração na composição funcional das assembleias de espécies. Uma vez que estas descobertas destacam a baixa resiliência do banco e da chuva de sementes a este método agrícola comum em florestas tropicais secas, a regeneração futura desta e potencialmente de outras florestas tropicais ricas em espécies expostas à agricultura de corte-e-queima não poderá depender do banco e da chuva de sementes, mas sim de outras fontes de regeneração menos vulneráveis a este método agrícola como a rebrota de plantas. Esses resultados têm profundas implicações para o potencial de resiliência das florestas tropicais secas e para a conservação da biodiversidade e sustentabilidade ecológica em paisagens modificadas humanas. Espera-se, assim, contribuir na implementação de estratégias capazes de conciliar a produção sustentável de alimentos em paisagens modificadas humanas e a implementação de paisagens mais amigáveis com a vida selvagem.

2 FUNDAMENTAÇÃO TEÓRICA

2.1 A crise da biodiversidade no Antropoceno: causas e consequências

A pegada humana sobre a Terra se expande, de tal forma que nenhum ecossistema escapa do contato humano, isso levou a argumentação de que estaríamos vivendo sob uma nova era geológica, o Antropoceno (CRUTZEN, 2002; STEFFEN et al., 2015). O termo antropoceno inclui a concepção de que: (1) a pegada humana na Terra exerce uma pressão tão forte que pode equivaler a algumas das maiores forças da Natureza em seu efeito sobre muitos processos ocorrendo na biosfera; (2) a influência das pressões humanas sobre o planeta ocorrem em várias escalas espaciais variando em níveis locais e globais; (3) durante a revolução industrial houve um desdobramento da influência humana em uma taxa e escala sem precedentes, o que criou a primeira economia de combustíveis fósseis do mundo; (4) os efeitos da pegada humana podem acarretar em grandes mudanças na estrutura e funcionamento dos ecossistemas da Terra, incluindo aqueles encontrados nas regiões mais remotas e de difícil acesso (MALHI et al., 2017; 2014).

Uma das características mais marcantes do antropoceno é a transformação abrupta dos ecossistemas florestais para sistemas de uso humano, um processo especialmente ligado a atividades como a agricultura, pecuária extensiva, mineração, geração de energia e outras infraestruturas (CURTIS et al., 2018). Juntas, estas atividades humanas resultam em uma alarmante perda de habitat diária de quase 11.500 ha das últimas florestas tropicais primárias do mundo (GLOBAL FOREST WATCH, 2022). De modo geral, as causas da mudança no uso do solo variam regionalmente (CURTIS et al., 2018). Enquanto em florestas temperadas e boreais as principais causas de degradação dos ecossistemas florestais consistem na silvicultura e queimadas florestais, nas florestas do sudeste da Ásia a produção de óleo de dendê é o principal motor de perda de habitat. Ao longo dos trópicos úmidos a agricultura de larga escala por meio de commodities agrícolas como a carne bovina, soja, óleo de dendê e produtos de madeira são responsáveis pela maior parte do desmatamento em todo o mundo. No mesmo caminho, na América do Sul, fazendas de gado e campos de soja estão devastando não apenas a Amazônia, mas também as paisagens do Chaco e do Cerrado brasileiro. Finalmente, nos trópicos secos da África Subsaariana, América Central e do Sul a agricultura de subsistência é a principal fonte de conversão de terras nativas em áreas agrícolas.

Nesse contexto de deflorestação dos ecossistemas naturais, uma consequência comum a qualquer motor de perda de habitat ao redor do mundo é a perda da biodiversidade. Uma premissa universal prediz que habitats interrompidos e de menor área suportam menos espécies, bem como favorecem um maior risco de extinção local para espécies com baixa densidade de indivíduos (CHASE et al., 2020). De modo geral, processos que levam a perda de espécies se iniciam a partir do momento em que a floresta passa a ser distribuída em incontáveis e minúsculos fragmentos florestais imersos em matrizes agrícolas e áreas antrópicas (tamanho médio global: 13-17 ha; para mais detalhes veja TAUBERT et al., 2018). Esses pequenos fragmentos florestais formam um grande arquipélago de pequenas manchas florestais com a conectividade biológica interrompida, o que leva ao isolamento dos fragmentos na paisagem (FAHRIG, 2003). Diante da fragmentação e isolamento da floresta, as comunidades de plantas das bordas recém-criadas passam a experimentar novas condições microclimáticas como a redução da umidade, aumento da luz e maior variabilidade da temperatura (HARPER et al., 2005; KAPOS et al., 1989).

Em resposta à interrupção da cobertura florestal, mudanças na estrutura da floresta remanescente são ocasionadas pelo aumento da mortalidade de espécies de crescimento tardio e posterior colapso da biomassa vegetal (LAURANCE et al., 2002). Por outro lado, espécies de crescimento rápido e de baixa biomassa são favorecidas e dão início ao processo de regeneração nas bordas da floresta (TABARELLI et al., 2008). Conforme a regeneração nas bordas avança em direção ao interior dos fragmentos, o empobrecimento da assembleia de árvores promove o domínio de espécies pioneiras e a simplificação das comunidades de plantas (SANTOS et al., 2008; TABARELLI et al., 2008).

Com a perda de espécies do habitat original, alterações na abundância de indivíduos das populações e interações bióticas são interrompidas, levando a mudanças em todos os compartimentos biológicos do sistema, incluindo a estrutura e composição da comunidade e os conjuntos de características e interações que afetam a resiliência de longo prazo das funções do ecossistema (MORRIS, 2010; SANTOS et al., 2010), e os serviços essenciais que elas prestam (NAEEM et al., 2012, SOUSA et al., 2019). De modo geral, as respostas das espécies a perturbações antrópicas também podem ser refletidas em características como o tamanho do corpo, capacidade de dispersão e tolerância ao fogo e, portanto, até certo ponto são

previsíveis (JACKSON; FAHRIG, 2012; MIGUET et al., 2016). Nesse sentido, a perda de funções ecossistêmicas dependerá de quanto o sistema consegue manter características que conferem resiliência, envolvendo fatores que interagem em maiores escalas espaciais, como a heterogeneidade no nível da paisagem ou conectividade do habitat, para determinar a resiliência da função do ecossistema (OLIVER et al., 2015). Por exemplo, a disponibilidade de fontes de sementes pode ser reduzida em sistemas com uma baixa proporção de florestas nativas na paisagem circundante e, assim, diminuir a dispersão de sementes imigrantes por animais (e.g. sementes grandes dentro de frutos carnosos) para áreas afetadas por distúrbios antrópicos (SAN-JOSÉ et al., 2020). Esse cenário impede a colonização de plantas nesses locais perturbados, originando um pool de espécies empobrecido localmente, o que pode causar extinções em cascata, impedir a recuperação da floresta e sobretudo deteriorar ainda mais funções do ecossistema que essas espécies suportam (ARROYO et al., 2020; OLIVER et al., 2015).

Em geral, a resiliência florestal após perturbação procede mais rapidamente em paisagens recentemente modificadas, onde a floresta de crescimento antigo ainda está presente na paisagem, bem como árvores adultas remanescentes e fontes de regeneração viáveis (revisado por ARROYO-RODRÍGUEZ et al., 2017). Assim, paisagens florestais (aquelas contendo mais de 80% da cobertura arbórea) que tenham sua cobertura florestal reduzida, mesmo que em pequenas proporções (reduções em até 60% da cobertura arbórea) podem ser tipicamente conduzidas a savanas (20% da cobertura florestal) ou áreas de vegetação arbustiva/pequeno porte (sem cobertura arbórea) em resposta a mudanças drásticas na abundância relativa de formas de vida vegetal, na estratificação e na biomassa da vegetação (HIROTA et al., 2011). De fato, qualquer perturbação que interrompa a cobertura florestal e/ou cause o esgotamento das fontes de regeneração da floresta (por exemplo, banco de sementes, chuva de sementes e banco de plântulas, VIEIRA et al., 2015; VIEIRA; SCARIOT, 2006) deve ser particularmente prejudicial para a regeneração e resiliência da floresta (BEZERRA et al., 2022; 2023; CHAZDON, 2014; DAÏNOU et al., 2011; DALLING et al., 1997; PLUE; COUSIN, 2013; SOUSA et al., 2017; WIJDEVEN; KUZEE, 2000).

2.2 Agricultura de corte-e-queima no Antropoceno: uma revisão dos impactos em florestas tropicais secas

Ocupando quase metade das florestas tropicais e subtropicais do mundo (MURPHY; LUGO, 1986), as florestas tropicais secas integram 54% da cobertura florestal global (MILES et al., 2006). Elas estão distribuídas em zonas climáticas similares onde uma das características mais marcantes é a sazonalidade, o que limita a ocorrência de grupos biológicos adaptados para enfrentar estiagens por mais de seis meses (MALHI; WRIGHT, 2004; MURPHY; LUGO, 1986; PENNINGTON et al., 2009). Em resposta às condições impostas pelo estresse hídrico, alta irradiação solar e evapotranspiração, a maioria das plantas lenhosas apresenta fenologia decídua e ciclos biológicos definidos pela sazonalidade (DIRZO et al., 2011; MURPHY; LUGO, 1986; PENNINGTON et al., 2009). Diferenças entre grupos vegetais surgem a partir de variações na estrutura florestal – árvores de pequeno porte, vegetação arbustiva e diferentes tolerâncias e estratégias como: para escapar da seca ou tolerar a perda de água, muitas plantas armazenam água em seus tecidos, produzem acúleos e espinhos (para mais detalhes veja GIULIETTI et al., 2004).

Como biota, as florestas secas abrigam uma grande diversidade de espécies de plantas arbóreas, arbustivas e cactos (BULLOCK et al., 1995). Espécies de mamíferos compreendem roedores, canídeos, marsupiais, cervídeos e felinos (ALVES et al., 2020; DIRZO et al., 2011). Outros grupos incluem espécies de aves, lagartos e insetos como formigas e borboletas (DIRZO et al., 2011; SILVA et al, 2017), incluindo altos níveis de endemismos (LINARES-PALOMINO et al., 2011). Em relação a provisão de serviços ecossistêmicos, essas florestas são poderosos sumidouros de carbono (BRIENEN et al., 2015; SAATCHI et al., 2011; SULLIVAN et al., 2017) com impactos na regulação do clima, estoque de carbono e mitigação das mudanças climáticas (PHILLIPS et al., 2009).

Apesar de abrigar um patrimônio biológico e cultural de importancia única, as florestas tropicais secas são habitadas por milhões de comunidades rurais de baixa renda que exercem forte pressão sobre a flora e fauna, retirando do meio produtos florestais madeireiros e não madeireiros (por exemplo, madeira, lenha, carvão vegetal e plantas medicinais) para fins de subsistência (ALBUQUERQUE et al., 2007; SÁNCHEZ-AZOFEIFA et al., 2014). Junto com atividades como a criação extensiva de caprinos e bovinos, caça e agricultura de corte-e-queima essas atividades

extrativistas criam um cenário de dependência intrínseca das populações humanas e recursos naturais.

A agricultura de corte-e-queima é a atividade de subsistência mais frequente no contexto das florestas secas (CURTIS et al., 2018; FAO, 2010). Estima-se que, globalmente, cerca de 36 milhões de km^2 de terras estejam sob domínio da agricultura de corte-e-queima e que este método de cultivo represente aproximadamente 30% do recurso global do solo (HAUSER; NORGROVE, 2013). Áreas cultivadas geralmente envolvem campos agrícolas de 0,5 a 5 ha (LOWDER et al., 2016; TANZITO et al., 2020). A criação dos cultivos se inicia com o corte manual de toda a biomassa lenhosa por meio de machados e facões. Em seguida, os agricultores recolhem madeiras com alta densidade para serem usadas como lenha, cercas e outras utilidades. Sem mais remoção dos detritos restantes, a biomassa é então deixada para secar naturalmente e no final da estação seca é queimada com posterior semeadura dos cultivares comumente plantados na região (HAUSER; NORGROVE, 2013; KLEINMAN et al., 1995; RIBEIRO-FILHO et al., 2013). Com exceção da mão de obra, este método agrícola geralmente opera com baixos insumos externos (SANCHEZ, 2002), onde se excluem a utilização de máquinas para limpeza, irrigação dos cultivos, e uso de fertilizantes e pesticidas (HAUSER; NORGROVE, 2013; KLEINMAN et al., 1995).

Esta forma tradicional de agricultura é utilizada há milhares de anos e por isso alguns autores a consideram sustentável, principalmente em regiões com baixa densidade populacional e alta cobertura florestal (BISHT et al., 2014; JOHNSON; CURTIS, 2001; KLEINMAN et al., 1995; PEDROSO-JUNIOR et al., 2008; 2009). No entanto, avaliações recentes estimam que esse método agrícola foi responsável por cerca de 24% da perda florestal global entre 2001 e 2015 (CURTIS et al., 2018). De fato, a agricultura de corte-e-queima é altamente disseminada ao longo dos trópicos e subtrópicos da América Central e do Sul, África, Ásia e Australia (CURTIS et al., 2018). Devido ao crescimento demográfico urbano e rural e às importantes transformações climáticas ocorridas nas últimas décadas nessas regiões (MERTZ, 2002; PEDROSO-JUNIOR et al., 2008; 2009; VAN-VLIET et al., 2012), esta atividade global pode limitar até mesmo sua própria sustentabilidade em cenários futuros (SOUZA et al., 2019).

A literatura científica gerada nas últimas décadas tem mostrado que os efeitos da agricultura de corte-e-queima podem ser muito variados. Por exemplo, em pequenas escalas espaciais e temporais, o fogo aumenta a fertilidade do solo, já que

incinera detritos como pequenos galhos e folhas, permitindo a entrada de nutrientes no solo como nitrogênio e fósforo via cinzas (MENEZES et al., 2012; RAISON, 1979). Outro efeito positivo do fogo em escala local é a eliminação imediata de ervas daninhas e outros inimigos das culturas, como artrópodes herbívoros, fungos e bactérias patógenas (EBEL, 2018). Em escalas espaciais e temporais maiores, um efeito positivo está associado à geração de áreas abertas e florestas secundárias na paisagem, uma vez que esses habitats são utilizados por muitas espécies de plantas e animais, como muitos mamíferos (por exemplo, javalis, veados) e aves migratórias (FERREIRA et al., 2018; KEAST; MORTON, 1980). A geração de novos habitats também pode ser um processo muito valioso, pois aumenta a heterogeneidade da paisagem, o que pode favorecer a coexistência de um maior número de espécies com diferentes exigências ecológicas (FAHRIG et al., 2011).

A investigação científica sobre a agricultura de corte-e-queima também demostrou que este método agrícola pode ter efeitos neutros nas comunidades bióticas. Por exemplo, Barros et al., (2021) e Filgueiras et al., (2021) analisaram a diversidade de plantas e besouros rola-bosta ao longo de uma cronossequência de florestas em sucessão (de 4 a 70 anos de abandono) que se dedicaram a essa atividade e encontraram níveis de diversidade semelhantes aos registrados em florestas maduras que nunca foram cultivadas. No entanto, o número de estudos mostrando efeitos negativos dessa atividade tem aumentado nas últimas décadas.

Por exemplo, embora a agricultura de corte-e-queima aumente a fertilidade do solo a curto prazo, os nutrientes que são rapidamente incorporados às culturas são perdidos por lixiviação e erosão do solo, bem como na forma de partículas de fumaça (ANDREAE; MERLET, 2001; CHRISTENSEN, 1977; LEWIS, 1974, UHL; JORDAN, 1984). O nitrogênio é particularmente sensível ao fogo, pois é muito volátil, a queima de folhas e galhos pode causar uma perda de mais de 90% de nitrogênio (DEBELL; RALSTON, 1970; LOBERT et al., 1990). Além disso, a liberação do carbono armazenado na vegetação para a atmosfera como dióxido de carbono é outra resposta esperada em relação à queima da vegetação. Em geral, a quantidade de CO^2 liberada dependerá da qualidade (e.g. árvores vs. arbustos) e quantidade da biomassa original, bem como do seu teor de água e das condições climáticas que governam a decomposição após a queima (HAUSER; NORGROVE, 2013). Embora os nutrientes do solo possam ser repostos com biomassa viva e serapilheira após o abandono da cultura, esse processo pode levar várias décadas até atingir os valores

encontrados em florestas maduras adjacentes (BROWN; LUGO, 1990). Do mesmo modo, o fogo também pode reduzir a porosidade do solo e causar compactação, o que aumenta a lixiviação de nutrientes e a erosão do solo (ALEGRE; CASSEL, 1996; HERNANI et al., 1999; PEREIRA; VIEIRA, 2001). Isso pode forçar o agricultor a abandonar as lavouras com mais frequência e encurtar o período de pousio, o que pode reduzir a produção agrícola e favorecer a entrada de espécies invasoras (LAWRENCE; FOSTER, 2002; KNOECHELMANN et al., 2020).

De fato, muitos fatores bióticos podem ser alterados pela agricultura de corte-e-queima, incluindo vários processos ecológicos importantes para o funcionamento do ecossistema (BEZERRA et al., 2022; KLANDERUD et al., 2010; RAMAN et al., 2001, OAKLEY; BICKNELL, 2022). Por exemplo, a queima pode reduzir a biomassa de microrganismos das camadas superficiais do solo e suas atividades de decomposição (ABOIM et al., 2008; RIBEIRO-FILHO et al., 2013; 2015). Bactérias fixadoras de nitrogênio são muito vulneráveis a mudanças de pH após o fogo. Efeitos da queima em microssimbiontes podem afetar a composição e produtividade da vegetação, bem como certas espécies que dependem de simbiontes para realizar suas atividades. Este é o caso de muitos cultivos que têm micorrizas e são hábeis para aumentar o acesso de fósforo orgânico usando a enzima fosfatase em uma reação de hidrólise. Embora a queima possa aumentar a disponibilidade de fosfato via cinzas, isso reduz a quantidade de micorrizas, e no geral esses efeitos podem ser negativos dependendo se os cultivos são micorrízicos e se o material de plantio está infectado (HAUSER; NORGROVE, 2013). Além disso, após a queima de grandes quantidades de biomassa as cinzas são dissolvidas nas primeiras chuvas. Essa solução contém um alto conteúdo de pH (acima de 10), o qual pode matar espécies como as minhocas, que usualmente vivem sob condições menos acidas e que estão tipicamente associadas a cobertura florestal (aproximadamente 4.0-4.5 em florestas úmidas) (ADEYOLANU et al., 2013).

Junto à eliminação da cobertura florestal também são alterados vários atributos das comunidades de animais como formigas arborícolas e de serapilheira, bem como agentes polinizadores e dispersores de sementes, rompendo assim serviços ecossistêmicos como a defesa de plantas contra herbívoros e processos ecológicos como a dispersão de sementes (CARBONE; AGUILAR, 2021; HAUSER; NORGROVE, 2013; SAN-JOSÉ et al., 2020; VENTER et al., 2017). Em espécies de vertebrados a queima afeta especialmente sua mobilidade. Embora mamíferos sejam

capazes de escapar do corte e queima da vegetação fugindo para áreas não afetadas da vegetação vizinha, muitos répteis e anfíbios são mortos quando a floresta é cortada e queimada, uma vez que não podem escapar rapidamente (RUSSEL et al., 1999). Além disso, quando vertebrados e particularmente as densidades de mamíferos e aves diminuem após agricultura de corte-e-queima, o potencial de resiliência da floresta é reduzido porque muitos vertebrados são responsáveis pela dispersão de sementes (ALVES et al., 2020; BEZERRA et al., 2020; RAMAN et al., 2001).

Além dos efeitos anteriormente citados, este método agrícola também pode aumentar interações antagônicas, como é o caso da herbivoria causada por formigas cortadeiras (LEAL et al., 2017; TABARELLI et al., 2017). As colônias dessas espécies de formigas cortam folhas e outros materiais vegetais que usam como substrato para o cultivo de fungos simbióticos - a principal fonte de alimento da colônia (ABRIL; BUCHER, 2004). Hoje sabemos que essas formigas proliferam em campos agrícolas abandonados, o que pode fazer com que esses insetos limitem ou impeçam a regeneração das plantas, principalmente em locais onde a cobertura florestal é menor (KNOECHELMANN et al., 2020).

Embora seja possível que, à escala da paisagem, as áreas cultivadas e as florestas secundárias sejam utilizadas por numerosas espécies de vertebrados, deve-se ter em conta que a utilização destas parcelas agrícolas pode expô-las à caça. Portanto, essas áreas poderiam funcionar como armadilhas e sumidouros ecológicos, um aspecto plausível e pouco explorado. De fato, a proliferação de cultivos e florestas secundárias na paisagem pode provocar sua homogeneização, prejudicando as espécies florestais comuns e ao mesmo tempo favorecendo certos traços funcionais ou algumas espécies adaptadas às perturbações humanas. Isso é particularmente provável em regiões densamente povoadas, onde o número e o tamanho dos fragmentos florestais convertidos em culturas agrícolas estão aumentando, às custas da cobertura florestal de crescimento primário (METZGER et al., 2002; 2003).

A remoção da vegetação também pode reduzir a precipitação localmente e aumentar a radiação solar e a temperatura do solo, causando uma redistribuição regional da precipitação (BALLING, 1989; CARLSON; GROOT, 1997; HAUSER; NORGROVE, 2013; HE et al., 2010; KURC; SMALL, 2004; MORECROFT et al., 1998). Por exemplo, a remoção da vegetação em regiões semiáridas do México mostrou estar associada a uma diminuição na precipitação e um aumento na temperatura do solo (ALTHOFF et al., 2016; BALLING, 1989; HE et al., 2010; KURC; SMALL, 2004).

Esses fatores reduzem o fornecimento de serviços ecossistêmicos essenciais para as comunidades humanas, como a regulação do clima, e aceleram o processo de desertificação (CHEHINE, 1995; KOSTER et al., 2004; SCHLESINGER, 1990).

Espera-se que todos esses impactos piorem nos próximos anos, pois as florestas tropicais secas continuam a sofrer taxas de desmatamento muito altas (CURTIS et al., 2018). Na verdade, essas florestas são um dos biomas mais desmatados, mas também um dos mais negligenciados em termos de políticas de conservação (SIYUM, 2020). Muitas evidências empíricas mostraram fortes impactos da agricultura de corte-e-queima na funcionalidade e saúde das florestas tropicais secas. Portanto, é crucial avaliar os efeitos deste modo de agricultura sobre fontes críticas de regeneração em florestas tropicais secas, a fim de entender melhor as consequências dessa prática e poder projetar estratégias adequadas de mitigação e remediação.

2.3 Impactos da agricultura de corte-e-queima sobre as fontes de regeneração da floresta

A regeneração dos ecossistemas tropicais é um processo chave para a resiliência florestal e está diretamente ligada à persistência da biodiversidade, manutenção da provisão de serviços ecossistêmicos e sustentabilidade socioecológica em nível global (CHAZDON et al., 2016; SOUZA et al., 2019). No caso da agricultura de corte-e-queima, que é a perturbação mais frequente no contexto das florestas tropicais secas, as florestas em regeneração emergem em resposta a pousios pós-cultivo (FAO, 2010). A regeneração florestal segue trajetórias sucessionais específicas que se iniciam com a conversão de áreas nativas para agricultura/pecuária, com posterior abandono da terra (LEBRIJA-TREJOS et al., 2011), o que desenvolve possibilidades para a regeneração da floresta (AIDE; GRAU, 2004; CHAZDON, 2012).

A recuperação de uma floresta geralmente está ligada a fontes de regeneração baseadas em sementes como a chuva e o banco de sementes, bem como o *pool* local de rebrotas de plantas sobreviventes após distúrbios (VIEIRA; SCARIOT, 2006). No caso da regeneração em paisagens modificadas pela agricultura de corte-e-queima, a regeneração da floresta depende não apenas da disponibilidade das fontes de regeneração, mas de quanto na verdade a agricultura as afeta e reduz a capacidade

de resiliência do sistema. Isto porque a regeneração futura da floresta pode ser imprevisível em áreas expostas a este tipo de agricultura, pois seus efeitos perpassam mais além dos danos causados durante o ciclo agrícola (e.g. perda da cobertura florestal e redução dos nutrientes do solo). Refiro-me particularmente à agricultura de corte-e-queima agindo como força deflagradora do processo de desertificação por meio de efeitos deletérios como o empobrecimento do solo e a eliminação das fontes de regeneração (VIEIRA et al., 2015). Isto deve ameaçar o potencial de regeneração da floresta por meio da redução da qualidade/quantidade de sementes e aumento da contribuição de espécies com capacidade de rebrota (COLÓN; LUGO, 2006), levando a sistemas que seguem perfis de degeneração, mesmo que algumas características isoladas do sistema como a recuperação da biomassa e fertilidade do solo estejam dando sinais de retorno/recuperação (LAWRENCE et al., 2010, SOUZA et al., 2019). De fato, evidencias já mostraram que a agricultura de corte-e-queima causa não apenas um somatório de restrições nas fontes de regeneração, mas também altera vários processos ecológicos essenciais para a manutenção e recuperação do banco e da chuva de sementes nas áreas de uso agrícola (e.g. polinização, produção de sementes, dispersão de sementes) (BEZERRA et al., 2022; KLANDERUD et al., 2010, OAKLEY; BICKNELL, 2022; RAMAN et al., 2001).

Por exemplo, após a conversão de áreas de floresta nativa para uso agrícola a polinização pode ser afetada, já que muitos grupos biológicos responsáveis pelos sistemas de polinização, como é o caso das abelhas, podem diminuir notavelmente nas áreas agrícolas em comparação com a floresta circundante ou mesmo nas parcelas com agricultura tradicional de baixa intensidade (LANDAVERDE-GONZÁLEZ et al., 2017). Assim, a agricultura de corte-e-queima pode promover a limitação da fonte de sementes, seja por falta de polinização ou pela eliminação de árvores adultas nos cultivos. De fato, a chuva de sementes parece conter menos sementes e espécies em áreas cultivadas do que em florestas adjacentes. Rocha et al., (2021) também registraram menor abundância de sementes dispersas por animais em áreas queimadas. Isso é verdade até mesmo em locais onde predomina a dispersão abiótica de sementes, pois a perda da cobertura florestal reduz a abundância de árvores adultas em nível local, o que afeta diretamente a densidade de sementes em áreas queimadas, afetando principalmente o número de espécies raras (CLARK et al., 1998; HOWE; SMALLWOOD, 1982; MULLER-LANDAU et al., 2002). Isso provavelmente se deve à limitação da fonte e à limitação da dispersão,

uma vez que a perda florestal aumenta a distância entre as fontes de sementes e as parcelas de cultivo (PIOTTO et al., 2019; SOUZA et al., 2014).

A limitação da fonte e/ou dispersão de sementes em parcelas de cultivo é particularmente preocupante no contexto da regeneração florestal, uma vez que a agricultura de corte-e-queima também parece ter impactos significativos no banco de sementes (MAMEDE; ARAÚJO, 2008). Por exemplo, em ecossistemas dependentes do fogo, ou seja, ecossistemas que evoluíram na presença de queimadas episódicas e dependem delas para manter seus processos ecológicos, como é o caso do Cerrado brasileiro, fogo direto, fumaça e cinzas podem estimular a germinação de sementes enterradas no solo (FIDELIS et al., 2016; PIVELLO et al., 2011; 2021). Contudo, ecossistemas independentes do fogo, ou seja, ecossistemas que não evoluíram com a presença de queimadas e cuja flora e fauna não têm adaptações ao fogo, como por exemplo a floresta Maya no México ou a Caatinga no Brasil, os bancos de sementes são altamente vulneráveis ao fogo (MAMEDE; ARAÚJO, 2008). Em particular, o fogo reduz drasticamente a abundância e diversidade de sementes no banco de sementes, e a maioria das sementes remanescentes queima ou perde sua viabilidade (KENNARD et al., 2002). A limitação da dispersão também pode estar associada à perda de dispersores de sementes nas áreas de cultivo, incluindo muitos mamíferos e aves (ALVES et al., 2020; RAMAN et al., 2001). Portanto, o fato de a dispersão de sementes ser limitada indica que ela não pode repor o banco de sementes após o fogo. Isso deve afetar a dinâmica florestal em paisagens habitadas por pessoas dependentes dos recursos florestais e afetar a diversidade de espécies em florestas perturbadas a longo prazo. Logo, se queremos promover práticas de gestão ambiental destinadas a aumentar a resiliência dos ecossistemas florestais, resguardar a biodiversidade e manter a sustentabilidade de comunidades humanas e não-humanas é necessário compreender o impacto da agricultura de corte-e-queima no banco e na chuva de sementes.

2.4 Caatinga: o que sabemos sobre impactos da agricultura de corte-e-queima sobre a regeneração da floresta

Desde os primeiros momentos do batismo por Martius em 1840 a Caatinga vem sendo demonizada como um ambiente semiárido escaldante, no qual espécies de árvores espinhosas e quase sem vida servem de cenário para uma população ossuda,

cuja agricultura de subsistência e a criação de pequenos rebanhos são arruinadas pelas estiagens que atingem a região (LEAL et al., 2003; SILVA et al., 2017). Ainda hoje as secas extremas que assolam o semiárido são resumidas como um argumento político quase irrefutável para conseguir recursos para planos de desenvolvimento rural (FARIAS et al., 2020). Muito distante dessa ideia, a Caatinga é mais apropriadamente descrita como um sistema socioecológico exuberante (ANDRADE-LIMA, 1981; PRADO, 2003; SILVA et al., 2017), mas que possui seu patrimônio natural e cultural sob constante ameaça (LEAL et al., 2003).

Cobrindo uma área de cerca de 912.529 km², a floresta seca da Caatinga integra o maior bloco de florestas secas do mundo (MMA/IBAMA, 2011; MILES et al., 2006; SILVA et al., 2017). Apesar da alta diversidade biológica, a Caatinga tem apenas ~1% de sua área de proteção integral, a menor extensão de área protegida de todos os ecossistemas brasileiros (LEAL et al., 2005; MELO et al., 2010). Esta floresta também é o lar de quase 28,6 milhões de pessoas, que exercem complexas interações com a natureza (SILVA et al., 2017). Desde a chegada dos europeus no século XVI, o uso da terra associado à presença de povos caçadores-coletores incorporou a criação extensiva e a agricultura de subsistência (TABARELLI et al., 2018). Séculos mais tarde, plantios de mamona, cana, sisal, e algodão branco e colorido integram alguns tipos de cultivos responsáveis pelo poder econômico no semiárido durante algum tempo (EVANGELISTA, 2010). No entanto, junto a posterior ruptura dessas culturas no sertão, surge um ecossistema à beira do colapso.

A Caatinga tal qual como conhecemos hoje representa o legado de três séculos de atividades baseadas no extrativismo e na subsistência (e.g. corte excessivo da vegetação para lenha e outros usos, criação extensiva de caprinos e bovinos, e agricultura de corte-e-queima), secas severas, restrições políticas e pobreza extrema (COIMBRA-FILHO; CÂMARA 1996; FAO, 2010), cuja biodiversidade e processos ecológicos fundamentais para manutenção da vida selvagem e humana como a regeneração florestal não têm acompanhado a transformação do ecossistema e o número crescente de espécies ameaçadas de extinção (TABARELLI et al., 2018).

Em resumo, a Caatinga hoje consiste em um ecossistema formado por paisagens modificadas humanas cada vez mais descaracterizadas devido a transformação da vegetação nativa em mosaicos compostos por florestas de diferentes idades de abandono pelo homem, campos agrícolas e manchas de floresta nativa (LAWRENCE; FOSTER, 2002; SINGH, 1998). Nesse sentido, florestas em

regeneração surgem assim após a ocorrência de distúrbios de origem antrópica (e.g. pecuária e agricultura), com posterior abandono da terra (LEBRIJA-TREJOS et al., 2011). Logo, florestas em regeneração são hoje o componente mais expressivo dos ecossistemas tropicais contexto regional e cabe a elas o dever de reter biodiversidade e fornecer serviços ecossistêmicos (FAO, 2018).

Este dever emergente na conservação e sustentabilidade socioecológica global trouxe de volta o interesse científico na regeneração de florestas secundárias de paisagens modificadas humanas (ARROYO-RODRÍGUEZ et al., 2017). Nesse contexto, a floresta seca da Caatinga surge como um excelente cenário para entender como perturbações de origem antrópica como a agricultura de corte-e-queima podem afetar a regeneração e a resiliência da floresta. No entanto, entender como funciona esse fenômeno ainda é um obstáculo pois: (1) faltam estudos experimentais para detalhar como a agricultura de corte-e-queima afeta as fontes de regeneração do sistema, já que a grande parte dos estudos trazem comparações em função de diferentes tipos de uso do solo, níveis de perturbação e precipitação; (2) estudos sobre o banco e a chuva de sementes geralmente contabilizam todas as formas de vida, o que torna difícil fazer generalizações para o ecossistema; (3) muitos desses estudos se concentram na densidade de sementes intactas após agricultura, o que pode mascarar os efeitos do fogo sobre a viabilidade das sementes; (4) a ausência de trabalhos sobre os padrões de diversidade beta torna difícil descrever os efeitos deste método agrícola na homogeneização da paisagem, (5) faltam estudos em nível funcional, já que a maioria foca massivamente na estrutura taxonômica da vegetação ao longo de gradientes de regeneração florestal (FERREIRA et al., 2015; PEREIRA et al., 2001). Como a produtividade e a sustentabilidade da agricultura de corte-e-queima dependem fortemente da capacidade da floresta se regenerar após perturbações (KUKLA et al., 2019; SANCHEZ, 2000), compreender o efeito deste método agrícola sobre o banco e a chuva de sementes da Caatinga é valioso para informar práticas de manejo e conservação, e de alguma forma, compreender os caminhos futuros de outras fronteiras agrícolas mais recentes das florestas secas.

Existem evidencias de que os bancos de sementes em florestas tropicais secas são naturalmente pobres (i.e. em áreas não perturbadas) em termos de abundância e diversidade de sementes de plantas lenhosas (e.g. DA SILVA et al., 2013; GARWOOD, 1989; SKOGLUND, 1992; GOMES et al., 2019). Logo, é provável que a agricultura de corte-e-queima atue como um fator crítico de estresse ambiental,

moldando a chuva e o banco de sementes na floresta seca da Caatinga (FERREIRA et al., 2014). Em particular, estudos em outras florestas tropicais demonstram que a densidade de sementes e a riqueza de espécies na chuva de sementes é menor até duas vezes em florestas queimadas/em sucessão do que em florestas nativas (CARRIERE et al., 2002; MARTINI et al., 2007; PIOTTO et al., 2019; ROCHA et al., 2021). Evidências anteriores também mostraram que a regeneração florestal na floresta da Caatinga por chuva de sementes tende a ocorrer lentamente mesmo em estágios intermediários de regeneração (SOUZA et al., 2014). Logo, os impactos da agricultura de corte-e-queima poderiam ser particularmente importantes no ecossistema da Caatinga, pois, é conhecido que as terras agrícolas em florestas secas tendem a apresentar falhas na chegada de sementes (CECCON et al., 2008; JARA-GUERRERO et al., 2020).

No caso do banco de sementes existe um número limitado de avaliações sobre o efeito da agricultura de corte-e-queima sobre esta fonte de regeneração. No geral, a literatura disponível sobre o tema demonstra que as florestas secundárias da Caatinga suportam um banco de sementes de plantas lenhosas de baixa densidade média mensal (4.89 sementes/m^2), as quais estão entre as mais baixas já relatadas para outras florestas tropicais sazonalmente secas (ou seja, 2.47 sementes/m^2) (DE PAULA et al., 2023). Uma única avaliação sobre os efeitos da agricultura de corte-e-queima sobre o banco de sementes da Caatinga demonstra que áreas recém queimadas apresentam reduções de até de 80% na densidade de sementes e 44% na riqueza de espécies (MAMEDE; ARAÚJO, 2008). A suscetibilidade de sementes ao fogo também foi demonstrada por Kennard et al., (2002) na floresta seca da Bolívia, onde sementes incineradas pelas altas temperaturas alcançadas pelo fogo perdem a viabilidade devido a desidratação das sementes e superaquecimento do embrião, causando assim a mortalidade de até 94% das sementes. Na Caatinga, esses processos de mortalidade de sementes poderiam resultar no declínio de espécies raras em escalas locais e regionais, pois evidências anteriores apontam uma alta vulnerabilidade de espécies raras de árvores a distúrbios antrópicos na Caatinga (MAMEDE; ARAÚJO, 2008; RITO et al., 2017; 2021).

Padrões observados em regiões mediterrâneas do Iran demonstraram que muitas áreas afetadas por queimadas antrópicas e naturais também sustentam menor diversidade α e β (HEYDARI et al., 2017). Como o fogo elimina muitas espécies de plantas intolerantes a altas temperaturas acaba reduzindo as populações destas

espécies na paisagem, resultando assim em alta homogeneização florística no espaço. Do ponto de vista adaptativo, as plantas lenhosas da Caatinga não apresentam nenhum tipo de adaptação ao fogo (PIVELLO et al., 2011), o que poderia implicar na co-ocorrência de espécies de plantas funcionalmente distintas (BARROS et al., 2021). No entanto, é possível que algumas características pudessem conferir algum nível de tolerância ao fogo (TANGNEY et al., 2019, 2020), como: (1) tamanho pequeno, já que poderia facilitar enterramento de sementes no solo (FERREIRA et al., 2014; THOMPSON et al., 1993), (2) modo de dispersão, pois a limitação de dispersão em florestas perturbadas é geralmente mais forte em sementes dispersas por animais do que em sementes dispersas pelo vento (SAN-JOSÉ et al., 2020), (3) sementes com testa dura e menos sensíveis à dessecação (KHURUMA; SINGH, 2001; TEEGALAPALLI et al., 2010), uma característica associada a sementes ortodoxas dentro de frutos secos que podem permitir que as sementes sobrevivem em solos expostos a altas temperaturas (CLARK, 1991).

É claro que teoricamente tanto o banco como a chuva de sementes poderiam ser reabastecidos pela dispersão de sementes de áreas próximas, mas é difícil dar uma estimativa de tempo. Alguns trabalhos como o de Mendes et al., (2014) sugerem que esse processo deve levar mais de 17 anos para o banco de sementes e mais de 20 anos para a chuva de sementes. Isso pode ser particularmente verdadeiro para paisagens expostas a falta de sementes devido a disponibilidade limitada de árvores e/ou produção limitada de sementes e da limitação de dispersão de sementes devido à falha de uma semente em chegar a um local apesar da disponibilidade suficiente de sementes (TRINDADE et al., 2020). Baixa produção de sementes e limitação de dispersão não são uma novidade na Caatinga (LEITE; MACHADO, 2010; TRINDADE et al., 2020). A baixa eficiência reprodutiva tem sido documentada como um fenômeno frequentemente observado em espécies da família Fabaceae (LEITE; MACHADO, 2010), onde a baixa taxa de produção de frutos e a alta taxa de aborto de sementes operam por uma deficiência na reprodução das espécies desta família (MUNIN et al., 2008; STEPHENSON, 1981; WEBB; BAWA, 1985). Além disso, apenas 0,003% das sementes que chegam a florestas queimadas representam sementes zoocóricas viáveis (Jakelyne S. Bezerra, dados não publicados). Logo, estas limitações na produção e dispersão de sementes já presentes na paisagem da Caatinga devem ser ampliadas devido a agricultura de corte-e-queima, levando a restrição no

reabastecimento do banco e da chuva de sementes e, naturalmente, da regeneração futura da floresta.

Outros estudos observaram que a regeneração da floresta da Caatinga é funcionalmente estruturada em estágios ontogenéticos mediados principalmente pela disponibilidade hídrica, mas não pelo tempo desde o abandono da terra. A limitação de dispersão seleciona apenas espécies com sementes pequenas e com alta capacidade dispersiva da região para o conjunto local e a limitação de recrutamento desfavorece a germinação ou persistência de espécies com sementes pequenas e com alta densidade da madeira (TRINDADE et al., 2020). Isto ajuda a explicar o caso das comunidades em regeneração dominadas por adultos e não por plântulas (TRINDADE et al., 2020; VANDERLEI et al., 2022). A floresta seca da Caatinga está exposta a uma assembleia de plântulas de baixa densidade de indivíduos (<0,5 plântula m^2) e taxonomicamente empobrecida em escalas espaciais locais e da paisagem (TRINDADE et al., 2020; VANDERLEI et al., 2022). Esse subconjunto de plântulas é dominado por um pequeno grupo de espécies, o que pode refletir limitações ao longo de paisagens modificadas na Caatinga (VANDERLEI et al., 2022). Mesmo assim, certas espécies de plântulas são capazes de manter algumas funções do ecossistema como é o caso da área foliar específica e conteúdo de matéria seca foliar – uma resposta decorrente da presença de estratégias conservadoras e aquisitivas de uso de recursos entre as espécies remanescentes (VANDERLEI et al., 2022).

Qualquer impacto negativo que a agricultura de corte-e-queima possa oferecer a regeneração da floresta pode ser particularmente importante na floresta seca da Caatinga (PIVELLO et al., 2021). Sendo assim, a regeneração da floresta seca da Caatinga não poderá contar com uma regeneração bem-sucedida baseada em sementes (i.e. banco de sementes, chuva de sementes e banco de plântulas), mas de outras fontes de regeneração como a rebrota de plantas. Espécies vegetais como a *Pityrocarpa moniliformis* (Fabaceae), que tem uma ampla capacidade de rebrotar plântulas através da propagação vegetativa, demonstrou ser particularmente valiosa para promover a regeneração da floresta da Caatinga após o abandono da área de cultivo (BARROS et al., 2021; VANDERLEI et al., 2021). Logo, como a rebrota também é uma fonte de regeneração menos vulnerável a distúrbios e que permite que as plantas sobrevivam ao corte e queima da vegetação, bem como a capina e diferentes regimes de perturbação (BARROS et al., 2021; CLARKE et al., 2013; VANDERLEI et

al., 2021), podemos supor que recuperação da floresta após a agricultura de corte-e-queima dependerá em grande parte da rebrota– uma importante característica de tolerância a práticas agrícolas insustentáveis.

3 ARTIGO 1 – DRASTIC IMPOVERISHMENT OF THE SOIL SEED BANK IN A TROPICAL DRY FOREST EXPOSED TO SLASH-AND-BURN AGRICULTURE

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Drastic impoverishment of the soil seed bank in a tropical dry forest exposed to slash-and-burn agriculture

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ABSTRACT

Forest ecosystems are increasingly threatened by unsustainable agricultural practices, especially by those that damage their regenerative potential. This can be the case of slash-and-burn agriculture – a farming method that can negatively impact the soil seed bank, potentially limiting the resilience of forest ecosystems. To test this hypothesis, and thus look for management practices aimed at enhancing forest recovery, we examined the impact of fire throughout an experiment of slash-and-burn agriculture on the soil seed bank of woody plants in the Caatinga tropical dry forest, northeast Brazil. We compared seed damage and viability, and the structure (seed density and diversity) and composition (taxonomic and functional) of seed bank assemblages before and after fire. We found a significant decrease in the frequency and proportion of intact (undamaged) seeds after fire, and a 3.6-fold decrease in the proportion of viable seeds. While seed density remained constant, species diversity drastically decreased after fire, especially the number of rare species. The compositional dissimilarity (β-diversity) between plots also dropped after fire, particularly its turnover component, thus causing the homogenization of seed assemblages across space. The functional composition of seed assemblages was also altered, with the relative frequency of shrub species increasing after fire, especially species with fleshy fruits and biotic dispersal. Taken together, our findings highlight the low resistance of the soil seed bank to this common farming method in tropical dry forests. Therefore, the recovery of this and potentially of other species-rich tropical forests exposed to slash-and-burn agriculture cannot rest on the soil seed bank, but on other processes such as seed dispersal and resprouting – an interesting avenue for future research.

1. Introduction

The 'Anthropocene' is characterized by an increasing conversion of forest ecosystems to agricultural lands (Malhi, 2017). Aside of forest loss (Hansen et al., 2020), such conversion has severe impacts on forest's regenerative potential (Arroyo-Rodríguez et al., 2017; Malhi et al., 2014). This is particularly true for unsustainable agricultural practices that disrupt key ecological processes for forest regeneration (e.g. pollination, seed dispersal, seed bank formation) (Arroyo-Rodríguez et al., 2017; Malhi et al., 2014). Therefore, if we are to promote management practices aimed at enhancing the resilience of forest ecosystems, we need to understand the impact of agriculture on important sources of forest regeneration, such as the soil seed bank.

Forest regeneration after disturbance is usually faster and more predictable in recently modified landscapes, where remnant trees and the soil seed bank persist, and where well-preserved native forests are still present in the landscape (reviewed by Arroyo-Rodríguez et al., 2017). Therefore, the farming methods that eliminate the tree cover and disrupt the soil seed bank ("seed bank" hereafter) are expected to be particularly harmful for forest regeneration and resilience (Chazdon, 2014; Daïnou et al., 2011; Dalling et al., 1997; Plue and Cousins, 2013; Sousa et al., 2017; Wijdeven and Kuzee, 2000). This can be the case of slash-and-burn agriculture – a common farming method in tropical dry forests where billions of people depend on it for their subsistence (Curtis

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et al., 2018). The slash-and-burn agriculture involves the cutting down of the trees and other woody plants in an area to leave the downed vegetation (slash) to dry, and then burn the plant biomass (Fig. 1). Burning promotes a rapid incorporation of nutrients to the soil and the elimination of weeds in agricultural areas that are used for cultivation for up to 4 years before abandonment takes place and forest regeneration starts (Hauser and Norgrove, 2013; Ribeiro-Filho et al., 2015, 2013).

The fire can have direct negative effects on the seed bank (Fig. 1). The loss of adult trees and seed dispersers in burned lands can also limit the abundance and diversity of seeds in the seed bank through the so-called 'seed source limitation' (Clark et al., 1998) and 'seed dispersal limitation' (Howe and Smallwood, 1982; Fig. 1), which together limit potentially forest recovery after disturbance. We expect that fire increases the frequency and proportion of damaged (i.e. dehydrated and burned) seeds, and decreases the proportion of viable seeds. In addition, as the seed bank in tropical dry forests is naturally poor in terms of seed abundance and diversity of woody plants (e.g. da Silva et al., 2013; Garwood, 1989; Gomes et al., 2019; Skoglund, 1992), it is reasonable to expect a drastic impoverishment of the seed bank after fire, with a significant decrease in seed density and diversity, particularly the diversity of rare (less abundant) species (Mamede and Araújo, 2008). This is not only because of the incineration of seeds, but because of seed source and seed dispersal limitations caused by the loss of adult trees (Fig. 1).

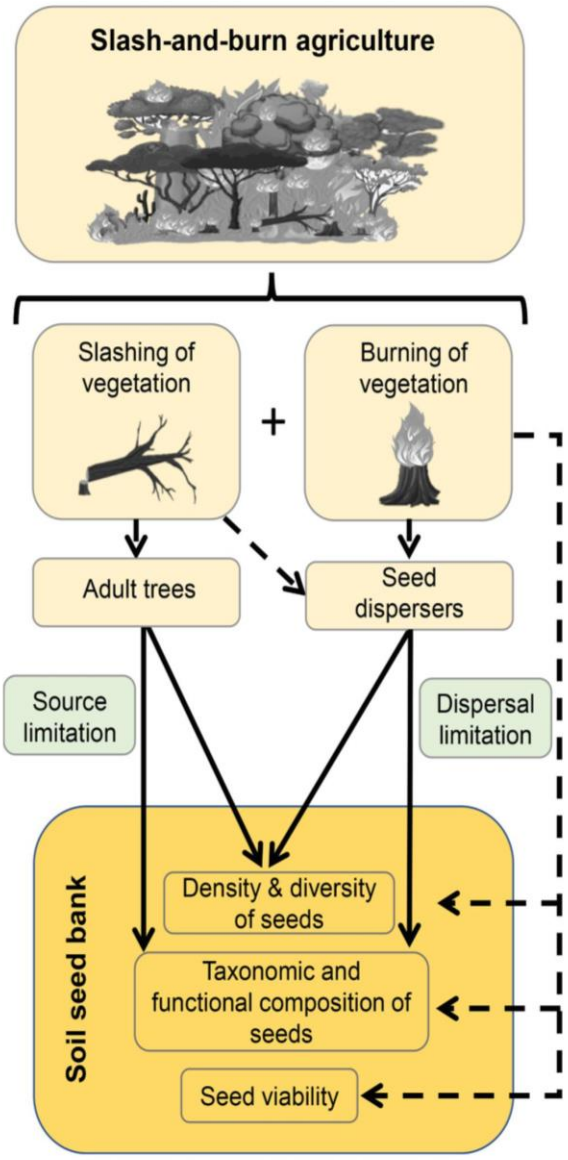

Fig. 1. Hypothesized effects of slash-and-burn agriculture on the soil seed bank. Positive associations are indicated with continuous arrows, and negative associations with dashed-line arrows. The loss of adult trees and seed dispersers in burned areas can cause limitations in seed source and seed dispersal, impoverishing seed assemblages in the soil. Fire can also have direct negative impacts on the seed bank, by dehydrating and/or incinerating the seeds and limiting its viability.

We can also expect that the strong environmental filtering imposed by fire should decrease the seed species turnover (β-diversity) between plots (floristic homogenization) after fire. The few remaining species after fire are predicted to be those with traits that confer tolerance to fire (Tangney et al., 2020, 2019), such as small size which makes it easier seed burial in the soil (Ferreira et al., 2014; Thompson et al., 1993). Dispersal mode can also be important, as dispersal limitation in disturbed forests is usually stronger in animal-dispersed than in wind-dispersed seeds (San-José et al., 2020). Another relevant trait includes a high seed hardness that favors physical dormancy – an attribute related to orthodox seeds inside dry fruits that could allow seeds to survive in soils exposed to high temperatures (Clark, 1991).

The slash-and-burn agriculture is widespread in the 'Caatinga' (Curtis et al., 2018; Kleinman et al., 1995) – a seasonally dry tropical forest endemic to Brazil (Silva et al., 2017). As other tropical dry forests, forest recovery after disturbance in this region is known to depend on plant resprouting (e.g. Barros et al., 2021; Kennard et al., 2002) and the seed bank; however, this later topic have been poorly investigated (reviewed by Meiado et al., 2012). About 75% of species in the Caatinga forest produces small seeds at the onset of the rainy season – a phenological synchronization that favors rapid seed germination for the successful establishment of seedlings (Meiado et al., 2012; Patrício and Trovão, 2020; Skoglund, 1992). Nevertheless, some species, particularly from the Fabaceae family, produce orthodox seeds that can remain in the soil for months or years until conditions become favorable for germination (Almeida-Cortez, 2004; Araújo-Neto et al., 2005; Barbosa et al., 2003; Gomes et al., 2019; Meiado, 2014; Nascimento and Meiado, 2016). The seed bank is generally dominated by herbaceous plants with a high dispersal ability (Mendes et al., 2015; Santos et al., 2013), which can reduce the compositional similarity between the seed bank and the local standing vegetation in regenerating forests (Gomes et al., 2019). Nevertheless, we only found one assessment of the effect of slash-and-burn agriculture on the seed bank, which demonstrates an 80% reduction of seed density and a 44% reduction of species richness following fire (Mamede and Araújo, 2008). However, the impact of fire on seed damage and viability, and on the taxonomic and functional composition of seed assemblages remains unknown. As the productivity and sustainability of this farming method strongly depend on the ability of the forest to recover after disturbance (Kukla et al., 2019; Sanchez, 2000), understanding the effect of slash-and-burn agriculture on the seed bank is valuable to inform management and conservation practices, particularly in seasonally dry tropical forests. Here, we assessed seed damage and viability, and the structure (seed density and diversity) and composition (taxonomic and functional) of seed assemblages in the seed bank in plots exposed to an experiment of slash-and-burn agriculture in the Caatinga dry forest, northeast Brazil.

2. Methods

2.1. Study area

This study was performed in the Catimbau National Park (8°23′17″-8°36′35″ S; 37°11′00″-37°33′32″W; ~600 m a.s.l.), a protected area covering 607 km^2 of Caatinga dry forest in northeastern Brazil. Flat lands covered by sandy soils predominate through the landscape, which is mostly exposed to a semi-arid climate (Koeppen's classification Bsh).

Annual temperature averages 23 °C, and annual rainfall ranges from 650 to 1100 mm (Rito et al., 2017). The original vegetation consists of small-statured dry forest dominated by Fabaceae, Euphorbiaceae and Myrtaceae (Rito et al., 2017). Previous surveys reported at least 151 woody plant species (de Paula, 2017; Rito et al., 2017), but in the study plots (see below) we recorded 74 species. Most woody plant species are trees, almost 60% of which have dry fruits, and almost 50% have abiotic dispersal mode (see Fig. S1 in Supplementary material). Land use in this park include slash-and-burn agriculture (e.g. maize, cassava, beans) and free-ranging cattle, that convert the old-growth forest into a mosaic of different-aged secondary forests (Barros et al., 2021; Souza et al., 2019; Specht et al., 2019).

2.2. Slash-and-burn experiment

To assess the potential effect of slash-and-burn agriculture on the seed bank of woody plant species we adopted an experimental approach. At the end of the dry season (November-December) of years 2018, 2019 and 2020, we prepared 9 forest plots (three plots per year) of 20 × 50 m (0.1 ha each) for agriculture by local farmers (Fig. 2). These plots were located at least 400 m apart to minimize spatial dependence, after verifying with the information provided by local people that these forest stands were not submitted to recent agriculture.

The woody vegetation was completely cut with the help of axes and machetes. As they usually do, all high-density poles were immediately collected by farmers to be used as firewood, fences and other household facilities. The remaining plant biomass was left to dry naturally for a period of 20 days, piled into small amounts and then completely burned through a controlled fire that lasted between 20 and 40 min (Fig. 2). Following the methods described below, we collected the seed bank 30 days before vegetation cutting (i.e. 'before fire' treatment), and immediately (2–3 days) after burning the fields ('after fire' treatment).

2.3. Seed bank sampling

In each plot, we recorded the seed bank in 20 randomly located samples, 10 samples before fire and 10 samples after fire. Each sample consisted of a 0.2 × 0.2 m (0.04 m^2 each) metal grid, and we collected the litter and soil layer up to 5 cm depth (i.e. sample unit = 2000 cm^3). Soil samples were sieved to collect the seeds, which were counted and identified up to the lowest taxonomic level possible with the help of literature, seed specialists and a catalog of Caatinga seeds stored at the Applied Plant Ecology Laboratory (Universidade Federal de Pernambuco, Recife).

2.4. State of seeds

To assess the state of the seeds before and after fire, we classified the seeds as either: (1) undamaged seeds (i.e. intact seeds without any physical damage), (2) damaged seeds (i.e. dehydrated, and/or burned seeds), (3) predated (i.e. with signs of predation by bruchids), or (4) with signs of rotting by fungi (moldy seeds). We also assessed changes in seed viability using the tetrazolium method (sensu Moore, 1973). We selected this test because it is a reliable method to assess the physiological quality of seeds, in addition to offering measurements similar to those found in germination methods (Witkowski and Wilson, 2001). In particular, we first scarified each seed with a sandpaper to expose the endosperm, but avoiding any damage to embryo tissue. We then pre-conditioned the samples in deionized water for 12 h, and immersed them in tetrazolium (0.075%) at 25 °C for approximately 240 min. We also washed the seeds

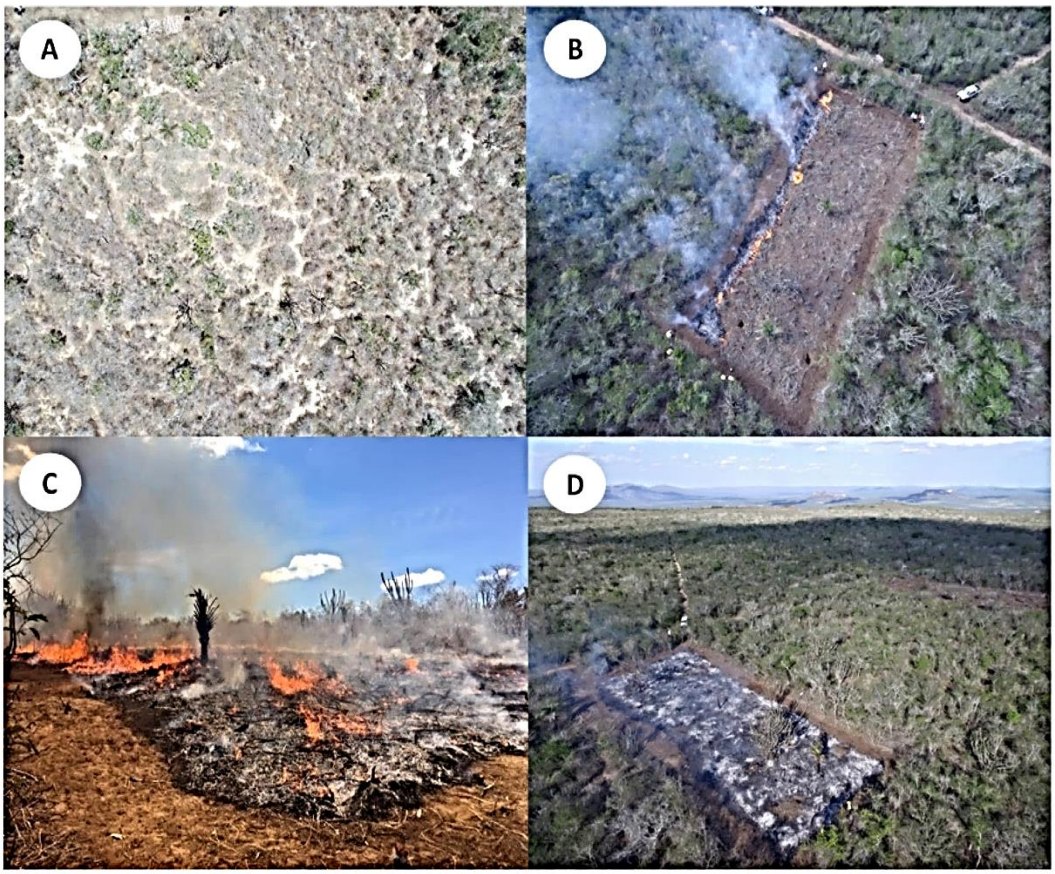

Fig. 2. The slash-and-burn experiment. In each plot, the native forest (A) was slashed and burned (B, C and D) to be converted into agricultural areas.

with running water and cut them longitudinally with the aid of a stylus and observed the color of the embryo tissues. A reddish color indicates the presence of living tissue (Moore, 1961; França-Neto and Krzyzanowski, 2019), while milky-white color means dead tissue. Thus, we considered the presence of living tissue in the embryo as a signal of seed viability, and estimated the proportion of viable seeds before and after fire.

2.5. The structure and composition of seed assemblages

As the seed bank refers to the seeds present in the soil that are able to germinate and become seedlings (i.e. viable seeds, Turnbull et al., 2000), the response variables and analyses that are described below include only the viable seeds. The structure of seed assemblages was described in each plot as the density and diversity of seeds summing up the information of the 10 samples per plot to avoid pseudoreplication problems. To estimate species diversity we used the Hill numbers of order 0 (^0D, species richness), 1 (^{1}D, exponential Shannon entropy) and 2 (^2D, inverse Simpson concentration) (Chao et al., 2014; Jost, 2006). ^0D is not sensitive to differences in seed abundance and it gives a disproportionate weight to rare species. ^1D weights each species according to its abundance in the community, without favoring rare or abundant species. ^2D favors very abundant species, and is therefore interpreted as the effective number of dominant species in the community. In particular, we calculated both α and γ diversities. α-diversity refers to the mean unweighted α-diversity per plot within each treatment, and was calculated with the "entropart" package (Marcon and Hérault, 2015), whereas γ-diversity is the accumulated diversity in all plots per treatment, and was calculated using the "iNEXT" package (Hsieh et al., 2016), for the R 3.3.0 software (R Core Team, 2016). To assess the accuracy of seed inventories in each plot, we estimated the sample coverage estimator (Chao and Jost, 2012), which vary from 0 to 1, and indicates the proportion of the total number of individuals in a community that belongs to the species found in the sample. Sample coverage was relatively high (>0.9) in all plots, suggesting that our sampling effort was adequate to assess changes in species diversity in all plots. However, to avoid any potential bias in our results due to differences in sample coverage among sites (see Chao and Jost, 2012), we considered not only the observed values of species richness, but also the expected values based on coverage-based rarefactions performed with the 'iNEXT' package (Hsieh et al., 2016).

To assess the differences in species composition between treatments, we calculated β-diversity between plots before and after fire with Hill numbers (Jost, 2006). We separately assessed β-diversity of all ($^0D_\beta$), typical ($^1D_\beta$) and dominant species ($^2D_\beta$) using the 'entropart' R package (Marcon and Hérault, 2015). These indices are interpreted as the effective number of completely different communities, and can vary between 1, when all plots are identical, and N communities, when all N plots are completely different from each other. To assess the mechanisms driving β-diversity patterns, we partitioned β-diversity into its turnover and nestedness components (Baselga, 2010) with the 'betapart' R package (Baselga and Orme, 2012). This procedure measures the overall dissimilarity (measured with the Sørensen dissimilarity index, β_{sor}), and partitions it into its turnover (β_{sim}) and nestedness resultant components (β_{sne}) (Legendre, 2014). These two components reflect (1) the replacement of some species by others as consequences of environmental filters or spatial and historical constraints (β_{sim}), and (2) the loss (or gain) of species across space causing a nested pattern (β_{sne}). We complemented these compositional analyses by assessing the differences in species abundances before and after fire with abundance-rank curves.

We also assessed the differences in functional composition of seed assemblages considering plant traits available in previous studies (de Paula, 2017; Rito et al., 2017). In particular, we considered traits potentially associated with seed resistance to fire and seed dispersal capacity, including (1) seed size (cm); (2) seed mass (g); (3) life form (tree or shrub); (4) fruit type (dry or fleshy); (5) seed dispersal mode (abiotic and biotic) and (6) seed type (orthodox or recalcitrant) (Díaz et al., 2016). Seed type was classified according to traits proposed by the literature, such as the presence of a hard coat (Turner, 2004). The abiotic dispersal syndrome includes species dispersed by wind, gravity and ballistic, whereas the biotic syndrome includes endozoochory and ectozoochory. We then calculated the community weighted mean (CWM) of each continuous trait (i.e. seed size and seed mass) in the plots before and after fire using the 'FD' R package for R, version 3.5 (Laliberté and Legendre, 2010). For the categorical traits, we calculated the relative abundance of seeds with each trait class.

2.6. Data analysis

We first tested whether the state of seeds (i.e. frequency of undamaged, damaged, predated and moldy seeds) was independent of the treatment (before and after fire) with a contingency table and an independence χ^2 test. The difference in the proportion of viable seeds before and after fire was tested using the prop.test function in R. However, given the paired nature of our experimental design, the difference in mean seed density and seed species diversity between treatments was tested with the non-parametric Wilcoxon signed-rank test. We did not use the parametric paired *t*-test because the residuals of several models did not meet the normality assumption. Regarding the functional composition of seed assemblages, we tested for differences between treatments in the frequencies of each categorical (binary) variable (i.e. life form, fruit type, dispersal mode, and seed type) with the Fisher's exact test for 2 × 2 contingency tables. For continuous variables (i.e. CWM of seed size and CWM of seed mass), we used the Wilcoxon test. We also tested for differences between treatments in total (γ) diversity comparing the mean values and 95% confidence intervals estimated for rarefied samples using the bootstrapping protocol described by Chao et al. (2014), and available in the 'iNEXT' package for R (Hsieh et al., 2016). Following Marcon et al. (2012), we also used 95% confidence intervals to test for changes in β-diversity between plots before and after fire using the bootstrap confidence intervals of diversity values provided by the 'entropart' package. Note that, as indicated above, all these statistical analyses were performed considering the viable seeds only.

3. Results

3.1. Seed damage and viability

In total, we recorded 449 seeds from 18 woody species belonging to 7 families. However, only 241 seeds (53%) were classified as undamaged, followed by predated (102 seeds, 23%), damaged (89 seeds, 20%), and moldy (17 seeds, 4%). Viable seeds belonged to 13 species, with Fabaceae and Euphorbiaceae representing 69% of species and 23% of viable seeds. Viable seeds mainly consisted of tree species (69% of all species) bearing dry fruits (84%) with abiotic dispersal (76%).

Seed state depended significantly on the treatment ($\chi^2 = 61.03$, df = 3, $p < 0.001$), with the observed frequency of undamaged seeds being higher than expected by chance before fire, but lower than expected after fire (Fig. 3). The frequency of damaged seeds followed the opposite pattern, with a higher frequency of damaged seeds after fire. The total number of viable seeds was 2.4 times higher before fire than after fire, and we found a 3.6-fold decrease in the proportion of viable seeds after fire (Table 1).

3.2. Structure of seed assemblages

Mean seed density did not differ significantly between treatments (Table 1). However, species diversity drastically decreased after fire, particularly the species richness ($^0D_\alpha$) (Table 1). This means that the negative impact of fire is stronger when considering rare species than when considering the number of typical ($^1D_\alpha$) or dominant species ($^2D_\alpha$) (Table 1). Considering the accumulated number of species in all plots

Fig. 3. Total frequencies of seeds (observed and expected values) within each seed state in 9 plots exposed to an experiment of slash-and-burn agriculture in the Catimbau National Park, Brazil. We tested for differences in frequencies between treatments (i.e. before and after fire) with a χ^2 test of independence ($p < 0.001$). Undamaged seeds are those without any physical damage, whereas the damaged ones are those dehydrated and/or burned.

Table 1
Description of seed assemblages in the seed bank of 9 plots exposed to an experiment of slash-and-burn agriculture in the Catimbau National Park, Brazil. The absolute and relative degree of seed viability is indicated, as well as the structure (seed density and diversity) and functional composition of seed assemblages before and after fire. When possible, we show mean values per plot and 95% confidence intervals.

Seed attributes	Before fire	After fire	Statistical test[b]
Total number of seeds	179	270	–
Number of viable seeds (total and %)	58 (32.4%)	24 (8.9%)	38.3**
Structure of seed assemblages			
Mean seed density (seeds/m^2)	16.11 (5.02–27.19)	6.66 (1.42–14.76)	28 ns
Mean species richness ($^0D_\alpha$)	2.33 (1.31–3.35)	0.77 (0.06–1.61)	21*
Mean number of typical species ($^1D_\alpha$)	1.91 (1.14–2.68)	0.71 (0.02–1.44)	33*
Mean number of dominant species ($^2D_\alpha$)	1.70 (1.06–2.34)	0.68 (0.01–1.37)	33*
Functional composition[a]			
Mean CWM - Seed size (cm)	0.21 (0.10–0.32)	0.30 (0.09–0.69)	2 ns
Mean CWM - Seed mass (g)	1.17 (0.11–2.45)	0.73 (0.67–2.12)	8 ns

[a] Only the two continuous traits are indicated, the community weighted mean (CWM) of seed size and seed mass, which indicates the mean trait value of all species present in the plots, weighted by their relative abundances.

[b] We tested for differences among treatments in the proportion of viable seeds with the prop.test function of R. The differences in the rest of variables were tested with the Wilcoxon test for dependent samples. *$p < 0.05$, **$p < 0.01$, ns $p > 0.05$.

(γ-diversity), species richness ($^0D_\gamma$) was 67% higher before fire than after fire, while the accumulated number of typical species ($^1D_\gamma$) was 69% higher before fire than after (Fig. 4a). In contrast, the accumulated number of dominant species ($^2D_\gamma$) did not differ between treatments (Fig. 4a).

3.3. Taxonomic and functional composition of seed assemblages

Forest stands before fire were dominated by two tree species (*Senna acurensis* and *Pityrocarpa moniliformis*) and a shrub species (*Croton tricolor*), together representing 66% of all viable seeds in these plots (Fig. 5; Table S1). Interestingly most species (75%) before fire were relatively rare, with nine species showing less than three seeds. In contrast, the plots after fire were composed of four similarly abundant species, three of them shrubs (*Croton tricolor, Byrsonima gardneriana* and *Senna rizzinii*), and only one tree species (*Pityrocarpa moniliformis*) (Fig. 5; Table S1).

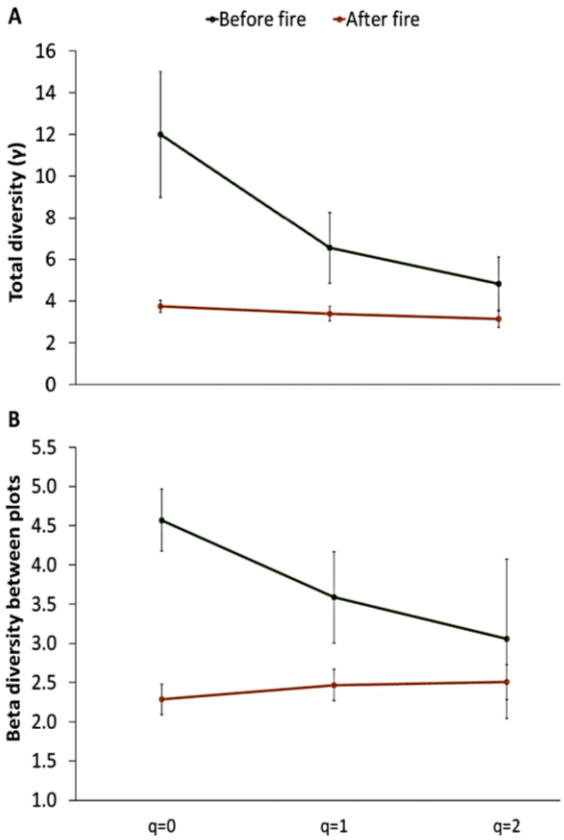

Fig. 4. Rarefied effective number of species (sample coverage = 0.91 in all cases) considering the total number of species ($^0D_\gamma$), the number of common species ($^1D_\gamma$), and number of dominant species ($^2D_\gamma$) before and after fire (A). Differences in species composition between plots (β-diversity) before and after fire is also indicated for q = 0, q = 1 and q = 2 (B). These measures of β-diversity indicate the effective number of completely different communities, and can vary between 1, if all plots (n = 9) are identical, and 9, if the plots are completely different from each other.

These compositional changes caused a significant decrease in β-diversity between plots (Fig. 4b). Considering all species ($^0D_\beta$), β-diversity was 50% higher before fire than after fire (Fig. 4b). Such differences between treatments decreased when considering the typical and dominant species (Fig. 4b), thus indicating that the loss of β-diversity was relatively stronger when considering rare species. Total β-diversity (i.e. β-JAC) was mainly caused by differences in species turnover among

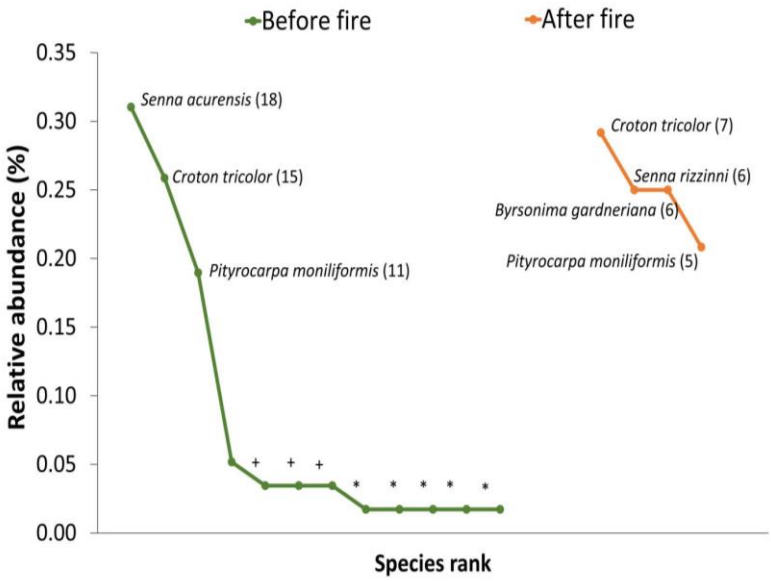

Fig. 5. Rank-abundance curves showing the relative abundance of viable seeds in nine 50 × 20-m plots (total sampling area = 0.9 ha) before (i.e. in forest stands) and after fire in a slash-and-burn experiment in the Catimbau National Park, Brazil. The species are ranked from highest to lowest abundance. The absolute abundance of the dominant species is also indicated (in parentheses), as well as those species with one (*singletons) and two (+doubletons) seeds. For further details see Table S1.

plots, but this component of β-diversity was slightly higher before fire (β-TUR = 0.91) than after fire (β-TUR = 0.73). The nestedness component of β-diversity followed the opposite pattern (β-NES before fire = 0.03; β-NES after fire = 0.22), thus indicating that there was a 7.3-fold increase in the relative contribution of nestedness to β-diversity after fire.

Functional composition of seed assemblages showed an increase in the frequency of shrubs after fire (Odds ratio, OR = 7.58, $p < 0.001$, Fig. 6a). The frequency of fleshy fruits also tended to increase after fire (OR = 0.22, p = 0.05, Fig. 6b), as did the frequency of seeds with biotic dispersal mode (OR = 0.07, $p < 0.001$, Fig. 6c). However, the relative frequency of recalcitrant and orthodox seeds did not differ between treatments (OR = 0, p = 1, Fig. 6d), and the two continuous seed traits (CWM of seed size and CWM of seed mass) were also similar before and after fire (Table 1).

4. Discussion

This study assessed the impact of experimental slash-and-burn agriculture on the soil seed bank in the Caatinga biome – a species-rich but vanishing tropical dry forest from northeastern Brazil. In agreement with previous studies (Mamede and Araujo, 2008), our findings support the hypothesis that this farming method promotes a drastic impoverishment of the seed bank. In particular, we found that fire: (1) increased seed damage and compromised seed viability; (2) decreased the diversity of seed species, particularly impacting rare species; (3) caused a significant homogenization (loss of β-diversity) of seed assemblages across space; and (4) changed its functional composition after fire. Together, these findings have critical applied implications that can be used to promote the sustainability of slash-and-burn agriculture in this and potentially other tropical dry forests.

As expected, we found evidence of strong deleterious effects of slash-and-burn agriculture on seed damage and viability. Thus, seeds of woody plants in this tropical forest are extremely vulnerable to this farming method. This is consistent with other studies that show the susceptibility of seeds to fire in the Caatinga forest (Mamede and Araújo, 2008) and other ecosystems (Auld and Denham, 2006; Kennard et al., 2002; Tarrega et al., 1992; Uhl et al., 1981), not only because fire can dehydrate the seeds, but also because it can overheat the embryo of seeds, causing the mortality of the seeds. Such negative impacts can be particularly important in the Caatinga biome, as unlike other fire-prone biomes such as the Brazilian Cerrado, the Caatinga's woody plants do not present adaptations to fire (Pivello et al., 2021).

We found a significant decrease in species diversity after fire. Such a loss of species diversity was evident at the local (α) and landscape (γ) scales. As the seed bank before and after fire was sampled with one month of temporal difference, the observed loss of species cannot be due to the loss of adult trees and seed dispersers in burned areas (i.e. seed source limitation and seed dispersal limitation, respectively), but simply to seed incineration by fire (Fig. 1). Importantly, the decline of species after fire was particularly evident when considering rare species, thus supporting previous evidence on the high susceptibility of rare tree species to forest disturbance in the region (Rito et al., 2017). In fact, our findings suggest that the most common species are likely less impacted by this farming method, as two dominant species in forest plots (i.e. *Croton tricolor* - Euphorbiaceae, and *Pityrocarpa moniliformis* - Fabaceae) remained dominant after fire. However, as other dominant species in forest plots (i.e. *Senna acurensis* - Fabaceae) were absent in burned plots, the effect of fire on dominant species needs to be investigated in more detail in the future.

Our finding also supports the hypothesis that, at the taxonomic level, this farming method homogenizes the composition of seed assemblages. This process of floristic homogenization can be associated with the loss of species discussed above, as the loss of β-diversity after fire was particularly evident when considering rare species ($^0D_\beta$), and these species were the most impacted by fire. Our assessment of the components of β-diversity also support the idea that floristic homogenization is mainly related to the loss of species in burned plots, as we found a 7.3-fold increase in the relative contribution of nestedness after fire, and this component is associated with the loss of species (Baselga, 2010). In contrast, species turnover – the substitution of species in one site by different species in another site – is usually related to species sorting (i.e. sites with different environmental conditions are occupied by different species; Baselga, 2010). Thus, the loss of β-diversity can also be partially

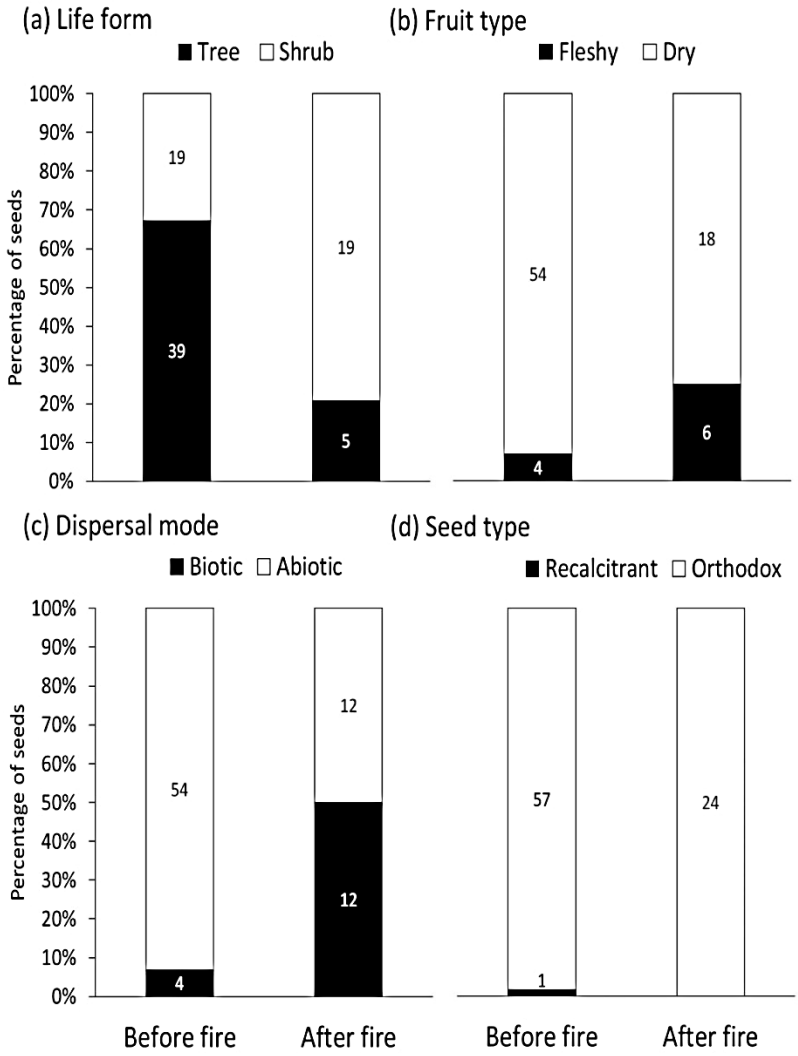

Fig. 6. Percentage of seeds (and absolute values within bars) per treatment, separately assessing different life forms (a), fruit types (b), dispersal modes (c), and seed types (d). The study plots were exposed to an experiment of slash-and-burn agriculture in the Catimbau National Park, Brazil, and we tested for differences between treatments (i.e. before and after fire) with a Fisher exact test for 2 × 2 contingency tables (see results in the main text).

related to the homogenization of environmental conditions after fire, which can cause the loss of species turnover in burned plots – a possibility supported by previous studies (Heydari et al., 2017).

4.1. Management implications

Taken together, these findings have important applied implications for the appropriate management and restoration of these (and potentially other) tropical dry forests. We not only found that slash-and-burn agriculture impoverishes the seed bank by decreasing α, β and γ diversity, but that this farming method causes severe physical damages on the remaining seeds after fire, compromising their viability. Importantly, as our sample plots are much smaller than the areas that are cultivated by the local population (i.e. slash-and-burn agriculture practiced in seasonally dry tropical forests usually involves crops of 0.5 to 5 ha; Lowder et al., 2016; Tanzito et al., 2020), we think that our assessment is conservative, as the impact of slash-and-burn agriculture should be more detrimental if extended over larger spatial extents.

From an applied perspective, our findings imply that forest recovery, and thus the productivity and sustainability of this farming method, cannot rely on the seed bank, but on other mechanisms of regeneration, such as seed dispersal. In fact, the seed bank could be replenished by seed dispersal from nearby areas, but we still do not know how long this could take. Thus, additional monitoring long-term studies are needed to fill this important knowledge gap. In any case, as this agricultural method is widespread in the region, a first and critical step to replenish the seed bank through seed dispersal and thus enhance forest recovery in sites exposed to slash-and-burn agriculture is to maintain a relatively high proportion of native old-growth forests in the surrounding landscape. This can increase the availability of seed sources, and thus enhance seed dispersal and plant colonization of regenerating stands (Piotto et al., 2021). Although we do not know exactly how much forest should be maintained in the landscape, there is evidence for other temperate and tropical forests that we should maintain at least 40% of landscape forest cover to prevent the extinction of most species (Arroyo-Rodríguez et al., 2020, 2021). Therefore, this could be used as reference data while we do not have specific information for the region.

Regarding the spatial configuration of old-growth forests in the landscape, we suggests that rather than preserving the 40% of forest cover in a single continuous forest, forest recovery is likely better if the remaining forest cover is preserved in many smaller forest patches scattered in the landscape (Arroyo-Rodríguez et al., 2020). We would

suggest this because by increasing the number of relatively smaller old-growth forest patches in the landscape we can increase the probability that different patches have different environmental conditions (e.g. different precipitation regime), thus covering a wider range of environmental heterogeneity in the landscape (Arroyo-Rodríguez et al., 2020; Fahrig et al., 2019). This is important to increase the compositional dissimilarity (β-diversity) of plant assemblages in the region (Arroyo-Rodríguez et al., 2013; Liu and Slik, 2014; Rito et al. 2021). Furthermore, by increasing the number of small patches we can also reduce the isolation distance between agricultural lands and old-growth forest patches – a key strategy to improve landscape connectivity and prevent seed source and dispersal limitations (Arroyo-Rodríguez et al., 2017; Piotto et al., 2021). However, as we there is no available information on the relative importance of single-large vs several-small patches in preserving the seed bank in the Caatinga forest, this suggestion of preserving many smaller forest patches scattered in the landscape should be taken with care.

Finally, it is important to note that forest recovery can also depend on the ability of the plants to resprout – an important tolerance trait that enable plants to survive different disturbance regimes (Clarke et al., 2013). We particularly refer to the resprouting of tree stumps that survive the slashing and burning of vegetation, as well as the stumps and roots able to persist weeding and initiating forest regeneration (Barros et al., 2021; Dufumier, 2006; Vanderlei et al., 2021). Unlike fire-prone ecosystems, the ability to resprout in the Caatinga may be a strategy to overcome water stress or nutrient deficiencies (Costa et al., 2014; Souza et al., 2021), but also a source of regeneration that is less vulnerable to unsustainable agricultural practices such as slash-and-burn agriculture (Barros et al., 2021; Vanderlei et al., 2021). In fact, given the impoverished seed bank found in the present research, and the available evidence on the importance of resprouting for forest recovery (Barros et al., 2021; Vanderlei et al., 2021), we can hypothesize that forest recovery after slash-and-burn agriculture will largely depend on seed dispersal and resprouting – two interesting avenues for future research.

CRediT authorship contribution statement

Jakelyne S. Bezerra: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. **Víctor Arroyo-Rodríguez:** Conceptualization, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. **Jonathan M. Tavares:** Methodology, Investigation. **Adrielle Leal:** Methodology, Investigation. **Inara R. Leal:** Conceptualization, Investigation, Funding acquisition. **Marcelo Tabarelli:** Conceptualization, Funding acquisition, Methodology, Validation, Supervision, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2022.120185.

References

Almeida-Cortez, J.S., 2004. Dispersão e banco de sementes. In: Ferreira, A.G., Borghetti, F. (Eds.), Germinação: do básico ao aplicado. Artmed, Porto Alegre, pp. 225–235.

Araújo Neto, J.C.d., Aguiar, I.B.d., Ferreira, V.M., Rodrigues, T.d.J.D., 2005. Armazenamento e requerimento fotoblástico de sementes de *Acacia polyphylla* DC. Rev. Bras. Sem. 27 (1), 115–124.

Arroyo-Rodríguez, V., Fahrig, L., Tabarelli, M., Watling, J.I., Tischendorf, L., Benchimol, M., Cazetta, E., Faria, D., Leal, I.R., Melo, F.P.L., Morante-Filho, J.C., Santos, B.A., Arasa-Gisbert, R., Arce-Peña, N., Cervantes-López, M.J., Cudney-Valenzuela, S., Galán-Acedo, C., San-José, M., Vieira, I.C.G., Slik, J.W.F., Nowakowski, A.J., Tscharntke, T., Jordan, F., 2020. Designing optimal human-modified landscapes for forest biodiversity conservation. Ecol. Lett. 23 (9), 1404–1420. https://doi.org/10.1111/ele.13535.

Arroyo-Rodríguez, V., Fahrig, L., Watling, J.I., Nowakowski, J., Tabarelli, M., Tischendorf, L., Melo, F.P.L., Santos, B.A., Benchimol, M., Morante-Filho, J.C., Slik, J.W.F., Vieira, I.C.G., Tscharntke, T., 2021. Preserving 40% forest cover is a valuable and well-supported conservation guideline: reply to Banks-Leite et al. Ecol. Lett. 24 (5), 1114–1116. https://doi.org/10.1111/ele.13689.

Arroyo-Rodríguez, V., Melo, F.P.L., Martínez-Ramos, M., Bongers, F., Chazdon, R.L., Meave, J.A., Norden, N., Santos, B.A., Leal, I.R., Tabarelli, M., 2017. Multiple successional pathways in human-modified tropical landscapes: new insights from forest succession, forest fragmentation and landscape ecology research. Biol. Rev. 92 (1), 326–340. https://doi.org/10.1111/brv.12231.

Arroyo-Rodríguez, V., Rös, M., Escobar, F., Melo, F.P.L., Santos, B.A., Tabarelli, M., Chazdon, R., Kitzberger, T., 2013. Plant β-diversity in fragmented rain forests: testing floristic homogenization and differentiation hypotheses. J. Ecol. 101 (6), 1449–1458. https://doi.org/10.1111/1365-2745.12153.

Auld, T.D., Denham, A.J., 2006. How much seed remains in the soil after a fire? Plant Ecol. 187 (1), 15–24. https://doi.org/10.1007/s11258-006-9129-0.

Barbosa, D.C.A., Barbosa, M.C.A., Lima, L.C.M., 2003. Fenologia de espécies lenhosas da Caatinga. In: Leal, I.R., Tabarelli, M., Silva, J.M.C. (Eds.), Ecologia e Conservação da Caatinga. Ed. Universitária da UFPE, Recife, pp. 657–693.

Barros, M.F., Ribeiro, E.M.S., Vanderlei, R.S., de Paula, A.S., Silva, A.B., Wirth, R., Cianciaruso, M.V., Tabarelli, M., 2021. Resprouting drives successional pathways and the resilience of Caatinga dry forest in human-modified landscapes. For. Ecol. Manage. 482, 118881. https://doi.org/10.1016/j.foreco.2020.118881.

Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. Glob. Ecol. Biogeogr. 19, 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x.

Baselga, A., Orme, C.D.L., 2012. Betapart: an R package for the study of beta diversity. Methods Ecol. Evol. 3, 808–812. https://doi.org/10.1111/j.2041-210X.2012.00224.x.

Chao, A., Colwell, R.K., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K., Ellison, A.M., 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecol. Monogr. 84, 45–67. https://doi.org/10.1890/13-0133.1.

Chao, A., Jost, L., 2012. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology 93 (12), 2533–2547.

Witkowski, E.T.F., Wilson, M., 2001. Changes in density, biomass, seed production and soil seed banks of thenon-native invasive plant, *Chromolaena odorata*, along a 15 year chronosequence. Plant Ecol. 152, 13–27.

Chazdon, R.L., 2014. Second growth: the promise of tropical forest regeneration in an age of deforestation. first ed. University of Chicago Press, Chicago. https://doi.org/10.1007/BF02394968.

Clark, J.S., Macklin, E., Wood, L., 1998. Stages and spatial scales of recruitment limitation in southern appalachian forests. Ecol. Monogr. 68 (2), 213. https://doi.org/10.2307/2657201.

Clark, L., 1991. The effect of fire on Yellowstone ecosystem seed banks. Montana State University, Bozeman, Montana, USA, Thesis.

Clarke, P.J., Lawes, M.J., Midgley, J.J., Lamont, B.B., Ojeda, F., Burrows, G.E., Enright, N.J., Knox, K.J.E., 2013. Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. New Phytol. 197 (1), 19–35. https://doi.org/10.1111/nph.12001.

Costa, T.L., Sampaio, E.V.S.B., Sales, M.F., Accioly, L.J.O., Althoff, T.D., Pareyn, F.G.C., Albuquerque, E.R.G.M., Menezes, R.S.C., 2014. Root and shoot biomasses in the tropical dry forest of semi-arid Northeast Brazil. Plant Soil. 378 (1-2), 113–123.

Curtis, P.G., Slay, C.M., Harris, N.L., Tyukavina, A., Hansen, M.C., 2018. Classifying drivers of global forest loss. Science 361 (6407), 1108–1111.

da Silva, K.A., dos Santos, D.M., dos Santos, J.M.F.F., de Albuquerque, U.P., Ferraz, E.M.N., Araújo, E.d.L., 2013. Spatio-temporal variation in a seed bank of a semi-arid region in northeastern Brazil. Acta Oecolo. 46, 25–32.

Daïnou, K., Bauduin, A., Bourland, N., Gillet, J.-F., Fétéké, F., Doucet, J.-L., 2011. Soil seed bank characteristics in cameroonian rainforests and implications for post-logging forest recovery. Ecol. Eng. 37 (10), 1499–1506. https://doi.org/10.1016/j.ecoleng.2011.05.004.

Dalling, J.W., Swaine, M.D., Garwood, N.C., 1997. Soil seed bank community dynamics in seasonally moist lowland tropical forest. Panamá. J. Trop. Ecol. 13, 659–680. https://doi.org/10.1017/S0266467400010853.

de Paula, A.S., 2017. Regeneração natural de uma área de Caatinga após o uso para a agricultura ao longo de uma cronossequência. Universidade Federal de Pernambuco, Recife, Pernambuco, Brasil, Tese.

Díaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P.B., Moles, A.T., Dickie, J., Gillison, A.N., Zanne, A.E., Chave, J., Joseph Wright, S., Sheremet'ev, S.N., Jactel, H., Baraloto, C., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., Casanoves, F., Joswig, J.S., Günther, A., Falczuk, V., Rüger, N., Mahecha, M.D., Gorné, L.D., 2016. The global spectrum of plant form and function. Nature 529 (7585), 167–171. https://doi.org/10.1038/nature16489.

dos Santos, D.M., da Silva, K.A., de Albuquerque, U.P., dos Santos, J.M.F.F., Lopes, C.G. R., Araújo, E.d.L., 2013. Can spatial variation and inter-annual variation in precipitation explain the seed density and species richness of the germinable soil seed bank in a tropical dry forest in north-eastern Brazil? Flora Morphol. Distrib. Funct. Ecol. Plants 208 (7), 445–452. https://doi.org/10.1016/j.flora.2013.07.006.

Dufumier, M., 2006. Slash-and-burn, intensification of rice production, migratory movements, and pioneer front agriculture in Southeast Asia. Moussons. 7–31.

Fahrig, L., Arroyo-Rodríguez, V., Bennett, J.R., Boucher-Lalonde, V., Cazetta, E., Currie, D.J., Eigenbrod, F., Ford, A.T., Harrison, S.P., Jaeger, J.A.G., Koper, N., Martin, A.E., Martin, J.L., Metzger, J.P., Morrison, P., Rhodes, J.R., Saunders, D.A., Simberloff, D., Smith, A.C., Tischendorf, L., Vellend, M., Watling, J.I., 2019. Is habitat fragmentation bad for biodiversity? Biol. Conserv. 230, 179–186. https://doi.org/10.1016/j.biocon.2018.12.026.

Ferreira, C.D., Souto, P.C., Lucena, D.S., Sales, F.D.C.V., Souto, J.S., 2014. Seed bank floristics in the soil at different stages of natural regeneration of caatinga. [Florística do banco de sementes no solo em diferentes estágios de regeneração natural de Caatinga] Ver. Bras. Cienc. Agra. 9, 562–569. https://doi.org/10.5039/agraria.v9i4a4497.

França-Neto, J. de B., Krzyzanowski, F.C., 2019. Tetrazolium: An important test for physiological seed quality evaluation. J. Seed Sci. 41, 359–366. https://doi.org/10.1590/2317-1545v41n3223104.

Garwood, N.C., 1989. Tropical Soil Seed Banks: a review. In: Leck, M.A., Parker, T.V., Simpson, R.L. (Eds.), Ecology of soil seed banks. Academic Press, pp. 149–209. https://doi.org/10.1016/B978-0-12-440405-2.50014-2.

Gomes, F.M., Oliveira, C.C.d., Rocha Miranda, R.d., Costa, R.C.d., Loiola, M.I.B., 2019. Relationships between soil seed bank composition and standing vegetation along chronosequences in a tropical dry forest in north-eastern Brazil. J. Trop. Ecol. 35 (4), 173–184. https://doi.org/10.1017/S0266467419000130.

Hansen, M.C., Wang, L., Song, X.P., Tyukavina, A., Turubanova, S., Potapov, P.V., Stehman, S.V., 2020. The fate of tropical forest fragments. Sci. Adv. 6, 1–10. https://doi.org/10.1126/sciadv.aax8574.

Hauser, S., Norgrove, L., 2013. Slash-and-burn agriculture, effects of. In: Levin S.A. (Ed.). Encyclopedia of biodiversity, pp. 551–562. https://doi.org/10.1016/B978-0-12-384719-5.00125-8.

Heydari, M., Omidipour, R., Abedi, M., Baskin, C., 2017. Effects of fire disturbance on alpha and beta diversity and on beta diversity components of soil seed banks and aboveground vegetation. Plant Ecol. Evol. 150 (3), 247–256.

Howe, H.F., Smallwood, J., 1982. Ecology of seed dispersal. Annu. Rev. Ecol. Syst. 13 (1), 201–228. https://doi.org/10.1146/annurev.es.13.110182.001221.

Hsieh, T.C., Ma, K.H., Chao, A., 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods Ecol. Evol. 7, 1451–1456. https://doi.org/10.1111/2041-210X.12613.

Jost, L., 2006. Entropy and diversity. Oikos 113 (2), 363–375. https://doi.org/10.1111/j.2006.0030-1299.14714.x.

Kennard, D.K., Gould, K., Putz, F.E., Fredericksen, T.S., Morales, F., 2002. Effect of disturbance intensity on regeneration mechanisms in a tropical dry forest. For. Ecol. Manage. 162 (2-3), 197–208. https://doi.org/10.1016/S0378-1127(01)00506-0.

Kleinman, P.J.A., Pimentel, D., Bryant, R.B., 1995. The ecological sustainability of slash-and-burn agriculture. Agric. Ecosyst. Environ. 52 (2-3), 235–249. https://doi.org/10.1016/0167-8809(94)00531-I.

Kukla, J., Whitfeld, T., Cajthaml, T., Baldrian, P., Veselá-Šimáčková, H., Novotný, V., Frouz, J., 2019. The effect of traditional slash-and-burn agriculture on soil organic matter, nutrient content, and microbiota in tropical ecosystems of Papua New Guinea. L. Degrad. Dev. 30 (2), 166–177. https://doi.org/10.1002/ldr.3203.

Laliberte, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91, 299–305.

Legendre, P., 2014. Interpreting the replacement and richness difference components of beta diversity. Glob. Ecol. Biogeogr. 23 (11), 1324–1334. https://doi.org/10.1111/geb.12207.

Liu, J.J., Slik, J.W.F., 2014. Forest fragment spatial distribution matters for tropical tree conservation. Biol. Conserv. 171, 99–106. https://doi.org/10.1016/j.biocon.2014.01.004.

Lowder, S.K., Bertini, R., Karfakis, P., Croppenstedt, A., 2016. Transformation in the size and distribution of farmland operated by household and other farms in select countries of sub-Saharan Africa. 5th Annu. Conf. African Assoc. Agric. Econ. 5, 1–25.

Malhi, Y., 2017. The concept of the Anthropocene. Annu. Rev. Environ. Resour. 42 (1), 77–104. https://doi.org/10.1146/annurev-environ-102016-060854.

Malhi, Y., Gardner, T.A., Goldsmith, G.R., Silman, M.R., Zelazowski, P., 2014. Tropical forests in the anthropocene. Annu. Rev. Environ. Resour. 39 (1), 125–159. https://doi.org/10.1146/annurev-environ-030713-155141.

Mamede, M.d.A., de Araújo, F.S., 2008. Effects of slash and burn practices on a soil seed bank of caatinga vegetation in Northeastern Brazil. J. Arid Environ. 72 (4), 458–470. https://doi.org/10.1016/j.jaridenv.2007.07.014.

Marcon, E., Hérault, B., 2015. Entropart: an R package to measure and partition diversity. J. Stat. Softw. 67, 1–26. https://doi.org/10.18637/jss.v067.i08.

Marcon, E., Hérault, B., Baraloto, C., Lang, G., 2012. The decomposition of Shannon's entropy and a confidence interval for beta diversity. Oikos 121 (4), 516–522. https://doi.org/10.1111/j.1600-0706.2011.19267.x.

Meiado, M.V., 2014. Banco de sementes no solo da Caatinga, uma floresta tropical seca no Nordestes do Brasil. Inf. Abrates 24, 39–43. https://doi.org/10.21707/gs.v9i2.26351.

Meiado, M.V., Silva, F.F.S. da;, Barbosa, D.C. de A., Filho, J.A. de S., 2012. Diaspores of the caatinga: A review. In: Siqueira-Filho, J.A. (Ed.). Flora of the Caatingas of the São Francisco River: Natural History and Conservation. Andrea Jakobsson Estúdio Editorial, pp.306-365.

Mendes, L.B., Silva, K.A., Melo, D.S., Santos, J.M.F.F., Albuquerque, U.P., Lima, E.A., 2015. What happens to the soil seed bank 17 years after clear cutting of vegetations? Rev. Biol. Trop. 63, 321–332. https://doi.org/10.15517/rbt.v63i2.14683.

Moore, R.P., 1961. Tetrazolium evaluation of the relationship between total germination and seed quality. Proceed. Assoc. Offic. Seed Anal. 51, 127–130.

Moore, R.P., 1973. Tetrazolium staining for assessing seed quality. In: Heydecker, W. (Ed.), Seed Ecology. Butterworths, pp. 347–366.

Nascimento, J.P.B., Meiado, M.V., 2016. In situ or ex situ seed conservation: which is the more effective way to maintain seed longevity of an endangered cactus? Plant Species Biol. 32 (2), 115–120. https://doi.org/10.1111/1442-1984.12131.

Patrício, M.C., Trovão, D.M.B.M., 2020. Seed biometry: Another functional trait in Caatinga. Acta Sci. - Biol. Sci. 42, 1–11. https://doi.org/10.4025/actascibiolsci.v42i1.51183.

Piotto, D., Magnago, L.F.S., Montagnini, F., Ashton, M.S., Oliver, C., Thomas, W.W., 2021. Nearby mature forest distance and regenerating forest age influence tree species composition in the Atlantic forest of Southern Bahia. Brazil. Biod. Cons. 30 (7), 2165–2180.

Pivello, V.R., Vieira, I., Christianini, A.V., Ribeiro, D.B., da Silva Menezes, L., Berlinck, C. N., Melo, F.P.L., Marengo, J.A., Tornquist, C.G., Tomas, W.M., Overbeck, G.E., 2021. Understanding Brazil's catastrophic fires: causes, consequences and policy needed to prevent future tragedies. Perspect. Ecol. Conserv. 19 (3), 233–255. https://doi.org/10.1016/j.pecon.2021.06.005.

Plue, J., Cousins, S.A.O., 2013. Temporal dispersal in fragmented landscapes. Biol. Conserv. 160, 250–262. https://doi.org/10.1016/j.biocon.2013.02.010.

R Core Team, 2016. R: a language and environment for statistical computing, version 3.3.0. R Foundation for Statistical Computing.

Ribeiro Filho, A.A., Adams, C., Manfredini, S., Aguilar, R., Neves, W.A., 2015. Dynamics of soil chemical properties in shifting cultivation systems in the tropics: a meta-analysis. Soil Use Manag. 31 (4), 474–482. https://doi.org/10.1111/sum.12224.

Ribeiro Filho, A.A., Adams, C., Murrieta, R.S.S., 2013. The impacts of shifting cultivation on tropical forest soil: a review. Bol. do Mus. Para. Emílio. Goeldi. Ciênc. Huma. 8 (3), 693–727. https://doi.org/10.1590/S1981-81222013000300013.

Rito, K.F., Arroyo-Rodríguez, V., Cavender-Bares, J., Santo-Silva, E.E., Souza, G., Leal, I. R., Tabarelli, M., 2021. Unraveling the drivers of plant taxonomic and phylogenetic β-diversity in a human-modified tropical dry forest. Biodivers. Conserv. 30 (4), 1049–1065. https://doi.org/10.1007/s10531-021-02131-9.

Rito, K.F., Arroyo-Rodríguez, V., Queiroz, R.T., Leal, I.R., Tabarelli, M., Norden, N., 2017. Precipitation mediates the effect of human disturbance on the Brazilian Caatinga vegetation. J. Ecol. 105 (3), 828–838. https://doi.org/10.1111/1365-2745.12712.

Sanchez, P.A., 2000. Linking climate change research with food security and poverty reduction in the tropics. Agric. Ecosyst. Environ. 82 (1-3), 371–383. https://doi.org/10.1016/S0167-8809(00)00238-3.

San-José, M., Arroyo-Rodríguez, V., Meave, J.A., 2020. Regional context and dispersal mode drive the impact of landscape structure on seed dispersal. Ecol. Appl. 30, 1–12. https://doi.org/10.1002/eap.2033.

Silva, J.M.C., Leal, I.R., Tabarelli, M., 2017. Caatinga the largest tropical dry forest region in South America. Springer International Publishing, Switzerland https://doi.org/https://doi.org/10.1007/978-3-319-68339-3.

Skoglund, J., 1992. The role of seed banks in vegetation dynamics and restoration of dry tropical ecosystems. J. Veg. Sci. 3, 357–360. https://doi.org/10.2307/3235760.

Sousa, T.R., Costa, F.R.C., Bentos, T.V., Leal Filho, N., Mesquita, R.C.G., Ribeiro, I.O., 2017. The effect of forest fragmentation on the soil seed bank of Central Amazonia. For. Ecol. Manage. 393, 105–112. https://doi.org/10.1016/j.foreco.2017.03.020.

Souza, C.R., Gianasi, F.M., Maia, V.A., Silva, A.M.d., Silva, W.B., Santos, R.M., 2021. Different heights of resprouting by trees: Response to small-scale environmental restrictions in a non-fire-prone Caatinga tropical dry forest. For. Ecol. Manage. 498, 119541. https://doi.org/10.1016/j.foreco.2021.119541.

Souza, D.G., Sfair, J.C., de Paula, A.S., Barros, M.F., Rito, K.F., Tabarelli, M., 2019. Multiple drivers of aboveground biomass in a human-modified landscape of the Caatinga dry forest. For. Ecol. Manage. 435, 57–65. https://doi.org/10.1016/j.foreco.2018.12.042.

Specht, M.J., Santos, B.A., Marshall, N., Melo, F.P.L., Leal, I.R., Tabarelli, M., Baldauf, C., 2019. Socioeconomic differences among resident, users and neighbour populations of a protected area in the Brazilian dry forest. J. Environ. Manage. 232, 607–614. https://doi.org/10.1016/j.jenvman.2018.11.101.

Tangney, R., Merritt, D.J., Callow, J.N., Fontaine, J.B., Miller, B.P., Seymour, C., 2020. Seed traits determine species' responses to fire under varying soil heating scenarios. Funct. Ecol. 34 (9), 1967–1978. https://doi.org/10.1111/1365-2435.13623.

Tangney, R., Merritt, D.J., Fontaine, J.B., Miller, B.P., 2019. Seed moisture content as a primary trait regulating the lethal temperature thresholds of seeds. J. Ecol. 107 (3), 1093–1105. https://doi.org/10.1111/1365-2745.13095.

Tanzito, G., Ibanda, P.A., Talaguma, R., Lusanga, N.M., 2020. Slash-and-burn agriculture, the major cropping system in the region of Faradje in Democratic Republic of Congo: ecological and socio-economic consequences. J. Dev. Agric. Econ. 12 (1), 25–36.

Tarrega, R., Calvo, L., Trabaud, L., 1992. Effect of high temperatures on seed germination of two woody Leguminosae. Vegetatio 102 (2), 139–147. https://doi.org/10.1007/BF00044730.

Thompson, K., Band, S.R., Hodgson, J.G., 1993. Seed size and shape predict persistence in soil. Funct. Ecol. 7 (2), 236. https://doi.org/10.2307/2389893.

Turnbull, L.A., Crawley, M.J., Rees, M., 2000. Are plant populations seed-limited? a review of seed sowing experiments. Oikos 88 (2), 225–238. https://doi.org/10.1034/j.1600-0706.2000.880201.x.

Turner, I.M., 2004. The ecology of trees in the tropical rain forest. Cambridge University Press.

Uhl, C., Clark, K., Clark, H., Murphy, P., 1981. Early plant succession after cutting and burning in the upper Rio Negro region of the amazon basin. J. Ecol. 69 (2), 631. https://doi.org/10.2307/2259689.

Vanderlei, R.S., Barros, M.F., Domingos-Melo, A., Alves, G.D., Silva, A.B., Tabarelli, M., 2021. Extensive clonal propagation and resprouting drive the regeneration of a Brazilian dry forest. J. Trop. Ecol. 37 (1), 35–42.

Wijdeven, S.M.J., Kuzee, M.E., 2000. Seed availability as a limiting factor in forest recovery processes in Costa Rica. Restor. Ecol. 8 (4), 414–424.

4 ARTIGO 2 – NEGATIVE IMPACT OF SLASH-AND-BURN AGRICULTURE ON THE SEED RAIN IN A TROPICAL DRY FOREST

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Negative impact of slash-and-burn agriculture on the seed rain in a tropical dry forest

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ABSTRACT

Forest's recovery potential in human-modified landscapes is increasingly threatened by agricultural activities that disrupt critical sources of forest regeneration, such as the seed rain. Slash-and-burn agriculture is a good example. By slashing and burning the vegetation, this farming method can promote seed source and seed dispersal limitation, but this hypothesis remains poorly tested. Here, we sampled the seed rain during a complete year in nine plots exposed to slash-and-burn agriculture (i.e., burned plots) and in forest stands (control plots) in the Caatinga biome – a species-rich tropical dry forest endemic to Brazil that is increasingly threatened by slash-and-burn agriculture. We compared seed density, seed species diversity, and the taxonomic and functional composition of seed assemblages between burned and control plots. As expected, seed density was 15 times lower in burned plots than in control plots. Species diversity was also lower in burned plots, but only when considering the number of rare species. However, burned plots showed a higher β-diversity of rare species than forest plots, mainly caused by species replacement (i.e. species turnover) from plot to plot. Burned plots also showed 30% more species with dry fruits and abiotic dispersal than control plots, but this difference was not statistically significant. Taken together, our findings highlight the low tolerance of the seed rain to this dominant agricultural practice in tropical dry forests. This is likely related to the lack of seed sources and seed dispersers in burned plots. Therefore, increasing the availability of seed sources and ecological connectivity in the surrounding landscape are critical management strategies for enhancing seed dispersal and forest recovery in forest areas exposed to this farming method.

1. Introduction

We are amid a planetary emergency, largely pushed by extensive forest loss, which causes a myriad of cascading effects on biodiversity, including our own species (Ripple et al., 2017; Rockström et al., 2009). Forest loss is largely driven by agriculture worldwide, especially by large-scale (commercial) agriculture (FAO, 2020). However, small-scale agriculture, such as slash-and-burn agriculture, also leads to the loss and disturbance of forest ecosystems (Curtis et al., 2018). This farming method is widespread in tropical dry forests (FAO, 2020), and although it usually involves relatively small (0.5 to 5 ha) areas (Lowder et al., 2016; Tanzito et al., 2020), it can have major impacts on biodiversity patterns and processes (Bezerra et al., 2022; Klanderud et al., 2010; Oakley and Bicknell, 2022; Raman, 2001). In particular, it can threaten the resilience of forest ecosystems by altering key sources of regeneration (e.g., soil seed bank; Bezerra et al., 2022). However, our knowledge on this topic is far from complete, especially regarding the impact of slash-and-burn agriculture on the seed rain.

The seed rain is defined as all seeds falling on the soil surface of a particular site. Seed arrival to a site depends on the availability of fruits and seeds in the surrounding vegetation, and on active seed dispersal by frugivores or passive dispersal (e.g. gravity, wind) (Carriere et al., 2002; Huanca-Nuñez et al., 2021; Nathan and Muller-Landau, 2000; San-José et al., 2020; Schott and Hamburg, 1997). Animal seed dispersal is

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particularly important in the tropics (Carriere et al., 2002; Gentry, 1982; Howe and Smallwood, 1982), but wind-dispersed seeds can become dominant in defaunated areas (Martínez-Garza et al., 2009; San-José et al., 2020). Thus, the composition and structure of the seed rain can be highly variable among sites, with direct consequences for forest recovery (Arroyo-Rodríguez et al., 2017; Cole et al., 2010; Huanca-Nuñez et al., 2021; Pickett et al., 1987; Svenning and Wright, 2005).

The seed rain is paramount during early successional stages (Carriere et al., 2002; Cole et al., 2010; Huanca-Nuñez et al., 2021; Svenning and Wright, 2005). This is particularly true in areas exposed to slash-and-burn agriculture (e.g. Carriere et al., 2002), as the seed rain can replenish the seed bank and increase the regenerative potential of burned areas, which typically show few seed species in the soil seed bank that are generally damaged by fire (Bezerra et al., 2022). Such a critical functional role of the seed rain could be, however, jeopardized if slash-and-burn agriculture erodes the seed rain. Therefore, understanding the effect of this farming method on the seed rain has major ecological and applied implications.

Slash-and-burn agriculture is particularly common in the Brazilian Caatinga biome (Curtis et al., 2018; Silva et al., 2017). In this tropical dry forest, some plant species can resprout after fire (Barros et al., 2021; Kennard et al., 2002), providing some level of resilience to regenerating forests (Lawrence et al., 2010). However, as this regenerative potential is biased to few resprouting species (Barros et al., 2021; Ceccon et al., 2006; Cury et al., 2020), the recovery of major community attributes such as species diversity and composition in burned areas largely depends on the seed rain (Souza et al., 2014). Yet, slash-and-burn agriculture can negatively affect the seed rain through two alternative but non-exclusive paths (Fig. 1): (i) by decreasing the availability of trees and seeds (i.e. seed source limitation; Clark et al., 1998); and/or (ii) by decreasing the abundance (and diversity) of seed dispersers thereby limiting seed dispersal (Howe and Smallwood, 1982). As most species (≈70 %) in the Caatinga forest show abiotic dispersal (e.g. gravity, wind, and ballistic; Griz and Machado, 2001; Barbosa et al., 2003), the former path is likely more important than the latter. However, many plant species have small- and medium-sized berries or drupes (with seeds < 1 cm in length) primarily dispersed by ants, birds and bats (Griz and Machado, 2001; Leal et al., 2007, E. Bernard, personal communication), so the impact of slash-and-burn agriculture on animal dispersed seeds should not be overlooked.

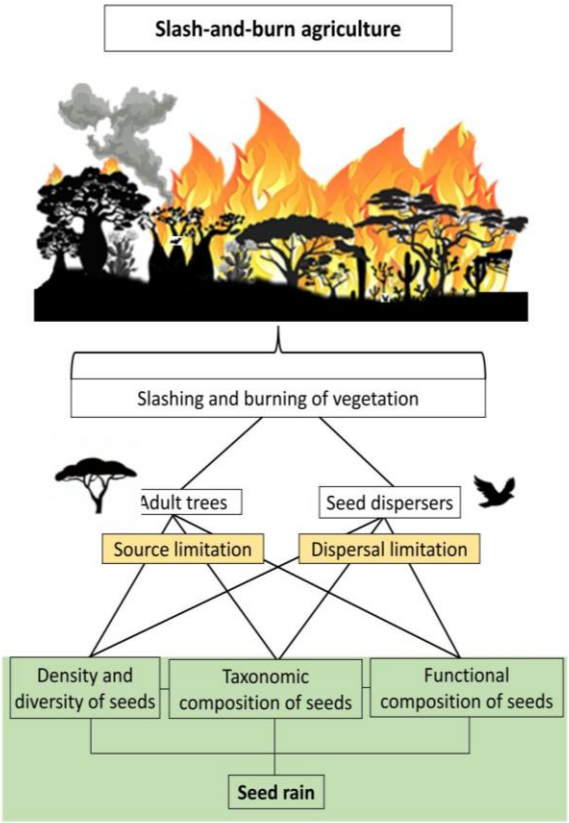

Fig. 1. Hypothesized effects of slash-and-burn agriculture on the seed rain. Adult trees and seed dispersers directly contribute to the structure and composition of seed rain through seed production and seed dispersal, respectively. Therefore, the loss of adult trees and seed dispersers after slashing and burning of vegetation can modify the structure and composition of seed assemblages through the so-called seed source and seed dispersal limitations.

In this study, we assessed for the first time the structure (seed density and diversity) and composition (taxonomic and functional) of seed assemblages in the seed rain in plots exposed to an experiment of slash-and-burn agriculture in the Caatinga dry forest. As this farming method can promote seed source and seed dispersal limitations (Fig. 1), it is reasonable to expect that the seed rain is extremely susceptible to slash-and-burn agriculture. In particular, compared to paired control plots (forest stands), we expected to find (i) a significantly lower number of seeds from a lower number of species in burned plots (i.e. areas exposed to slash-and-burn agriculture). We expected that this particularly affect rare species because forest loss in the region usually has stronger negative effects on adult trees of rare species than on common or dominant species (Rito et al., 2017). As burned plots are extremely homogeneous environments compared to forest plots, we also expected to find (ii) a lower β-diversity between burned plots (floristic homogenization) than between forest plots, especially the species turnover component of β-diversity. In addition, we predicted that (iii) the seed rain of burned plots would be composed of few species, particularly those with ecological traits that provide high dispersal ability (Trindade et al., 2020). Examples of such traits include small seeds with abiotic dispersal, which are commonly produced in large numbers by woody plants (Leishman, 2001); these traits are predicted to be particularly frequent in burned plots.

2. Methods

2.1. Study area

We carried out the study in the Catimbau National Park, northeastern Brazil (8°23′17″-8°36′35″ S; 37°11′00″-37°33′32″W; ~600 m a.s.l.). This protected area was created in 2002 and covers 607 km^2 of the Caatinga biome – a tropical dry forest endemic to Brazil. The climate is semi-arid (Koppen classification), with annual temperature averaging 25 to 30 °C, and annual rainfall ranging from 450 to 1100 mm, concentrated in a few (but variable) months (Nimer, 1972; Rito et al., 2021). Most (≈70 %) of the area is composed of litosol soils, and has been strongly impacted by human activities since the beginning of European colonization in the 16th century (Coimbra-Filho and Câmara, 1996). Small groups of farmers are still present within this national park, where they traditionally practice slash-and-burn agriculture to produce mainly beans, cassava, corn, and watermelon. Free-ranging cattle raising is also practiced, and both activities have converted old-growth forests into a mosaic of different-aged secondary forests (Barros et al., 2021; Souza et al., 2019; Specht et al., 2019).

2.2. Slash-and-burn experiment

The study design was described elsewhere (Bezerra et al., 2022), but a summary is provided here. We adopted an experimental approach to assess the effects of slash-and-burn agriculture on the seed rain of woody plant species (i.e., trees and shrubs; Fig. 2). We selected nine blocks of two paired plots of 50 m × 20-m (0.1 ha) each, with no record of recent agricultural practices. One plot was exposed to slash-and-burn

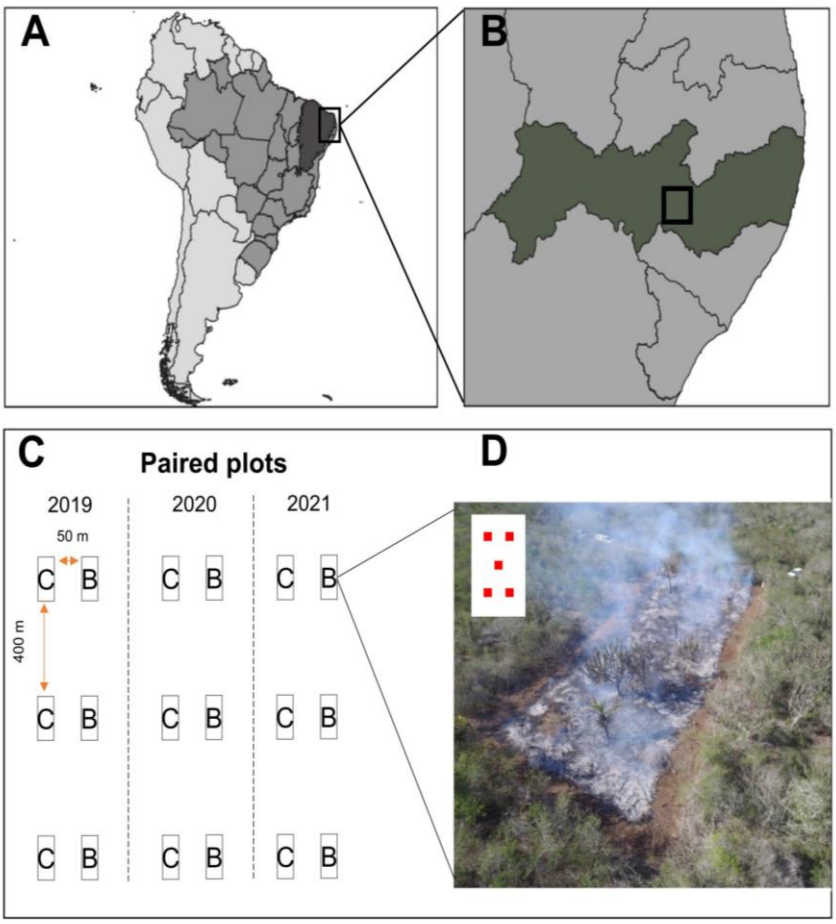

Fig. 2. Distribution of the Caatinga dry forest (dark gray area in A) and location of the Catimbau National Park (black square in B) within the Pernambuco state of Brazil (dark gray area in B), in which we sampled the seed rain using the experimental approach described in panels C and D. We sampled 9 paired (C = control; B = burned) plots in three different years (C) and sampled the seed rain along a complete year in 5 seed traps (red squares in D) within each plot. An example of burned plot is also indicated (D), courtesy of Jens Brauneck.

agriculture (i.e. burned plots), and as a reference (control), we located another plot in a forest area near (50 m apart) the burned plot. As all burned plots had the same size and were surrounded by forest, the isolation distance between sampling areas (i.e. the seed traps, see below) and the extant forest remained constant across burned plots (Fig. 2C), allowing us to control the potential effect of such a distance on the seed rain. The entire experiment was carried out with official permission from ICMBio (the Brazilian agency for protected areas). The information on historical land use was confirmed by the local community.

The blocks were located at an average distance of 400 m apart from each other to avoid spatial autocorrelation. The woody vegetation present in the nine plots exposed to slash-and-burn agriculture was completely cut by local farmers with the help of axes and machetes at the end of the dry season (November-December). Following the practices they usually do, all high-density poles were immediately collected by farmers, as they use them for firewood, fences and other household facilities. The remaining plant biomass was left to dry naturally for a period of 20 days, piled into small amounts and then completely burned (during between 20 and 40 min) through a controlled fire by the park's fire brigade team (Fig. 2). After that, without further removal of the remaining debris, farmers seeded manually-three kilograms of each of the crop types commonly seeded by local farmers (i.e. beans, corn, and watermelon).

2.3. Seed rain sampling

We randomly placed five square (1 m × 1 m) seed traps of nylon mesh in each plot but keeping a minimum distance of 2.5 m from each other. Each trap was maintained 50 cm above the ground with plastic (PVC) poles. We collected the content of the traps every 30 d during a complete year. Three blocks (including burned and control plots) were sampled from February 2019 to February 2020, three additional blocks from February 2020 to February 2021, and three blocks from February 2021 to February 2022. This allowed us to have a more representative seed rain assemblage, as some species have triannual cycles of reproduction and can be overlooked if sampling all plots along a single year. Samples were sorted to separate leaves, flowers and/or fruits from the seeds of woody plant species (i.e., trees and shrubs), which were quantified and identified at species or genus level with the help of literature, seed specialists and a guide of Caatinga seeds available at the Applied Plant Ecology Laboratory (Universidade Federal de Pernambuco, Recife). It is important to note that annual rainfall during the sampling years (2019, 2020 and 2021) was 439 mm, 582 mm and 414 mm, respectively, which are normal values according to data collected by meteorological stations installed by the Long-Term Ecological Research Network (https://www.peldcatimbau.org.br) close to the study sites.

2.4. Structure and composition of seed assemblages

To avoid pseudoreplication, we combined (summed) the data from the five seed traps from each plot and considered each plot as an independent sample. To characterize the structure of seed assemblages in the seed rain, we calculated the total number of seeds (seed density hereafter) and seed species diversity. This later response variable was estimated with Hill numbers of order 0 (${}^0D$, species richness), 1 (${}^1D$,

exponential Shannon entropy) and 2 (^2D, inverse Simpson concentration) (Chao et al., 2014; Jost, 2006). ^0D is not sensitive to differences in seed abundance, so it gives a disproportionately high weight to rare species. ^1D weights each species according to its relative abundance in the community, without favoring rare or abundant species, and thus it is considered a measure of the effective number of common or typical species (Jost, 2006). Finally, ^2D favors very abundant species, and is therefore interpreted as the effective number of dominant species in the community (Jost, 2006). To assess the accuracy of our seed inventories in each plot, we estimated the sample coverage index (C_n) proposed by Chao and Jost (2012). This index ranges from 0 to 1 and indicates the proportion of seeds in a plot that belongs to the species found in it. Sample coverage was very high ($C_n > 0.9$) in all plots, which suggests that our sampling effort was adequate to assess changes in species diversity in all plots. However, to avoid any potential bias in our results due to differences in sample coverage among sites (see Chao and Jost, 2012), we carried out diversity analyses with coverage-based rarefied values of $^0D_\alpha$, $^1D_\alpha$ and $^2D_\alpha$, performed with the 'iNEXT' package for R, version 3.5. We also evaluated the patterns of β-diversity between control plots and between burned plots with Hill numbers (i.e. $D_\beta = D_\gamma / D_\alpha$; Jost, 2006). We assessed β-diversity considering all species ($^0D_\beta$), and focusing on typical ($^1D_\beta$) and dominant ones ($^2D_\beta$) using the 'entropart' R package (Marcon and Hérault, 2015). We calculated these three metrics using a function designed by Sfair et al. (2016) to construct a matrix that contained β-diversity values of each pairwise comparison within each treatment. Independently of order of q (i.e. $^0D_\beta$, $^1D_\beta$ and $^2D_\beta$), β-diversity values within the matrix could range between 1, when two plots were identical in composition, and 2, when both plots were completely different from each other. Then, following Sfair et al. (2016), we calculated the mean pairwise β-diversity values and 95 % confidence intervals to compare β-diversity between treatments. To assess to some extent the mechanisms driving β-diversity differences between treatments, we also assessed the species turnover and nestedness-resultant components of β-diversity with the metrics proposed by Baselga (2010) and calculated by the 'betapart' R package (Baselga and Orme, 2012). In particular, we calculated overall dissimilarity (measured as Jaccard dissimilarity, βJac) and partitioned it into its turnover (βSim) and nestedness (βSne) components (Legendre, 2014). βSim reflects the substitution of some species by others, usually associated with environmental filters and historical contractions, whereas βSne is related to the loss (or gain) of species through space in a nested pattern. We complemented our compositional analyses with abundance-rank curves to assess how the composition and dominance of species differed between control and burned plots. Finally, we assessed the functional composition of seed assemblages considering plant traits that can affect seed dispersal capacity, including (i) seed size (cm^3); (ii) life form (tree or shrub); (iii) fruit type (dry or fleshy); and (iv) seed dispersal mode (abiotic or biotic) (Díaz et al., 2016; Rito et al., 2017; Turner, 2004; Alexandre de Paula, unpublished data). For seeds identified only at the genus level, we considered the mean characteristics of all species within this taxon. For the continuous trait (seed size), we calculated the community weighted mean per plot with the 'FD' R package (Laliberté and Legendre, 2010). Following Bezerra et al. (2022), for categorical traits, we calculated the relative abundance of seeds with each trait class.

2.5. Data analyses

To test for differences in response variables between treatments (control and burned plots) we used parametric paired *t*-test after verifying that residuals of all models followed the normality assumptions (Shapiro-Wilk test): (i) seed density, (ii) total number of species ($^0D_\alpha$), (iii) number of typical species ($^1D_\alpha$), (iv) number of dominant species ($^2D_\alpha$), and (v) CWM of seed size. Following Bezerra et al. (2022), for categorical seed traits, we tested for differences between treatments in the total frequencies of each binary variable (i.e., life form, fruit type, dispersal mode, and seed type) with the Fisher's exact test for 2 × 2 contingency tables. Finally, the differences between treatments in pairwise β-diversity values were assessed by comparing mean and 95 % confidence interval values.

3. Results

3.1. Overview

In total, we found 8417 seeds belonging to 50 species, 37 genera and 18 families. The most abundant species was *Guapira graciliflora*, followed by *Croton heliotropiifolius*, and *Pityrocarpa moniliformis*, together representing 55 % of seeds. Most species (54 %) belonged to Fabaceae and Euphorbiaceae. Seed density averaged 467 seeds per plot (range = 6 to 3556 seeds), and the observed species richness averaged 10 species (range = 1 to 29 species). Seeds mainly consisted of tree species (76 % of all species) bearing dry fruits (70 %) with abiotic dispersal mode (62 %).

3.2. Structure of seed assemblages in burned and control plots

Both the total and the mean density of seeds were 15 times higher in control plots than in burned plots (Table 1). The total number of species was also 1.7-times higher in control plots (47 species) than in burned plots (27 species). Considering the rarefied values, seed species diversity was also significantly higher in control plots, but only when considering species richness ($^0D_\alpha$) (Table 1, Fig. 3). As the number of typical ($^1D_\alpha$) and dominant ($^2D_\alpha$) species did not differ between treatments, our findings indicate that the species that are lost in burned plots are relatively rare (with few seeds) (Table 1, Figs. 3 and 4).

3.3. Differences in taxonomic and functional composition of seed assemblages

Control plots were dominated by two species, a tree (*Guapira graciliflora*) and a shrub (*Croton heliotropiifolius*), together representing 46 % of all seeds in control plots (Fig. 4). Other common tree species in control plots were *Pityrocarpa moniliformis*, *Guapira laxa* and *Senegalia piauhiensis*. However, most species (46 %) in control plots were relatively rare (i.e. 23 species showed < 15 seeds; Fig. 4). In contrast, burned plots were by far dominated by a tree species (*Moquiniastrum oligocephalum*) that represented 43 % of all seeds recorded in these plots (Fig. 4). *Senegalia piauhiensis*, *Combretum leprosum*, *Cnidosculus bahianus*, and

Table 1
Structure of seed assemblages in the seed rain in 9 plots exposed to an experiment of slash-and-burn agriculture (i.e. burned plots) and 9 forest stands (i.e. control plots) in the Catimbau National Park, Brazil. The total number of seeds (i.e. summing all plots per treatment), as well as the mean (and range) values per plot are indicated. Significant differences between treatments are indicated with asterisks (*p < 0.05; **p < 0.01; ns p > 0.05).

Response variables	Control plots	Burned plots	test-value
Total number of seeds	7888	529	–
Total number of species	47	27	–
Structure of seed assemblages[a]			
Seed density (seeds/plot)	876.4 (74 – 3556)	58.7 (6 – 307)	2.32**
Species richness ($^0D_\alpha$)	9 (5 – 22)	4 (1 – 14)	8***
Number of typical species ($^1D_\alpha$)	4 (1 – 8)	3(1 – 12)	1.38 ns
Number of dominant species ($^2D_\alpha$)	3 (1 – 6)	3 (1 – 10)	0.14 ns
Functional composition			
CWM - Seed size (cm)[b]	0.54 (0.23 – 0.83)	0.56 (0.10 – 0.91)	– 0.52 ns

[a] Note that our unit of analysis is the plot (50 m × 20 m; 0.1 ha each), and that we sampled 5 m^2 per plot.
[b] The community weighted mean (CWM) of seed size is the mean value of all species per plot, weighted by their relative abundances.

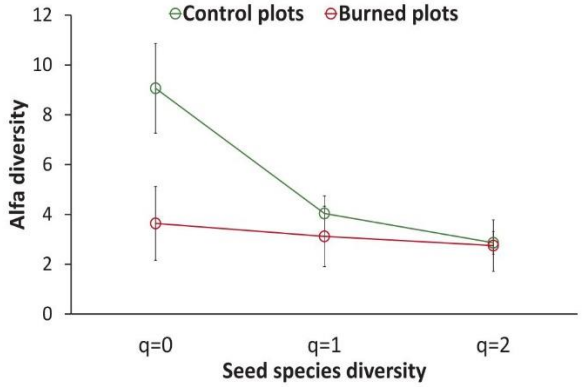

Fig. 3. Mean (±SE) rarefied effective number of species recorded in 9 plots exposed to slash-and-burn agriculture (burned plots) and 9 control (forest stands) plots in the Catimbau National Park, Brazil. We considered three orders of q (${}^{0}D_{\alpha}$ = species richness; ${}^{1}D_{\alpha}$ = number of typical species, and ${}^{2}D_{\alpha}$ = number of dominant species).

Pityrocarpa moniliformis were also relatively common in burned plots, together representing 39 % of seeds. The rest of the species (78 %) in burned plots were rare (i.e. 21 species showed < 15 seeds).

β-diversity was significantly higher between burned plots than between control plots, but only when considering all species (${}^{0}D_{\beta}$; Fig. 5). As β-diversity did not differ between treatments when assessing typical (${}^{1}D_{\beta}$) and dominant species (${}^{2}D_{\beta}$), our findings indicate that the relatively higher compositional differentiation between burned plots was driven by differences in rare species between plots. The partitioning of total β-diversity (β-Jac) in its turnover (β-Sim) and nestedness (β-Sne) components indicated that in both treatments β-diversity was mainly driven by species replacement from plot to plot (β-Sim), but the contribution (in percentage) of species turnover to total β-diversity was 90 % in burned plots and 92 % in control plots, whereas the nestedness component of β-diversity followed the opposite pattern (burned plots = 10 %; control plots = 8 %).

Regarding the functional composition of seed assemblages, we found that the seed rain in both control and burned plots was dominated by trees (77 % and 81 % of the species, respectively; Odds ratio = 0.75, p = 0.77, Fig. 6). Seed size varied more in control (0.03 to 2.43 g) than burned plots (0.03 to 1.74 g), but the community-level weighted mean (CWM) of seed size was similar in both treatments (Table 1). The percentage of species with dry fruits was 1.3-times (i.e. 30 %) higher in burned plots (85 % of species) than in control plots (68 %), but this difference was not significant according to Fisher's exact test (fleshy vs dry; OR = 2.66, p = 0.17, Fig. 6). Similarly, the percentage of species with abiotic dispersal was also 30 % higher in burned (78 %) than control (60 %) plots, but again the Fisher's test suggest this difference is not significant (biotic vs abiotic; OR = 2.35, p = 0.13).

4. Discussion

This study evaluates the impact of experimental slash-and-burn agriculture on the seed rain in the Caatinga biome – a species-rich but threatened tropical dry forest from northeastern Brazil. Our findings indicate that, as expected, this agricultural practice causes a drastic impoverishment of the seed rain, not only because seed density was 15 times lower in burned plots, but because seed species diversity was also significantly lower, particularly the number of rare species. Contrary to our expectations, β-diversity was significantly higher (not lower) in

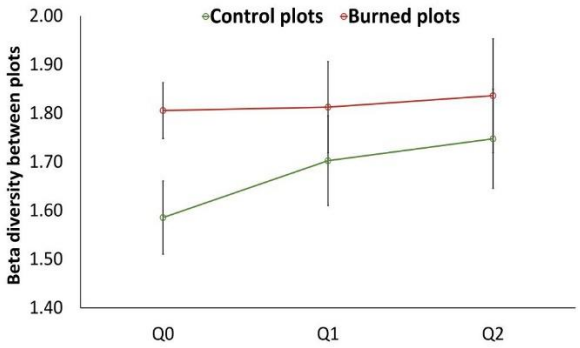

Fig. 5. Mean pairwise β-diversity values (and 95 % confidence intervals) between control and burned plots separately for different q orders (q = 0 assesses all species irrespective to their abundances, q = 1 focuses on typical species, and q = 2 focuses on highly abundant or dominant species). Note that these three β-diversity metrics can vary between 1 (if two plots are identical), and 2 (the plots are completely different from each other).

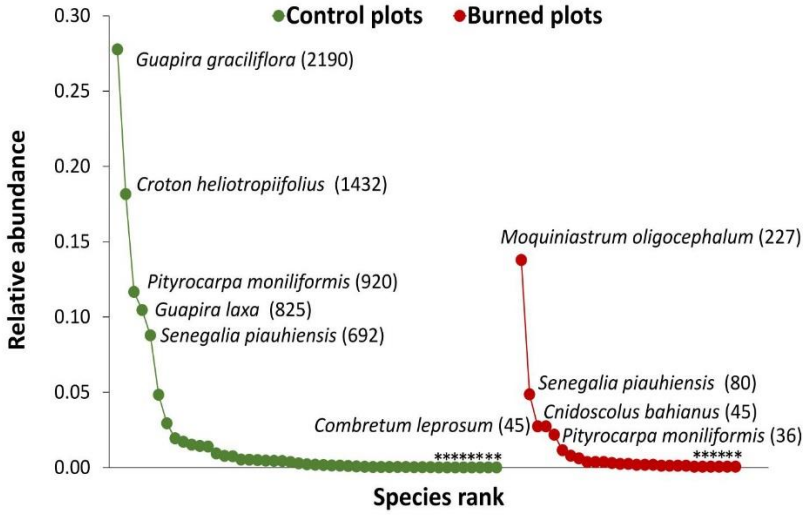

Fig. 4. Rank-abundance curves showing the proportion of seeds per species in control (forest stands) and burned plots in the Catimbau National Park, Brazil. The species are ranked from highest to lowest abundance, and we indicate the absolute abundance of each species in parentheses, as well as those species with one (* singletons) individuals.

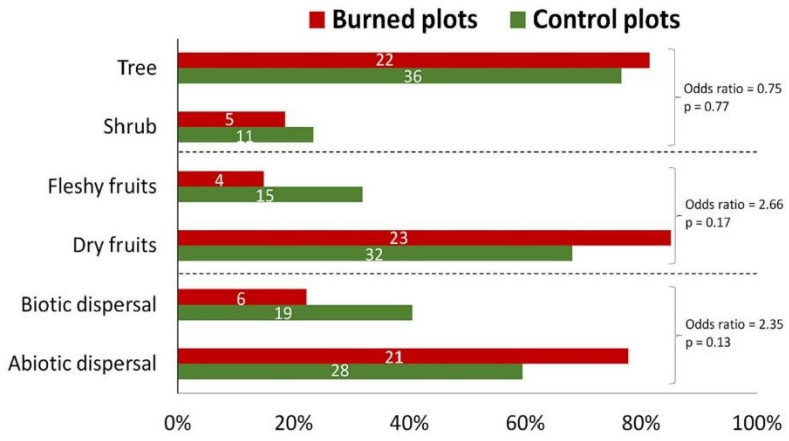

Fig. 6. Total percentage of species (and absolute frequency within bars) with different life forms (tree and shrub), fruit types (dry and fleshy) and dispersal modes (abiotic and biotic) in control and burned plots. The differences between treatments were tested with Fisher exact tests for 2 × 2 contingency tables, and the odds ratio and p-value of each test is indicated for each seed trait.

burned plots than in control plots, but only when considering rare species. Although the functional composition of seed rain did not differ significantly between treatments, we found some interesting trends that merit special attention. As discussed below, our findings can be explained by the lack of seed sources and seed dispersers in burned plots, which together limit the arrival of seeds to areas exposed to slash-and-burn agriculture. Therefore, we highlight some important applied implications for increasing the resilience of these degraded lands.

As expected, seed dispersal was extremely limited in burned plots. The significantly lower seed density and diversity in burned plots add to emerging evidence of the widespread impact this farming method has on different biodiversity patterns and processes (Bezerra et al., 2022; Klanderud et al., 2010; Oakley and Bicknell, 2022; Raman, 2001). For example, Rocha et al. (2021) and Cury et al. (2020) found that seed density and richness in the seed rain was significantly lower (up to two times) in burned forests than in control ones. This is likely caused by the removal of adult trees (and seeds) in burned sites (i.e. seed source limitation; Clark et al., 1998), especially in the Caatinga forests, where most plant species (≈70 %) have abiotic dispersal (e.g. gravity, wind, and ballistic; Barbosa et al., 2003; Griz and Machado, 2001), so they do not depend on animals for dispersing their seeds. Yet, the removal of adult trees not only causes seed source limitation, as it also increases the distance to seed sources, causing seed dispersal limitation (Piotto et al., 2019; Souza et al., 2014).

Slash-and-burn agriculture seems to be causing stronger negative impacts on rare species. This is consistent with previous studies of adult trees (Rito et al., 2017) and the soil seed bank (Bezerra et al., 2022) in the region, thus suggesting that rare species in the Caatinga forest are the most sensitive to human disturbances throughout ontogeny. This is not surprising, as the factors that limit seed dispersal in burned plots are expected to be even more limiting in species that have smaller populations (Pinho et al., 2022). What is likely more interesting is the fact that even relatively common plants in forest stands, such as *Croton heliotropiifolius* and *Senna macranthera*, showed a lower number of seeds in burned plots, and some of them (e.g. *Croton nepetifolius*) where actually absent in these plots. All these species have dry fruits with abiotic dispersal and are geographically restricted across the landscape, so the lack of seeds in burned plots could be simply caused by the removal of adult trees in burned plots, and/or by the absence of adult trees in the nearby forest. Nevertheless, as most tree species in this tropical dry forest are relatively rare (Bezerra et al., 2022; Pinho et al., 2022; Rito et al., 2017), and our findings suggest that they are exposed to strong dispersal limitations, the recovery of community attributes such as species diversity in the seed rain will be difficult.

Surprisingly, this farming method does not seem to promote the compositional homogenization (loss of β-diversity) of seed assemblages in burned plots, but rather the opposite. Our pairwise comparisons of β-diversity indicated that most burned plots were completely different from each other independently of species abundances (i.e. for all order q). This pattern is similar to that observed in adult trees in the region (Rito et al., 2021), likely because most species have abiotic dispersal and depend strongly on the composition of the remaining adult trees in the surrounding areas. Thus, such a relatively high β-diversity in adult trees and seeds is probably caused by the clumped spatial distribution of trees across the Caatinga forest (Pinho et al., 2022; Rito et al., 2021, 2017; Alexandre de Paula, unpublished data), which promotes a very high species replacement (turnover) from plot to plot. But why was β-diversity of rare species higher between burned plots than between control plots? The partitioning of β-diversity into its turnover and nestedness components suggests the answer is in both the loss and replacement of rare species from some burned plots to others. In addition to the aforementioned effects of tree spatial distribution on the turnover component of β-diversity, the loss of rare species in some burned plots can explain why the nestedness component of β-diversity was 2 % higher in burned plots, as this component is associated with the loss (or gain) of species from some plots to others (Baselga, 2010). In any case, our findings imply that because of the very high β-diversity between plots, each burned plot will follow different successional pathways after disturbance depending on the composition of surrounding adult trees (Arroyo-Rodríguez et al., 2017).

Our findings suggest that animal seed dispersal is not significantly impacted by this farming method. Previous studies in secondary (regenerating) tropical forests (Martínez-Garza et al., 2009) and fragmented tropical forests (San-José et al., 2020) suggest that seed dispersal limitation causes a proportionally stronger impact on animal-dispersed species than in species with abiotic dispersal. Yet, in our study the percentage of species with biotic and abiotic dispersal did not differ significantly between treatments, probably because burned plots were relatively small (0.1 ha), which would not be expected to have a major impact on seed-dispersing fauna. Alternatively (but not exclusively), our findings could be explained by centuries of overhunting and habitat degradation in the Caatinga forest. These processes have gradually defaunated the whole region (Alves et al., 2020, 2022; Bezerra et al., 2020), contributing to a generalized loss of animal-dispersed seeds across the ecosystem (Leal et al. 2014a, 2014b; Lins et al., 2022). It is worth noting, however, that the percentage of species with fleshy fruits

and biotic dispersal was 30 % lower in burned plots – a non-negligible trend that might (to some extent) reflect the fact that the remaining fauna, although scarce, may avoid burned lands, either because these areas have fewer resources (e.g. food, shelter), or because they are perceived by animals as places of risk, and they avoid using them (see the "landscape of fear" conceptual framework; Frid and Dill, 2002). However, additional studies are needed to identify the composition and structure of animal assemblages, and their behaviors in burned lands to better understand the potential cascading effects of slash-and-burn agriculture on plant-animal interactions in the Caatinga.

All in all, our results have important implications. As argued in the introduction section, seed rain is paramount for replenishing the seed bank and thus increasing the resilience (regenerative potential) of burned areas, which usually have an impoverished soil seed bank (Bezerra et al., 2022). Therefore, the first and likely the most important implication of our findings is that such a critical functional role of the seed rain is likely compromised in burned plots, as the seed rain was significantly poorer in the number and diversity of seeds than in control (forest stands) plots. This finding is not trivial, as the study plots are smaller than the areas that are usually dedicated to this farming method in tropical dry forests (0.5 to 5 ha; Lowder et al., 2016; Tanzito et al., 2020). Therefore, as argued in previous studies (Bezerra et al., 2022), another important implication is that the impact of slash-and-burn agriculture on the seed rain is likely to be worse than that reported here (i.e. it should be more detrimental if extended over larger spatial extents). The third implication is that such impact is likely weaker on some dominant species, especially those with dry fruits and abiotic dispersal (e.g. *Senegalia piauhiensis*, *Moquiniastrum oligocephalum*). Yet, the presence and recruitment of rare species in burned plots will probably require effective management actions (see below). Finally, the very high β-diversity between burned plots implies that, after disturbance, the plots will follow multiple successional pathways (Arroyo-Rodríguez et al., 2017, 2022). This is good news, as it can contribute to maintaining this important component of species diversity and its critical role for preserving total (γ) diversity at the landscape and regional scales (Arroyo-Rodríguez et al., 2013; Flohre et al., 2011).

5. Management implications

The most important recommendation from enhancing seed dispersal and ecosystem resilience is preventing as much forest loss as possible. We understand that this is extremely challenging in a region where local people depend on slash-and-burn agriculture for subsistence (Souza et al., 2019). However, agricultural lands could at least be placed as far apart as possible from each other to leave old-growth forest patches between them so that seed sources can persist around the burned lands (Piotto et al., 2021). This is of critical importance because as discussed above, most plant species have passive dispersal modes, so they depend on nearby seed sources. Second, to promote the dispersal of rare tree species, which are the first to become extirpated from both the seed rain and the soil seed bank (see Bezerra et al., 2022), we must avoid losing adult trees of these species in the region. For this reason, when slashing the vegetation, we should avoid the removal of adult individuals of these species, not only within agricultural lands, but also outside these areas. Finally, we must recognize that in some places we may need to directly plant individuals of these rare species to enrich areas/regions of the forest where they are disappearing. In this sense, there are some successful restoration efforts in the Caatinga forest, which have increased the diversity of rare species and raised the species survival rate by 70 % in degraded agricultural lands in the National Forest Açu Federal Reserve, Rio Grande do Norte, Brazil (https://brazildry.wixsite.com/treediv). Taken together, these complementary management strategies can be valuable to promote the recovery of burned areas. Without these strategies, forest recovery will largely depend on plant resprouting, being biased to the few plant species that are able to resprout after fire (see Barros et al., 2021; Ceccon et al., 2006; Cury et al., 2020; Kennard et al., 2002), significantly limiting the future diversity and composition of this species-rich ecosystem.

CRediT authorship contribution statement

Jakelyne S. Bezerra: Conceptualization, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. **Víctor Arroyo-Rodríguez:** Conceptualization, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. **Juan Manuel Dupuy:** Investigation, Writing – review & editing. **Inara R. Leal:** Conceptualization, Investigation, Funding acquisition, Supervision, Writing – review & editing. **Marcelo Tabarelli:** Conceptualization, Investigation, Funding acquisition, Supervision, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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References

Alves, T.S., Alvarado, F., Arroyo-Rodríguez, V., Santos, B.A., 2020. Landscape-scale patterns and drivers of novel mammal communities in a human-modified protected area. Landsc. Ecol. 35, 1619–1633. https://doi.org/10.1007/s10980-020-01040-6.

Alves, T., Alvarado, F., Arroyo-Rodríguez, V., Santos, B.A., 2022. Foxes and goats: the outcome of free-ranging livestock farming in Brazilian dry forests. Biodiv. Conserv. https://doi.org/10.1007/s10531-022-02520-8.

Arroyo-Rodríguez, V., Rito, K.F., Farfán, M., Navía, I.C., Mora, F., Arreola-Villa, F., Balvanera, P., Bongers, F., Castellanos-Castro, C., Catharino, E.L.M., Chazdon, R.L., Dupuy-Rada, J.M., Ferguson, B.G., Foster, P.F., González-Valdivia, N., Griffith, D.M., Hernández-Stefanoni, J.L., Jakovac, C.C., Junqueira, A.B., Jong, B.H.J., Letcher, S. G., May-Pat, F., Meave, J.A., Ochoa-Gaona, S., Meirelles, G.S., Muñiz-Castro, M.A., Muñoz, R., Powers, J.S., Rocha, G.P.E., Rosário, R:P.G., Santos, B.A., Simon, M.F., Tabarelli, M., Tun-Dzul, F., van den Berg, E., Vieira, D.L.M., Williams-Linera, G., Martínez-Ramos, M., 2022. Landscape-scale forest cover drives the predictability of forest regeneration across the Neotropics. Proc. Roy. Soc. B. 290, 20222203. https://doi.org/10.1098/rspb.2022.2203.

Arroyo-Rodríguez, V., Ros, M., Escobar, F., Melo, F.P.L., Santos, B.A., Tabarelli, M., Chazdon, R., Kitzberger, T., 2013. Plant β-diversity in fragmented rain forests: testing floristic homogenization and differentiation hypotheses. J. Ecol. 101, 1449–1458. https://doi.org/10.1111/1365-2745.12153.

Arroyo-Rodríguez, V., Melo, F.P.L., Martínez-Ramos, M., Bongers, F., Chazdon, R.L., Meave, J.A., Norden, N., Santos, B.A., Leal, I.R., Tabarelli, M., 2017. Multiple successional pathways in human-modified tropical landscapes: new insights from forest succession, forest fragmentation and landscape ecology research. Biol. Rev. 92, 326–340. https://doi.org/10.1111/brv.12231.

Barbosa, D.C.A., Barbosa, M.C.A., Lima, L.C.M., 2003. Fenologia de espécies lenhosas da Caatinga. In: Leal, I.R., Tabarelli, M., Silva, J.M.C. (Eds.), Ecologia E ConsErvação Da, Caatinga. Ed. Universitária da UFPE, Recife, pp. 657–693.

Barros, M.F., Ribeiro, E.M.S., Vanderlei, R.S., de Paula, A.S., Silva, A.B., Wirth, R., Cianciaruso, M.V., Tabarelli, M., 2021. Resprouting drives successional pathways and the resilience of Caatinga dry forest in human-modified landscapes. For. Ecol. Manage. 482, 118881 https://doi.org/10.1016/j.foreco.2020.118881.

Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. Glob. Ecol. Biogeogr. 19, 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x.

Baselga, A., Orme, C.D.L., 2012. Betapart: an R package for the study of beta diversity. Methods Ecol. Evol. 3, 808–812. https://doi.org/10.1111/j.2041-210X.2012.00224.x.

Bezerra, J.S., Arroyo-Rodríguez, V., Tavares, J.M., Leal, A., Leal, R.I., Tabarelli, M., 2022. Drastic impoverishment of the soil seed bank in a tropical dry forest exposed to slash-and-burn agriculture. For. Ecol. Manage. 513, 120185 https://doi.org/10.1016/j.foreco.2022.120185.

Bezerra, D.M.M., de Araujo, H.F.P., Alves, R.R.N., 2020. Understanding the use of wild birds in a priority conservation area of Caatinga, a Brazilian tropical dry forest. Environ. Dev. Sustain. 22, 5297–5316. https://doi.org/10.1007/s10668-019-00425-1.

Carriere, S.M., Andre, M., Letourmy, P., Oliver I., McKey, D.B., 2002. Seed rain beneath remnant trees in a slash-and-burn agricultural system in southern Cameroon. J. Trop. Ecol. 18, 353–374. 10.10 17/S0266467402002250.

Ceccon, E., Huante, P., Rincón, E., 2006. Abiotic factors influencing tropical dry forests regeneration. Brazilian Arch. Biol. Technol. 49, 305–312. https://doi.org/10.1590/S1516-89132006000300016.

Chao, A., Colwell, R.K., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K., Ellison, A.M., 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecol. Monogr. 84, 45–67. https://doi.org/10.1890/13-0133.1.

Chao, A., Jost, L., 2012. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology 93, 2533–2547. https://doi.org/10.1890/11-1952.1.

Clark, J.S., Macklin, E., Wood, L., 1998. Stages and spatial scales of recruitment limitation in southern appalachian forests. Ecol. Monogr. 68, 213. https://doi.org/10.2307/2657201.

Coimbra-Filho, A.F., Câmara, I.G., 1996. Os limites originais do bioma Mata Atlântica na região Nordeste do Brasil. Fundação Brasileira para a Conservação da Natureza, Rio de Janeiro.

Cole, R.J., Holl, K.D., Zahawi, R.A., 2010. Seed rain under tree islands planted to restore degraded lands in a tropical agricultural landscape. Ecol. Appl. 20, 1255–1269. https://doi.org/10.1890/09-0714.1.

Curtis, P.G., Slay, C.M., Harris, N.L., Tyukavina, A., Hansen, M.C., 2018. Classifying drivers of global forest loss. Science 361, 1108–1111. https://doi.org/10.1126/science.aau3445.

Cury, R.T.S., Montibeller-Santos, C., Balch, J.K., Brando, P., Torezan, J.M.D., 2020. Effects of fire frequency on seed sources and regeneration in southeastern Amazonia. Front. For. Glob. Change 3, 82. https://doi.org/10.3389/ffgc.2020.00082.

Díaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bonisch, G., Westoby, M., Poorter, H., Reich, P.B., Moles, A.T., Dickie, J., Gillison, A.N., Zanne, A.E., Chave, J., Joseph Wright, S., Sheremet'ev, S.N., Jactel, H., Baraloto, C., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., Casanoves, F., Joswig, J.S., Günther, A., Falczuk, V., Rüger, N., Mahecha, M.D., Gorné, L.D., 2016. The global spectrum of plant form and function. Nature 529, 167–171. https://doi.org/10.1038/nature16489.

Fao, 2020. The State of the World's Forests 2020. FAO, Rome.

Flohre, A., Fischer, C., Aavik, T., Bengtsson, J., Berendse, F., Bommarco, R., et al., 2011. Agricultural intensification and biodiversity partitioning in European landscapes comparing plants, carabids, and birds. Ecol. Appl. 21, 1772–1781. https://doi.org/10.1890/10-0645.1.

Frid, A., Dill, L., 2002. Human-caused disturbance stimuli as a form of predation risk. Conserv. Ecol. 6, 11.

Gentry, A.H., 1982. Patterns of Neotropical plant species diversity. In: Hecht, M.K., Wallace, B., Prance, G.T. (Eds.), Evolutionary Biology. Springer, Boston, MA. https://doi.org/10.1007/978-1-4615-6968-8_1.

Griz, L.M., Machado, I.C.S., 2001. Fruiting phenology and seed dispersal syndromes in Caatinga, a tropical dry forest in the northeast of Brazil. J. Trop. Ecol. 17, 303–321. https://doi.org/10.1017/S0266467401001201.

Howe, H.F., Smallwood, J., 1982. Ecology of seed dispersal. Annu. Rev. Ecol. Syst. 13, 201–228. https://doi.org/10.1146/annurev.es.13.110182.001221.

Huanca-Nuñez, N., Chazdon, R.L., Russo, S.E., 2021. Seed rain–successional feedbacks in wet tropical forests. Ecology 859, e03362.. https://doi.org/10.1002/ECY.3362.

Jost, L., 2006. Entropy and diversity. Oikos 113, 363–375. https://doi.org/10.1111/j.2006.0030-1299.14714.x.

Kennard, D.K., Gould, K., Putz, F.E., Fredericksen, T.S., Morales, F., 2002. Effect of disturbance intensity on regeneration mechanisms in a tropical dry forest. For. Ecol. Manage. 162, 197–208. https://doi.org/10.1016/S0378-1127(01)00506-0.

Klanderud, K., Mbolatiana, H.Z.H., Vololomboahangy, M.N., Radimbison, M.A., Roger, E., Totland, Ø., Rajeriarison, C., 2010. Recovery of plant species richness and composition after slash-and-burn agriculture in a tropical rainforest in Madagascar. Biodiv. Conserv. 19, 187–204. https://doi.org/10.1007/s10531-009-9714-3.

Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91, 299–305. https://doi.org/10.1890/08-2244.1.

Lawrence, D., Radel, C., Tully, C., Schmook, B., Schneider, L., 2010. Untangling a Decline in Tropical Forest Resilience: Constraints on the sustainability of shifting cultivation across the Globe. Biotropica 42, 21–30. https://doi.org/10.1111/j.1744-7429.2009.00599.x.

Leal, L.C., Andersen, A.N., Leal, I.R., 2014a. Anthropogenic disturbance reduces seed-dispersal services for myrmecochorous plants in the Brazilian Caatinga. Oecologia 174, 173–181. https://doi.org/10.1007/s00442-013-2740-6.

Leal, I.R., Wirth, R., Tabarelli, M., 2007. Seed dispersal by ants in the semi-arid Caatinga of North-east Brazil. Ann. Bot. 99, 885–894. https://doi.org/10.1093/aob/mcm017.

Leal, I.R., Wirth, R., Tabarelli, M., 2014b. The multiple impacts of leaf-cutting ants and their novel ecological role in human-modified neotropical forests. Biotropica 46, 516–528. https://doi.org/10.1111/btp.12126.

Legendre, P., 2014. Interpreting the replacement and richness difference components of beta diversity. Glob. Ecol. Biogeogr. 23, 1324–1334. https://doi.org/10.1111/geb.12207.

Leishman, M.R., 2001. Does the seed size/number trade-off model determine plant community structure? An assessment of the model mechanisms and their generality. Oikos 93, 294–302. https://doi.org/10.1034/j.1600-0706.2001.930212.x.

Lins, L., Santos, D., Lira, R., Oliveira, F.M.P., Wirth, R., Menezes, T., Tabarelli, M., Leal, I. R., 2022. Exotic goats do not affect the seed bank but reduce seedling survival in a human-modified landscape of Caatinga dry forest. For. Ecol. Manage. 522, 120491 https://doi.org/10.1016/j.foreco.2022.120491.

Lowder, S.K., Bertini, R., Karfakis, P., Croppenstedt, A., 2016. Transformation in the size and distribution of farmland operated by household and other farms in select countries of sub-Saharan Africa. 5th Annu. Conf. African Assoc. Agric. Econ. 5, 1–25.

Marcon, E., Hérault, B., 2015. Entropart: an R package to measure and partition diversity. J. Stat. Softw. 67, 1–26. https://doi.org/10.18637/jss.v067.i08.

Martínez-Garza, C., Flores-Palacios, A., De La Peña-Domene, M., Howe, H.F., 2009. Seed rain in a tropical agricultural landscape. J. Trop. Ecol. 25, 541–550. https://doi.org/10.1017/S0266467409990113.

Nathan, R., Muller-Landau, H.C., 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends. Ecol. Evol. 15, 278–285.

Nimer, E., 1972. Climatologia da região Nordeste do Brasil. Introdução à climatologia dinâmica. Rev. Bras. Geogr. 34, 3–51.

Oakley, J.L., Bicknell, J.E., 2022. The impacts of tropical agriculture on biodiversity: a metaanalysis. J. Appl. Ecol. 59, 3072–3082. https://doi.org/10.1111/1365-2664.14303.

Pickett, S.T.A., Collins, S.L., Armesto, J.J., 1987. A hierarchical consideration of causes and mechanisms of succession. Vegetatio 69, 109–114.

Pinho, B.X., Trindade, D.P.F., Peres, C.A., Jamelli, D., de Lima, R.A., Ribeiro, E.M.S., Melo, F.P.L., Leal, I.R., Tabarelli, M., 2022. Cross-scale drivers of woody plant species commonness and rarity in the Brazilian drylands. Divers. Distrib. 28, 1497–1511. https://doi.org/10.1111/ddi.13587.

Piotto, D., Craven, D., Montagnini, F., Ashton, M., Oliver, C., Thomas, W.W., 2019. Successional, spatial, and seasonal changes in seed rain in the Atlantic forest of southern Bahia. Brazil. PLoS One 14, e0226474. https://doi.org/10.1371/journal.pone.0226474.

Piotto, D., Magnago, L.F.S., Montagnini, F., Ashton, M.S., Oliver, C., Thomas, W.W., 2021. Nearby mature forest distance and regenerating forest age influence tree species composition in the Atlantic forest of Southern Bahia. Brazil. Biodiv. Conserv. 30, 2165–2180. https://doi.org/10.1007/s10531-021-02192-w.

Raman, T.R.S., 2001. Effect of slash-and-burn shifting cultivation on rainforest birds in Mizoram, northeast India. Conserv. Biol. 15, 685–698.

Ripple, W.J., Wolf, C., Newsome, T.M., Galetti, M., Alamgir, M., Crist, E., Mahmoud, M. I., Laurance, W.F., et al., 2017. World scientists' warning to humanity: a second notice. BioScience 67, 1026–1028. https://doi.org/10.1093/biosci/bix125.

Rito, K.F., Arroyo-Rodríguez, V., Queiroz, R.T., Leal, I.R., Tabarelli, M., Norden, N., 2017. Precipitation mediates the effect of human disturbance on the Brazilian Caatinga vegetation. J. Ecol. 105, 828–838. https://doi.org/10.1111/1365-2745.12712.

Rito, K.F., Arroyo-Rodríguez, V., Cavender-Bares, J., Santo-Silva, E.E., Souza, G., Leal, I. R., Tabarelli, M., 2021. Unraveling the drivers of plant taxonomic and phylogenetic β-diversity in a human-modified tropical dry forest. Biodivers. Conserv. 30, 1049–1065. https://doi.org/10.1007/s10531-021-02131-9.

Rocha, J.I.S., Menezes, G.S.C., Cazetta, E., Dodonov, P., Talora, D.C., 2021. Seed rain across fire-created edges in a neotropical rainforest. Plant Ecol. 223, 247–261. https://doi.org/10.1007/s11258-021-01205-6.

Rockström, J., Steffen, W., Noone, K., et al., 2009. A safe operating space for humanity. Nature 461, 472–475. https://doi.org/10.1038/461472a.

San-José, M., Arroyo-Rodríguez, V., Meave, J.A., 2020. Regional context and dispersal mode drive the impact of landscape structure on seed dispersal. Ecol. Appl. 30, 1–12. https://doi.org/10.1002/eap.2033.

Schott, G.W., Hamburg, S.P., 1997. The seed rain and seed bank of an adjacent native tallgrass prairie and old field. Can. J. Bot. 75, 1–7. https://doi.org/10.1139/b97-001.

Sfair, J., Arroyo-Rodríguez, V., Santos, B.A., Tabarelli, M., 2016. Taxonomic and functional divergence of tree assemblages in a fragmented tropical forest. Ecol. Appl. 26, 1816–1826. https://doi.org/10.1890/15-1673.1.

Silva, J.M.C., Leal, I.R., Tabarelli, M., 2017. Caatinga the largest tropical dry forest region in South America. Springer International Publishing, Switzerland.

Souza, J.T., Ferraz, E.M.N., Albuquerque, U.P., Araújo, E.L., 2014. Does proximity to a mature forest contribute to the seed rain and recovery of an abandoned agriculture area in a semiarid climate? Plant Biol. 16, 748–775. https://doi.org/10.1111/plb.12120.

Souza, D.G., Sfair, J.C., de Paula, A.S., Barros, M.F., Rito, K.F., Tabarelli, M., 2019. Multiple drivers of aboveground biomass in a human-modified landscape of the Caatinga dry forest. For. Ecol. Manage. 435, 57–65. https://doi.org/10.1016/j.foreco.2018.12.042.

Specht, M.J., Santos, B.A., Marshall, N., Melo, F.P.L., Leal, I.R., Tabarelli, M., Baldauf, C., 2019. Socioeconomic differences among resident, users and neighbor populations of a protected area in the Brazilian dry forest. J. Environ. Manage. 232, 607–614. https://doi.org/10.1016/j.jenvman.2018.11.101.

Svenning, J.C., Wright, S.J., 2005. Seed limitation in a Panamanian forest. J. Ecol. 93, 853–862.

Tanzito, G., Ibanda, P.A., Talaguma, R., Lusanga, N.M., 2020. Slash-and-burn agriculture, the major cropping system in the region of Faradje in Democratic Republic of Congo: ecological and socio-economic consequences. J. Dev. Agric. Econ. 12, 25–36.

Trindade, D.P.F., Sfair, J.C., de Paula, A.S., Barros, M.F., Tabarelli, M., 2020. Water availability mediates functional shifts across ontogenetic stages in a regenerating seasonally dry tropical forest. J. Veg. Sci. 1–12 https://doi.org/10.1111/jvs.12896.

Turner, I.M., 2004. The ecology of trees in the tropical rain forest. Cambridge University Press, Cambridge, UK.

5 CONSIDERAÇÕES FINAIS

Os resultados encontrados nesta tese sustentam a hipótese de que a agricultura de corte-e-queima pode limitar a regeneração florestal da Caatinga após agricultura de corte-e-queima, já que impacta negativamente duas fontes de regeneração fundamentais que são a chuva e o banco de sementes. Ao contrário do que já foi proposto de que a agricultura de corte-e-queima seria uma atividade sustentável, este método agrícola pode ter repercussões negativas para a regeneração da floresta, e, portanto, para a sustentabilidade do sistema agrícola. Logo, a produtividade e sustentabilidade deste método de cultivo não pode depender apenas da chuva e do banco de sementes, mas também da capacidade de rebrota das plantas, que deverá exercer um papel-chave impulsionando a regeneração inicial da floresta.

A agricultura de corte-e-queima praticada na Caatinga tem características similares em outras regiões de florestas secas do mundo em que as comunidades humanas dependem ativamente da floresta como meio de subsistência. Como resposta às secas frequentes, baixos índices de desenvolvimento humano (IDH),

coronelismo e pouca assistência governamental, esse cenário de pobreza extrema tem levado as populações do semiárido a dependerem cada vez mais da agricultura de corte-e-queima para manter sua qualidade de vida. Logo, o uso continuado e em longo prazo deste método a agrícola deve ser ainda mais prejudicial em maiores extensões espaciais, pois o crescimento das populações humanas deve promover a expansão espacial e tempos de abandono da terra cada vez mais curtos. Além disso, a produtividade agrícola e o sistema socioecológico baseado em exploração e agricultura de subsistência pode entrar em colapso no médio prazo, favorecendo o desenvolvimento de vegetação arbustiva/estado inicial de regeneração biologicamente empobrecidos, que, junto com as mudanças climáticas (aumento de temperatura e redução da precipitação), podem acelerar o processo de desertificação de florestas tropicais secas como a Caatinga.

Esta ameaça emerge com grandes desafios para propor caminhos alternativos para explorar a floresta seca da Caatinga por meio de uma agricultura de corte-e-queima mais sustentável. Para isso são necessárias futuras investigações que avaliem: 1) o impacto da agricultura de corte-e-queima em maiores escalas espaciais e temporais; 2) o tempo de recuperação das fontes de regeneração; 3) se a rebrota de plantas é suficiente para manter as funções do ecossistema e uso de recursos florestais por populações humanas; 4) como processos e interações ecológicas são impactados pela agricultura de corte-e-queima. Tendo em conta que o cenário de dependência intrínseca entre as populações do semiárido e recursos florestais se expande, os efeitos da agricultura de subsistência sobre a floresta seca da Caatinga não devem podem permanecer negligenciadas em estratégias de conservação e de melhores práticas produtivas no semiárido. Como medidas para promover uma agricultura de corte-e-queima mais amigável com a biodiversidade da floresta seca da Caatinga e rumo à sustentabilidade e desenvolvimento rural no semiárido sugiro levar em conta os seguintes quesitos:

1) Investigações e criação de estratégias agrícolas mais sustentáveis (por exemplo, enriquecer o banco de sementes após o abandono da terra);

2) Investimento em planos de desenvolvimento rural que levem em conta práticas de manejo mais amigáveis à biodiversidade (por exemplo, agricultura agroecológica e regenerativa) porque melhoram a resiliência florestal e a prestação de serviços em escala regional;

3) Desenvolvimento de fontes de renda alternativas focadas na melhoria da qualidade de vida (e.g. artesanato, apicultura, ecoturismo, selo verde, pagamento por serviços ecossistêmicos, plantios perenes);

4) Aumento no número de áreas devotadas a conservação, bem como a criação do plano de manejo delas.

Finalmente, a conservação da biodiversidade e manutenção da qualidade de vida das populações humanas na Caatinga carecem de investimentos/incentivos governamentais, investigação científica de longo prazo e compromisso das comunidades rurais para aumentar o potencial de resiliência e mudar o destino desta floresta seca rica em espécies.

REFERENCIAS

ABOIM, M. C. R. et al. Soil bacterial community structure and soil quality in a slash-and-burn cultivation system in Southeastern Brazil. **Applied Soil Ecology**, v. 38, p. 100–108, 2008.

ABRIL, A. B.; BUCHER, E. H. Nutritional sources of the fungus cultured by leaf-cutting ants. **Applied Soil Ecology**, v. 26, n. 3, p. 243–247, 2004.

ADEYOLANU, O. D. et al. Evaluation of two methods of soil quality assessment as influenced by slash and burn in tropical rainforest ecology of Nigeria. **Archives of Agronomy and Soil Science**, v. 59, p. 1725–1742, 2013.

AIDE, T. M.; GRAU, H. R. Globalization, migration, and Latin American ecosystems. **Science**, v. 305, p. 1915–1916, 2004.

ALBUQUERQUE, E. R. G. M; MENEZES, R. S. C. Root and shoot biomasses in the tropical dry forest of semi-arid Northeast Brazil. **Plant Soil**, v. 378, p. 113–123, 2014.

ALBUQUERQUE, U. P. et al. Medicinal plants of the caatinga (semi-arid) vegetation of NE Brazil: a quantitative approach. **Journal of Ethnopharmacology**, v. 114, p. 325–354, 2007.

ALEGRE, J. C.; CASSEL, D. K. Dynamics of soil physical properties under alternative systems to slash-and-burn. **Agriculture, Ecosystems & Environment**, v. 58, n. 1, p. 39–48, 1996.

ALTHOFF, T. D. et al. Climate change impacts on the sustainability of the firewood harvest and vegetation and soil carbon stocks in a tropical dry forest in Santa Teresinha municipality, Northeast Brazil. **Forest Ecology and Management**, v. 360, p. 367–375, 2016.

ALVES, T. S. et al. Landscape-scale patterns and drivers of novel mammal communities in a human-modified protected area. **Landscape Ecology**, v. 35, p. 1619–1633, 2020.

ANDRADE-LIMA, D. The caatingas dominium. **Revista Brasileira de Botânica**, v. 4 p. 149–153, 1981.

ANDREAE, M. O; MERLET, P. Emission of trace gases and aerosols from biomass burning. **Global Biogeochemical Cycles**, v. 15, p. 955–966, 2001.

ARROYO-RODRÍGUEZ, V. et al. Multiple successional pathways in human-modified tropical landscapes: new insights from forest succession, forest fragmentation and landscape ecology research. **Biological Reviews**, v. 92, p. 326–340, 2017.

ARROYO-RODRÍGUEZ, V. et al. Designing optimal human modified landscapes for forest biodiversity conservation. **Ecology Letters**, v. 23, p. 1404–1420, 2020.

ARROYO-RODRÍGUEZ, V. et al. Preserving 40% forest cover is a valuable and well-supported conservation guideline: reply to Banks- Leite et al. **Ecology Letters**, v. 24, p. 1114–1116, 2021.

BARBOSA, D. C. A; BARBOSA, M. C. A; LIMA, L. C. M. Fenologia de espécies lenhosas da Caatinga. In: **Ecologia e Conservação da Caatinga**. Editora Universitária, Universidade Federal de Pernambuco, Recife, pp. 657–693, 2003.

BARROS, M. F. et al. Resprouting drives successional pathways and the resilience of Caatinga dry forest in human-modified landscapes. **Forest Ecology and Management**, v. 482, p. 118881, 2021.

BEZERRA, D. M. M; DE ARAUJO, H. F. P; ALVES, R. R. N. Understanding the use of wild birds in a priority conservation area of Caatinga, a Brazilian tropical dry forest. **Environment, Development and Sustainability**, v. 22, p. 5297–5316, 2020.

BEZERRA, J. S. et al. Drastic impoverishment of the soil seed bank in a tropical dry forest exposed to slash-and-burn agriculture. **Forest Ecology and Management**, v. 513, p. 120185, 2022.

BEZERRA, J.S. et al. Negative impact of slash-and-burn agriculture on the seed rain in a tropical dry forest. **Forest Ecology and Management**, v. 531, 120821, 2023.

BISHT, I. S. et al. Subsistence farming, agrobiodiversity, and sustainable agriculture: A case study. **Agroecology and Sustainable Food Systems**, v. 38, n. 8, p. 890–912, 2014.

BRIENEN, R. J. W. et al. Long-term decline of the Amazon carbon sink. **Nature**, v. 519, p. 344–348, 2015.

BULLOCK, S. H.; H. A. MOONEY, MEDINA, E. **Seasonally dry tropical forests**. Cambridge University Press, New York, 1995.

CARBONE, L. M.; AGUILAR, R. Abiotic and biotic interactions as drivers of plant reproduction in response to fire frequency. **Arthropod-plant interactions**, v. 15, n. 1, p. 83–94, 2021.

CARLSON, D. W; GROOT, A. Microclimate of clear-cut, forest interior, and small openings in trembling aspen forest. **Agricultural and Forest Meteorology**, v. 87, p. 313–329, 1997.

CARRIÈRE, S. M; LETOURMY, P; MCKEY, D. B. Effects of remnant trees in fallows on diversity and structure of forest regrowth in a slash-and-burn agricultural system in southern Cameroon. **Journal of Tropical Ecology**, v. 18, p. 375–396, 2002.

CECCON, E.; HUANTE, P.; RINCÓN, E. Abiotic factors influencing tropical dry forests regeneration. **Brazilian Archives of Biology and Technology**, v. 49, p. 305–312, 2006.

CHASE, J. M. et al. Ecosystem decay exacerbates biodiversity loss with habitat loss. **Nature**, v. 7820, p. 238–243, 2020.

CHAZDON, R. L. (Ed). **Second growth: the promise of tropical forest regeneration in an age of deforestation**. University of Chicago Press, 2014.

CHAZDON, R. L. et al. Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics. **Science Advances**, v. 2, p. e1501639, 2016.

CHAZDON, R. Regeneração de florestas tropicais. **Boletim do Museu Paraense Emílio Goeldi. Ciências Naturais**, v. 7, p. 195–218, 2012.
Chihuahuan desert, **Journal of Geophysical Research**, v. 115, D21120, 2010.

CHRISTENSEN, N. L. Fire ans soil-plant nutrient relations in a pine-wiregrass savanna on the coastal plain of North Carolina. **Oecologia**, v. 31, p. 27–44, 1977.

CLARK, D. L. **The effect of fire on Yellowstone ecosystem seed banks.** Thesis (Doctoral dissertation, College of Letters & Science) - Montana State University-Bozeman, 1991.

CLARK, J. S; MACKLIN, E; WOOD, L. Stages and spatial scales of recruitment limitation in southern appalachian forests. **Ecology Monographs**, v. 68, p. 213, 1998.

CLARKE, P. J. et al. Resprouting as a key functional trait: How buds, protection and resources drive persistence after fire. **New Phytologyst**, v. 197, p. 19–35, 2013.

COIMBRA-FILHO, A. F; CÂMARA, I. G. **Os limites originais do bioma Mata Atlântica na região Nordeste do Brasil**. **Fundação Brasileira para Conservação da Natureza**, Rio de Janeiro, 1996.

COLÓN, S. M; LUGO, A. E. Recovery of a subtropical dry forest after abandonment of different land uses. **Biotropica**, v. 38, p. 354–364, 2006.

CRUTZEN, P. J. Geology of mankind. **Nature**, v. 415, p. 23, 2002.

CURTIS, P. G. et al. Classifying drivers of global forest loss. **Science**, v. 361, p. 1108–1111, 2018.

DA SILVA, K. A. et al. Spatio-temporal variation in a seed bank of a semi-arid region in northeastern Brazil. **Acta Oecologia**, v. 46, p. 25–32, 2013.

DAÏNOU, K. et al. Soil seed bank characteristics in cameroonian rainforests and implications for post logging forest recovery. **Ecological Engineering**, v. 37, p. 1499–1506, 2011.

DALLING, J. W.; SWAINE, M. D.; GARWOOD, N. C. Soil seed bank community dynamics in seasonally moist lowland tropical forest, Panama. **Journal of Tropical Ecology**, v. 13, p. 659–680, 1997.

DE PAULA, A. S. et al. The role of seed rain and soil seed bank in the regeneration of a Caatinga dry forest following slash-and-burn agriculture. **Journal of Arid Environments,** v. 211, p. 104948, 2023.

DEBELL, D. S.; RALSTON, C. W. Release of nitrogen by burning light forest fuels. **Soil Science Society of America Journal**, v. 34, p. 936–938, 1970.

DIRZO, R. et al. **Seasonally Dry Tropical Forests: Ecology and Conservation**. Island Press, 2011.

EBEL, R. Effects of slash-and-burn-farming and a fire-free management on a cambisol in a traditional maya farming system. **Ciencia ergo-sum**, v. 25, n. 2, 2018.

EVANGELISTA, A. DOS R. S. **O processo de ocupação do bioma caatinga e suas repercussões socioambientais na sisalândia, Bahia**. Dissertação (mestrado em Geografia) – Universidade Federal da Bahia, 2010.

FAHRIG, L. Effects of habitat fragmentation on biodiversity. **Annual Review of Ecology, Evolution, and Systematics**, v. 34, p. 487–515, 2003.

FAHRIG, L. et al. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. **Ecology letters**, v. 14, n. 2, p. 101–112, 2011.

FAO. Food and Agriculture Organization. **Global Forest Resources Assessment 2010**.
FAO, Rome, Italy, 2010.

FAO. **The state of the world's forests 2018 - forest pathways to sustainable development**. FAO, Rome, Italy, 2018.

FARIAS, L. M; MARQUESAN, F. F. S; FIGUEIREDO, M. D. Migração e políticas públicas de convivência com o semiárido brasileiro. **Revista Pensamento Contemporâneo em Administração**, v. 14, p. 55–73, 2020.

FERREIRA, C. D. et al. Seed bank floristics in the soil at different stages of natural regeneration of Caatinga. **Revista Brasileira de Ciencias Agrárias**, v. 9, p. 562–569, 2014.

FIDELIS, A; DAIBES, L. F; MARTINS, A. R. To resist or to germinate? The effect of fire on legume seeds in Brazilian subtropical grasslands. **Acta Botanica Brasilica**, v. 30, p. 147–151, 2016.

FILGUEIRAS, B. K. C. et al. Recovery of dung beetle assemblages in regenerating Caatinga dry forests following slash-and-burn agriculture. **Forest Ecology and Management**, v. 496, p. 119423, 2021.

GARWOOD, N. C. Tropical Soil Seed Banks: A Review. In: **Ecology of Soil Seed Banks**. pp. 149–209, 1989.

GFW. Global Forest Watch. Disponível em: https://www.globalforestwatch.org/. The Global Forest Goals Report 2022.

GIULIETTI, A. M. et al. Diagnóstico da vegetação nativa do bioma Caatinga. In: **Biodiversidade da Caatinga: áreas e ações prioritárias para a conservação**. Ministério do Meio Ambiente, Brasília, pp. 48–90, 2004.

GOMES, F. M. et al. Relationships between soil seed bank composition and standing vegetation along chronosequences in a tropical dry forest in north-eastern Brazilian. **Journal of Tropical Ecology**, v. 35, p. 173–184, 2019.

HARPER, K. A. et al. Edge influence on forest structure and composition in fragmented landscapes. **Conservation Biology**, v. 19, p. 768–782, 2005.

HAUSER, S.; NORGROVE, L. Slash-and-burn agriculture, effects of **in Encyclopedia of biodiversity**, pp. 551–562, 2013.

He, Y. et al. On the impact of shrub encroachment on microclimate conditions in the northern

HERNANI, L. C.; KURIHARA, C. H.; SILVA, W. M. Sistemas de manejo de solo e perdas de nutrientes e matéria orgânica por erosão. **Revista Brasileira de Ciências do Solo**, v. 23, n. 1, p. 145–154, 1999.

HEYDARI, M.; et al. Effects of fire disturbance on alpha and beta diversity and on beta diversity components of soil seed banks and aboveground vegetation. **Plant Ecology and Evolution**, v. 150, p. 247–256, 2017.

HIROTA, M.; et al. Global resilience of tropical forest and savanna to critical transitions. **Science**, v. 334, p. 232–235, 2011.

HOWE, H. F.; SMALLWOOD, J. Ecology of seed dispersal. **Annual Review of Ecology, Evolution, and Systematics**, v. 13, p. 201–228, 1982.

JACKSON, H. B.; FAHRIG, L. What size is a biologically relevant landscape? **Landscape Ecology**, v. 27, p. 929–941, 2012.

JARA-GUERRERO, A.; et al. Dispersal syndrome influences the match between seed rain and soil seed bank of woody species in a Neotropical dry forest. **Journal of Vegetation Science**, v. 31, p. 995–1005, 2020.

JOHNSON, D. W.; CURTIS, P. S. Effects of forest management on soil C and N storage: metaanalysis. **Forest Ecology and Management**, v. 140, p. 227–238, 2001.

KAPOS, V. et al. Effects of isolation on the water status of forest patches in the Brazilian Amazon. **Journal of Tropical Ecology**, v. 5, p. 173–185, 1989.

KEAST, A.; MORTON, E. S. **Migrant Birds in the Neotropics: ecology, behavior, distribution, and conservation**. Washington, DC: Smithsonian Institution Press, 1980.

KENNARD, D. K.; et al. Effect of disturbance intensity on regeneration mechanisms in a tropical dry forest. **Forest Ecology and Management**, v. 162, p. 197–208, 2002.

KHURANA, E; SINGH, J. S. Ecology of seed and seedling growth for conservation and restoration of tropical dry forest: a review. **Environmental Conservation**, 28, 39– 52, 2001.

KLANDERUD, K. et al. Recovery of plant species richness and composition after slash-and-burn agriculture in a tropical rainforest in Madagascar. **Biodiversity and Conservation**, v. 19, n. 1, p. 187–204, 2010.

KLEINMAN, P. J. A.; PIMENTEL, D.; BRYANT, R. B. The ecological sustainability of slash-and-burn agriculture. **Agriculture, Ecosystems and Environment**, v. 52, p. 235–249, 1995.

KNOECHELMANN, C. M. et al. Leaf-cutting ants negatively impact the regeneration of the Caatinga dry forest across abandoned pastures. **Biotropica**, v. 00, p. 1–11, 2020.

KOSTER, R. D. et al. Regions of strong coupling between soil moisture and precipitation. **Science**, v. 305, p. 1138–1140, 2004.

KUKLA, J. et al. The effect of traditional slash-and-burn agriculture on soil organic matter, nutrient content, and microbiota in tropical ecosystems of Papua New Guinea. **Land Degradation and Development**, v. 30, p. 166–177, 2019.

KURC, S. A. SMALL; E. E. Dynamics of evapotranspiration in semiarid grassland & shrubland ecosystems during the summer monsoon season, central New Mexico. **Water Resources Research,** v. 40, n. 9, 2004.

LANDAVERDE-GONZÁLEZ, P. et al. Sweat bees on hot chillies: Provision of pollination services by native bees in traditional slash-and-burn agriculture in the Yucatán Peninsula of tropical Mexico, **Journal of Applied Ecology**, v. 54, n. 6, p. 1814–1824, 2017.

LAURANCE, W. F. et al. Ecosystem decay of Amazonian forest fragments: a 22 year investigation. **Conservation Biology**, v. 16, p. 605–618, 2002.

LAWRENCE, D. et al. Untangling a decline in tropical forest resilience: constraints on the sustainability of shifting cultivation across the globe. **Biotropica**, v. 42, p. 21–30, 2010.

LAWRENCE, D.; FOSTER, D. Changes in forest biomass, litter dynamics and soils following shifting cultivation in southern Mexico: an overview. **Interciencia**, v. 27, p. 400–408, 2002.

LEAL, I. R. et al. Changing the course of biodiversity conservation in the caatinga of northeastern Brazil. **Conservation Biology**, v. 19, p. 701–706, 2005.

LEAL, I. R.; TABARELLI, M.; SILVA, J. M. C. **Ecologia e conservação da Caatinga**. Editora Universitária, Universidade Federal de Pernambuco, Recife, 2003.

LEBRIJA-TREJOS, E. et al. Environmental changes during secondary succession in a tropical dry forest in Mexico. **Journal of Tropical Ecology**, v. 27, p. 477–489, 2011.

LEITE, A. V. L.; MACHADO, I. C. Reproductive biology of woody species in Caatinga, a dry forest of northeastern Brazil. **Journal of Arid Environments**, v. 74, p. 1374–1380, 2010.

LEWIS, W. M. Effects of fire on nutrient movement in a South Carolina pine forest. **Ecology**, v. 55, p. 1120–1127, 1974.

LINARES-PALOMINO, R.; OLIVEIRA-FILHO, A. T.; PENNINGTON, R. T. Neotropical seasonally dry forests: diversity, endemism, and biogeography of woody plants. In: **Seasonally dry tropical forests**, pp. 3–21. Island Press, 2011.

LOBERT, J. M. et al. Importance of biomass burning in the atmospheric budgets of nitrogen-containing gases. **Nature**, v. 346, p. 552–554, 1990.

LOWDER, S. K. et al. Transformation in the size and distribution of farmland operated by household and other farms in select countries of sub-Saharan Africa. **5th African Association of Agricultural Economists**, v. 5, p. 1–25, 2016.

MALHI, Y. et al. Tropical forests in the Anthropocene. **Annual Review of Environment and Resources**, v. 39, p. 125–59, 2014.

MALHI, Y. The concept of the Anthropocene. **Annual Review of Environment and Resources**, v. 42, p. 77–104, 2017.

MALHI, Y.; WRIGHT, J. Spatial patterns and recent trends in the climate of tropical rainforest regions. **Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences**, v. 359, p. 311–329, 2004.

MAMEDE, M. D. A.; DE ARAÚJO, F. S. Effects of slash and burn practices on a soil seed bank of caatinga vegetation in Northeastern Brazil. **Journal of Arid Environments**, v. 72, p. 458–470, 2008.

MARTINI, A. M. Z; SANTOS, F. A. M. Effects of distinct types of disturbance on seed rain in the Atlantic forest of NE Brazil. **Plant Ecology**, v. 190, p. 81–95, 2007.

MELO, F. P. L. et al. Forest fragmentation reduces recruitment of large-seeded tree species in a semi-deciduous tropical forest of southern Mexico. **Journal of Tropical Ecology**, v. 26, p. 35, 2010.

MELO, F. P. L. et al. On the hope for biodiversity-friendly tropical landscapes. **Trends in Ecology and Evolution**, v. 28, p. 462-468, 2013.

MENDES, L. B. et al. What happens to the soil seed bank 17 years after clear cutting of vegetations? **Revista de Biologia Tropical**, v. 63, p. 321–332, 2015.

MENEZES, R. et al. Biogeochemical cycling in terrestrial ecosystems of the Caatinga Biome. **Brazilian Journal of Biology**, v. 72, p. 643–653, 2012.

MERTZ, O. The relationship between length of fallow and crop yields in shifting cultivation: a rethinking. **Agroforestry Systems**, v. 55, n. 2, p. 149–159, 2002.

METZGER, J. P. Effects of slash-and-burn fallow periods on landscape structure. **Environmental Conservation**, v. 30, p. 325–333, 2003.

METZGER, J. P. Landscape dynamics and equilibrium in areas of slash-and-burn agriculture with short and long fallow period (Bragantina region, NE Brazilian Amazon). **Landscape Ecology**, v. 17, p. 419–431, 2002.

MIGUET, P. et al. What determines the spatial extent of landscape effects on species? **Landscape Ecology**, v. 31, p. 1177–1194, 2016.

MILLES, L. et al. A global overview of the conservation status of tropical dry forests. **Journal of Biogeography**, v. 33, p. 491–505, 2006.

MMA/IBAMA. Monitoramento do desmatamento nos Biomas Brasileiros por satélite. **Acordo de Cooperação Técnica MMA/Ibama – Monitoramento do Bioma Caatinga 2008-2009**, p. 46, Brasília, 2011.

MORECROFT, M. D. et al. Air and soil microclimates of deciduous woodland compared to an open site. **Agricultural and Forest Meteorology**, v. 90, p. 141–156, 1998.

MORRIS, R. J. Anthropogenic impacts on tropical forest biodiversity: a network structure and ecosystem functioning perspective. **Philosophical transactions of the Royal Society of London. Series B, Biological sciences**, v. 365, n. 1558, p. 3709–18, 2010.

MULLER-LANDAU, H. C. et al. Assessing recruitment limitation: concepts, methods and case studies from a tropical forest. In: **Seed dispersal and frugivory: ecology, evolution and conservation**. CAB International, Wallingford, 2002.

MUNIN, R. L.; TEIXEIRA, R. C.; SIGRIST, M. R. Esfingofilia e sistema de reprodução de Bauhinia curvula Benth. (Leguminosae: Caesalpinioideae) em cerrado no Centro-Oeste brasileiro. **Revista Brasileira de Botanica**, v. 31, p. 15–25, 2008.

MURPHY, P. G.; LUGO, A. E. Ecology of tropical dry forest. **Annual Review of Ecology and Systematics**, v. 17, p. 67–88, 1986.

NAEEM, S. et al. The functions of biological diversity in an age of extinction. **Science**, v. 336, p. 1401–1406, 2012.

OAKLEY, J. L.; BICKNELL, J. E. The impacts of tropical agriculture on biodiversity: A meta-analysis. **Journal of Applied Ecology**, v. 59, n. 12, p. 3072–3082, 2022.

OLIVER, T. H. et al. Biodiversity and resilience of ecosystem functions. **Trends in Ecology & Evolution**, v. 30, p. 673–684, 2015.

PEDROSO-JUNIOR, N. N. (2008). **No caminho dos antigos: agricultura de corte-e-queima e intensificação agrícola em populações quilombolas do Vale do Ribeira, SP**. Tese (doutorado em Administração) – Universidade de São Paulo, 2008.

PEDROSO-JUNIOR, N. N., ADAMS, C., MURRIETA, R. S. (2009). Slash-and-burn agriculture: a system in transformation. **Current trends in human ecology**, v. 2, n. 34, p.12–34, 2009.

PENNINGTON, R. T; LAVIN, M; OLIVEIRA-FILHO, A. Woody plant diversity, evolution, and ecology in the tropics: Perspectives from Seasonally Dry Tropical Forests. **Annual Review of Ecology, Evolution, and Systematics**, v. 40, p. 437–457, 2009.

PEREIRA, A. C.; VIEIRA, I. C. G. A importância das florestas secundárias e os impactos de sua substituição por plantios mecanizados de grãos na Amazônia. **Interciência,** v. 26, n. 8, p. 337–341, 2001.

PEREIRA, I. M. et al. Regeneração natural em um remanescente de Caatinga sob diferentes níveis de perturbação, no agreste paraibano. **Acta Botanica Brasilica**, v. 15, p. 413–426, 2001.

PHILLIPS, O. L. et al. Drought Sensitivity of the Amazon Rainforest. **Science**, v. 323, p. 1344–1347, 2009.

PIOTTO, D. et al. Successional, spatial, and seasonal changes in seed rain in the Atlantic forest of southern Bahia, Brazil. **PLoS One**, v. 14, p. e0226474, 2019.

PIVELLO, V. R. et al. Understanding Brazil's catastrophic fires: causes, consequences and policy needed to prevent future tragedies. **Perspectives in Ecology and Conservation**, v. 19, p. 233–255, 2021. PIVELLO, V. R. The use of fire in the Cerrado and Amazonian rainforests of Brazil: past and present. **Fire Ecology**, v. 7, n. 1, p. 24–39, 2011.

PLUE, J.; COUSINS, S. A. O. Temporal dispersal in fragmented landscapes. **Biological Conservation**, v. 160, p. 250–262, 2013.

PRADO, D. As caatingas da América do Sul. In: **Ecologia e conservação da Caatinga**. Editora Universitária, Universidade Federal de Pernambuco, Recife, 2003.

RAISON, R. J. Modification of the soil environment by vegetation fires, with particular reference to nitrogen transformations: a review. **Plant and Soil**, v. 51, p. 73–108, 1979.

RAMAN, T. R. S. Effect of slash-and-burn shifting cultivation on rainforest birds in Mizoram, northeast India. **Conservation Biology**, v. 15, p. 685–698, 2001.

RIBEIRO-FILHO, A. A. et al. Dynamics of soil chemical properties in shifting cultivation systems in the tropics: a meta-analysis. **Soil use and management**, v. 31, n. 4, p. 474–482, 2015.

RIBEIRO-FILHO, A. A.; ADAMS, C.; MURRIETA, R. S. S. The impacts of shifting cultivation on tropical forest soil: a review. **Boletim do Museu Paraense Emílio Goeldi. Ciências Humanas**, v. 8, n. 3, p. 693-727, 2013.

RITO, K. F. et al. Unraveling the drivers of plant taxonomic and phylogenetic β-diversity in a human-modified tropical dry forest. **Biodiversity and Conservation**, v. 30, p. 1049–1065, 2021.

RITO, K. F. Precipitation mediates the effect of human disturbance on the Brazilian Caatinga vegetation. **Journal of Ecology**, v. 105, p. 1–11, 2017.

ROCHA, J. I. S. et al. Seed rain across fire-created edges in a neotropical rainforest. **Plant Ecology**, v. 223, p. 247–261, 2021.

SAATCHI, S. S. et al. Benchmark map of forest carbon stocks in tropical regions across three continents. **Proceedings of the National Academy of Sciences**, v. 108, p. 9899–9904, 2011.

SAMPAIO, E. et al. Tree biomass estimation in regenerating areas of tropical dry vegetation in northeast Brazil. **Forest Ecology and Management**, v. 259, p. 1135–1140, 2010.

SANCHEZ, P. A. Linking climate change research with food security and poverty reduction in the tropics. **Agriculture, Ecosystems and Environments**, v. 82, p. 371–383, 2000.

SANCHEZ, P. A. Soil fertility and hunger in Africa. **Science**, v. 295, p. 64–66, 2002.

SÁNCHEZ-AZOFEIFA, A. et al. **Tropical dry forest in the Americas: Ecology, conservation, and management**. CRC Press, 2014.

SAN-JOSÉ, M.; ARROYO-RODRÍGUEZ, V.; MEAVE, J. A. Regional context and dispersal mode drive the impact of landscape structure on seed dispersal. **Ecological Applications**, v. 30, p. 1–12, 2020.

SANTOS, B. A. et al. Drastic erosion in functional attributes of tree assemblages in Atlantic forest fragments of Northeastern Brazil. **Biological Conservation**, v. 141, p. 249-260, 2008.

SANTOS, B. A. et al. Edge-related loss of tree phylogenetic diversity in severely fragmented Brazilian Atlantic Forest. **PLoS ONE**, v. 5, p. e12625, 2010.

SCHLESINGER, W. H. Evidence from chronosequence studies for a low carbono storage potential of soils. **Nature**, v. 348, p. 232–234, 1990.

SIGNH, S. P. Chronic disturbance, a principal cause of environmental degradation in developing countries. **Environmental Conservation**, v. 25, p. 1–2, 1998.

SILVA, J. M. C.; LEAL, I. R.; TABARELLI, M. **Caatinga the largest tropical dry forest region in South America**. Springer International Publishing, Switzerland, 2017.

SIYUM, Z. G. Tropical dry forest dynamics in the context of climate change: syntheses of drivers, gaps, and management perspectives. **Ecology Process**, v. 9, n. 25, p. 1–16, 2020.

SKOGLUND, J. The role of seed banks in vegetation dynamics and restoration of dry tropical ecosystems. **Journal of Vegetation Science**, v. 3, p. 357–360, 1992.

SOUSA, J. S.; LONGO, M. G.; SANTOS, B. A. Landscape patterns of primary production reveal agricultural benefits from forest conservation. **Perspectives in Ecology and Conservation**, v. 17, p. 136–145, 2019.

SOUSA, T. R. et al. The effect of forest fragmentation on the soil seed bank of Central Amazonia. **Forest Ecology and Management**, v. 393, p. 105–112, 2017.

SOUZA, D. G. et al. Multiple drivers of aboveground biomass in a human-modified landscape of the Caatinga dry forest. **Forest Ecology and Management**, v. 435, p. 57–65, 2019.

STEPHENSON, A. G. Flower and fruit abortion: proximate causes and ultimate functions. **Annual Review of Ecology and Systematics**, v. 12, p. 253–279, 1981.

SULLIVAN, M. et al. Diversity and carbon storage across the tropical forest biome. **Scientific Reports**, v. 7, 2017.

TABARELLI, M. et al. Caatinga: legado, trajetória e desafios rumo à sustentabilidade. **Ciência e Cultura**, v. 70, p. 25–29, 2018.

TABARELLI, M. et al. The Future of the Caatinga. In: **Caatinga: The largest tropical dry forest region in South America**. Springer, Switzerland, pp. 461–474, 2017.

TABARELLI, M.; LOPES, A. V.; PERES, C. A. Edge-effects drive forest fragments towards an early-successional system. **Biotropica**, v. 40, p. 657-661, 2008.

TANGNEY, R. et al. Seed moisture content as a primary trait regulating the lethal temperature thresholds of seeds. **Journal of Ecology**, v. 107, p. 1093–1105, 2019.

TANGNEY, R. et al. Seed traits determine species' responses to fire under varying soil heating scenarios. **Functional Ecology**, v. 34, p. 1967–1978, 2020.

TANZITO, G. et al. Slash-and-burn agriculture, the major cropping system in the region of Faradje in Democratic Republic of Congo: ecological and socio-economic consequences. **Journal of Development and Agricultural Economics**, v. 12, p. 25–36, 2020.

TAUBERT, F. et al. Global patterns of tropical forest fragmentation. **Nature**, v. 554, p. 519–522, 2018.

TEEGALAPALLI, K.; HIREMATH, A. J.; JATHANNA, D. Patterns of seed rain and seedling regeneration in abandoned agricultural clearings in a seasonally dry tropical forest in India. **Journal of Tropical Ecology**, v. 26, p. 25–33, 2010.

THOMPSON, K.; BAND, S. R.; HODGSON, J. G. Seed size and shape predict persistence in soil. **Functional Ecology**, v. 7, p. 236–241, 1993.

TRINDADE, D. P. F. et al. Water availability mediates functional shifts across ontogenetic stages in a regenerating seasonally dry tropical forest. **Journal of Vegetation Science**, v. 31, p. 1088–1099, 2020.

UHL, C.; JORDAN, C. F. Succession and nutrient dynamics following forest cutting and burning in Amazonia. **Ecology**, v. 65, p. 1476–1490, 1984.

VAN VLIET, N. et al. Trends, drivers and impacts of changes in swidden cultivation in tropical forest-agriculture frontiers: a global assessment. **Global Environmental Change** v. 22, n. 11, p. 418–429, 2012.

VANDERLEI, R. S. et al. Extensive clonal propagation and resprouting drive the regeneration of a Brazilian dry forest. **Journal of Tropical Ecology**, v. 37, p. 35–42, 2021.

VANDERLEI, R. S. et al. Impoverished woody seedling assemblages and the regeneration of Caatinga dry forest in a human-modified landscape. **Biotropica**, v. 00, p. 1–12, 2022.

VENTER, Z. S.; HAWKINS, H. J.; CRAMER, M. D. Implications of historical interactions between herbivory and fire for rangeland management in African savannas. **Ecosphere**, v. 8, n. 10, p. e01946, 2017.

VIEIRA, D. L. M.; SCARIOT, A. Principles of natural regeneration of Tropical Dry Forests for restoration. **Restoration Ecology**, v. 14, p. 11–20, 2006.

VIEIRA, R. M. S. P. et al. Identifying areas susceptible to desertification in the Brazilian northeast. **Solid Earth**, v. 6, p. 347–360, 2015.

WEBB, C. J.; BAWA, K. S. Patterns of fruit and seed production in Bauhinia ungulate (Leguminosae). **Plant Systematics and Evolution**, v. 151, p. 55–65, 1985.

WIJDEVEN, S. M. J.; KUZEE, M. E. Seed availability as a limiting factor in forest recovery processes. **Restoration Ecology**, v. 8, p. 414-424, 2000.