Universidade Estadual de Londrina

ROBERTA THAYS DOS SANTOS CURY

RESPOSTAS DA VEGETAÇÃO A DIFERENTES FREQUÊNCIAS E INTENSIDADES DE INCÊNDIOS NO SUDESTE DA BACIA AMAZÔNICA

Londrina
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Tese apresentada ao programa de Pós-Graduação do Centro de Ciências Biológicas da Universidade Estadual de Londrina (UEL), como requisito à obtenção do título de Doutora em Ciências Biológicas.

Orientador: Dr. José Marcelo Domingues Torezan.
Coorientador: Dr. Paulo Monteiro Brando.

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2016

Ficha de identificação da obra elaborada pelo autor, através do Programa de Geração Automática do Sistema de Bibliotecas da UEL

Cury, Roberta Thays dos Santos.
Respostas da vegetação a diferentes frequências e intensidades de incêndios no sudeste da Bacia Amazônica / Roberta Thays dos Santos Cury. - Londrina, 2016.
169 f. : il.

Orientador: José Marcelo Domingues Torezan.
Coorientador: Paulo Monteiro Brando.
Tese (Doutorado em Ciências Biológicas) - Universidade Estadual de Londrina, Centro de Ciências Biológicas, Programa de Pós-Graduação em Ciências Biológicas, 2016.
Inclui bibliografia.

1. Florestas Tropicais - Tese. 2. Conservação da Biodiversidade - Tese. 3. Ecologia de Fogo - Tese. 4. Mudanças Climáticas Globais - Tese. I. Domingues Torezan, José Marcelo . II. Monteiro Brando, Paulo. III. Universidade Estadual de Londrina. Centro de Ciências Biológicas. Programa de Pós-Graduação em Ciências Biológicas. IV. Título.

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Londrina, 28 de abril de 2018.

Universidade
Estadual de Londrina

201123090091

CENTRO DE CIÊNCIAS BIOLÓGICAS
PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS

DEFESA DE TESE DE DOUTORADO

Discente: **Roberta Thays dos Santos Cury**

Título: **"Respostas da vegetação sob diferentes freqüências e intensidades de incêndios no sudeste da bacia Amazônica".**

Data da Defesa: 28 de abril de 2016 – 08:00 hs, na sala CCB S/10 do Centro de Ciências Biológicas, desta Universidade.

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Dedico este trabalho às Florestas Tropicais, as quais despertam a minha curiosidade, vontade de aprender e ensinar por um mundo melhor... ☺

AGRADECIMENTOS

Neste momento aproveito para agradecer aos professores e pesquisadores, amigos de Londrina, Canarana e Boulder, funcionários e técnicos de campo e familiares que tiveram grande importância na realização deste trabalho de Tese, bem como os orgãos de fomento que viabilizaram as pesquisas nos últimos cinco anos.

Agradeço ao orientador José Marcelo D. Torezan da Universidade Estadual de Londrina (UEL) pela motivação e amizade nos últimos nove anos. Em especial, aos pesquisadores Jennifer K. Balch, que me recebeu na Universidade do Colorado em Boulder-USA durante o doutorado sanduíche e Paulo M. Brando, do Instituto de Pesquisa Ambiental da Amazônia (IPAM), os quais contribuíram enormemente com meu crescimento acadêmico, me ajudaram a enxergar processos ecológicos na floresta de transição Amazônia-Cerrado, e sobretudo pelos incríveis momentos de aprendizado nas áreas experimentais na Fazenda Tanguro, no estado de Mato Grosso, Brasil.

Aos membros da banca pelas contribuições e disponibilidade. Dra. Beatriz S. Marimon (UNEMAT), Dra. Simone A. Vieira (UNICAMP), Dr. Efraim Rodrigues (UEL), Dr. Halley Caixeta de Oliveira (UEL), Dr. José Antônio Pimenta (UEL) e Dr. José Eduardo Lahoz S. Ribeiro (UEL).

Aos amigos de longa data de Londrina “Carolina Cainelli, Pedro Ícaro G. Marchese, Alba Cavalheiro e Regia Cristina” pelo companheirismo. Aos novos recrutas do Laboratório de Biodiversidade e Restauração de Ecossistemas (LABRE), em especial à Cinthia Montibeller, Alexandre Bordignon, Jéssica Magon, Renata Picollo e Jézili Dias pela companhia no laboratório e finais de semana. Obrigada pela amizade e também pelas longas horas de discussão, as quais contribuíram para elaboração desse manuscrito.

Aos queridos amigos que me acolheram em Canarana – MT, Edilaine Ciotti, Marcio Gomes, Cândida Mews e Silvana Belizario, saudades. Aos amigos de Boulder no Colorado que possibilitaram minha adaptação durante o doutorado sanduíche, especialmente ao casal Rafael e Gabriela Andrade que me acolheram nos primeiros dias; Paula Yamashita, Paricher Rosseini, Roberta Moura, Guilherme Passamani e Tyler D Lagasse pela agradável companhia.

Um agradecimento especial aos funcionários do IPAM, que tornaram as coletas de campo menos árduas e divertidas. Obrigada Raimundo Quintino, Darlisson Souza, Ebis Nascimento, Sebastião Nascimento, Sandro Rocha, Adilson Coelho e Lúcia Nascimento por todos estes anos de convivência. Ao chefe, Dr. Oswaldo Carvalho Jr pelas inúmeras dicas.

Um agradecimento especial aos meus pais Marily S. Cury e Oscar B. Cury, e minha irmã Nicole Maria S. Cury pelo suporte emocional, sempre.

Aos orgãos de fomento: Coordenação de Aperfeiçoamento Pessoal de Nível Superior (CAPES) pela bolsa de Doutorado Sanduíche; Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) pela bolsa de estudos no Brasil; Instituto de Pesquisa Ambiental da Amazônia (IPAM) pelo suporte junto a Fazenda Tanguro; Grupo André Maggi (AMAGGI) por autorizar a realização das pesquisas na Fazenda Tanguro; Programa de Pós-Graduação em Ciências Biológicas da Universidade Estadual de Londrina (PPG-UEL) por financiar parte dos trabalhos de campo.

Universidade Estadual de Londrina

IPAM Instituto de Pesquisa Ambiental da Amazônia

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CURY, Roberta Thays dos Santos. **Respostas da vegetação a diferentes frequências e intensidades de incêndios no sudeste da Bacia Amazônica**. 2016. 169 f. Tese (Doutorado em Ciências Biológicas) – Universidade Estadual de Londrina, Londrina, 2016.

RESUMO

O desmatamento, a fragmentação florestal e as mudanças no clima têm chamado a atenção pelos seus efeitos na intensificação das secas e nos regimes de incêndios nas florestas tropicais, alterando a diversidade nos fragmentos remanescentes. Este estudo traz informações sobre algumas das respostas da vegetação a diferentes frequências e intensidades de incêndios no sudeste da Bacia Amazônica. No capítulo 1, analisamos o efeito da variação de combustível (serapilheira) na mortalidade de indivíduos lenhosos, nos danos, na área queimada e na regeneração pós-fogo. Observamos que o aumento de 50% no combustível elevou a mortalidade espécies de lenhosas em 14% (indivíduos entre 1-5 cm de DAP), os danos em 21% (indivíduos ≥ 5 cm DAP) e a área queimada em 33%. No capítulo 2, investigamos os efeitos de incêndios anuais (repetidos seis vezes; tratamento B6) e trienais (repetidos três vezes; tratamento B3) na diversidade de espécies regenerantes em comparação com o controle, não queimado (B0). A riqueza de espécies florestais da Amazônia, florestais coocorrentes no Bioma de Cerrado, espécies de hábito arbóreo-arbustivo e lianas foi reduzida na mesma proporção em ambos os tratamentos. *Pyrostegia venusta* foi a liana mais abundante em ambos os tratamentos, com ~42% dos indivíduos. *Myrcia multiflora* e *Mabea fistulifera* foram as arbóreas mais abundantes em B3. Todas as espécies arbóreas tardias na sucessão foram excluídas de B6. O número de espécies foi menor em B6 devido à redução do rebrotamento. Em contrapartida, o potencial de invasão da gramínea *Aristida longifolia* foi aumentado em B6. No capítulo 3, discutimos como os incêndios anuais e trienais alteram as fontes de sementes, plântulas e rebrotas; como estes são afetados pela borda florestal, e se as plântulas e as rebrotas persistem nos primeiros anos após os incêndios. Houve redução na chuva de sementes (-36%) e no banco de sementes (-56%) em B3 em comparação com B6. As sementes também foram reduzidas nas bordas. As plântulas foram afetadas em ambos os tratamentos (2,4% de recrutamento no controle, contra 0,6% em B3 e 0,7 em B6) e ao longo da borda. As rebrotas aumentaram no primeiro ano pós-fogo, principalmente em B3 (+5,5 rebrotas), mas declinaram nos anos subsequentes. Concluímos que deve haver maior investimento público no combate aos incêndios na floresta de transição Amazônia-Cerrado, a qual não está adaptada a incêndios recorrentes e intensos, uma vez que as principais vias de regeneração são negativamente afetadas.

Palavras-chave: Biodiversidade. Conservação. Ecologia de Fogo. Floresta Tropical. Mato Grosso. Mudanças Climáticas Globais. Regeneração. Seca.

Cury, Roberta Thays dos Santos. **Forest vegetation responses to different burning frequencies and intensities in southeastern Amazon Basin.** 2016. 169 p. Thesis. (Doctoral Degree in Biological Sciences) – Universidade Estadual de Londrina, Londrina, 2016.

ABSTRACT

Deforestation, forest fragmentation and climate change have drawn attention to their effects on the drought intensification and changing fire regimes in tropical forests, reducing the diversity of remaining forest fragments. The current study assesses the vegetation responses to different burn frequencies and intensities in southeastern Amazon Basin. In chapter 1, we analyzed the effects of variation in fine fuel load (litter) on woody plant damages and mortality, burned area and post-fire regeneration. We showed that an addition of 50% more fine fuel increased in 14% the woody plant mortality (individuals within 1-5 cm DBH range), and increased in 21% the number of damaged boles (individuals ≥ 5 cm in DBH), after an increase in 33% in burned area. In chapter 2, we investigated the effects of annual burns (burned six times; B6 treatment) and triennial burns (burned three times; B6 treatment) on regeneration species diversity, comparing with a control (not burned, B0). Tree, shrub and liana species both exclusive from Amazon forests and forest-Cerrado cooccurring species were reduced at the same proportion in both treatments. *Pyrostegia venusta* was the liana species more abundant in both burned treatments (~42% of all individuals). *Myrcia multiflora* and *Mabea fistulifera*, both early succession tree species, were the most abundant species in B3. All late-succession tree species were excluded of B6. This treatment also showed a reduced number of woody species resprouts and an increase in abundance of *Aristida longifolia*, a dominant invasive grass. In chapter 3, we discussed how B3 and B6 treatments alter the seed sources (seed rain and seed bank), recruits (seedling and saplings) and resprouts and how the forest edge influence each treatment; and also whether the recruits and resprouts were persisting after fires. Our findings showed a reduced number of seeds in the litterfall traps (-36%) and in the soil seed bank (-56%) in B3 compared with B6. Seeds were also reduced at the forest edge. Recruits were altered in both burned treatments (2.4% of seeds recruited in control site versus 0.6% in B3 and 0.7 in B6) and along the forest edge. We found that B3 was linked with a 5.5-fold increase in resprouts, however, they declined across the three years post-fire. We concluded that public investments are needed to inhibit wildfires in Amazonia-Cerrado transition forest, which are not adapted to recurrent and intense fires, since the main regeneration pathways were negatively affected.

Keywords: Biodiversity. Conservation. Drought. Fire Ecology. Global Climate Changes Mato Grosso. Regeneration. Tropical Forest.

SUMÁRIO

INTRODUÇÃO GERAL

As zonas de baixa latitude abrigam as Florestas Tropicais Úmidas, as quais em conjunto contabilizam mais de 5000 espécies de plantas por hectare e abrigam 25 *hotspots*, ou seja, áreas com no mínimo 1500 plantas endêmicas e com menos de 30% da vegetação original remanescente (Dirzo & Raven 2003). As Américas são particularmente ricas em diversidade, especialmente na porção ocidental da Amazônia, costa leste do Brasil e Mesoamérica (Dirzo & Raven 2003; Puig 2008). Os prejuízos derivados da perda da cobertura florestal e das alterações abruptas no clima tornam-se incalculáveis ao considerar que as florestas tropicais e seus *hostpots* abrigam pelo menos metade de todas as plantas e um terço de todos os vertebrados terrestres do mundo (Myers et al 2000), gerando benefícios econômicos e serviços ambientais em escala local, regional e global (Gardner *et al.* 2009).

No entanto, entre os anos de 1990 e 1997 as florestas tropicais foram reduzidas a uma taxa anual de 0.38% na América Latina, 0.43% na África e 0.91% no sudeste da Ásia (Achard *et al.* 2002). De 2000 a 2005, 2,4% de desmatamento reduziram extensos blocos de floresta tropical úmida globalmente (Hansen *et al.* 2010). Estudos recentes mostraram que entre 2000 e 2012, 35% de florestas foram perdidas no Brasil, 18% na Indonésia, 5% na Malásia, 3% na Bolívia, 3% no Paraguai e 1% no Cambodia, totalizando mais de 50% de perda de cobertura florestal nos trópicos (Sam Lawson 2014).

As causas do desmatamento e da degradação florestal aparentemente são as mesmas nas diferentes regiões tropicais do planeta (Armenteras *et al.* 2013), resultantes conjuntamente de ações diretas: conversão das florestas em áreas para a agricultura e criação de gado, exploração madeireira insustentável e incêndios florestais ilegais. Resultam também de ações indiretas: subsídios para o agronegócio e a pecuária, política de investimento em infraestrutura (*e.g.,* rodovias e hidroelétricas), conflitos fundiários, ausência de governança e fiscalização do governo, demanda por produtos florestais (*e.g.*, crescimento populacional) e mercado favorável à produção de grãos e carne (Gardner *et al.* 2009; Moutinho *et al.* 2011; Armenteras *et al.* 2013; Sam Lawson 2014).

No Brasil, as obras de infraestrutura deram início ao desmatamento em larga escala na Floresta Amazônica com a inauguração da Rodovia Transamazônica durante a década de 60. Desde então, cerca de dois terços do desmatamento na Amazônia esteve concentrado num raio de 50 km adjacentes às rodovias pavimentadas (Nepstad *et al.* 2001), facilitando o acesso de madeireiras às áreas de floresta e tornando as mesmas mais propensas aos incêndios (Fearnside 2005). Oscilações econômicas também foram propulsores para o desmatamento na Amazônia, por exemplo, a maior taxa já registrada ocorreu em 1995, com 29.059 km^2 (INPE 2014), dado concomitante com a recuperação econômica, a implantação do Plano Real e o aumento do crédito agrícola em 1994 (Fearnside 2005).

A taxa média de desmatamento registrada na Amazônia entre 1996 e 2005 (19.625 km^2/ano) se tornaria uma marca histórica de referência para futuras ações de combate ao desmatamento. Assim, o governo brasileiro propôs voluntariamente durante a *Conferência das Partes* em 2008 (COP 15), ações inseridas no Plano Nacional sobre Mudança do Clima, como reduzir em 80% o desmatamento na Amazônia Legal (em relação à média histórica) e 40% no Cerrado até 2020 e mitigar as emissões dos gases do efeito estufa (GEE) oriundas de desmatamentos no Brasil (BRASIL 2010).

Indicadores de governança ambiental, como a criação de Unidades de Conservação (UCs) e territórios de ocupação tradicional (Terras Indígenas e Territórios Remanescentes de Quilombo) que foram incluídas no Plano Nacional de Áreas Protegidas (PNAP) em 2006, somaram 43,9% da Amazônia legal, reduzindo a expansão do desmatamento (Veríssimo *et al.* 2011). Ainda, o monitoramento e o controle do desmatamento através de ações integradas de fiscalização e combate ao crime organizado entre 2009-2011, contribuíram para redução do desmatamento na Amazônia nos últimos anos (MMA 2014). A partir de 2006 o país passou a registrar taxas decrescentes de desmatamento na Amazônia Legal em relação à média histórica, com: 6.400 km^2 de desmatamento em 2010, 4.571 km^2 em 2012 e 5.891 km^2 em 2013 (INPE 2014), reduzindo o desmatamento em 79% em relação à taxa média (19.625 km^2; MMA 2014). Contudo, a fiscalização não parece ser suficiente para conter o avanço da degradação florestal, principalmente, devido às deficiências na estrutura de fiscalização, a corrupção e a impunidade, fatores que dificultam o cumprimento da lei (Moutinho *et al.* 2011).

A Floresta Amazônica possui 68% de cobertura florestal remanescente, é formada por 77.038 fragmentos, os quais possuem tamanho médio de 8.376 ha (Pütz *et al.* 2014). No entanto, o desmatamento e a fragmentação florestal estão concentrados sobretudo ao leste e sudeste da Bacia Amazônica, região chamada de “arco do desmatamento” (Pütz *et al.* 2014), despontando com 137.241 km^2 já desmatados desde 1988 no estado de Mato Grosso (Figura 1) e 136.094 km^2 no Pará (INPE 2014). Essa região caracteriza-se pela prevalência de incêndios de origem antropogênica próximos às áreas desmatadas (Figura 1; INPE 2013), disputa e especulação por terras entre pequenos e grandes produtores, populações indígenas e madeireiras, impulsionadas pela expansão da fronteira desmatada para a criação de gado (≈70%) e a produção de soja (Malhi *et al.* 2008; Brando *et al.* 2013; DeFries *et al.* 2013; Sam Lawson 2014).

Na Amazônia, a conversão do uso do solo de áreas que originalmente possuíam cobertura florestal para a agricultura e a criação de gado pode elevar a temperatura da região entre 1,8 a 5,1°C e reduzir a precipitação (Malhi et al 2008). A floresta se tornaria mais seca na porção sudeste da Amazônia, sugerindo mudanças no ciclo hidrológico, incêndios florestais mais intensos e frequentes e alterações na ciclagem e no estoque de carbono (Nepstad *et al.* 2001; Malhi *et al.* 2008). A liberação dos gases do efeito estufa provenientes do desmatamento e das queimadas e as consequências para o clima regional e global são preocupantes. Atualmente, o desmatamento é a principal fonte de emissão de carbono, contribuindo com cerca de 10 a 15% as emissões antropogênicas anuais. Globalmente, as formações vegetais armazenam hoje cerca de 610 Pg de carbono e somente a fragmentação das florestas tropicais e a criação de bordas resultam em uma perda de 0,2 Pg de carbono por ano (Pütz *et al.* 2014). Somente a Amazônia possui 86 Pg de carbono armazenado (±20%; Saatchi *et al.* 2007) e, nos últimos anos, a Floresta Amazônica emitiu 599 Tg de carbono através da fragmentação florestal (Pütz *et al.* 2014).

Dentre as áreas mais ameaçadas está a Floresta Estacional Sempre Verde, situada na borda sul da Amazônia Legal, também conhecida como floresta de transição por apresentar espécies ocorrentes na Floresta Amazônica Úmida e no Bioma Cerrado (IBGE 2012). A floresta de transição compõe um mosaico paisagístico, com zonas de sensível transição ecológica e climatológica (Coe *et al.* 2013), possuindo vegetação pouco conhecida (Marimon *et al.* 2006; Ivanauskas *et al.* 2004; 2008), e de relevante interesse político, social e econômico devido à expansão da fronteira agrícola (Brando *et al.* 2013).

A perda da cobertura florestal torna os fragmentos remanescentes mais inflamáveis e susceptíveis aos incêndios (Nepstad *et al.* 1999; Nepstad *et al.* 2008; Gardner *et al.* 2009; Coe *et al.* 2013; Brando *et al.* 2014). Estudos mostram que os incêndios ocorrerão na presença de (1) biomassa suficiente para queima (*i.e.*, combustível), (2) predisposição para queima, decorrentes da baixa umidade, (3) clima favorável para ignição e espalhamento do fogo e (4) fontes de ignição (Bradstock 2010). Atualmente, as zonas de expansão da fronteira agrícola no Brasil apresentam conjuntamente esses quatro elementos, sendo que as principais fontes de ignição são provenientes das práticas agrícolas rudimentares que utilizam o fogo na limpeza e na manutenção das “roças” e pastagens de baixa produtividade (Carmenta *et al.* 2013) que, acidentalmente ou não, escapam das áreas agrícolas e atingem as bordas florestais (Nepstad *et al.* 2001; Mendonça *et al.* 2004).

Propágulos de gramíneas de origem africana, utilizados para a formação e a manutenção das pastagens, invadem as bordas florestais e aumentam o combustível disponível para queima (Silvério *et al.* 2013). Após a passagem do fogo, a mortalidade de árvores reduz a cobertura de dossel (Balch *et al.* 2008), eleva a temperatura do ar e reduz a umidade do sub-bosque. A floresta degradada favorece, novamente, a entrada de gramíneas, criando um ciclo positivo onde o fogo torna-se reincidente na paisagem (D'Antônio & Vitousek 1992; Brooks *et al.* 2004; Balch *et al*. 2009). Adicionalmente, a maior inflamabilidade florestal associada aos anos de secas extremas aumentam a probabilidade de incêndios subsequentes de maior intensidade (Nepstad *et al.* 2004; Balch *et al.* 2008; Brando *et al*. 2015).

A ocorrência dos incêndios é predominante no período de estiagem (*e.g.*, 4 a 5 meses no estado de Mato Grosso), quando o interior da floresta se torna mais susceptível à queima devido à baixa umidade e elevada quantidade de material combustível (*e.g.*, serapilheira; Brando *et al.* 2014; 2015). A severidade do período seco pode ser aumentada pela supressão da convecção nas estações chuvosas na região central e leste da Amazônia, tornando-se cada vez mais frequente devido aos anos de El Niño (Malhi *et al.* 2008; Chen *et al.* 2011). Ainda, as Oscilações do Atlântico Norte, tornam as estações secas mais intensas, aumentando a sua duração nas regiões oeste e sul da Amazônia (Malhi *et al.* 2008; Chen *et al.* 2011; Saatchi *et al.* 2013). Por exemplo, somente em 1997/98, 40.000 km^2 de floresta Amazônica foi queimado, com 13 vezes mais incêndios registrados quando comparados com anos não secos (Alencar *et al.* 2006), chamando a atenção pela severidade e impactos ecológicos. Em 2010, foi queimado 12% do sudeste da Bacia Amazônica, sendo que em anos não secos esse valor é menos de 1% (Brando *et al.* 2014).

Segundo Bowman *et al.* (2014), não só os modelos de alteração do clima, mas também a composição da vegetação em escala regional pode guiar os regimes de incêndios, tornando-os mais frequentes. Naturalmente, as florestas tropicais não possuem espécies adaptadas à presença do fogo (Slik *et al.* 2010). Dados preocupantes documentam que a presença de incêndios em florestas tropicais resulta no empobrecimento e na substituição de ampla gama de espécies florestais não adaptadas à presença do fogo por poucas espécies representantes da flora original e o predomínio de espécies adaptadas aos incêndios, como as gramíneas, especialmente as de origem africana (Balch *et al.* 2011; Veldman & Putz 2011; Balch *et al.* 2013; Balch *et al.* 2015). Assim, os incêndios transformam extensas porções florestais de alta produtividade em áreas de produtividade primária intermediária e estruturalmente similar às savanas, favorecendo que os incêndios se tornem mais intensos e frequentes (Cochrane & Schulze 1999; Veldman & Putz 2011; Pausas & Ribeiro 2013).

Incêndios na Amazônia alteram drasticamente a estrutura florestal e a diversidade de espécies (Ray *et al.* 2005; Chen *et al.* 2011; Saatchi *et al.* 2013). Os mesmos comprometem a funcionalidade do ecossistema florestal (Balch *et al.* 2015), alterando a dinâmica das relações interespecíficas como a competição, predação, polinização, dispersão dos diásporos e frugivoria (Puig 2008). Tais alterações, afetam negativamente a disponibilidade de recursos, como néctar, pólen e frutos (Puig 2008), especialmente na estação seca após os incêndios (Barlow & Peres 2006), e comprometem o recrutamento e a persistência das espécies vegetais remanescentes (Balch *et al*. 2013; 2015)

Diferentes frequências e intensidades de incêndios podem resultar em diferentes respostas da vegetação. Incêndios mais frequentes podem eliminar a biomassa aérea no sub-bosque sistematicamente, ano após ano, comprometendo a regeneração das espécies após os incêndios (Balch *et al*. 2013; 2015; Slik *et al*. 2010). No entanto, incêndios menos frequentes podem se tornar mais intensos, devido ao acúmulo de biomassa entre um incêndio e outro, elevando, assim, a mortalidade desde as plântulas até os adultos reprodutivos (Brando *et al*. 2014). A mortalidade dos indivíduos reprodutivos pode reduzir a chuva de sementes e afetar o abastecimento de sementes no banco de sementes (Montibeller-Santos 2013). Ainda, o banco de sementes no solo pode ser negativamente afetado quanto maior a intensidade dos incêndios, devido a mortalidade de sementes nas camadas superiores do solo. Tanto o banco, como as rebrotas são as principais vias para permanência das espécies da flora original após os incêndios (Hoffmann *et al.* 2003), uma vez que, mesmo incêndios de baixa intensidade, podem eliminar massivamente o banco de plântulas (Slik *et al*. 2010). No entanto, não se tem conhecimento sobre o limiar de degradação suportado pela floresta de transição diante de tais incêndios recorrentes e intensos.

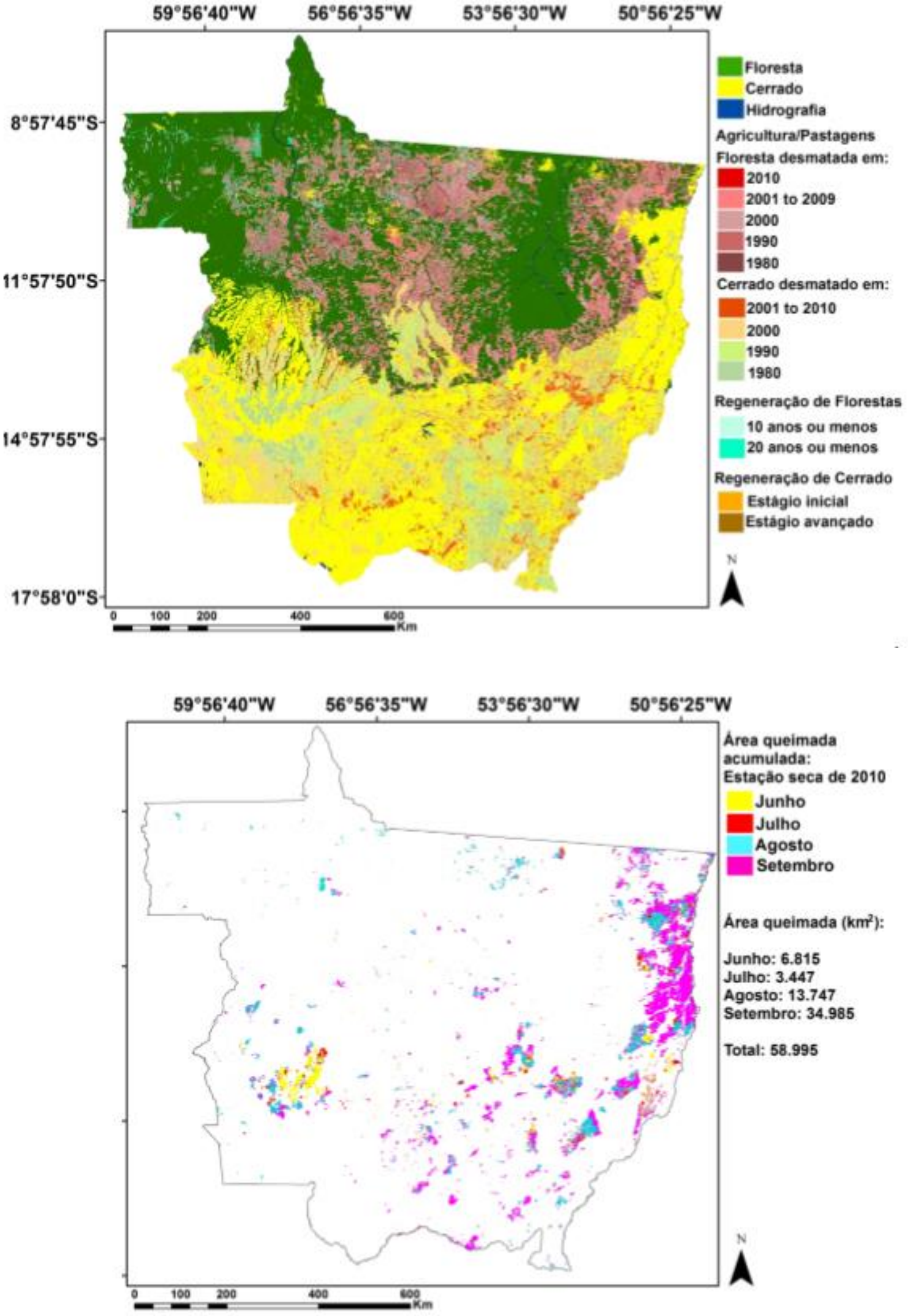

Figura 1. Na imagem acima temos a cobertura do estado de Mato Grosso, incluindo a área florestal, o Cerrado, áreas desmatadas de 1980 até 2010 e vegetação em início de sucessão. Abaixo, cicatrizes de incêndios registradas em 2010. Fonte: Projeto Pan Amazônia – INPE (2013).

OBJETIVOS

O objetivo geral deste estudo foi analisar algumas das respostas da vegetação a diferentes frequências e intensidades de incêndios no sudeste da Bacia Amazônica. Especificamente, foi investigado a mortalidade e os danos causados aos indivíduos lenhosos submetidos a diferentes intensidades de incêndios (*Capítulo 1*), alterações na diversidade de espécies lenhosas e gramíneas no estrato regenerante submetidos a duas frequências de incêndios (*Capítulo 2*), bem como o papel das espécies de plantas sobreviventes a ambas as frequências de incêndios para a manutenção da diversidade de recrutas, por meio da contribuição destas para a chuva de sementes e o banco de sementes (*Capítulo 3*) e o modo de estabelecimento das mudas (*i.e.*, recrutas ou rebrotas; *Capítulos 1, 2 e 3*). Neste estudo apontamos indicadores de resiliência florestal e abordamos o fenômeno da “savanização”, um dos possíveis cenários associados ao empobrecimento e/ou substituição da vegetação nativa por uma vegetação similar às savanas africanas.

No capítulo 1, *“Experimental fire-induced tree mortality in southeastern Amazonia: fine fuel loads matters”*, foram analisados os efeitos de diferentes intensidades de incêndios sobre a mortalidade, os danos, área queimada e a regeneração florestal pós-fogo. O experimento foi realizado na área de estudo 2 (Figura 2; a2), onde foram conduzidos incêndios controlados em duas áreas experimentais: 1 ha queimado com a adição de combustível (*i.e.*, folhas e galhos finos) simulando o aumento da biomassa que ocorre durante os eventos de secas anômalas; e 1 ha queimado sem a manipulação de combustível. Os tratamentos foram comparados com 1 ha não queimado, utilizado como controle. Esse estudo teve como objetivos analisar se: (i) o aumento de combustível fino (*i.e.*, folhas e galhos) resultaria em maior severidade de incêndios, aumentando a mortalidade de plantas lenhosas, os danos nos troncos e a área queimada; (ii) o aumento de combustível fino levaria a alterações nos padrões de regeneração (*i.e.*, rebrotas e recrutas) e chuva de sementes após o fogo.

No capítulo 2, *"Higher fire frequency impaired woody species regeneration in a transitional forest of southeastern Amazonia"*, foram analisados os efeitos de diferentes frequências de incêndios sobre a diversidade de espécies regenerantes dois anos após o último incêndio. O experimento foi realizado na área de estudo 1 (Figura 2; a1), onde foram conduzidos incêndios em duas frequências: queimado trienalmente, por três vezes, e queimado anualmente, por seis vezes. No experimento foram avaliados: (i) alterações na diversidade de espécies lenhosas regenerantes dois anos após a supressão dos incêndios; (ii) alterações nas proporções entre espécies florestais e espécies florestais coocorrentes no Bioma de Cerrado, espécies florestais tardias e iniciais (*i.e.*, pioneiras e secundárias) e espécies de porte arbóreo-arbustivo e lianas; (iii) a ocorrência e cobertura de gramíneas; e (iv) a contribuição das rebrotas para a persistência das espécies nativas, analisando a proporção entre rebrotas e recrutas.

No capítulo 3, *"Effects of increasing fire frequency on seed sources and early regeneration in Southeastern Amazonia"*, também realizado na área de estudo 1 (Figura 2; a1), analisamos: (i) se a diversidade da chuva de sementes, banco de sementes no solo e recrutas seriam afetados negativamente quanto maior a frequência de incêndios; (ii) se a diversidade da chuva de sementes, banco de sementes no solo e recrutas seriam afetados negativamente quanto maior a proximidade com a borda florestal e (iii) se o número de rebrotas se manteria elevado durante os primeiros três anos após a supressão dos incêndios.

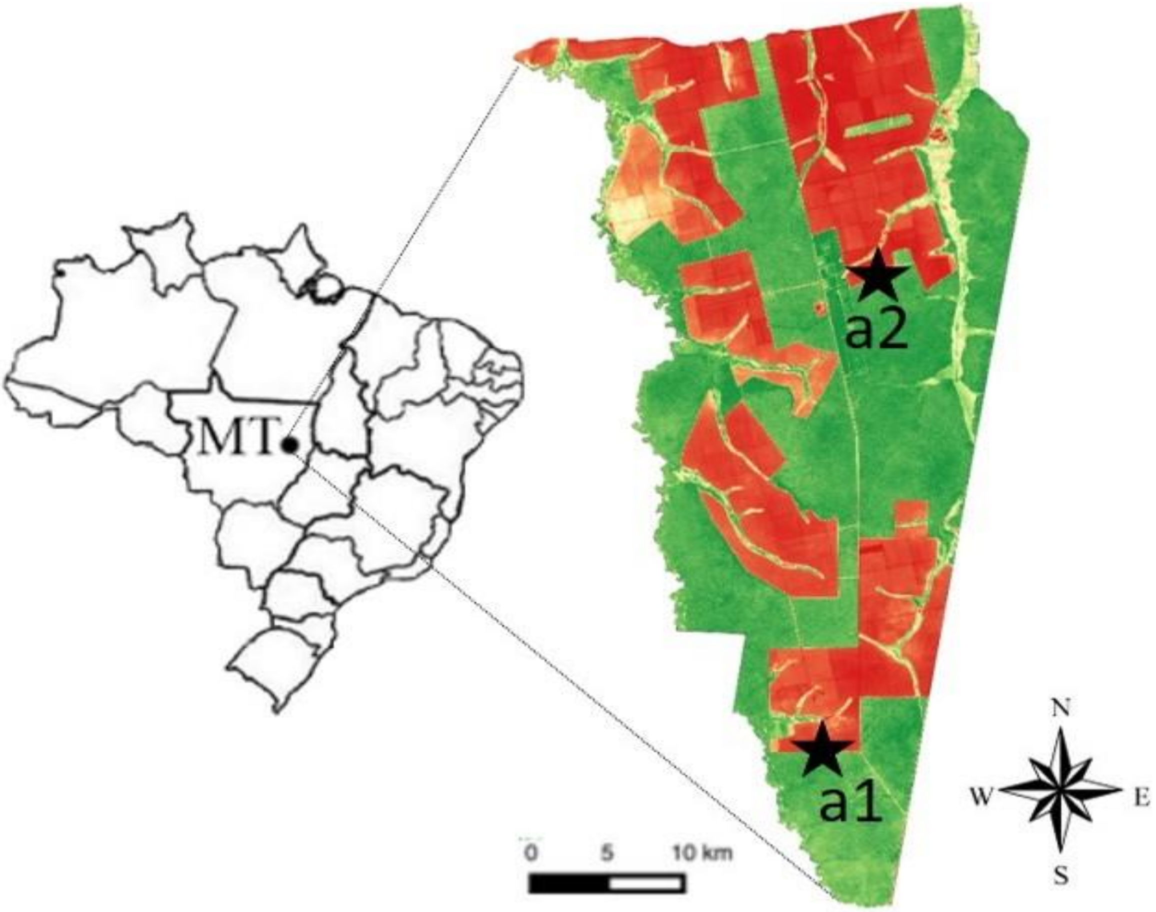

Figura 2. Da esquerda para direita, localização da Fazenda Tanguro no estado de Mato Grosso, porção sudeste da Bacia Amazônica; delimitações da fazenda Tanguro (≈80.000 ha) e áreas experimentais com incêndios controlados: área experimental 1 (a1; 150 ha), ao sul, referente aos Capítulos 2 e 3; e área experimental 2 (a2; 3 ha), ao norte, referente ao Capítulo 1. As áreas em verde representam a matriz florestal e em vermelho as porções desmatadas destinadas, principalmente, ao cultivo de soja.

METODOLOGIA GERAL

Histórico do Projeto Savanização

Os experimentos apresentados nos capítulos seguintes fazem parte do "Projeto Savanização", o qual foi desenvolvido e coordenado pelo Instituto de Pesquisa Ambiental da Amazônia (IPAM; www.ipam.org) sendo, atualmente, um dos maiores experimentos com fogo em florestas tropicais. O projeto consiste na constante avaliação florestal diante da exposição da mesma a incêndios controlados.

Na área de estudo 1 (Figura 2; a1), os experimentos tiveram início em 2004, quando foram simuladas diferentes frequências de incêndios florestais, sendo 50 ha queimados trienalmente, por três vezes, e 50 ha queimados anualmente, por seis vezes, em 7 anos. As últimas queimadas foram realizadas em agosto de 2010. As áreas queimadas foram comparadas com 50 ha não queimados – controle. Os *Capítulos 2 e 3* trazem resultados sobre a alguns aspectos da recuperação florestal três anos após os incêndios. Na área de estudo 2 (Figura 2; a1), o experimento teve início em 2011, com o objetivo de avaliar os efeitos de incêndios mais intensos e as respostas da vegetação associadas aos mesmos. Mais especificamente, o *Capítulo 1* descreve os efeitos do acúmulo de combustível fino na severidade dos incêndios (*i.e.*, mortalidade, danos e área queimada) e na regeneração pós-fogo.

Caracterização da Área de Estudo

Ambas as áreas de estudo se localizam na Bacia do Rio Xingu, região sudeste da Amazônia Legal, em uma propriedade privada (Fazenda Tanguro, ≈ 80.000 ha; Figura 2) situada no município de Querência, Mato Grosso, Brasil (13°04'S, 52°23'W). A vegetação é classificada como Floresta Estacional Perenifólia, possui baixa deciduidade na estação seca e passa por duas estações climáticas definidas (IBGE 2012). Segundo IBGE (2004), é uma zona de contato entre a Floresta Estacional e Cerradão no entanto diferenciam-se floristicamente (Marimon *et al.* 2006; Kunz *et al.* 2009), apresentando menor número de espécies arbóreas [*e.g.*, ≈ 97 espécies de árvores e lianas ≥ 10 cm de diâmetro a altura do peito (DAP); Balch *et al.* 2008] em comparação com a floresta Amazônica mais ao norte, além de possuírem menor altura média e maior luminosidade no sub-bosque (Balch *et al.* 2008). Ainda, é amplamente conhecida como "floresta de transição" devido à sua proximidade com o Bioma de Cerrado, apresentando tanto espécies florestais quanto savânicas (Kunz *et al.* 2009). Assim, devido ao amplo uso e aceitação, convencionamos utilizar o termo "floresta de transição" ao longo dos capítulos.

A média anual histórica de precipitação da região é de 1839 mm (dados coletados entre 2000 e 2015, INMET 2016). Possui estação chuvosa de outubro a abril e intensa estação seca entre os meses de maio a setembro (INMET 2016). Entre os anos de 2000 e 2015, no auge da seca (agosto), a temperatura média foi 35°C (máxima de 36°C) e umidade relativa média foi 44% (mínima 38%; INMET 2016). O solo é do tipo Latossolo Vermelho-Amarelo Distrófico típico (Oxissolo; IBGE 2009), profundo, de boa drenagem e, normalmente, de baixa fertilidade natural (IBGE 2007).

Desenho experimental: área de estudo 1 (Capítulos 2 e 3)

A área experimental 1 possui 150 ha e está inserida em um maciço de floresta madura, que não sofreu extração seletiva de madeira ou incêndios anteriores. A face norte (1,5 km) é adjacente a um campo agrícola aberto há mais de 10 anos, utilizado previamente como pastagem e atualmente sendo utilizado para o plantio de soja, a qual chamamos de borda.

A área foi dividida em três parcelas de 50 ha (0,5 x 1,0 km; Figura 3): uma parcela não queimada – controle (B0); uma parcela queimada trienalmente por três vezes (B3; queimado em 2004, 2007 e 2010); e uma parcela queimada anualmente por seis vezes (B6; tratamento queimado em 2004, 2005, 2006, 2007, 2009 e 2010).

O levantamento florístico foi realizado em 270 sub-parcelas de 0,5 m^2 (0,5 x 1,0 m; N = 90) desde a borda com agricultura (0 m) até o interior florestal (1000 m). As parcelas amostrais foram distribuídas sistematicamente a 0, 10, 15, 30, 50, 100, 250, 500 e 750 m de distância, sendo que próximo de 0 m, as distâncias entre parcelas foram reduzidas a fim de mensurar com maior detalhamento os efeitos que a borda exerce nas variáveis analisadas.

Os censos foram realizados por três anos consecutivos, 2011, 2012 e 2013, sendo que o primeiro censo foi realizado no mês de agosto, um ano após as últimas queimadas realizadas em 2010. Todos os indivíduos lenhosos com DAP $\leq$ 1 cm (incluindo os menores que 130 cm de altura) foram marcados e identificados (Figura 5a). Quando o modo de estabelecimento do indivíduo (germinação de sementes ou rebrota a partir troncos e raízes subterrâneas) não era de fácil identificação eram realizadas pequenas escavações na base da planta. A porcentagem de cobertura de gramíneas foi estimada visualmente e pela contagem do número de ocorrências (moitas) em cada sub-parcela.

As espécies foram comparadas com o acervo do herbário NX (Universidade do Estado de Mato Grosso, campus Universitário de Nova Xavantina) e com a coleção botânica mantida pelo IPAM. A nomenclatura científica foi atualizada segundo o Missouri Botanical Garden (www.tropicos.org). No *Capítulo 2* as espécies arbóreas e arbustivas identificadas nas sub-parcelas de 0,5 m^2 em 2012 foram classificadas em somente florestal e florestal coocorrentes no bioma de Cerrado; iniciais (*i.e.*, presentes ou não em áreas iniciais na sucessão ecológica, portanto, incluindo pioneiras e secundárias) e tardias (*i.g.*, as espécies que somente ocorreram em áreas florestais). Para as classificações foram utilizados levantamentos florísticos realizados na Floresta Amazônica, no Cerrado e em florestas secundárias. As lianas não foram classificadas devido à escassez de literatura.

Foram instaladas 270 bandejas de 0,5 m^2 (0,5 x 1,0 cm) para a coleta de chuva de sementes (Figura 5b). As bandejas foram dispostas a 1 m acima do solo e adjacentes às parcelas de regeneração desde a borda (0 m) até 750 m (Figura 3). O material depositado nas bandejas foi recolhido e triado quinzenalmente durante 2010, 2011, 2012 e 2013. Todos os frutos e sementes coletados foram quantificados e identificados através de comparação com material previamente coletado e mantido pelo IPAM (*Capítulos 3*).

Em 2012, 120 amostras de solo foram coletadas nos tratamentos e na área controle para análise do banco de sementes do solo (N = 40). Foram utilizados cilindros com 20 cm de diâmetro e 5 cm de profundidade para retirada do solo (Figura 5c). As amostras eram compostas pela mistura de duas sub-amostras retiradas a menos de dois metros de distância das sub-parcelas de regeneração e das bandejas de chuva de sementes. As coletas foram realizadas a 0, 30, 100, 500 e 750 metros de distância da borda. O solo de cada amostra foi depositado em bandejas plásticas e mantido em casa de vegetação (figura 5c) com irrigação mecanizada duas vezes ao dia na Universidade Estadual de Londrina, Estado do Paraná. As plântulas lenhosas germinadas nas bandejas foram contabilizadas semanalmente durante um ano. As plântulas germinadas nas bandejas foram identificadas através de comparações com plântulas, indivíduos juvenis e material vegetativo de indivíduos maduros previamente coletados durante os trabalhos *in loco* (*Capítulo 3*).

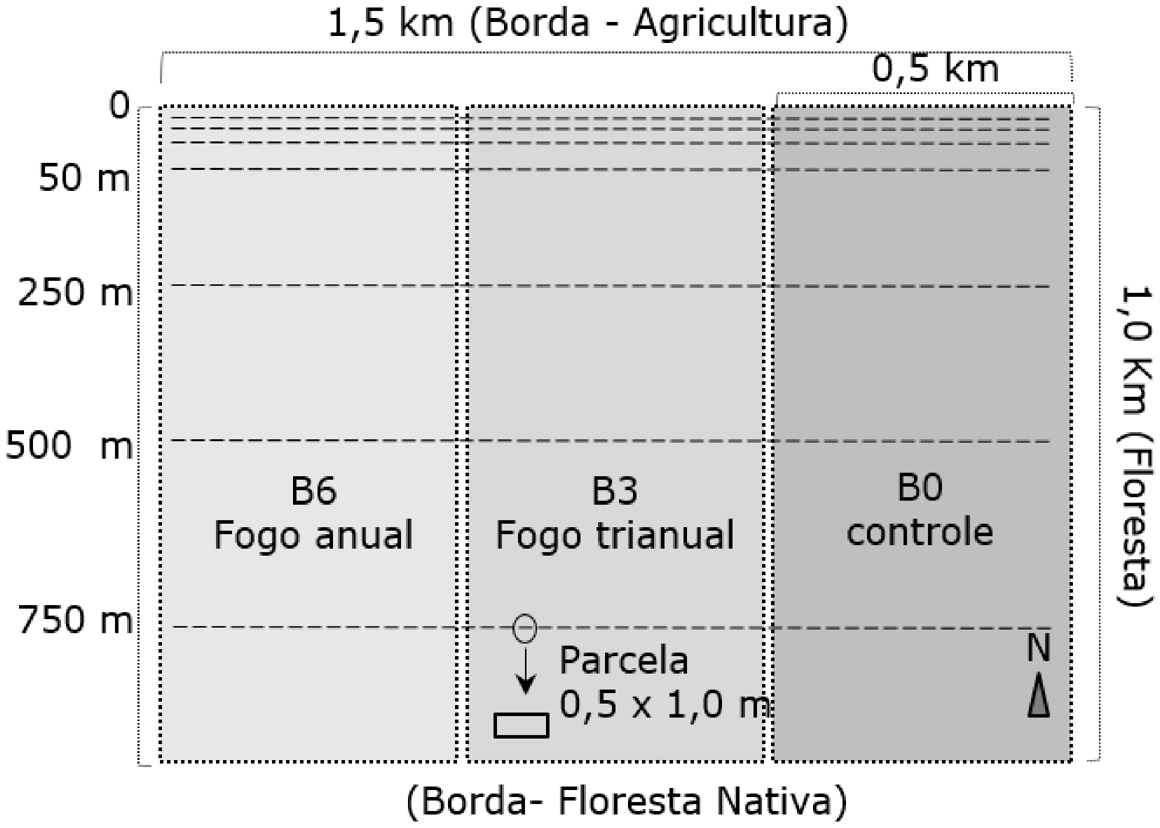

Figura 3. Área experimental inserida em uma floresta madura na área de estudo 1 no estado de Mato Grosso, Brasil. Ao norte da imagem há uma borda abrupta com cultura de soja. Desenho esquemático mostrando o tratamento queimado anualmente (B6 – queimado seis vezes); trienalmente (B3 - queimado três vezes); e não queimado (B0). As linhas tracejadas indicam a posição das parcelas amostradas.

Desenho experimental: área de estudo 2 (Capítulo 1)

Na área de estudo 2 foram delimitados quatro blocos experimentais no interior da floresta nativa, sendo dois localizados a 250 m de distância da borda e dois a 500 m (Figura 4). Cada bloco continha três parcelas de 0,25 ha (50 x 50 m): 1) parcela não queimada (*Controle*); 2) parcela queimada com adição de combustível (*i. e.*, folhas e ganhos finos; simulando maior abscisão foliar em períodos de seca; tratamento *B+*); 3) parcela queimada sem a adição de combustível (tratamento *B0*).

Todas as espécies lenhosas, como árvores, arbustos e lianas foram contabilizadas, marcadas com placas metálicas e identificadas ≈20 meses antes do início dos incêndios para observação da diversidade e taxa de mortalidade prévia aos incêndios. Os mesmos indivíduos foram recenseados no mês anterior e oito meses após as queimas.

A amostragem florística dos indivíduos com diâmetro a altura do peito (DAP) ≥ 5 cm foi realizada em parcelas de 1600 m^2 (40 x 40 m; N=4). Parcelas de 10 m^2 (1 x 10 m; N=16) foram alocadas no centro das parcelas de 40 x 40 m para amostragem dos indivíduos > 1 cm e < 5 cm de DAP. Parcelas de 2 m^2 (1 x 2 m; N=16) foram distribuídas a 10 m dos cantos das parcelas de 40 x 40 m, onde foram registrados todos os indivíduos entre 5 e 130 cm de altura ou ≤ 1 cm de DAP. Todas as parcelas foram delimitadas por estacas metálicas. As parcelas de 40 x 40 m foram isoladas entre si por aceiros para evitar que o fogo se espalhasse para áreas fora do experimento.

A serapilheira utilizada para o tratamento *B+* (queimado com adição de combustível), foi coletada em áreas de 40 x 40 m adjacentes as parcelas experimentais, onde todas as folhas e galhos finos foram coletados, armazenados em sacos e distribuídos regularmente nas parcelas (Figura 5e).

Após a adição da serapilheira, a mesma foi coletada adjacente as sub-parcelas de 2 m^2 com anel volumétrico, sendo que o material foi posteriormente pesado em laboratório para obtenção do peso seco. No mesmo ponto foram medidos a espessura da massa de raízes finas e a altura da serapilheira. No interior das sub-parcelas, os galhos finos com até 0,6 cm de diâmetro foram contados seguindo um transecto de dois metros. Os galhos maiores que 0,6 cm até 2,5 cm de diâmetro foram contados em um transecto de três metros.

Para verificar a severidade dos incêndios, foi avaliada a mortalidade dos indivíduos previamente marcados, estimado visualmente a porcentagem de área queimada nas parcelas de 2 m^2, determinado o número de árvores que apresentavam cicatrizes de incêndios e medida a altura das cicatrizes de fogo nos troncos dos indivíduos ≥ 5 cm de DAP.

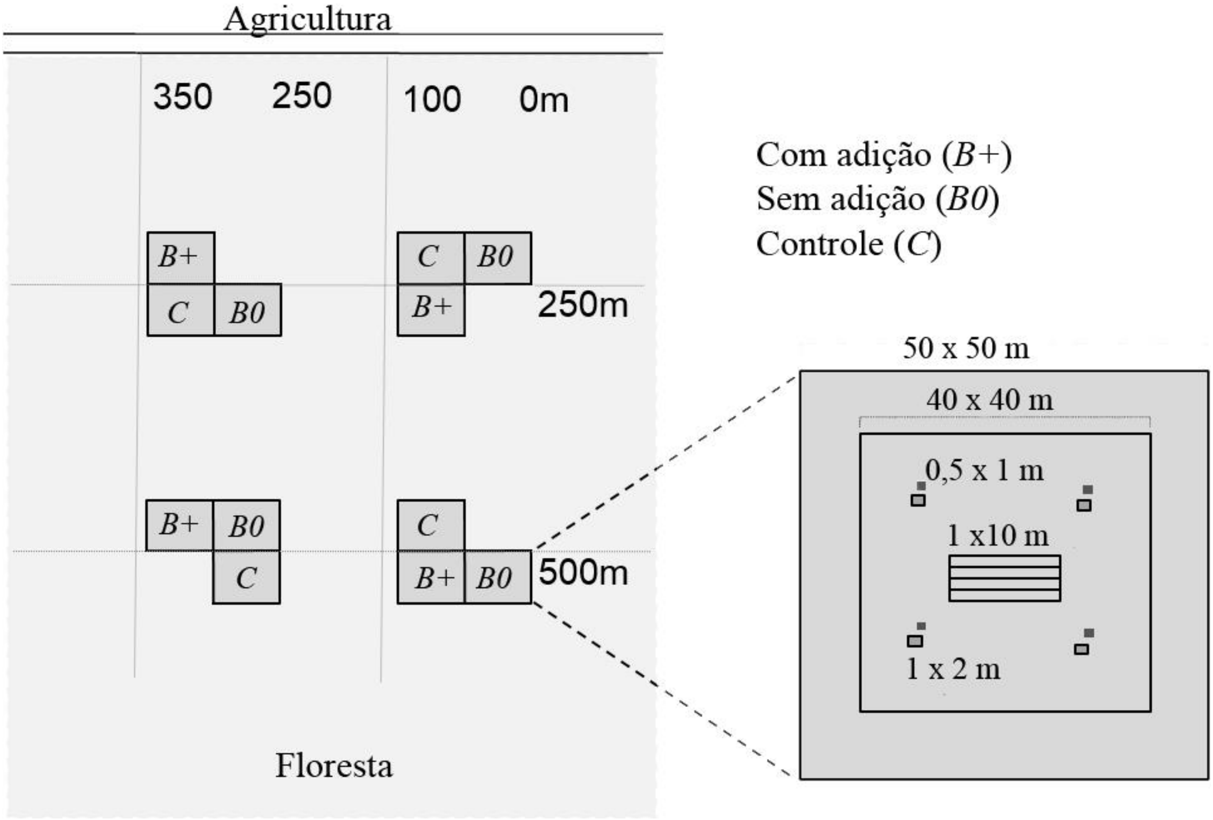

Figura 4. Desenho esquemático da área de estudo 2: tratamentos queimados com adição de serapilheira (combustível fino; *B+*), queimados sem adição de serapilheira (*B0*) e não queimado (*Controle*). Distribuição das parcelas de 40 x 40 m, 1 x 10 m e 1 x 2 m para levantamento florístico. Bandejas de para 0,5 x 1 m. Floresta de transição no estado de Mato Grosso, Brasil.

Queimada controlada

Todas as queimas (áreas 1 e 2) foram realizadas no mês de agosto, período de maior incidência de incêndios na região. Os incêndios foram autorizados pelo Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA) e realizados pela equipe técnica e científica do IPAM, com auxílio de pesquisadores e estudantes de diversas instituições acadêmicas e organizações não governamentais, pela brigada de incêndio e funcionários da Fazenda Tanguro.

Após delimitadas as parcelas e construídos os aceiros, em ambas as áreas experimentais, o fogo foi induzido com tochas de querosene (ver "pinga-fogo"; Figura 5f) criando-se assim, linhas de fogo. Variáveis ambientais como velocidade do vento, temperatura e umidade do ar e do solo, foram medidos concomitante com os incêndios.

Na área experimental 1 (*Capítulos 2 e 3*) o fogo foi induzido no sentido norte-sul ao longo de 10 transectos de 1000 m cada. O fogo foi reiniciado a cada 50 m, totalizando 10 km percorridos a cada 50 ha. As chamas se extinguiam naturalmente durante a noite e foram reiniciadas no dia seguinte, totalizando três a quatro dias com queimas consecutivas entre às 9:00 e 16:00 horas. Para mais detalhes sobre os procedimentos de queima, comportamento do fogo, alterações na inflamabilidade da floresta e dinâmica da vegetação nos primeiros anos do experimento consultar Balch *et al.* (2008; 2011; 2013; 2015).

Na área experimental 2 (*Capítulo 1*), as parcelas foram queimadas aos pares, no período da tarde durante dois dias. O fogo foi ateado no sentido do vento em uma das margens das parcelas de 40 x 40 m. A velocidade do vento, a umidade e a temperatura do ar, a altura, a velocidade e o espalhamento das chamas e a serapilheira consumida foram medidas durante as queimas (ver detalhes em Brando *et al.* 2016).

Figura 5. (a) levantamento florístico dos indivíduos juvenis e posterior comparação com exsicatas do adulto para identificação, (b) coletor para chuva de sementes, (c) cano de 20 cm de diâmetro para coleta do banco de sementes do solo e casa de vegetação, (d) aceiro, (e) coleta de serapilheira na área 2 e (f) pinga fogo. Floresta de transição no sudeste da Bacia Amazônica, Mato Grosso, Brasil. Fotos: Roberta T. S. Cury e (c) Cinthia M. Santos.

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Capítulo 1

Experimental fire-induced tree mortality in southeastern Amazonia: fine fuel loads matters

Acta Amazonica

Experimental fire-induced tree mortality in southeastern Amazonia: fine fuel loads matters

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Experimental fire-induced tree mortality in southeastern Amazonia: fine fuel loads matters

ABSTRACT

Synergistic interactions between forest fragmentation and severe drought events have increased the flammability of Amazonian forests by changing fuel amounts and moisture. However, little is known about the effects of increased fuel loads on fire behavior and severity in the region. To fill this gap, we investigated woody plant mortality, damages, seed rain and regeneration in an experimental fires conducted in plots that were treated with (*B+*) and without (*B0*) fine fuel additions (leaves and small branches) and in an unburned plot (*Control*). Both burning treatments strongly promoted stem mortality of individuals ≤ 1 cm DBH (including individuals between 5 and 130 cm height) compared with unburned plots (99% in *B+* and 88% in *B0*, against 14% in the *Control*). Individuals with 1 to 5 cm in DBH were more negatively affected in *B+* treatment (-86%) compared with *B0* (-72%) and the *Control* (-2%). Although the mortality of individuals ≥ 5 cm in DBH had showed no differences between treatments (21% and 15% in *B+* and *B0*, respectively) they were higher compared with the *Control* (4%). Also, 70% of the post-fire surviving stems (≥ 5 cm DBH) showed fire scars on the trunk in B+, against 49% in *B0*. Bark fire scars can lead to afterwards tissue exposure to pathogens, which potentially increases further mortality of large individuals. In both burned treatments, post-fire regenerating diversity was much lower than in the *Control* plot even counting the recruits and resprouts pulse. The density of seeds from seed rain showed no significant reductions among treatments and the *Control*. Our outcomes from fine fuel load manipulation corroborated that fires are more severe during “simulated” dry-season conditions, as observed in *B+* treatment which led to more severe fires, strongly altering the vegetation community, and may turn closed-canopy forests extremely vulnerable to loss of forest diversity and carbon releases in southeastern Amazon Basin.

KEYWORDS: carbon stocks; drought; global climate change; El Niño; Tropical Forest

Incêndios experimentais induzem a mortalidade de espécies lenhosas no sudeste da Amazônia: a importância do acúmulo de serapilheira.

RESUMO

Interações sinérgicas entre a fragmentação florestal e eventos de secas severas tem aumentado a inflamabilidade da floresta Amazônica devido a mudanças na quantidade de combustível e na umidade. No entanto, pouco é conhecido sobre os efeitos do acúmulo de combustível no comportamento e na severidade dos incêndios. Para preencher esta lacuna, investigamos a mortalidade, os danos, chuva de sementes e a regeneração da vegetação lenhosa em parcelas queimadas experimentalmente, tratadas com (*B+*) e sem (*B0*) a adição de combustível (folhas e galhos finos) e não queimadas (*Controle*). Ambos os tratamentos promoveram a mortalidade de indivíduos lenhosos ≤ 1 cm de DAP (incluindo indivíduos entre 5 e 130 cm de altura) comparado com o *Controle* (99% em *B+* e 88% em *B0*, contra 14% no *Controle*). Indivíduos entre 1 e 5 cm de DAP foram negativamente afetados no tratamento B+ (-86%) comparado ao tratamento B0 (-72%) e com o *Controle* (-2%). Embora os indivíduos ≥ 5 cm de DAP não tenham apresentado diferenças na mortalidade entre os tratamentos (21% em *B+* e 15% em *B0*) elas foram superiores às registradas no *Controle* (4%). Ainda, 70% dos indivíduos remanescentes (≥ 5 cm DAP) tiveram cicatrizes nos troncos em *B+*, contra 49% em *B0*. Cicatrizes nos troncos podem expor os tecidos ao ataque de patógenos, as quais potencialmente, aumentam a mortalidade dos indivíduos maiores a longo prazo. Em ambos os tratamentos, após o fogo, a diversidade do estrato regenerante foi reduzida em comparação com o *Controle*, mesmo após o incremento de recrutas e rebrotas. Não houve redução na densidade de sementes nos tratamentos em relação ao *Controle*. Nossos resultados, a partir da manipulação de combustível, corroboraram que os incêndios se tornaram mais severos devido a simulação de secas extremas, como observado no tratamento *B+*, onde os incêndios foram mais severos, alterando a comunidade vegetal, e podem tornar densas florestas extremamente susceptíveis a perda de diversidade e emissões de carbono no sudeste da bacia Amazônica.

PALAVRAS-CHAVE: estoque de carbono; seca; El Niño; Mudança Climática Global; Floresta Tropical.

INTRODUCTION

The fire regime of tropical forests responds to complex interactions among drought events, forest disturbances, land use and cover, and ignition sources (Ray *et al.* 2005; Nepstad *et al.* 2008; Nepstad *et al.* 1999; Asner *et al.* 2005; Lindenmayer *et al.* 2009; Bradstock 2010; Chen *et al.* 2011; Saatchi *et al.* 2013; Brando *et al.* 2014). Furthermore, the fires that move through the understory of tropical forests can cause substantial losses in biodiversity, in socio-economic indicators, and in the capacity of tropical forests to store and cycle carbon (Mendonça *et al.* 2004).

For example, understory forest fires burned more than 85.000 km^2 in the "arc of deforestation" in southeastern Amazonia during the past decade (1999-2010), mostly during extreme droughts events (Morton *et al.* 2013) caused by sea surface anomalies (Chen *et al.* 2011). These current climatic conditions may have potentially large effects on frequency, intensity and severity of burning (Alencar *et al.* 2006; Morton *et al.* 2013; Saatchi *et al.* 2013). As a result of these shifts, we are witnessing an unprecedented loss of forest cover, changes in stand structure, loss of species and their functional services, but our understanding about these drought-fires events and the vegetation responses is still poor.

Many studies point that mature Amazon forests are moist enough to substantially reduce fire forest risks in most non-drought years (Ray *et al.* 2010; 2005). However, during anomalous dry-warm periods two linked key processes can increase forest inflammability: moisture and fuel dynamics (Nepstad *et al.*1999; Brando *et al.* 2016). First, higher temperatures cause declines in soil moisture below critical thresholds, and the cumulative canopy water stress that results from this process (Meir *et al.* 2009; Ray *et al.* 2005; Saatchi *et al.* 2013) increase the tree mortality and associated litterfall accumulation (Brando *et al.* 2008). Second, higher temperatures can also turn the biomass aboveground dryer compared with non-drought seasons. Therefore, fire may penetrate in undisturbed forests that have lost parts of their canopy and make these forests more prone to fire spread and intense burns, increasing fire severity (Keeley 2009).

Some studies show a variety of vegetation responses because of fire behavior. For example: light burns may remove > 70% of saplings and vines (Cochrane and Schulze, 1999), varying substantially by species (Balch *et al.* 2011). There is diversity reduction and loss of fruit-frugivorous interactions (Barlow and Peres 2006), seeds and seed sources become scarce (Kennard *et al.* 2002, Barlow and Peres 2006, Norden *et al.* 2007), occurs failure of recovery processes, such as recruitment and regrowth, and mortality of large individuals due to increases with char height (Balch *et al.* 2011; Barlow *et al.* 2003a), not only in the year following the fires (Brando *et al.* 2012), but many years thereafter (Barlow *et al.* 2003b; Brando *et al.* 2012; Balch *et al.* 2015). However, the mechanisms that control mortality of tropical woody species from seedlings to reproductive individuals, recovery, and seed availability remain uncertain due to heterogeneity of fine fuel load variation associated with atypical canopy defoliation.

We evaluated the fire severity by testing if an increase of fine fuels would result in differences in the aboveground organic matter loss in southeastern Amazon forest. Thus, we hypothesized that more fine fuel load could result in fire severity observed by increasing mortality of stems, surface litter consumed, number of burned boles and fire scars height, resulting poor vegetation diversity. We also evaluated initial recovery by analyzing the regenerating individuals and seed rain after fires.

MATERIAL AND METHODS

Study site

The experimental fires were conducted in a primary transitional forest growing between Amazonia and Cerrado Biome at Fazenda Tanguro, a privately owned agricultural holding (80.000-ha) located in Querência, Mato Grosso State, Brazil (12°49’S; 52°23’W; Figure 1A). The farm was originally cleared for pasture in the 1980s and afterwards converted into soybean fields between 2003 and 2008. The deep, well-drained soils are classified as dystrophic red-yellow Oxisols by IBGE (2009). The average annual precipitation is around 1.770 mm (data from 2005 to 2011; Rocha *et al.* 2014), and the rainy season extents from September to April and the dry season from May to August, when monthly rainfall typically is below 10 mm (Rocha *et al.* 2014). Dry-season temperature averages 25°C and relative humidity 66% (Balch *et al.* 2008). The vegetation is classified as Evergreen Seasonal Forest (IBGE 2012), with a little seasonality (leaf area index averaged 4.13 m^2 m^{-2}; Rocha *et al.* 2014). These forest are also classified as “transitional forest” (Kunz *et al.* 2009) due to their proximity to the Cerrado Biome. Our study forest has lower canopy height and lower plant diversity than wetter Amazonian forests (Balch *et al.* 2008). For example, 97 species of trees and lianas ≥10 cm diameter at 1.3 m stem diameter breast height (DBH hereafter) were identified at Tanguro Farm (Balch *et al.* 2008; 2011). The 10 most common species account for 50% of the Vegetation Importance Index (Balch *et al.* 2008), and more than 74% of tree and shrub species also occur in the adjacent Cerrado Biome (See the chapter 2).

Experimental design

The experimental site was located in 3-ha of a primary forest (N = 4) with no recent signs of logging (*e.g.*, stumps) or previous fires (*e.g.*, scars or charcoal). Fully randomized blocks were placed at 250 m and 500 m from the forest edge (crop fields). Each block was comprised of three 0.25-ha plots (Figure 1B). The fire experiment consisted of three treatments: one burned after fine fuels were augmented by 50% (*B+*); one burned with no fuel manipulation (no fuel addition; *B0*); and an unburned control (*Control*).

Pre fire fuel manipulation

The experimental fine fuel additions were aimed to mimic litterfall increases during anomalous drought years, and consisted of manually adding ≈3.2 Mg ha^{-1} of fine fuel that was collected in 50 x 50 m plots, adjacent to the *B+* treatment. Four hours before conducting the experimental fires, downed woody debris we measured in all 2 m^2 plots: fine and coarse woody fuel loads (N=16; 0-0.6 cm and 0.6-2.5 cm diameter) and the thickness of the litter layer (N=16). Adjacent to the 2 m^2 plots the biomass was collected using a 40 cm diameter wire circle to measure the dry biomass weight of litter (N=16; Table 1).

Experimental fires

The experimental fires were carried during two successive days between 12:00 and 17:00 hours in August 2013, near the end of the dry season (for details about the methods see Brando *et al.* 2016). Six days following the experimental fires, we estimated the percent litter that was charred by the fires in all regeneration plots (burned area hereafter).

Floristic inventories

We conducted three inventories to estimate species richness, size distribution, and mortality rates of seedlings, juveniles, and adult individuals. The first inventory was performed ~20 months prior the experimental fires (on November 2011), the second inventory was conducted one month before (on July 2013), and eight months following the fires, we conducted another inventory to quantify fire-induced mortality rates of all tagged plants (April to June 2014; Table 2).

In these inventories, we tagged and identified all individuals based on different sampling areas. Trees, shrubs and lianas with DBH ≤ 1 cm and individuals between 5 and 130 cm height (hereafter referred to as "≤ 1 cm DBH"), were measured in 2 m^2 plots (1 x 2 m; N=16); trees, shrubs and lianas with DBH between 1 to 5 cm were measured in 10 m^2 plots (1 x 10 cm; N=16); and, trees and lianas with ≥ 5 cm in DBH were measured in 0.25-ha plots (40 x 40 m; N=4; Figure 1C).

Basal resprouts and seedlings were recorded. When the regeneration mode was not evident, the basal resprouts or emerged seedlings from seeds were determined through small excavations from plant base. Dry stems and missed tagged plants were considered dead. We also counted the number of trees charred stems and measured char height for all trees with DBHs ≥ 5 cm.

Species identification were based on comparisons between on-site plant collections and the botanical collections of the Amazon Environmental Research Institute (IPAM) and the Herbarium NX at Universidade do Estado de Mato Grosso at Nova Xavantina campus.

Seed rain

Seed rain was collected biweekly for 22 months before the fire experiment (October 2011 – August 2013) and eight months after fires (September 2013 – April 2014) from 0.5 m^2 mesh traps (N = 16). Traps were suspended ≈1m above the forest floor and were placed adjacent to the 2 m^2 plots (Figure 1C). The number of seeds was quantified per plot.

Data analysis

Fine fuel load parameters (*i.e.*, fine and coarse fine woody, thickness of litter layer, and litter biomass weight), percent of burned area, amount of fire scars, fire scar height on the trunk and the amount of seeds from seed rain were compared between treatments using Kruskal-Wallis test indicated for non-normal data (Zar 1999). Burned area was correlated with fine fuel parameters using the Spearman's correlation test. We also correlated the mortality of plants with DBH ≤ 1cm with the percent of burned area using the Spearman's correlation test. Shapiro-Wilk normality test was used to indicate normality of residuals.

Each plant size class had their abundance and richness compared by treatments using individual-based species accumulation curves (Colwell *et al.* 2004). For community composition and structure, we used non-metric multidimensional scaling (NMDS), based on Bray–Curtis similarity index matrices (Legendre and Legendre 2012), and ANOSIM test (Clarke 1993).

A generalized linear model (GLM) was used to account for differences in density of dead stems, the number of damaged stems (fire scar height), resprouts from base after stem death, new recruits, post-fire surviving stems, and seed from seed rain among burning treatments (*B+* and *B0*) and them with unburned site. GLM was performed using Poisson distribution, indicated for counts with Quasi-Poisson correction when the variance was higher than the average (Crawley 2013).

RESULTS

Our findings showed that both fire treatments reduced the vegetation density of all plant sizes. In general, regenerating and small individuals were more vulnerable to heat exposure than larger ones and, they were correlated with burned area during surface fires. However, 50% more fine fuel load resulted in more species loss and stem deaths for individuals between 1 to 5 cm in DBH range, and more damage of individuals ≥ 5 cm in DBH, which showed higher fire scar height on the trunks. We further explore these results and, also the pathways of regeneration in the first months after fire degradation.

Pre-burn forest diversity

Two years prior to the experimental fire, we registered 3,086 (32 ind m^{-2}) individuals ≤ 1 cm in DBH (97 species); 579 (1.2 ind m^{-2}) individuals with DBH between 1 and 5 cm (70 species); and 3,049 (1.5 ind m^{-2}) individuals with DBH ≥ 5 cm (82 species). Accumulation curves, indicated that species richness and abundance did not differ among the *Control*, *B+* and *B0* plots. Between 2011 and 2013, mortality rates were also similar among the three treatments, averaging per year 18.2% (individuals ≤ 1 cm in DBH), 5.2% (1-5 cm) and 2.8% (≥ 5 cm; Table 2).

Extent of the burned area and damages

The 50% increase in fine fuel loads (*B+*) resulted in a 33% increase in burned area compared with *B0* (98% versus 65%, respectively; Kruskal-Wallis = 15.9, p = 0.000). The burned area was positively correlated with litter thickness (Spearman’s correlation: S = 2025.2, p = 0.000, rho = 0.627) and the amount of dry biomass (Spearman’s correlation: S = 2663.7, p = 0.002, rho = 0.512).

Overall, more surviving individuals ≥ 5 cm in DBH were charred in *B+* (70%) than in *B0* (49%; Kruskal-Wallis = 5.33, p = 0.02; Figure 2). Char height was also higher in *B+* than *B0* (Kruskal-Wallis = 89.38, p = 0.000).

Effects of fire on plant mortality

Both burning treatments strongly promoted stem mortality of individuals ≤ 1 cm DBH compared with unburned plots, 99, 88, and 14% of stem death in *B+*, *B0*, and in the *Control*, respectively (Figure 2; GLM, p < 0.001), leading to a reduction in the number of species near to zero in *B+* (five species remaining) and 34 species in *B0* compared with 80 species in the *Control*.

One single fire with 50% more fine fuel load caused 14% more stem deaths of individuals with DBH between 1 and 5 cm than in *B0* (86 against 72%, respectively; Figure 2 and 3; GLM, p < 0.001), which represented a loss of 2,750 individuals per hectare. Accumulation curves showed that species richness was also negatively affected, showing a total of 16 species in *B+* and 28 species in *B0*, against 41 species in the *Control* (Figure 3). Eight months since the fire experiment took place, 54 and 49% of all burned stems showed a basal or epicormic resprout response in *B+* and *B0*, respectively, contributing to species recovery near to the *Control* patterns.

Although the mortality of individuals ≥ 5 cm in DBH had no differences between treatments, it increased fivefold in *B+* and fourfold in *B0* compared with the unburned site (Figure 2; GLM; p = 0.002), with loss of 283 individuals per hectare in *B+*. Surviving individuals slightly reduced the richness and abundance, and the structure and composition of community had a non-significant difference when comparing burning treatment plots and them with the *Control*.

Post-fire regeneration dynamics

Eight months after the beginning of the fire experiments, we observed that live stem density were still low, with 83% and 73% of individuals showing no basal resprouts in *B+* and *B0*, respectively, compared with the *Control* (14%; GLM: $p < 0.001$). This result represented a loss of 25 individuals per m^2 in *B+*. When we analyzed mortality by life form (trees, shrubs and lianas) we had a similar patterns of mortality (Table 2). The percent of regenerating plant mortality (*i.g.*, individuals with no basal resprouts) was also positively correlated with percent of burned area (Spearman's correlation: S = 3446.7, p = 0.038, rho = 0.368; Figure 4).

At the same time, the number of recruits of regenerating species increased in *B+* near to the *Control* plot levels (≈9 ind m^{-2}); resprouts were larger in both burning treatments (≈7 ind m^{-2}; 18.5% with multi-stems) compared with the *Control*; and, only *B0* had few surviving plants ≤ 1 cm in DBH (2.6 ind m^{-2}) differing from *B+* and the *Control* (GLM, $p < 0.05$; Figure 5). This size class still showed a loss of 47% of total richness (loss of 35 species) in *B+* compared with *B0*, where a loss of 31% was recorded (loss of 22 species; Figure 6). The structure and composition of regeneration plant community were still negatively affected by fires compared with the *Control* (Figure 7; ANOSIM; R = 0.1901; p = 0.001).

Accumulated seeds from seed rain were similar comparing pre-fire treatments with the *Control* from October 2011 to August 2013. However, in post-fire seed rain density, from September 2013 to April 2014, the amount of seeds increased expressively in *B0*, with 2.4-fold more propagules, compared with the *B+* treatment (36 vs. 15 seeds m^{-2}, respectively); whilst *B+* remained similar to the *Control,* with 16 seeds m^{-2} (Kruskal-Wallis = 12.34, p = 0.002).

DISCUSSION

Overall, we found that our fuel addition treatment increased burned area and associated mortality of seedlings, juveniles, and adult trees. These losses are essentially explained by forest vegetation characteristics which has few evolutionary adaptations to fire (Hoffmann *et al.* 2003). When a forest tree is girdled even by a low-intense fire the resulting cambium necrosis is frequently accompanied by phloem necrosis leading to stem death. For example, according to Poorter *et al.* (2014), who studied dry and moist forests in Bolivia, about 50% of the species never developed enough bark thickness to avoid fire damage to their vascular cambium.

As we expected, both treatments, with- and without fine fuel manipulation, suffered an expressive reduction of density of all plant sizes after one single surface fire event compared with the unburned site. Also, the pattern of stem mortality was similar to those reported in previous studies, showing the highest mortality of smaller stems, while larger and thicker-barked trees (≥ 5 cm in DBH) had a tendency to survive (Cochrane and Schulze, 1999; Barlow *et al.* 2002; Balch *et al.* 2011; Barlow *et al.* 2003b). This result would be expected because, first, as a tree grows larger, the basal bark thickness may increase until it is thick enough to insulate the cambium from the fire (Barlow *et al.* 2003a; Brando *et al.* 2012); second, the tree also grows taller, elevating the vegetative buds above the lethal plume temperatures (Michaletz and Johnson, 2007). However, we witnessed the increase in 50% of litter biomass also resulted in an increase of mortality of individuals in 1 to 5 cm DBH range, increasing the vulnerability of larger individuals. And, the increase in mortality for young individuals (≤ 1 cm DBH and between 1 and 5 cm in DBH) were large enough to reduce species richness and abundance, and change the species compositions and structure of community. These losses may lead to a failure of recovery process for years after fires (Balch *et al.* 2015).

Our results also showed that the larger surviving plants had more fire scars on the trunk (70% in *B+* against 49% in *B0*); it may respond by future increasing in tree mortality and carbon emissions. Further tree mortality may be caused by several complex, coupled processes, which can be direct (*e.g.*, heat transfer and the resulting tissue necrosis; Brando *et al.* 2012; Poorter *et al.* 2014) or indirect (such as altering physiology, reducing resistance to insect infestation, rot and fungus, increasing vulnerability to wind throw). For example, the crown of a girdled tree will continue to fix carbon and grow, but with a damaged phloem will not be transported to roots. The root system must rely on carbohydrate reserves; eventually, these reserves will be depleted, fine-root production will cease and the tree will die from water stress (Michaletz and Johnson, 2007). In the Central Brazilian Amazon, another study showed that there was a significant additional mortality of large trees between 1 and 3 years after fire that reduced live tree density by a further 74 trees ha^{-1} (Barlow *et al.* 2003b). Holdsworth and Uhl (1997) also demonstrated that tree mortality was linked to the degree of fire damage, whilst Balch *et al.* (2011) found that trees that had died exhibited significantly higher char marks.

Surprisingly, although seedling and sapling were critically susceptible to one single fire event in both fuel conditions, we observed that thinner fuel layer resulted in 33% more unburned portions, which were significant to warrant survival of plants of smaller sizes ($\leq$ 1 cm in DBH). This result is attributable to reduced fuel and likely more understory moisture under portions of denser canopy, which combined, extinguished the fires (Ray *et al.* 2005; 2010). Thus, we highlight the importance to maintenance of undamaged canopy in fire prone-forests via controlling forest degradation.

Our findings indicated that eight months after fires the establishment mode of smaller individuals shifted, increasing single- and multi-stems originated from basal resprouts in both burning treatments compared with the *Control* plot, where the germination mode was dominant. This result can arise from differences in species-specific traits, which help to support the initial forest resilience to fires via resprout (Chapter 2 and 3; Balch *et al.* 2015). Comparing both treatments, the regenerating individuals had an expressive pulse, showing a trade-off between the density of resprouting and seeding species. Particularly, we witnessed an increase of emerging seedlings in *B+*, likely explained by the abundance of seeds arriving from seed rain in both fire treatments. According to Norden *et al*. (2007), the seeds reaching the forest floor or stored in the soil may contribute with the seedling assemblage being recruited after fire and, recruits from both patches were likely benefited of higher irradiance levels (Brando *et al.* 2016) and lower root competition after fires, predominantly where fires were more severe. These results indicate that the transitional forest even during extreme droughts periods, with increasing fuels, are still resilient to maintain some regenerating diversity after one fire event.

Our results suggest that increases in fine fuel addition and resulting fire severity may therefore have large effects on the forest by reducing diversity and carbon stocks in all size of plants in southeastern Amazon Basin. To minimize these effects, once severe droughts cannot be prevented, the only possibility is to control ignition sources and to maintain forest cover.

CONCLUSIONS

This study documents that accumulated fuel can affect negatively the transitional forest diversity after fires. Overall, we found that i) although smaller individuals were more likely to be killed by fires than large trees, fine fuel addition increased the mortality of larger individuals; ii) fuel addition also caused more damages, such as fire scars on the bole, which suggest further tree mortality; iii) unburned paths, which occurred in without litter addition treatment, may strongly contribute for surviving of small stems; iv) combined recruits, resprouts and surviving stems can slightly increment species richness in a short time, contrasting with extended loss of larger individuals. Due to current severe droughts are changing fuel loads all over the Amazon we emphasize the importance to control ignition sources and also to avoid canopy disturbance, such as caused by selective logging and forest fragmentation, particularly in fire sensitive zones, as is the case of transitional forest in southeastern Amazon Basin.

ACKNOWLEDGEMENTS

We thank all IPAM and LABRE-UEL for financial support. Raimundo M. Quintino, Sebastião Nascimento, Adilson R. Coelho and Darlisson N. Costa who provided valuable field assistance. RTSC benefited from a CNPq grant (process # 248491/2013-0, Science Without Borders program) during the study term at University of Colorado-Boulder, USA. JMDT grant 305854/2012-7.

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TABLES

Table 1. Branches with diameter smaller than 0.6 cm and between 0.6 to 2.5 cm of diameter, litter thickness, and dry biomass weight. Burned with fine fuel loads addition (*B+*), burned with no fuel manipulation (*B0*), and unburned site (*Control*). Transitional forest in southeastern Amazon Basin. Asterisks compare *B+* with *B0* using Kruskal-Wallis test: (*) p < 0.05 and (**) p < 0.01.

Treatments	Branch (< 0.6 cm)	Branch (0.6-2.5 cm)	Litter thickness (cm)	Biomass (g)
B+	12.5*	6.8	6.2**	64.5**
B0	8.9	4.9	4.4	43.8
Control	14.1	4.8	5.7	49.4

Table 2. Percent of total, tree, shrub and liana mortality per month. Pre- and post-mortality data were recorded ~20 months before and eight months after fire experiment, respectively. Individuals ≤ 1 cm DBH (including individuals between 5 and 130 cm height), within 1 to 5 cm DBH, and ≥ 5 cm DBH. Burned with fine fuel loads addition (*B+*), burned with no fuel manipulation (*B0*), and unburned site (*Control*). Fire experiment located in southeastern Amazon Basin.

DBH	Treat.	Total (%)		Tree (%)		Shrub (%)		Liana (%)	
		Pre	Post	Pre	Post	Pre	Post	Pre	Post
≤ 1 cm	*B+*	1,3	9,8	1,8	10,5	0,9	9,0	0,7	9,0
	B0	1,6	8,6	2,0	9,4	0,9	5,6	0,9	7,9
	Control	1,2	1,2	1,3	1,5	0,9	1,0	0,9	0,6
1-5 cm	*B+*	0,4	3,8	0,4	3,8	1,1	4,5	0,0	3,9
	B0	0,5	2,8	0,5	2,6	0,0	1,8	0,9	2,2
	Control	0,3	0,3	0,2	0,2	0,4	1,0	0,4	0,0
≥ 5 cm	*B+*	0,3	2,6	0,3	2,6	-	-	0,1	2,2
	B0	0,2	1,9	0,2	1,8	-	-	0,1	2,5
	Control	0,3	0,5	0,2	0,5	-	-	0,2	0,8

FIGURES AND LEGENDS

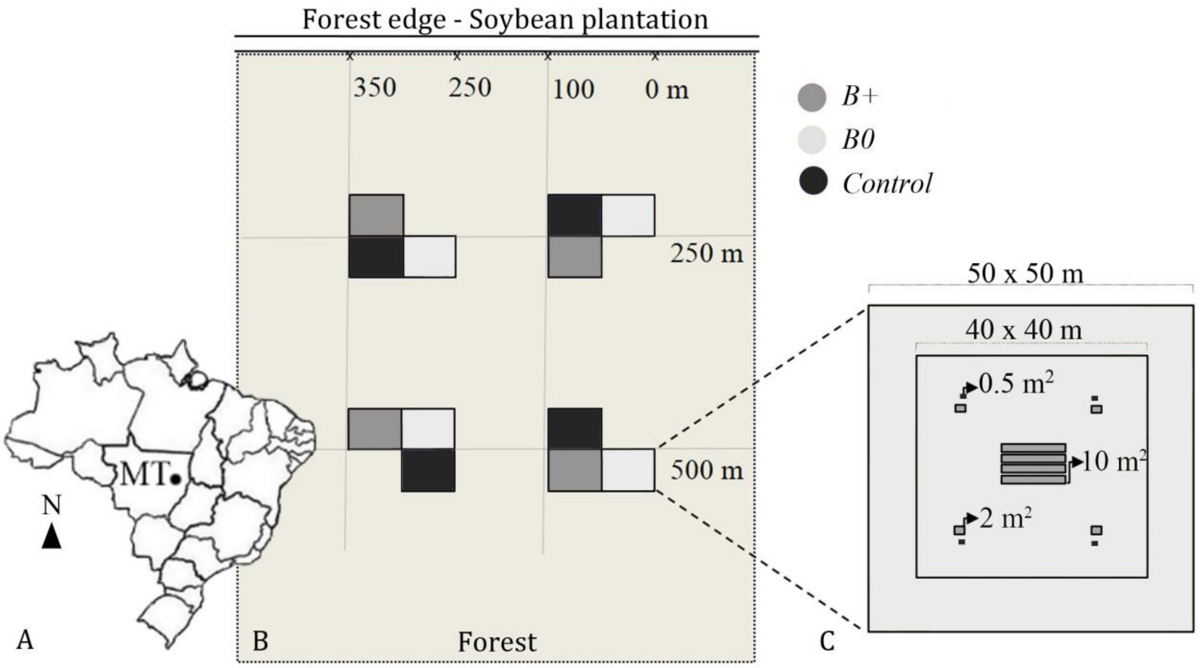

Figure 1. (A) Field experiment location in Mato Grosso state in southeastern Amazon Basin. (B) Design of field experiment showing the replicated burned plots (N=4): burned treatment with 50% fine fuel load addition (*B+*), burned in natural conditions (*B0*), and unburned control (*Control*). (C) Floristic inventory plots: individuals ≤ 1 cm DBH (including individuals between 5 and 130 cm height; 2 m^2; N=16), 1-5 cm DBH (10 m^2; N=16), and ≥ 5 cm DBH (40 x 40 m; N=4). Seed rain: 0.5 m^2 mesh traps (N=16).

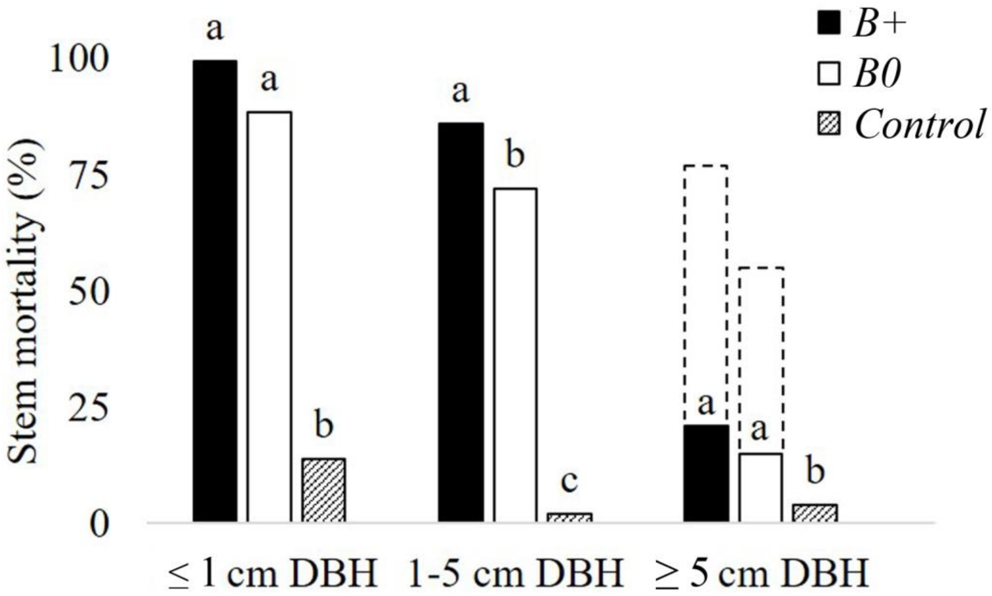

Figure 2. Columns represent the percent of total stem death after burning experiments by treatment and size classes in the southeastern Amazon Basin. Dashed columns represent the percent of surviving large individuals (≥ 5 cm DBH) showing fire scars on the trunks. Stems were grouped using the diameter at breast: DBH ≤ 1 cm (including the individuals between 5 and 130 cm height), 1-5 cm DBH, and ≥ 5 cm DBH. Black columns represent burned plots with 50% fine fuel load addition (*B+*), white columns, burned with no fuel manipulation (*B0*), and striped columns, unburned control (*Control*).

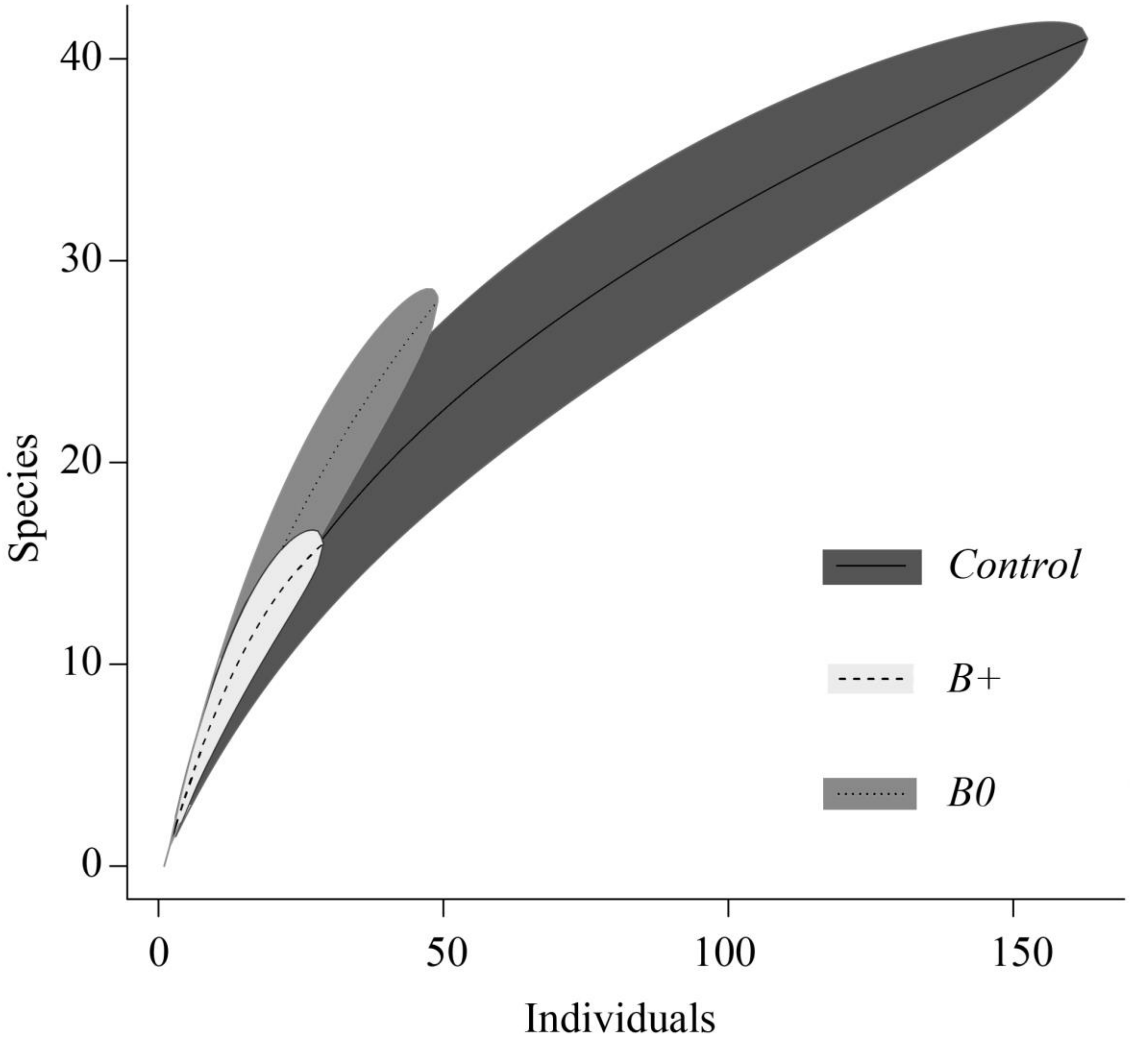

Figure 3. Accumulation curves for richness species by individuals. Surviving individuals of intermediate class (between 1 and 5 cm DBH) by treatment. Burned treatment with ≈50% more fine fuel load (*B+*), burned with no fuel load manipulation (*B0*) and unburned, as the control (*Control*), placed in the southeastern Amazon Basin. Using 95% of confidence interval.

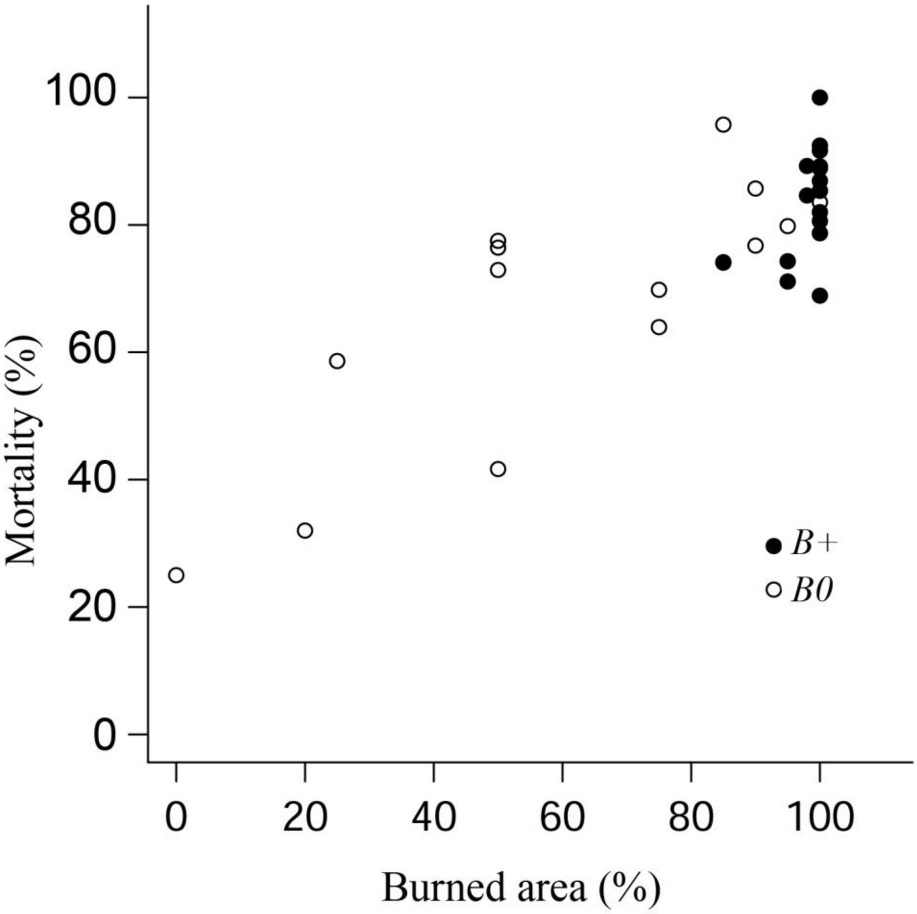

Figure 4. Correlation between the percent of burned area and percent of regeneration mortality, which showed no basal resprouts. Black dots indicate burned plots with 50% fine fuel load addition (*B+*) and hollow dots, burned with no fuel manipulation (*B0*). Experiment located in the southeastern Amazon Basin. Spearman's correlation, rho = 0.3682, p < 0.03.

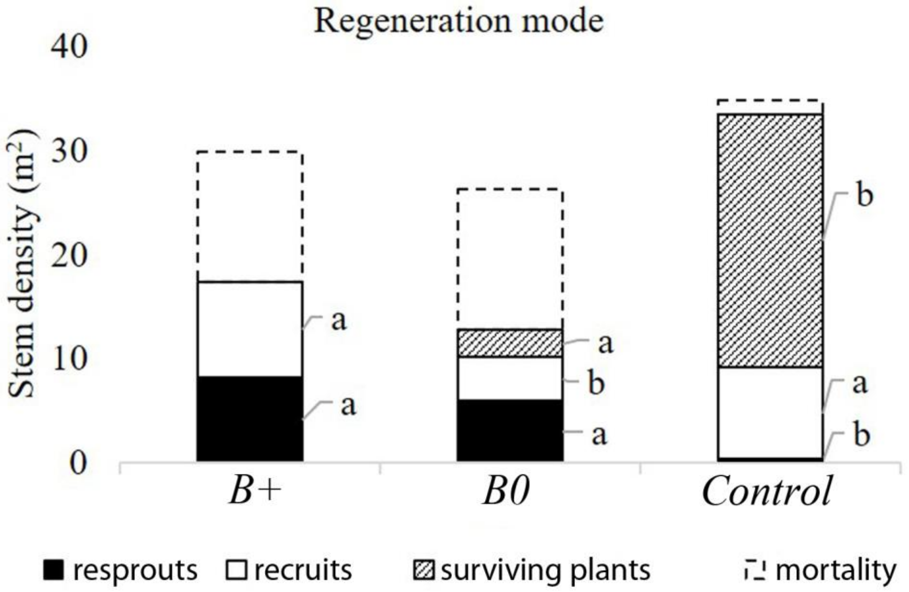

Figure 5. Classification of regeneration mode - resprouts, recruits and surviving individuals - of new plant community eight months after the beginning burning experiments. Dashed columns show plant density censed before fires. Burned treatment with ≈50% more fine fuel load (*B+*), burned with no fuel load manipulation (*B0*) and unburned control (*Control*), placed in the southeastern Amazon Basin. The same letters indicate no differences among treatments according to general linear model with Poisson family.

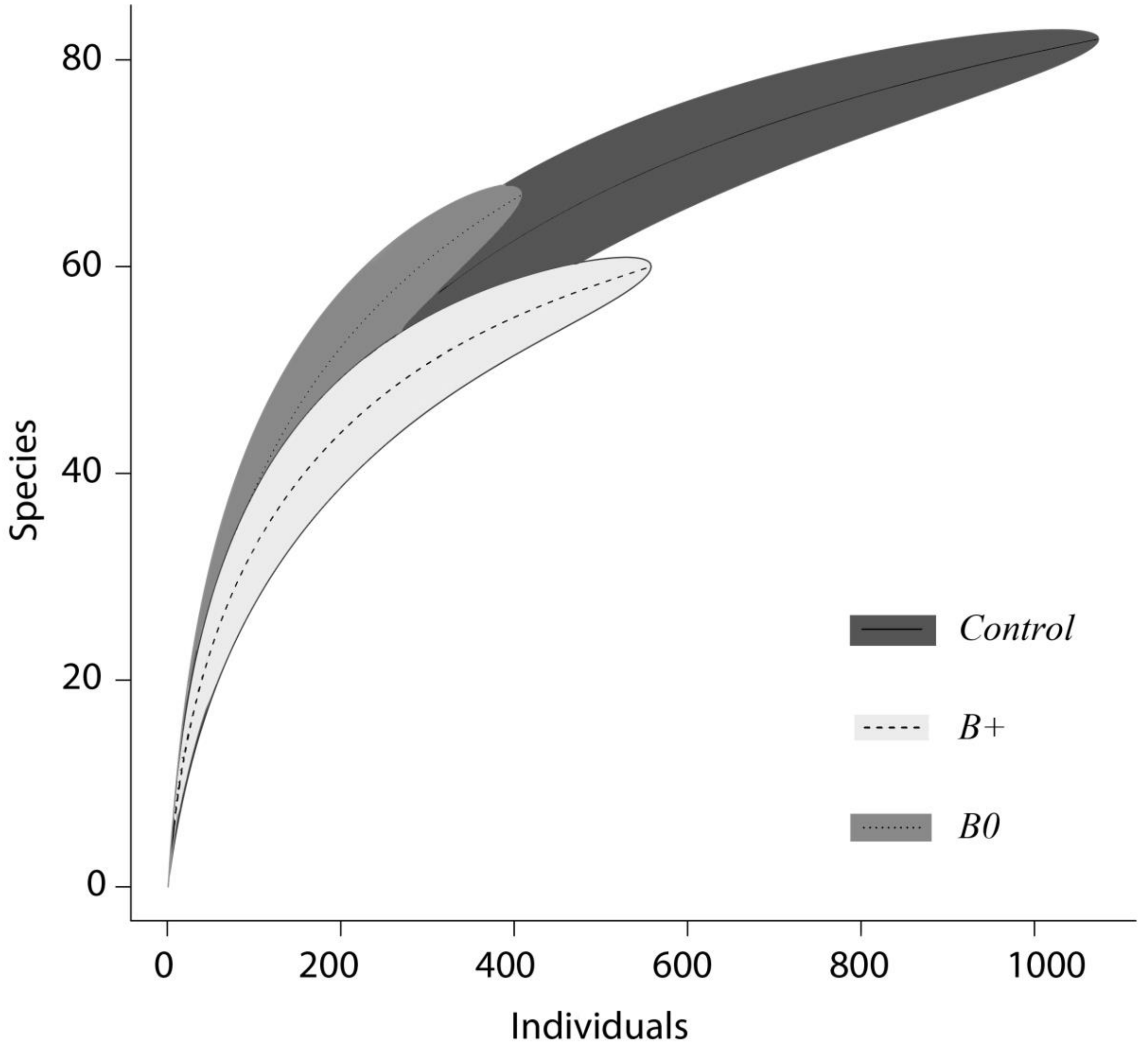

Figure 6. Accumulation curves for richness species by individuals. Resprouts, recruits and surviving individuals composing the regeneration community eight months after fires. Burned treatment with ≈50% more fine fuel load (*B+*), burned with no fuel load manipulation (*B0*) and unburned, as the control (*Control*), placed in the southeastern Amazon Basin. Using 95% of confidence interval.

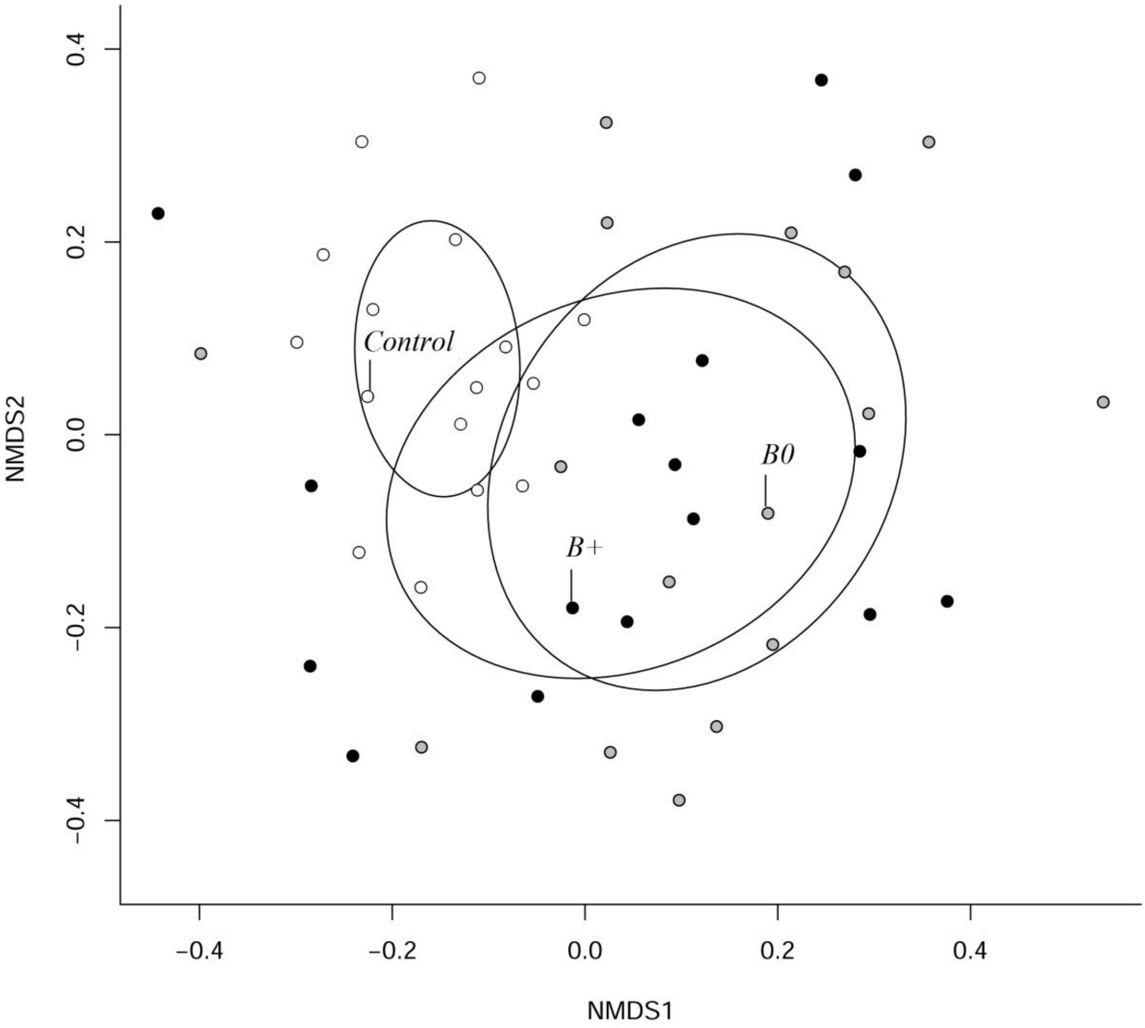

Figure 7. Analysis of similarities (ANOSIM) plot, based on nonmetric multidimensional scaling (NMDS - Bray-Curtis similarity index). Resprouts, recruits and surviving individuals composing the regeneration community eight months after fires. Burned treatment with ≈50% more fine fuel load (black dots; *B+*), burned with no fuel load manipulation (grey dots; *B0*) and unburned control (white dots; *Control*) placed in the southeastern Amazon Basin.

ANEXO 1. NORMAS DA REVISTA ACTA AMAZONICA

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21. Conclusions. This section should contain a concise interpretation of main results and a final message, which should highlight the scientific implications of the study. Write the conclusions in a separate section (one paragraph).

22. Acknowledgements should be brief and concise. Include funding agency. Do NOT abbreviate names of institutions.

23. References. At least 70% of references must be scientific journal articles. Citations should preferentially be from last 10 years. It is suggested not to exceed 40 references. They should be cited in alphabetical order of author names, and should be restricted to citation included in the text. If a reference has more than ten authors, use only the six first names and *et. al.* In this section, the journal title is NOT abbreviated. See the examples below:

a) Articles from periodicals:

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Articles from periodicals that do not follow traditional pagination:

Ozanne, C.M.P.; Cabral, C.; Shaw, P.J. 2014. Variation in indigenous forest resource use in Central Guyana. *PLoS ONE,* 9: e102952.

b) Dissertations and theses:

Ribeiro, M.C.L.B. 1983. *As migrações dos jaraquis (Pisces: Prochilodontidae) no rio Negro, Amazonas, Brasil.* Dissertação de Mestrado, Instituto Nacional de Pesquisas da Amazônia/Fundação Universidade do Amazonas, Manaus, Amazonas. 192p.

c) Books:

Steel, R.G.D.; Torrie, J.H. 1980. *Principles and procedures of statistics: a biometrical approach.* 2nd ed. McGraw-Hill, New York, 633p.

d) Book chapters:

Absy, M.L. 1993. Mudanças da vegetação e clima da Amazônia durante o Quaternário. In: Ferreira, E.J.G.; Santos, G.M.; Leão, E.L.M.; Oliveira, L.A. (Ed.). *Bases científicas para estratégias de preservação e desenvolvimento da Amazônia. v.2.* Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, p.3-10.

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Accessed on 19/05/1999.

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FIGURES

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Capítulo 2

Higher fire frequency impaired woody species regeneration in a transitional forest of southeastern Amazonia

Journal of Tropical Ecology

Title: Higher fire frequency impaired woody species regeneration in a transitional forest of southeastern Amazonia

Short title: Fire effects on regenerating plant diversity

Key Words: Cerrado, Deforestation, Experimental burn, Fire Ecology, Land-use change, Mato Grosso, Recruitment, Resprout, Savannization, Tropical Forest

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Abstract: Understory wildfires affect natural regeneration in tropical forests, but the recovery trajectories of fire-disturbed forests after disturbance are poorly understood. To fill this gap, we conducted experimental burns in a transitional forest between the Amazonia and the Cerrado Biome and investigated their effects on regenerating plant community. First, we investigated the effects of fire-frequency on diversity of early regenerating community. Second, we analyzed the proportions among Amazon and Cerrado (*lato sensu*), late and early successional, and among tree-shrub and liana species. Then, we examined grass cover by fire treatment and edge distances. Finally, we analyzed the contribution of sprouting for persistence of native tree species. The experiment consisted of three 50-ha plots. One was burned six-times annually (B6), another burned three-times triennially (B3) and the last was not burned at all (Control-B0). The diversity of tree species (recruits and resprouts) was reduced in B6 compared with B3 (-62% richness and -84% abundance), while both treatments were reduced compared with B0. The treatment B6 was also associated with more negative floristic changes, led to dominance by few species early successional species, such as *Myrcia multiflora* and *Pyrostegia venusta*, and allowed increased grass colonization when compared with B3. We observed that resprouts were the main pathway for forest restoration in both burned regimes, particularly in B3, likely explained by the three years interval between fires which allowed greater growth of saplings and more vigorous resprouting. Transitional forests can recover from fires by resprouting until a threshold in fire frequency is reached, when resprouts declined for most of the species, with a few fire-tolerant species becoming dominant.

Resumo: Incêndios rasteiros alteram a regeneração natural em florestas tropicais, no entanto as trajetórias envolvidas na recuperação dessas florestas degradadas são pouco conhecidas. Para preencher esta lacuna, foram conduzidos experimentos com incêndios em uma floresta transicional entre a Amazônia e o Bioma Cerrado e investigados os seus efeitos na comunidade de plantas em regeneração. Primeiro, foram investigados os efeitos da frequência dos incêndios na diversidade da comunidade regenerante. Segundo, foram analisadas as proporções entre espécies Amazônicas e de Cerrado (*lato sensu*), tardias e iniciais na sucessão e entre arbóreas-arbustivas e lianas. Ainda, foram examinadas a ocorrência de gramíneas por tratamento e pela distância da borda. Por fim, foram analisados a contribuição das rebrotas para a persistência das espécies arbóreas nativas. O experimento foi conduzido em três parcelas de 50-ha. Uma queimada seis vezes anualmente (B6), outra queimada seis vezes trienalmente (B3) e uma não queimada (Controle-B0). A diversidade de espécies arbóreas (recrutas e rebrotas) foi reduzida em B6 em comparação com B3 (-62% de espécies e -84% de abundância), enquanto que ambos os tratamentos sofreram perdas quando comparados com B0. O tratamento B6 também resultou em alterações negativas na composição florísticas, favorecendo a dominância de poucas espécies arbóreas, como *Myrcia multiflora* e *Pyrostegia venusta*, e aumentando na colonização por gramíneas quando comparado ao tratamento B3. Houve aumento das rebrotas em ambos os tratamentos, especialmente no tratamento B3, tornando-se o principal meio para a restauração florestal, provavelmente devido ao intervalo entre os incêndios que permitiu maior crescimento das plântulas e rebrotas mais vigorosas. A Floresta de transição pode se recuperar dos incêndios via rebrotas até um limiar de frequência de incêndios, após esse limiar ser atingindo, a maioria das espécies declinam, quando poucas espécies tolerantes ao fogo se tornam dominantes.

INTRODUCTION

In the 1970s, a new frontier of Amazon deforestation advanced over the southern and eastern portion of the Basin. During this process, large tracts of forests were converted primarily into pasturelands and more recently also into soybean fields (Brando *et al*. 2013, Davidson *et al*. 2012, Fearnside 2005, Nepstad *et al*. 2008). This frontier expansion was accompanied by the use of fire to remove fallen forests and manage pastures (Mendonça *et al*. 2004, Nepstad *et al*. 2001). Unfortunately, these fires commonly escape into adjacent forests (Mendonça *et al*. 2004), especially during severe drought episodes (Alencar *et al*. 2006).

Wildfires are not common in humid tropical forests, explaining why most rainforest species are not adapted to fire (Brando *et al*. 2012, Slik *et al*. 2010), contrasting with tropical savanna species, which evolved under much higher natural rates of fire (Hoffmann *et al*. 2003). Additionally, forest fragments are particularly vulnerable to fires given that their edges are drier and warmer than forest interiors (Cochrane & Laurance 2002) and with more fuel load, such as biomass of grasses. Fire is a strong driver of change in plant community in tropical forests, as even a single, low-intensity fire event can reduce soil seed bank, and density of seedlings and saplings (Balch *et al*. 2011, Balch *et al*. 2013, Slik *et al*. 2008). Besides, regeneration mode can also be altered according to fire frequency and intensity, by means of an increase in sprouting and decrease in seedling regeneration (Balch *et al*. 2013).

This is also true for the “transitional forests” of southeastern Amazonia, a formation with an original extent of 400,000 km^2 and adjacent to the Cerrado Biome (the Brazilian savanna; Kunz *et al*. 2009). This forest has a marked dry season, with five months in the year with precipitation lower than 10 mm (Rocha *et al*. 2014), which make this forest more susceptible to fire recurrence. After several fires, those forests become impoverished, with lower tree species richness and increasing dominance by lianas, early succession species (Balch *et al*.

2011) and graminoids (Silvério *et al*. 2013) under an open overstory of scattered trees. This formation has been called “derived savanna” (Veldman & Putz 2011), however, these ecosystems should be very different from the species-rich Cerrado Biome (Balch *et al*. 2009, Cochrane & Schulze 1999, Cochrane *et al*. 1999, Veldman & Putz 2011). Nonetheless, it is not clear whether such derived savannas are stable, resilient ecosystems, or if the burned forests retained some resilience itself and thus are able to recover after a time without fire. And, if different fire frequencies could result in more or less harm to forest resilience.

The resilience of the forest after fire events is key to understand the likelihood of the replacement of forests by derived savannas. Long-term recovery of aboveground biomass, ecosystem function and diversity in burned forests are largely dependent on successful of early post-fire regeneration (Slik *et al*. 2008). However, post-fire succession under the current increasing fire regimes remains unknown. In this context, the present study aimed to investigate the effects of two different fire frequencies - burned 3 and 6 times in 7 years - on forest regeneration, two years after the last fire burning experiment in the transitional forest between Amazon and Cerrado.

First, we analyzed how much of the transitional forest species were co-occurring in the adjacent physiognomies of Cerrado Biome, such as Cerrado *stricto sensu,* Cerradão, riparian forest, and open areas in this Biome. Also, how much of the transitional forest species (pioneer and early secondary species) were colonizing secondary forests, likely increasing the tolerance of the Amazon to fire degradation by means of an increase of diversity of regenerating woody plants. Second, we asked the following questions to elucidate how increasing fire frequency affects forest regeneration: i) Is the diversity of tree species regeneration - a good indicator of future forest condition - still altered two years after fire exclusion? ii) Is there an increased recruitment of Cerrado, early successional or liana species after several fires? iii) Is there an increase in grass cover, which can be predicted by fire frequency and/or edge effects, increasing competition? iv) What is the contribution of sprouting for persistence of native tree species?

STUDY SITE

A large-scale burning experiment was conducted in a primary forest, located in the Brazilian Amazon (IBGE 2014), in the southern boundary of the Amazon rainforest and Cerrado Biome, in a privately owned farm (Fazenda Tanguro, ≈ 80.000 ha) in the state of Mato Grosso, Brazil (13º04' S; 52º23' W). Experimental fires were conducted from 2004 to 2010 (except for 2008), during late dry season (August), when accidental wildfires are common in the region. The experimental site occupied 1.5 x 1.0 km (150 ha) and was divided in three plots of 0.5 x 1.0 km (50 ha; Figure 1): control (unburned plot; B0), burned triennially plot (burned three times; B3) and burned annually plot (burned six times; B6). Fires were set with kerosene drip torches along the north-south trails, during three to four consecutive days between 9:00 and 16:00 hours. During the fire events, temperature and humidity were around 26.5ºC and 54%, respectively. Details about the experimental design and fire behavior are referred in Balch *et al.* (2008).

The vegetation is classified by IBGE (2012) as Evergreen Seasonal Forest, with deciduousness on dry season lower than other Brazilian seasonal forests (see detail about aboveground biomass, canopy height and canopy density in Balch *et al*. (2008). According to Köppen's classification, the climate is tropical Aw, with an average annual precipitation of 1,700 mm (data from 2004 to 2011; Rocha *et al.* 2014), with the rainy season extending from September to April, and the dry season between May and August, when precipitation typically is below 10 mm per month (Rocha *et al.* 2014). During the dry season, the average temperature was 25 °C and relative humidity was 66% (average daily values used to calculate in 2004-2006; Balch *et al.* 2008). Soil is classified as dystrophic red-yellow Oxisols, with a sandy clay texture and flat terrain (IBGE 2009). It is also deep, well drained, and with low natural fertility (IBGE 2007).

METHODS

Regeneration sampling

In 2012, two years after the last experimental burn (2010), we sampled seedlings and saplings (*i.e.*, recruits and resprouts) of tree and liana species in 90 sub-plots of 0.5 m^2 in each one of three 50-ha plots. All plants with stems ≤ 1 cm DBH (diameter at breast height or 130 cm above ground), including individuals between 10 and 130 cm in height were recorded. Ten sub-plots were distributed along 0, 10, 15, 30, 50, 100, 250, 500 and 750 m from the edge with agriculture area into the forest (Figure 1). The regeneration mode (seeds or resprouts) of all regenerating plants was also recorded through small excavations. Grass cover percentage was estimated in all sub-plots, and grass clumps were counted.

We collected floristic samples and identified it using the botanical collection of IPAM and the herbarium NX at Universidade do Estado de Mato Grosso at Nova Xavantina campus and Universidade Estadual de Londrina (UEL). Species names followed the Missouri Botanical Garden – TROPICOS database (www.tropicos.org). Tree species were categorized by occurring in transitional forest exclusively and in transitional forest co-occurring in different physiognomies of Cerrado Biome. The species were also classified by successional stage (*i.e.*, early or late successional). Both classifications were made checking published floristic inventories conducted in 13 Cerrado *lato sensu* and in 19 secondary forest (see Appendix 1 for species list, Appendix 2 for species occurrence and successional status classification).

Lianas were not classified due scarcity of specialized literature, except the most abundant liana species, *Pyrostegia venusta*.

Data analysis

To evaluate the degree in which fire disturbance affects diversity of woody species regeneration, we analyzed species richness (*i.e.*, how many species) and abundance (*i.e.*, how many individuals) using individual-based species accumulation curves (Colwell *et al*. 2004). Community composition (*i.e.*, which species) and structure (*i.e.*, how many of each species) was analyzed using nonmetric multidimensional scaling (NMDS) ordination, generated from a Bray-Curtis dissimilarity matrix (Legendre & Legendre 2012), and compared by means of an Analysis of Similarity (ANOSIM test; Clarke 1993). The analyses were performed using R (R Core Team 2014) and the package Vegan (Oksanen *et al*. 2013).

We also compared rank abundance distribution using a Whittaker plot (Magurran 2004). We compared Shannon-Wiener index (H'; used for evaluated the contribution of rare species) and Simpson's (1-D'; that describes species evenness) diversity indexes between two samples (B0 and B3, B0 and B6, and B3 and B6) with t-test. Finally, percentage of floristic similarity was also estimated using Jaccard index (Magurran 2004).

To test if repeated burns, B3 and B6, can increase the occurrence of Cerrado, early successional and lianas species, we compared the species proportions by category using Chi-Square test (X^2). In addition, we performed similarity percentage analysis (SIMPER), which provides the contribution of each species for the dissimilarity between treatments (Clarke 1993). We also performed an IndVal test to detect which species are associated with each treatment.

To test the importance of sprouting for the maintenance of tree species regeneration, we compared the proportions between sprouts and seedling and saplings with Chi-Square (X^2)

with treatments and control site. Richness of Forest and co-occurring in Cerrado Biome, early and late succession, lianas and trees, resprouts and recruit species and the percentage of grass cover (0-250 m and 0-750 m) and the number of clumps were compared among treatments with analyses of variance test (ANOVA). Non-normal data (forest and late successional categories, recruits and number of clumps) were transformed by square root (Zar 1999).

RESULTS

Reduction of species diversity

Combined, the burned and unburned treatment plots, tree species comprised 46 species (353 live stems) of recruits and sprouts, which were distributed across 27 botanical families (See sampled species list in the Appendix 1).

Overall, species regeneration diversity was still altered two years after the last fire. The accumulation curve showed a loss of 69% tree species in B6 and 17% in B3, compared with B0 (B6, B3 and B0 had 11, 29 and 35 tree species, respectively; Figure 2). Also, we observed notable reduction of recruits and resprouts of tree diversity in B6 compared with B3 treatment (62% less species and 84% live stems in B6). Likewise, both burned treatments reduced regeneration abundance compared with B0 (N = 197; 4.4 individuals.m^{-2}), however, the number of live stems was much lower in B6 (N = 36; 0.8 individuals.m^{-2}), where the abundance was 81% lower than in the control B0, than in B3 (N = 120; 2.7 individuals.m^{-2}).

Lianas comprised 37% of total species richness (S = 27) and 31% of total abundance (N = 157) of all woody plants measured in regeneration of all plots (Appendix 1). Lianas, also, exhibited the same pattern as the trees, with a loss of species in B6 (S = 6), in comparison with B3 (S = 15) and B0 (S = 19; $F_{(2,24)} = 6.379$, $P < 0.001$).

The understory community composition and structure, including recruits and resprouts of tree and liana species, were also different between B6 and B0, while B3 partially shared species with both, B0 and B6 study sites (ANOSIM: R = 0.208, $P < 0.001$; Figure 3).

The diversity of species, considering the Shannon-Wiener index, was lower in B6 [H' = 1.99 (*t* test; $P < 0.001$)] and similar between B0 (H' = 2.87) and B3 (H' = 2.69). Likewise, the diversity of species according to Simpson's index (1-*D*), was slightly lower in B6 (1-*D* = 0.82) compared with the control site (1-*D* = 0.90; *t* test, $P = 0.05$), while B0 and B3 (1-*D* = 0.88) had no differences. Using Jaccard's index, there was 30.3% of tree floristic similarity between B0 and B3, 11.3% between B0 and B6 and 11.3 between B3 and B6. Likewise, the set of liana species showed low floristic similarity between B0 and B3, with 16%, B0 and B6, with 6.5% and B3 and B6 6.5%.

Woody tree and liana species turnover

Species that are also found in the Cerrado Biome (vegetation physiognomies) accounted for 74% of the species and 77% abundance growing in B0. Cerrado Biome and Amazonian species declined by the same proportion in both treatments (~74%) and in B0 (~80%; not differing by Chi-Square test; Figure 5A). However, although Cerrado Biome species had reduced by the same proportion across treatments and B0, the absolute amount of Cerrado Biome species were strongly affected in B6, with more than 60% of species loss in comparison with B0 and B3 ($F_{(2,24)} = 5.80$, $P < 0.01$). Similarly, B6 also had a decrease in the amount of forest species richness comparing to B0 and B3 ($F_{(2,24)} = 13.8$, $P < 0.001$), with 78% less forest species than in B0.

The two burning regimes caused a decline in plant diversity and a shift in species community toward greater abundance of early successional and liana species, particularly in B3. We recorded a lower absolute number of early successional species in B6 than both B3 and B0

($F_{(2,24)}$ = 6.15, $P < 0.01$; Figure 5B) but, after six annually fire events (B6), the proportion between late and early species changed. All species in B6 were early successional species, while B0 exhibited 61% of such species (x^2 = 6.15, g.l. = 1, $P < 0.05$). In contrast, late successional species richness decreased from B0 to B3, and they were completely excluded from B6 (Kruskal-Wallis = 11.74, d.f. = 2, $P < 0.01$; Figure 5B).

Two species, *Marlierea umbraticola* (IndVal = 0.716, $P < 0.05$) and *Tachigali vulgaris* (IndVal = 0.617, $P < 0.05$) occurred only in B3. On the other hand, five species were recorded only in B0, such as *Protium guianensis* (IndVal = 0.764, $P < 0.001$), a late successional, forest tree species, with 6% of contribution to community dissimilarity.

The regenerating community showed the strong contribution of *Myrcia multiflora*, *Pyrostegia venusta* and *Mabea fistulifera* in B3 treatment compared with B0, where *Elachyptera floribunda* the most contributed for the sample (SIMPER test; Appendix 3). Also, *M. multiflora* and *M. fistulifera* comprised almost 42% of individuals in B3 and 30% in B6, against 15% in control site, reinforcing the floristic dissimilarity between the burned treatments and the control. Whittaker plot also showed the higher dominance *M. multiflora* e *P. venusta*, both early successional species in B3 and in B6 (Figure 4).

Liana species reduced by the same proportion across burned treatment and B0 (≈34%), however, their total abundance where smaller in B6 compared with B3 and B0 (Figure 5C). The liana *P. venusta, a* wide spread ruderal species (Flora do Brasil 2016), alone showed expressive abundance in both burned plots, accounting for more than 42% of total liana stems in each B3 and B6 treatments, about 3.5 times more than registered in B0 (11%).

Establishment of resprouts and recruits

There was a significant increase in sprouting individuals from B0 (21%) to B6 (55%) and to B3 (79%). Seventy-nine and 65% of total sprouting individuals in B3 and in B6, respectively, came from species that also occur in the Cerrado Biome versus 31% in B0. We also noted the threshold of fire resistance was reached in B6, when resprouts and recruits declined for most of the species.

Although resprout number increased in both burning treatments, the B3 treatment presented higher species richness ($F_{(2,24)} = 10.49$, $P < 0.001$; Figure 5D) and abundance ($F_{(2,24)} = 7.05$, $P < 0.01$) of regenerating resprouts. Although, there was a decrease in recruit species richness in both fire treatments ($F_{(2,24)} = 13.86$, $P < 0.001$; Figure 5D), B6 had four times less species and 9.6 times less live stems recruited by seeds in comparison to B0

Overall, 62% of the species resprouted after fire treatments, highlighting a clear change in regeneration mode in both burned sites. B3 exhibited a remarkable inversion of proportion of resprouting-originated species (76%; $x^2 = 18.19$, df = 1, $P < 0.01$; Figure 5D) than B6. The same pattern was observed for the resprout abundance with 79 % of sprouts in B3 ($x^2 = 101.68$, df = 1, $P < 0.01$) and 55% in B6 ($x^2 = 71.68$, df = 1, $P < 0.01$) when they were compared to B0 (21%).

Grass invasion and competition

Both burned regimes showed expressive invasion by grasses. However, the grasses were observed mainly from cleared edge (0 m) up to 250 m in both burned treatments, but occurred only at the border in B0 (<10 m) and were virtually absent in the forest interior. Moreover, grasses covered 50% of the plots in B6, against 14.5% in B3 and 2.5 in B0 ($F_{(2,18)} = 10.06$, $P < 0.001$; Figure 6), from 0 to 250 m from the cleared edge. Likewise, the number of clumps increased in B6, reaching 53% in B6 against 38% in B3 and 9% in B0 ($F_{(2,18)} = 6.3$, $P < 0.01$). We identified nine grass species in total (Table 1). *Aristida longifolia* was the most abundant, accounting for 94% of all clumps recorded. Another 6% of grass cover corresponded to a mix of native and exotic especies, such as *Steinchisma laxum* (Sw.) Zuloaga, and *Andropogon gayanus* Kunt., an invasive African grass (Rossiter-Rachor *et al*. 2009). When we analized establishment of woody tree species (Figure 7A) and grass cover (Figure 7B) along the cleared edge up to 750, we also noted a reduction of grass cover in 0 to 10 m where regenerating tree species (recruirts plus resprouts) were more adundant in B3.

DISCUSSION

Fire has been reported as hindering the regeneration process and harming tropical forest recovery, mostly because their species cannot endure fire damage (Slik *et al*. 2008, Slik *et al*. 2010). Here, we witnessed different patterns in vegetation responses to both fire frequencies, which drastically altered negatively forest recovery compared with B0.

In fact, two years was not enough time for the forest to recover, particularly in B6 (*i.e.*, lose 77% of recruits and 45% of sprout-based regeneration species when compared with B0). First, the reduced number of seeds could be one driver of the lower recruit species observed in both fire treatments, as higher mortality of reproductive trees was observed (Brando et al. 2014), likely reducing local seed rain (Barlow & Peres 2006). Second, the soil seed bank could also be affected by repeated fires, as it has been documented in other studies (See Chapter 3; Barlow & Peres 2006, Melo *et al*. 2007, Montibeller-Santos 2013). Third, seed predator populations may increase (*e.g.*, leaf-cutting ants; Carvalho *et al*. 2012, Massad *et al*. 2013), leading to higher pressure on remaining seeds, seedlings and saplings. Fourth, the number of suitable microsites for seed germination could be reduced as humidity drops and temperature increases due to loss of canopy cover (Balch *et al*. 2015). Jointly, these factors may be impairing forest restoration from seeds to seedling recruitment.

The most remarkable result of this experiment was to find a critical threshold of Amazon forest resilience to fires. Comparing burned treatments, B3 were not necessarily a threshold for regenerating plants, and tended to cause less harm to regenerating woody plant richness and abundance, mainly through allowing for the regrowth of native woody species by means of resprouting, more than in B6, which led to a strong decline in the forest resilience.

The three-year interval between fires in B3 allowed a regrowth of saplings (Grady & Hoffmann 2012) and a vigorous sprouting ability for some species, thus maintaining the plant community composition and structure more similar to B0. While, B6 could be annually eliminating all aerial biomass of juveniles, suggesting a reduction in root and shoot sprouting capacity and, consequently, sprout-originated stems (Bond & Midgley 2001, Vesk 2006, Grady & Hoffmann 2012). As a result of B3, root-sprouting became an important trait for forest regeneration process, increasing the abundance of live stems and favoring self-replacement of damaged individuals after stem death (Bellingham & Sparrow 2000, Bond & Midgley 2001), likely explaining the similarity of observed diversity (*e.g.*, *H’* = 1.99 in B6, *H’* = 2.69 in B3, and *H’* = 2.87 B0).

Although most rainforest species show little or no fire tolerance (Hoffmann *et al.* 2003), we have found that most of the tree species present in our sample of transitional forests also occur in the Cerrado Biome (74% of the species were listed in 15 compilations of floristic inventories in different physiognomies in the Cerrado Biome; Appendix 2). Thus, the species in transitional forests may have evolved with some degree of fire adaptation, which may contribute to some degree of resilience in burned forests. In our study, more than 79% of all sprouts originated from species also occurring in Cerrado Biome. Hoffmann *et al.* (2003) emphasized the species similarity between Cerrado Biome and Amazon-Cerrado transitional forest and suggested that these forests should have high sprouting ability, presenting higher carbohydrate content in the roots than in the stem, which can help to explain the higher proportion of basal sprouting, mostly in the plot B3.

We also observed that, although the B3 plot exhibited regenerating species richness and abundance more similar to B0, both burned forests had substantial changes in community structure and composition. The high proportion of early successional species in these transitional forests (around 63%) could also help to enhance forest recovery in B3 scenario, given the potential of these fast-growing tree species to colonize open sites (Slik *et al.* 2008).

We registered that both fire frequencies favored liana and grass invasion. In the B3, the high mortality of large trees (*e.g.*, increase in fire-induced adult tree mortality by 462% during drought events in 2007; Brando *et al.* 2014) and reduced canopy cover (Balch *et al.* 2011) favoring germination and establishment of invasive species (Nepstad *et al*. 2008, Silvério *et al*. 2013, Veldman & Putz 2011). Contrastingly, in the B6, where fire slowly moved through the forest understory, more negative effects were observed on regenerating plants. Probable, there was a reduction in the number of regenerating native species and in the abundance of juveniles, followed by dominance by a single liana species (*P. venusta,* a ruderal species; Pool 2008) and invasion by a grass species (*A. longifolia,* a native C3 grass, lower light requirement species; Cerros-Tlatilpa & Columbus 2009). These favored species may outcompete with seedlings of native trees species, likely explaining the increase of woody tree species versus the reduction of grass cover near the cleared edge in B3 (Gunaratne *et al.* 2010; Silvério *et al.* 2013). Furthermore, the grass species showed a gradual invasion into the burned forest (*e.g.*, 0 to 250 m from cleared edge), which points to a positive feedback cycle among fuel accumulation, drought and new fires (Balch *et al.* 2008, Brooks *et al.* 2004, Cochrane *et al.* 1999, Silvério *et al.* 2013).

In conclusion, our results point to two main findings. First, B6 led to higher loss in the diversity of native forest species and greatest increase in heliophytic and ruderal species, such as disturbance-adapted liana and grass species (*P. venusta* and *A. longifolia*, respectively). This increase in opportunistic species can increase the likelihood of future fire events given the increase in fine fuels and compete with native tree species. Second, a massive regeneration from resprouting may be a result of many species in the transitional forests also occur in the Cerrado Biome and are supposed to be more fire-adapted than forest-only species, while seedling regeneration was scarce. However, we highlight that resprouting ability also decreased with B6, such as observed in other studies in Cerrado, showing a threshold in forest ability to regenerate by resprouting. Long-term monitoring is essential to understand how these patterns will change in the future, in scenarios with or without fire suppression, shedding light on whether these forests can recover from fire disturbance or transition into stable derived savanna ecosystems.

ACKNOWLEDGEMENTS

We thank all IPAM and LABRE-UEL for financial support. IPAM staff for help in fieldwork. A. Bordignon and G. Gonzaga helped in species classification. Dr. E. Bianchini, Dr. J. E. Ribeiro, Dr. W. Zangaro-Filho, R. Moratelly, C. Montibeller-Santos, Nicole Cury and Tyler Lagasse provided helpful suggestions on an earlier draft of this paper. Roberta T. S. Cury benefited both from a CAPES and CNPq grant (248491/2013-0) and José M. D. Torezan from a CNPq research grant (process # 305854/2012-7).

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TABLES

Table 1. Species, number of clumps, photosynthetic metabolism and distribution of all grasses sampled in unburned site (B0), triennial burns (B3) and annual burns (B6) registered two years after fire exclusion. SAm = South America, CAm = Central America, NAm = North America, Aus = Australia, Afr = Africa, As = Asia.

Species	Clumps/Treatment			Phot.	Distribution
	B0	B3	B6		
Andropogon gayanus Kunth		10	26	C4	Afr; Aus; SAm; Cam
Andropogon leucostachyus Kunth		2		C4	SAm; CAm
Aristida longifolia Trin.	147	607	839	C3	Sam
Digitaria insularis (L.) Fedde		1		C4	SAm; CAm; NAm; As
Imperata brasiliensis Trin.		1		C4	SAm; CAm; Nam
Pennisetum setosum (Sw.) Rich.		8		C4	SAm; CAm; Nam
Setaria parviflora (Poir.) Kerguélen		2	14	C4	Afr, As, Sam
Steinchisma laxum (Sw.) Zuloaga	2	17	11	C4	SAm; CAm; Aus,
Streptogyna americana C.E. Hubb.	4			C3	CAm; Sam

Source: www.tropicos.org

FIGURES AND LEGENDS

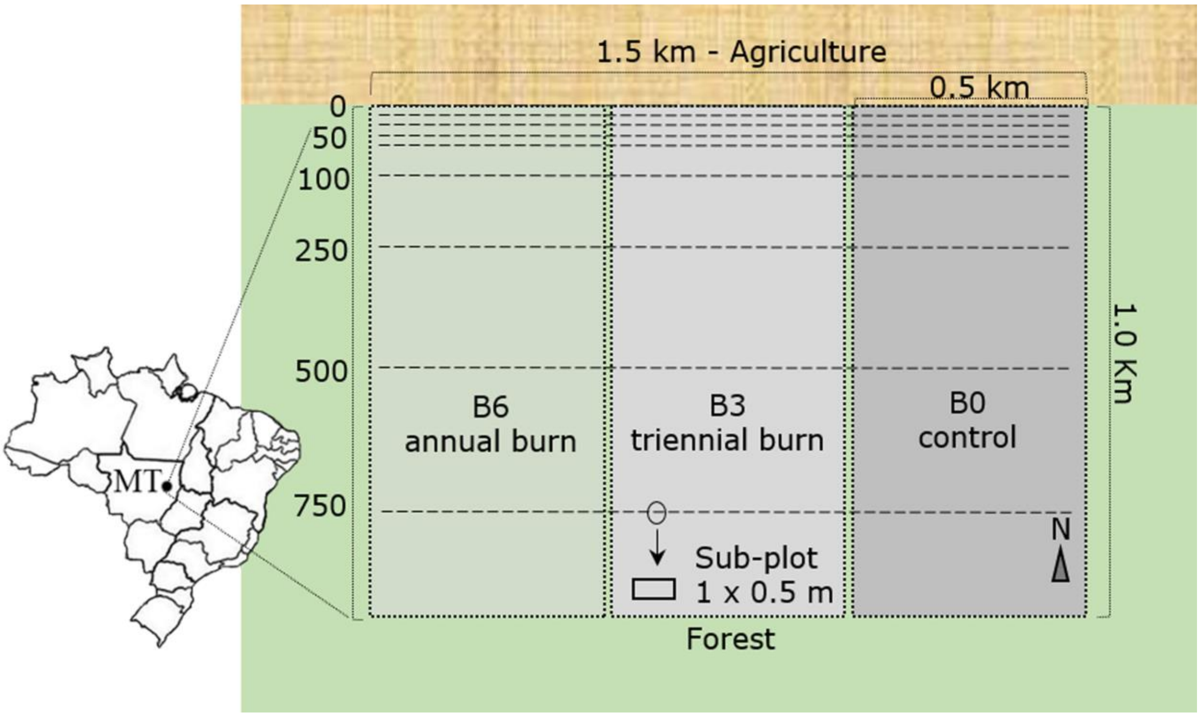

Figure 1. Delimitation of burned plots and regeneration sub-plots located in a mature forest, southeastern Amazon Basin, Brazil. Unburned control (B0; 50 ha), burned three times, triennially (B3; 50 ha) and burned six times, annually (B6; 50 ha) plots. Each plot contains 90 sub-plots of 0.5 cm^2, distributed in nine distances from the edge to forest interior (represented by dashes).

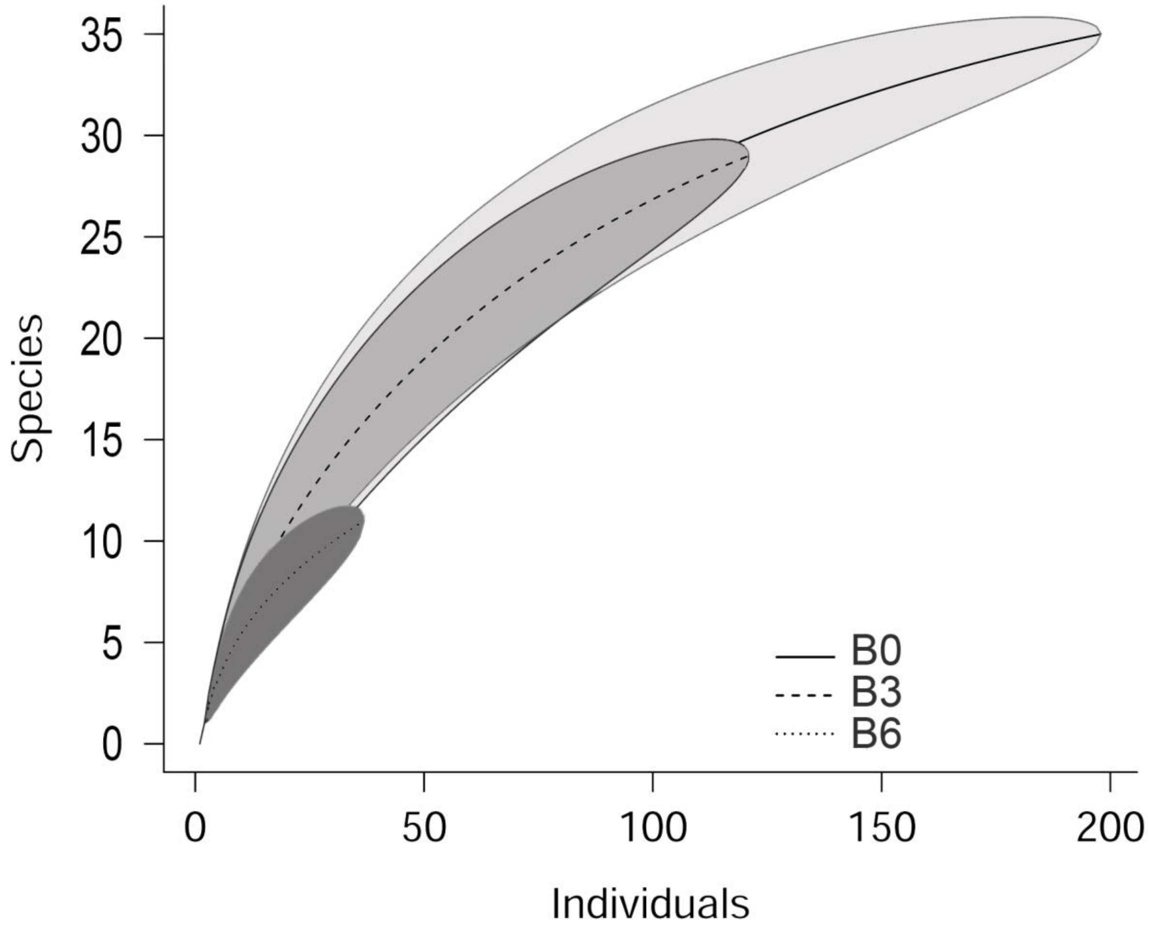

Figure 2. Accumulation curve for tree species recruits and resprouts with stems ≤ 1 cm DBH (including individuals ≥ 10 cm in height and until 130 cm height) sampled two years after the last fire in unburned, triennial burns (burned thrice), and annual burns plots (burned six times). Gray shaded area denotes 95% confidence interval.

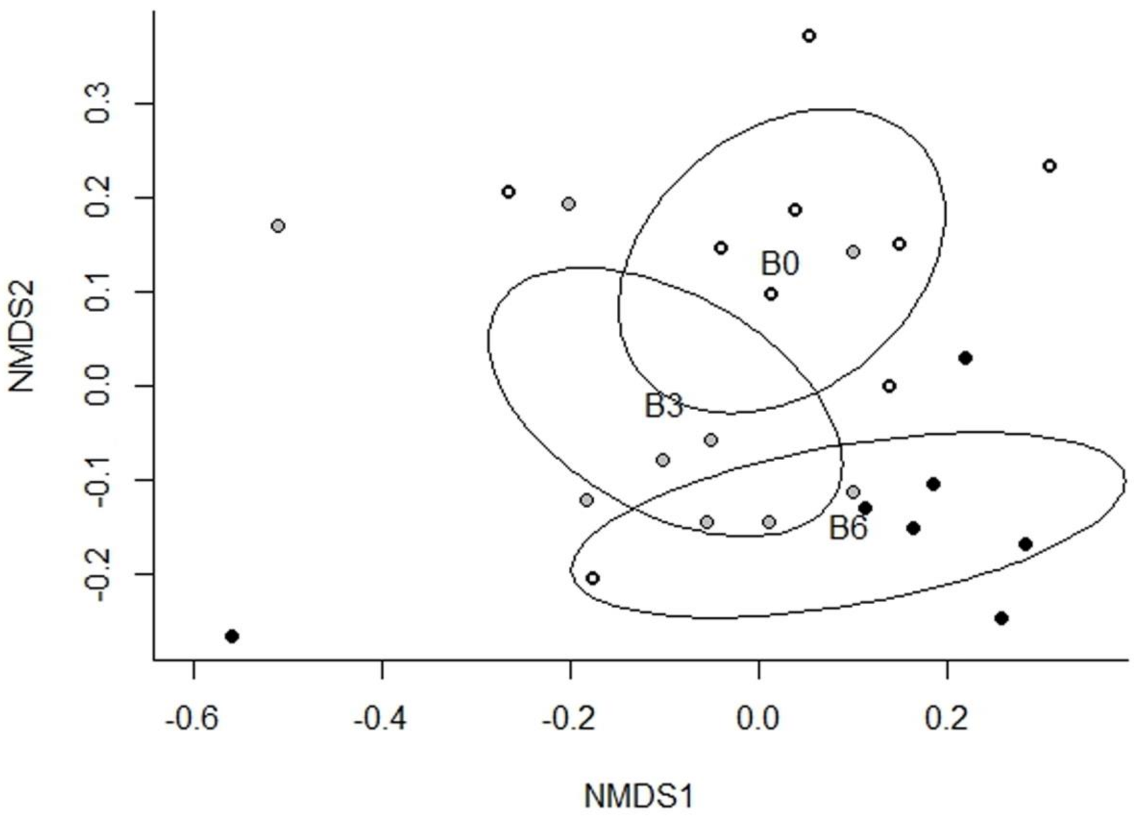

Figure 3. Structure and composition of tree species of recruits and resprouts with stems ≤ 1 cm DBH (including individuals between ≥ 10 cm to 130 cm in height) sampled two years after the last fire in a burning experiment at southern border of Amazon Basin. Nonmetric multidimensional scaling (NMDS) plot and ellipses based on Bray-Curtis similarity index. Each dot represents a set of 10 sub-plots sample unit. Hollow dots for unburned (B0), grey dots for forest burned tree times, every three years (B3), and black dots for forest burned six times, annually (B6).

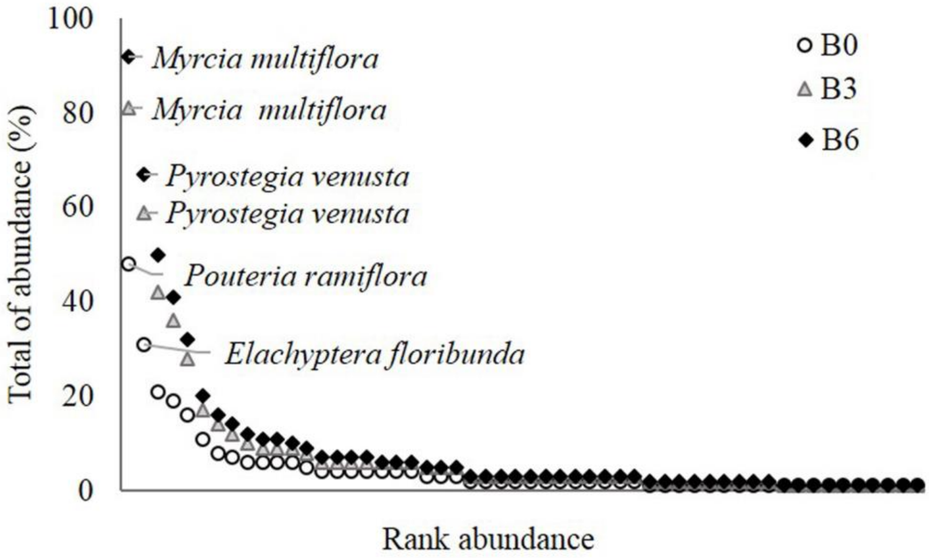

Figure 4. Ranked percentage contribution to total abundance of tree and liana species of recruits and resprouts with stems ≤ 1 cm DBH (including individuals between ≥ 10 cm to 130 cm in height) sampled two years after the last fire in a burning experiment at southern border of Amazon Basin. White marks for unburned control forest (B0), grey marks for forest burned tree times, every three years (B3), and black marks for forest burned six times annually (B6).

Figure 5. Tree species of recruits and resprouts with stems ≤ 1 cm in DBH (including individuals between ≥ 10 cm to 130 cm in height) sampled two years after the last fire in a burning experiment at southern border of Amazon Basin. Amazonia-only and Cerrado Biome co-occurring (A), successional stage (B), life form (C) and regeneration mode (D) species richness and proportions. Undetermined or non-classified species were excluded from figure A and B. Figure A and B Percentage of species recorded in unburned (B0), triennially (B3) and annually burned (B6). * represent statistical differences among treatments and the control (ANOVA; *P* < 0.05).

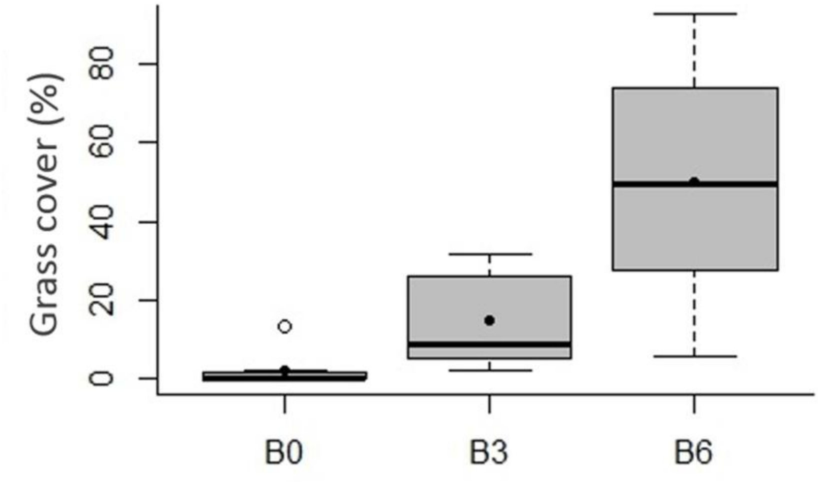

Figure 6. Percentage of mixed-species grass cover from 0 to 250 m from forest edge. Sampling done two years after fires in a burning experiment at southern border of Amazon Basin. Unburned control (B0), triennial burns (burned thrice; B3), and annual burns plots (burned six times; B6).

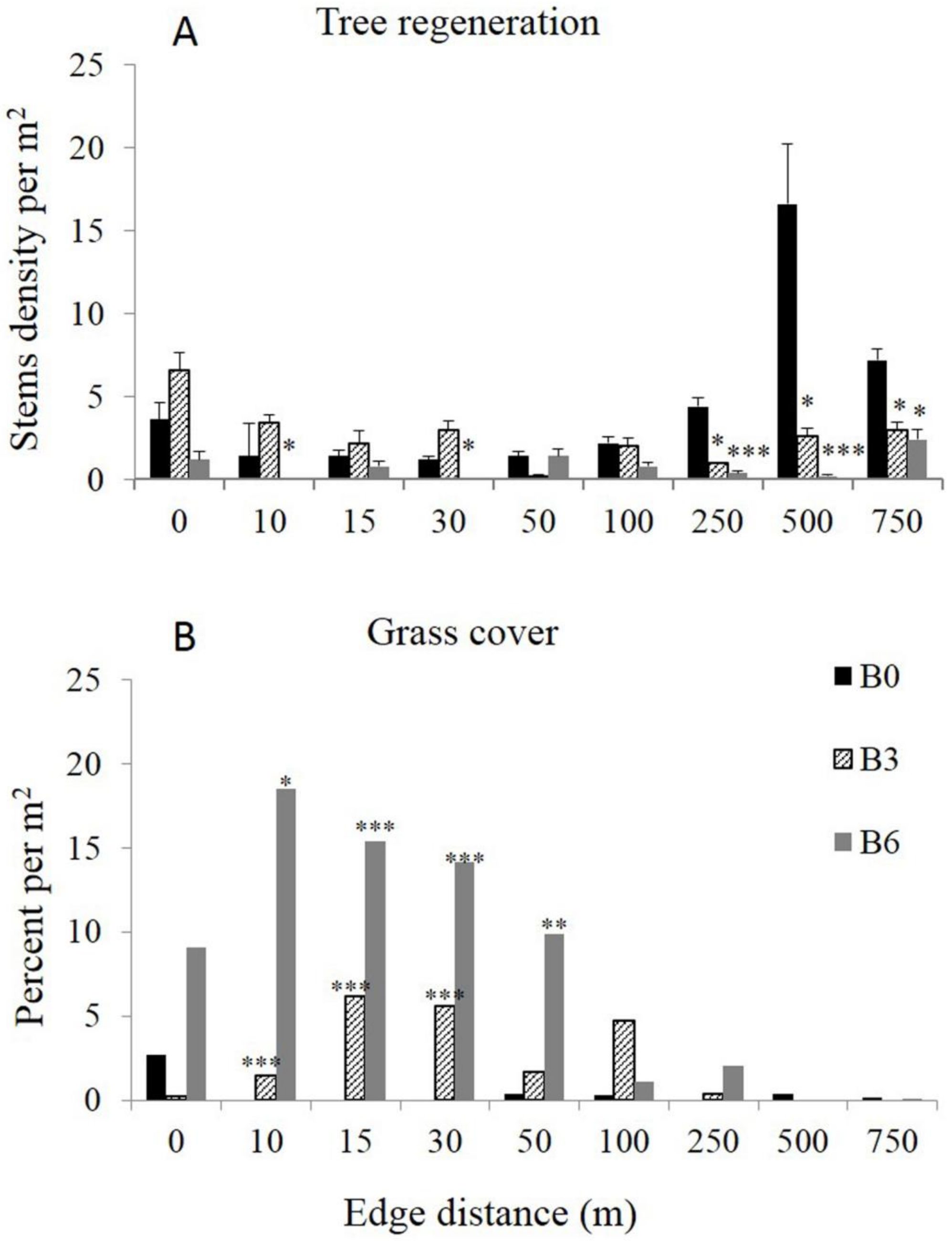

Figure 7. (A) Density of tree species with stems ≤ 1 cm DBH (including individuals between ≥ 10 cm to 130 cm in height and (B) grass cover percent from 0 to 750 m of cleared edge. Sampling done two years after fires in a burning experiment at southern border of Amazon Basin. Triennial burns (B3) and annual burns (B6) compared with unburned plot (B0). Error bars. * represent statistical differences according to Mann-Whitney U test at $P < 0.05$, ** $P < 0.01$, ***$P < 0.001$.

SUPPORTING INFORMATION

APPENDIX 1

Botanical families, woody species and number of individuals regenerating in each 45 m^2 treatment two years after fires: unburned (B0), triennially burned (B3) and annually burned plots (B6). Life form (LF): tree, shrubs and lianas.

Botanical family and species name	B0	B3	B6	LF
Anacardiaceae				
Tapirira guianensis Aubl.	1	3		Tree
Annonaceae				
Guatteria blepharophylla Mart.	6	1		Tree
Guatteria schomburgkiana Mart.	2	1		Tree
Xylopia amazonica R.E. Fr.	2			Tree
Apocynaceae				
Aspidosperma excelsum Benth.	4			Tree
Aspidosperma obscurinervium Azambuja	1			Tree
Forsteronia affinis Müll. Arg.		2		Liana
Himatanthus sucuuba (Spruce ex Müll.Arg.) Woodson	1		1	Tree
Secondatia densiflora A. DC.	1	2		Liana
Araliaceae				
Schefflera morototoni (Aubl.) Maguire, Steyem & Frodin		1		Tree
Bignoniaceae				
Adenocalymma longilineum (A.Samp.) L.G. Lohmann		2		Liana
Bignonia cf. *aequinoctialis* L.			2	Liana
Cuspidaria inaequalis (DC. ex Splitg.) L.G. Lohmann		1	4	Liana
Fridericia cinnamomea (DC.) L.G. Lohmann	4			Liana
Indet 1	1	1		Liana
Indet 2		1		Liana
Indet 3		1		Liana
Pleonotoma melioides (S. Moore) A.H. Gentry	2	1		Liana
Pyrostegia venusta (ker Gawl.) Miers	8	28	8	Liana
Boraginaceae				
Cordia bicolor A. DC.		2		Tree
Burseraceae				
Protium unifoliolatum Engl.	1			Tree
Protium guianense (Aubl.) Marchand	21	3		Tree
Celastraceae				
Elachyptera floribunda (Benth.) A.C. Sm.	31	21	2	Liana
Hippocratea volubilis L.	4			Liana
Tontelea corymbosa (Ruber) A.C. Sm.	1			Liana

Botanical family and species name	B0	B3	B6	LF
Chrysobalanaceae				
Licania egleri Prance	1	2		Tree
Licania gracilipes Taub.	4	1		Tree
Combretaceae				
Combretum sp.		1		Liana
Connaraceae				
Connarus perrottetii (DC.) Planch	6	2		Tree
Dilleniaceae				
Davilla kunthii A. St.-Hil.	3			Liana
Doliocarpus spatulifolius Kubitzki	2	1	2	Liana
Elaeocarpaceae				
Sloanea eichleri K. Schum.	4		1	Tree
Erythroxylaceae				
Erythroxylum rufum Cav.	2	1		Tree
Euphorbiaceae				
Mabea fistulifera Mart.	11	17		Tree
Maprounea guianensis Aubl.		2	1	Tree
Fabaceae				
Abrus precatorius L.	1			Liana
Copaifera reticulata Ducke		1		Tree
Derris floribunda (Benth.) Ducke	7	1		Liana
Inga heterophylla Willd.	6	3		Tree
Inga thibaudiana DC.	2			Tree
Machaerium myrianthum Spruce ex Benth.	1			Liana
Ormosia paraensis Ducke	1			Tree
Tachigali vulgaris L.F. Gomes da Silva & H.C.Lima	1	6		Tree
Humiriaceae				
Sacoglottis guianensis Benth.	2			Tree
Hypericaceae				
Vismia cf. *latifolia* (Aubl.) Choisy	6	1	5	Tree
Lauraceae				
Nectandra cuspidata Nees & Mart	5		1	Tree
Ocotea guianensis Aubl.	16	2	2	Tree
Ocotea leucoxylon (Sw.) Laness.	4			Tree
Loganiaceae				
Strychnos xinguensis Krukoff	1			Liana
Malpighiaceae				
Banisteriopsis sp.	1	1		Liana
Indet 4	2			Liana
Tetrapterys styloptera A. Juss.			1	Liana
Melastomataceae				
Mouriri brachyanthera Ducke	2			Tree
Moraceae				
Pseudolmedia macrophylla Trécul		2		Tree
Myristicaceae				

Botanical family and species name	**B0**	**B3**	**B6**	**LF**
Virola sebifera Aubl.	2	6		Tree
Myrtaceae				
Marlierea umbraticola (Kunth) O. Berg	1	12		Tree
Myrcia multiflora (Lam.) DC.	19	33	11	Tree
Myrcia sylvatica (G. Mey.) DC.	3	4		Tree
Ochnaceae				
Ouratea discophora Ducke	2			Tree
Peraceae				
Chaetocarpus echinocarpus (Baill.) Ducke		3		Tree
Polygalaceae				
Securidaca bialata Benth.	1	1		Liana
Rubiaceae				
Amaioua guianensis Aubl.	4	1	2	Tree
Indet		1		Tree
Psychotria prunifolia (Kunth) Steyerm.	3			Shrub
Psychotria tomentella (S. Moore) Zappi	1			Shrub
Sapindaceae				
Matayba guianensis Aubl.		5		Tree
Paullinia sp.	1			Liana
Serjania sp.	1			Liana
Sapotaceae				
Pouteria ramiflora (Mart.) Radlk.	48	1	8	Tree
Micropholis egensis (A.DC.) Pierre	2			Tree
Siparunaceae				
Siparuna guianensis Aubl.			1	Tree
Solanaceae				
Solanum mauritianum Scop.		2	3	Tree
Urticaceae				
Cecropia cf. *distachya* Huber		1		Tree
Total abundance	**270**	**185**	**55**	
Total species	**54**	**44**	**11**	

APPENDIX 2

Species classification and reference list. Species occurring in Cerrado physiognomies (C) and Amazon Forest (F). Species occurring in secondary or only in mature forests (E = early or L = late successional species). (-) species with no information.

Family and Species	Occurrence and references		Successional stage and references	
Anacardiaceae				
Tapirira guianensis Aubl.	F, C	1 (Cerrado, Floresta, Pantanal), 4 (Cerrado Denso, Cerradão, Savanas Amazônicas, Mata Ciliar, Mata Seca Semidecidual, Mata de Galeria, Vereda), 6 (Cerradão, Mata de Galeria), 7 (Cerrado *lato sensu*, Mata de galeria), 9 (Mata de Galeria), 10 (Cerrado *lato sensu*)	E	16 (floresta secundária com aproximadamente 30 anos de idade, abandonada após sucessivos ciclos de agricultura itinerante, Pará), 17 (Complexo de vegetação de campos e matas abertas dos Campos Naturais de Humaitá-Puciari, Amazonas), 18 (Pioneira - Checklist IBAMA e Museu Emílio Goeldi), 19 (Planta heliófita, característica de formações secundárias da Floresta Latifoliada Semidecidual, menos frequente no interior de floresta primária densa), 25 (Floresta secundária com 4, 8 e 12 anos, após pousio de sistema agrícola de culturas anuais e queimas, Pará)
Annonaceae				
Guatteria blepharophylla Mart.	F	1 (Floresta), 5 (Floresta de Terra Firme)	L	18 (Secundária Tardia - Checklist IBAMA e Museu Emílio Goeldi)
Guatteria schomburgkiana Mart.	F, C	1 (Floresta), 5 (Savana Amazônica, Campinarana, Floresta de Igapó, Floresta de Terra Firme, Floresta de Várzea, Floresta Ombrófila), 12 (Cerradão)	E	18 (Pioneira - Checklist IBAMA e Museu Emílio Goeldi)
Xylopia amazonica R.E. Fr.	F, C	1 (Floresta), 5 (Savanas Amazônicas), 9 (Mata de Galeria), 10 (Cerrado *lato sensu*), 12 (Cerradão)	E	21 (Pioneira, heliófita)

Family and Species	Occurrence and references		Successional stage and references	
Apocynaceae				
Aspidosperma desmanthum Benth. ex Müll.Arg., Sin. *A. obscurinervium*	F	1 (Floresta), 5 (Floresta de Terra Firme)	L	18 (Secundária Tardia - Checklist IBAMA e Museu Emílio Goeldi)
Aspidosperma excelsum Benth.	F	5 (Floresta de Terra Firme, Floresta Estacional Decidual)	L	18 (Secundária Tardia - Checklist IBAMA e Museu Emílio Goeldi)
Himatanthus articulatus (Spruce ex Müll.Arg.) Woodson; Sin. *H. sucuuba*	F, C	1 (Cerrado, Florestal), 5 (Cerrado *lato sensu*, Savanas Amazônicas, Floresta de Terra Firme), 7 (Mata de galeria), 10 (Cerrado *lato sensu*), 12 (Cerradão)	E	16 (floresta secundária com aproximadamente 30 anos de idade, abandonada após sucessivos ciclos de agricultura itinerante, Pará), 17 (Complexo de vegetação de campos e matas abertas dos Campos Naturais de Humaitá-Puciari, Amazonas), 18 (Pioneira - Checklist IBAMA e Museu Emílio Goeldi), 20 (Planta heliófita secundária, ocorre no interior de matas primárias e secundárias)
Araliaceae				
Schefflera morototoni (Aubl.) Maguire, Steyem & Frodin	F, C	1 (Cerrado, Florestal), 5 (Cerrado *lato sensu*, Floresta Ciliar ou Galeria, Floresta de Terra Firme, Floresta Estacional Semidecidual, Floresta Ombrófila), 7 (Mata de Galeria), 12 (Cerradão, Cerrado Denso, Cerrado Típico)	E	17 (Complexo de vegetação de campos e matas abertas dos Campos Naturais de Humaitá-Puciari, Amazonas), 18 (Pioneira - Checklist IBAMA e Museu Emílio Goeldi), 19 (Planta heliófita, ocorre em matas pouco densas ou em formações secundárias, como capoeiras e capoeirões), 22 (Secundária inicial; presente em clareira em diferentes estágios sucessionais, frequentemente dominada por trepadeiras), 23 (Floresta secundária),
Boraginaceae				
Cordia bicolor A. DC.	F, C	1 (Cerrado, Florestal), 7 (Cerrado lato sensu), 9 (Mata de Galeria), 10	L	18 (Secundária Tardia - Checklist IBAMA e Museu Emílio Goeldi)
Burseraceae				

Family and Species	Occurrence and references		Successional stage and references	
Protium guianense (Aubl.) Marchand	F, C	1 (Florestal), 7 (Cerradão, Cerrado *lato sensu*)	L	18 (Secundária Inicial - Checklist IBAMA e Museu Emílio Goeldi)
Protium unifoliolatom Engl.	F, C	1 (Cerrado, Florestal), 7 (Mata seca), 12 (Cerradão)	L	18 (Secundária Tardia - Checklist IBAMA e Museu Emílio Goeldi)
Chrysobalanaceae				
Licania egleri Prance	F, C	1 (Cerrado, Florestal), 7 (Cerradão, Mata)	L	18 (Secundária Tardia - Checklist IBAMA e Museu Emílio Goeldi)
Licania gracilipes Taub.	F	5 (Floresta de Terra Firme, Floresta Ombrófila)	-	-
Connaraceae				
Connarus perrottetii (DC.) Planch	F, C	1 (Cerrado, Floresta), 7 (Cerrado *lato sensu*)	E	16 (Floresta secundária com aproximadamente 30 anos de idade, abandonada após sucessivos ciclos de agricultura itinerante, Pará), 18 (Pioneira - Checklist IBAMA e Museu Emílio Goeldi)
Elaeocarpaceae				
Sloanea eichleri K. Schum.	F, C	1 (Florestal), 7 (Mata de Galeria), 12 (Cerradão)	E	18 (Secundária Inicial - Checklist IBAMA e Museu Emílio Goeldi)
Erythroxylaceae				
Erythroxylum rufum Cav.	F, C	5 (Savanas Amazônicas, Campinarana, Afloramentos rochosos), 10 (Cerrado *lato sensu*)	-	-
Euphorbiaceae				
Mabea fistulifera Mart.	F, C	1 (Cerrado, Floresta), 7 (Cerrado *lato sensu*), 10 (Cerrado *lato sensu*)	E	19 (Planta heliófita, pioneira, característica da vegetação secundária de terrenos arenosos, principalmente do Cerrado e de sua transição para Floresta Semidecidual)

Family and Species	Occurrence and references		Successional stage and references	
Maprounea guianensis Aubl.	F, C	1 (Cerrado, Floresta), 2 (Cerrado *stricto sensu*), 7 (Cerradão, Cerrado *lato sensu*), 10 (Cerrado *lato sensu*), 14 (Cerrado *stricto sensu*)	E	16 (Floresta secundária com aproximadamente 30 anos de idade, abandonada após sucessivos ciclos de agricultura itinerante, Pará), 18 (Pioneira - Checklist IBAMA e Museu Emílio Goeldi), 21 (Planta heliófita, secundária, ocorre em formações secundárias e primárias, com maior frequência em cerradões e mata Semidecidual), 22 (Secundária inicial; presente em clareira em diferentes estágios sucessionais, frequentemente dominada por trepadeiras)
Fabaceae				
Copaifera reticulata Ducke	F	5 (Floresta de Terra Firme), 15 (Cresce em Mata de Terra Firme)	L	15 (Árvore de crescimento lento, ocupa o dossel florestal)
Inga heterophylla Willd.	F, C	1 (Cerrado, Floresta), 7 (Mata de Galeria), 9 (Mata de Galeria)	E	16 (Floresta secundária com aproximadamente 30 anos de idade, abandonada após sucessivos ciclos de agricultura itinerante, Pará), 18 (Pioneira - Checklist IBAMA e Museu Emílio Goeldi)
Inga thibaudiana DC.	F, C	1 (Florestal), 7 (Mata de Galeria), 12 (Cerradão)	E	18 (Pioneira - Checklist IBAMA e Museu Emílio Goeldi), 25 (Floresta secundária com 4, 8 e 12 anos, após pousio de sistema agrícola de culturas anuais e queimas, Pará)
Ormosia paraensis Ducke	F	1 (Florestal), 5 (Floresta de Terra Firme)	L	16 (Floresta secundária com aproximadamente 30 anos de idade, abandonada após sucessivos ciclos de agricultura itinerante, Pará), 18 (Secundária Tardia) - Checklist IBAMA e Museu Emílio Goeldi)
Tachigali vulgaris L.F. Gomes da Silva & H.C.Lima	F, C	1 (Cerrado, Floresta, Pantanal), 5 (Cerrado *lato sensu*, Floresta Ciliar ou Galeria, Floresta Estacional Decidual, Floresta Estacional Semidecidual, Savana Amazônica), 7	E	17 (Complexo de vegetação de campos e matas abertas dos Campos Naturais de Humaitá-Puciari, Amazonas), 18 (Pioneira - Checklist IBAMA e Museu Emílio Goeldi), 22 (secundária inicial; presente em clareira em diferentes estágios sucessionais, frequentemente

Family and Species		Occurrence and references		Successional stage and references
		(Cerradão, Cerrado *lato sensu*)		dominado por trepadeiras)
Humiriaceae				
Sacoglottis guianensis Benth.	F, C	1 (Cerrado, Floresta), 7 (Mata de Galeria), 10 (Cerrado *lato sensu*)	L	18 (Secundária Tardia - Checklist IBAMA e Museu Emílio Goeldi), 20 (Planta heliófita, característica de formações semiabertas da Amazônia como campos e campinas)
Hypericaceae				
Vismia latifolia (Aubl.) Choisy	F	5 (Floresta de Terra Firme, Floresta Ciliar ou Galeria)	E	17 (Complexo de vegetação de campos e matas abertas dos Campos Naturais de Humaitá-Puciari, Amazonas), 5 (Área antrópica)
Lauraceae				
Nectandra cuspidata Nees & Mart	F, C	1 (Florestal), 6 (Cerradão), 7 (Mata), 10 (Cerrado *lato sensu*), 12 (Cerrado Denso, Cerrado Típico)	L	18 (Secundária Tardia - Checklist IBAMA e Museu Emílio Goeldi), 24 (A espécie pode ser coletada na floresta ombrófila densa aluvial e na savana florestada das regiões central), 9 (Clímax)
Ocotea guianensis Aubl.	F, C	1 (Cerrado, Floresta), 5 (Cerrado *lato sensu*, Floresta de Terra Firme, Floresta Ombrófila)	E	16 (Floresta secundária com aproximadamente 30 anos de idade, abandonada após sucessivos ciclos de agricultura itinerante, Pará), 18 (Secundária Tardia - Checklist IBAMA e Museu Emílio Goeldi), 21 (Planta pioneira, heliófita, ampla distribuição na Amazônia e ocorre com frequência em vegetação secundária), 25 (Floresta secundária com 4, 8 e 12 anos, após pousio de sistema agrícola de culturas anuais e queimas, Pará)
Ocotea leucoxylon (Sw.) Laness.	F	1 (Florestal), 5 (Floresta de Terra Firme, Floresta Ombrófila, Floresta de Igapó)	L	18 (Secundária Tardia - Checklist IBAMA e Museu Emílio Goeldi)

Family and Species	Occurrence and references		Successional stage and references	
Melastomataceae				
Mouriri brachyanthera Ducke	F	5 (Floresta de Terra Firme)	E	18 (Secundária Inicial - Checklist IBAMA e Museu Emílio Goeldi)
Moraceae				
Pseudolmedia macrophylla Trécul	F	5 (Floresta de Terra Firme, Floresta Ombrófila)	E	18 (Secundária Inicial - Checklist IBAMA e Museu Emílio Goeldi)
Myristicaceae				
Virola sebifera Aubl.	F, C	1 (Cerrado, Florestal), 4 (Cerrado *lato sensu*, Savanas Amazônicas, Cerradão, Mata Seca Semidecidual, Mata de galeria), 6 (Cerradão), 7, 10 (Cerrado *lato sensu*), 12 (Cerradão, Cerrado Denso, Cerrado Típico)	E	17 (Complexo de vegetação de campos e matas abertas dos Campos Naturais de Humaitá-Puciari, Amazonas), 18 (Pioneira - Checklist IBAMA e Museu Emílio Goeldi) 19 (Heliófita, característica de formações secundárias da Floresta Latifoliada Semidecidual), 22 (Secundária inicial; presente em clareira em diferentes estágios sucessionais, frequentemente dominada por trepadeiras)
Myrtaceae				
Marlierea umbraticola (Kunth) O. Berg	F	5 (Floresta de Terra Firme, Floresta de Várzea), 13 (Floresta)	-	-
Myrcia multiflora (Lam.) DC.	F, C	1 (Cerrado, Florestal), 2 (Cerrado *stricto sensu*), 7 (Mata de Galeria), 8 (Cerrado *lato sensu*, Campina de solos arenosos e argilosos, Floresta de Várzea, Floresta de Terra Firme), 10 (Cerrado *lato sensu*), 12 (Cerrado Denso, Cerrado Típico)	E	18 (Pioneira - Checklist IBAMA e Museu Emílio Goeldi), 8 (Floresta Secundária)
Myrcia sylvatica (G. Mey.) DC.	F, C	5 (Floresta de Terra Firme, Floresta de Várzea, Floresta Ombrófila); 8 (Cerrado *lato sensu*, Savana, Campina, Floresta de Várzea, Floresta de Terra Firme)	E	25 (Floresta secundária com 4, 8 e 12 anos, após pousio de sistema agrícola de culturas anuais e queimas, Pará), 8 (Floresta Secundária)

Family and Species	Occurrence and references		Successional stage and references	
Ochnaceae				
Ouratea discophora Ducke	F, C	1 (Florestal), 5 (Savana Amazônica, Floresta Estacional Semidecidual, Floresta Ombrófila)	-	-
Peraceae				
Chaetocarpus echinocarpus (Baill.) Ducke	F, C	5 (Campinarana, Campo Limpo, Cerrado *lato sensu*, Floresta Ciliar ou Galeria, Restinga), 7 (Cerrado *lato sensu*)	E	21 (Planta heliófita, característica da Mata Pluvial Atlântica e de áreas abertas)
Rubiaceae				
Amaioua guianensis Aubl.	F, C	1 (Florestal), 7 (Mata de Galeria), 10 (Cerrado *lato sensu*), 12 (Cerradão)	E	18 (Secundária Inicial - Checklist IBAMA e Museu Emílio Goeldi), 20 (Ocorre em matas primárias e em capoeirões)
Indet	-	-	-	-
Psychotria prunifolia (Kunth) Steyerm.	F, C	1 (Cerrado), 5 (Campo de Várzea, Floresta Ciliar ou Galeria, Floresta Estacional Perenifólia, Floresta Estacional Semidecidual), 7 (Cerradão)	E	22 (Presente em clareira em diferentes estágios sucessionais, frequentemente dominada por trepadeiras)
Psychotria tomentella (S. Moore) Zappi	F	5 (Floresta Ciliar ou Galeria, Floresta Estacional Perenifólia)	-	-
Sapindaceae				
Matayba guianensis Aubl.	F, C	1 (Cerrado, Floresta, Pantanal), 2 (Cerrado *stricto sensu*), 7 (Cerradão, Cerrado *lato sensu*), 10 (Cerrado *lato sensu*), 11(Cerradão, Carrasco), 12 (Cerrado Denso, Cerrado Típico)	E	18 (Pioneira - Checklist IBAMA e Museu Emílio Goeldi), 22 (Secundária inicial), 21 (Planta pioneira, heliófita, ocorre em formações florestais fechadas ou abertas; é considerada invasora de pastagens)

Family and Species	**Occurrence and references**		**Successional stage and references**	
Sapotaceae				
Micropholis egensis (A.DC.) Pierre	F, C	1 (Florestal), 5 (Floresta de Terra Firme, Floresta de Várzea, Floresta de Igapó), 12 (Cerradão)	L	18 (Secundária Tardia - Checklist IBAMA e Museu Emílio Goeldi)
Pouteria ramiflora (Mart.) Radlk.	F, C	1 (Cerrado, Florestal), 3 (Cerrado *stricto sensu*), 4 (Cerrado *stricto sensu*, Savanas Amazônicas, Carrasco, Vereda, Cerradão, Mata de galeria), 6 (Cerradão, Mata de Galeria), 7 (Cerrado *lato sensu*, Vereda), 10 (Cerrado *lato sensu*), 12 (Cerradão, Cerrado Denso, Cerrado Típico), 14 (Cerrado *stricto sensu*)	L	18 (Secundária Tardia - Checklist IBAMA e Museu Emílio Goeldi)
Siparunaceae				
Siparuna guianensis Aubl.	F, C	1 (Cerrado, Florestal), 4 (Cerrado *stricto sensu*, Cerradão, Mata Seca Semidecidual, Mata de galeria), 7 (Campo sujo, Vereda), 9 (Mata de Galeria), 10 (Cerrado *lato sensu*)	E	17 (Complexo de vegetação de campos e matas abertas dos Campos Naturais de Humaitá-Puciari, Amazonas), 22 (Planta secundária inicial, presente em clareira em diferentes estágios sucessionais, frequentemente dominada por trepadeiras), 25 (Floresta secundária com 4, 8 e 12 anos, após pousio de sistema agrícola de culturas anuais e queimas, Pará)
Solanaceae				
Solanum mauritianum Scop.	F, C	5 (Cerrado *lato sensu*, Floresta Estacional Decidual, Floresta Ombrófila, Floresta Ombrófila Mista	E	5 (Área antrópica)

Family and Species	Occurrence and references		Successional stage and references	
Urticaceae				
Cecropia cf. *pachystachya* Trécul	F, C	1 (Cerrado, Floresta), 5 Cerrado *lato sensu*, Floresta de Galeria, Floresta de Terra Firme, Floresta Estacional Semidecidual, Floresta Ombrófila, Floresta Ombrófila Mista, Restinga)	E	22 (Planta pioneira, secundária inicial; presente em clareira em diferentes estágios sucessionais, frequentemente dominada por trepadeiras), 19 (Planta pioneira, heliófita, ocorre em clareiras, bordas de florestais e matas secundárias)

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APPENDIX 3

Species presenting higher contribution to dissimilarity in composition and structure between treatments (*i.e.*, species with more than 5% of abundance between the two treatments). Percent of contribution to dissimilarity, standard deviation (s.d.) and average abundance per treatment, based on SIMPER analysis. Data from unburned (B0), triennially burned (B3) and annually burned sites (B6) recorded two years after fires.

Species	Contribution (%)	s.d.	Average	
			B0	B3
Elachyptera floribunda	7.71	0.07	3.44	2.33
Myrcia multiflora	7.69	0.06	2.11	3.66
Pyrostegia venusta	7.67	0.08	0.88	3.11
Mabea fistulifera	5.38	0.07	1.22	1.88
Species	Contribution (%)	s.d.	B0	B6
Pouteria ramiflora	7.96	0.13	5.33	1.00
Elachyptera floribunda	6.66	0.06	3.44	0.25
Protium guianense	5.97	0.04	2.33	0.00
Myrcia multiflora	5.92	0.05	2.11	1.37
Pyrostegia venusta	5.22	0.09	0.88	1.00
Species	Contribution (%)	s.d.	B3	B6
Myrcia multiflora	12.14	0.08	3.66	1.37
Pyrostegia venusta	11.66	0.11	3.11	1.00
Elachyptera floribunda	7.21	0.10	2.33	0.25
Mabea fistulifera	5.23	0.06	1.88	0.00

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Capítulo 3

Effects of Increasing Fire Frequency on Seed Sources and Early Regeneration in Southeastern Amazonia

Biotropica

Effects of Increasing Fire Frequency on Seed Sources and Early Regeneration in Southeastern Amazonia

RRH: Seed Sources and Post-Fire Recruitment

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ABSTRACT

Seed availability and resprouting from existing structures are key sources for germination and species persistence after fire disturbance. We investigated the link between seed availability (via seed rain and the soil seed bank) and resulting woody plant species recruitment a post-fire. Also, we evaluated resprouting occurrence. Data were collected for three years after the last experimental fire in two 50-ha plots that were burned 3 (triennial) and 6 times (annual) in 7 years and in a control plot (also 50-ha) in the southeastern Amazon Basin. Seedlings represent only 2.4 percent of seeds deposited in unburned site, but this rate was even small in both burned treatments (≈0.65%). Triennial burn showed a reduction in the number of seeds gathered in seed traps (-43%) and viable seeds in the soil seed bank (-77%), which likely explain the low density of new recruits (0.4 ind/m^2.yr) compared to the annually burned treatment (0.8 ind/m^2.yr). The three-year interval between fires in triennial fire treatment, resulted in more intense fires due to fuel accumulation and concurrent drought, which killed more reproductive trees and seeds stored in the soil than in the annual burn treatment where fires were less severe. Also, lower fire frequency resulted in 5.5 times more sprouting stems than in higher fire frequency, but in both treatments sprouts declined across the three years post-fire. In conclusion, both sources of seed and resprouting occurrence were negatively affected by both fire frequencies, reducing the likelihood of native species recovery by altering the regeneration pathways in southeastern Amazon.

RESUMO

A disponibilidade de sementes e as rebrotas são recursos chaves para o recrutamento e persistência das espécies florestais após a degradação por incêndios. Foram analisados a disponibilidade de sementes (chuva de sementes e banco de sementes no solo) e o recrutamento de espécies lenhosas após os incêndios. Adicionalmente, foi analisado a ocorrência de rebrotas. Os dados foram coletados por três anos após exclusão do fogo em duas parcelas de 50-ha que foram queimadas três vezes (trienalmente) e 6 vezes (anualmente) durante 7 anos e em uma parcela controle (50-ha) no sudeste da Bacia Amazônica. As plântulas representaram apenas 2.4 por cento do total de sementes depositadas no controle, mas foi ainda menor em ambos os tratamentos queimados (≈0.65%). Incêndios trienais resultaram na redução no número de sementes coletadas na chuva de sementes (-43%) e no banco de sementes do solo (-77%), explicando a baixa densidade de recrutas (0.4 ind/m^2.ano) comparado com os incêndios anuais (0.8 ind/m^2.ano). O intervalo de três anos entre os incêndios no tratamento queimado trienalmente resultou em incêndios mais intensos devido ao acúmulo de combustível e à seca, os quais aumentaram a mortalidade de indivíduos reprodutivos e de sementes estocadas no solo em comparação com os incêndios anuais, os quais foram menos severos. Incêndios trienais resultaram em 5.5 vezes maior número de rebrotas do que incêndios anuais; no entanto, ambos os tratamentos mostraram um declínio no número de rebrotas ao longo dos três anos após fogo. Concluímos que as fontes de sementes e a ocorrência de rebrotas foram negativamente afetadas em ambas as frequências de fogo e que os incêndios podem reduzir a regeneração das espécies nativas no sudeste da Amazônia.

Key words: drought; fire ecology; global climate change; secondary forest; seed dispersion; tropical forest; understory fire.

THE CONTEMPORARY FIRE REGIMES OF TROPICAL FORESTS ARE STRONGLY INFLUENCED BY LOGGING, DEFORESTATION, FOREST FRAGMENTATION AND EPISODIC DROUGHT EVENTS (Nepstad *et al*. 2008, Lindenmayer *et al*. 2009, Coe *et al*. 2013, Brando *et al*. 2014). In Amazonia, widespread understory fires are commonly observed along the "arc of deforestation" (Morton *et al.* 2013), where droughts, forest fragmentation, disturbances, and sources of ignition are common. For example, between 2000-2014 nearly 70 percent of forest cover were lost in Amazonia (INPE 2015) and the region experienced four extreme drought events (Morton *et al.* 2013). These current disturbances had a large effects on forest flammability (Alencar *et al.* 2006, Balch *et al.* 2008, Morton *et al.* 2013), increasing forest sensitivity to fires in large areas (Coe *et al.* 2013).

As a result, fires become recurrent and severe in moist tropical forests, therefore, it is important to evaluate the recovery potential to these fire-disturbed areas. Thus, the main resources to forest recovery after a disturbance are seedling recruitment from seed rain, from the soil seed bank and from sprouts (Clark *et al.* 1999, Bond & Midgley 2003, Wright *et al.* 2005, Poorter *et al*. 2010). However, the recovery pathways will depend on fire frequency, intensity and severity (Kennard *et al.* 2002, Balch *et al*. 2013). Therefore, the trajectories of fire-disturbed forests are still unclear.

Understory fires are expected to influence forest dynamics in two different moments. In the first, understory fires can affect directly recovery by killing regenerating stems (Balch *et al*. 2013) and reducing the stock of viable seeds of forest species by heat shock and high temperatures (Kennard *et al*. 2002, Cochrane 2003; Ribeiro & Borghetti 2014). Particularly, seedling bank and soil seed bank can be even more affected at boundary between forest and cleared edge (mostly agriculture and pasture), where fires are more severe due to increased fuels and drier microclimate (Melo *et al*. 2007, Montibeller-Santos 2014, Balch *et al*. 2015). In the second, tree and liana mortality may lead to changes in the forest structure and reproductive processes. For example, tree mortality led to an scarcity of reproductive trees, which results in limited fruiting production inside burned forests and alter microclimatic conditions in the understory, which results in recovery failures by reduced seed germination and seedling establishment (Clark *et al.* 1999, Cochrane & Schulze 1999, Cochrane 2003, Peres *et al*. 2003, Wright *et al*. 2005, Barlow & Peres 2006; Balch *et al.* 2015).

Thus, the abundance and species composition of propagules reaching the forest floor or stored on soil are the major determinants of the seedling assemblage being recruited (Norden *et al*. 2007), determining the direction and recovery time. However, when seed to seedling recruitment failures, resprouting (root, basal or epicormic) shows to be an important pathway of community recovery and maintenance of diversity for many woody species in disturbed forest (Poorter *et al*. 2010), but these mechanisms are still poorly understood in moist fire-prone forest.

We assessed how different fire frequencies affect forest regeneration and two associated processes: seed rain and storage of seeds in the soil seed bank. We studied these processes in the transitional forest between southwestern Amazonia and Cerrado Biome (*i.e.*, the Brazilian savanna). We tested three hypotheses: (1) fire drives reductions in forest regeneration due to reduced number of recruits, seed rain, and seed bank availability, particularly when fires are more frequent (3 vs. 6 burns in 7 years); (2) forest regeneration and associated processes (seed rain, seed bank) will be lower along the forest edge – where fires are more intense – than in the forest interior (>250 m from an open field); and, (3) regeneration mode is more dependent on resprouting than seedling germination, and resprouts will be more resilient along the first years post-fire.

METHODS

STUDY SITE — In 2004, a large-scale burning experiment was conducted in a transitional forest growing between Amazon rainforest and Cerrado Biome (Brazilian savanna), in a privately owned agricultural holding (80,000-ha), in Querência municipality, Mato Grosso state, Brazil (13º04’ S; 52º23’ W; Fig. 1). The farm was partially cleared (~50%) for pasture in the 1980s and was converted for soybean cultivation between 2003 and 2008.

The soil is classified as dystrophic red-yellow Oxisols by IBGE (2009), being deep, well drained and with low natural fertility (IBGE 2007). According to Köppen’s classification, the climate is tropical Aw, with an average annual precipitation of 1.770 mm (data from 2005 to 2011; Rocha *et al*. 2014), with the rainy season extending from September to April, and the dry season between May and August, when monthly rainfall is typically below 10 mm (Rocha *et al*. 2014). Dry season temperature was 25°C and relative humidity was 66 percent (average daily values used to calculate from 2004-2006 data; Balch *et al*. 2008).

The vegetation is classified as Evergreen Seasonal Forest, with lower deciduousness on dry season (IBGE 2012). Due to the proximity of the Cerrado Biome these forest are also known as “Transitional Forests” (Kunz *et al.* 2009). The forest has a relatively low canopy (averaging 20 m) and lower plant diversity in comparison with the wetter forests of the central Amazon (Balch *et al.* 2008). Furthermore, about 97 species of trees and lianas ≥10 cm diameter at 1.3 m stem diameter breast height (DBH) were identified over the entire 150-ha experimental area (Balch *et al.* 2011). The nine most common species accounted for 50 percent of the Vegetation Importance Index (Balch *et al.* 2008; 2011), and more than 74 percent of tree and shrub species also occur in the adjacent Cerrado Biome (See Chapter 2).

EXPERIMENTAL DESIGN ─ The experimental site was located in a forest with no signs of logging or previous fires. The experimental area of 1.5 x 1.0 km (150-ha; Fig. 1) was subdivided in three 50-ha plots: an unburned (as a control; B0), burned three times every three years (B3) and burned six times annually (B6). The experimental fires were conducted annually towards the end of the dry season (August) from 2004 to 2010 (except for 2008) (details in Balch *et al.* 2008, Brando *et al.* 2014).

SEED RAIN ─ Seed rain was collected biweekly for 36 months (September 2010 – August 2013) after the last fire in August 2010, from 0.5 m^2 mesh traps (N = 90 per 50-ha plot) placed systematically throughout the experimental plots, from the cleared edge to the forest interior (0, 10, 15, 30, 50, 100, 250, 500, 750 m; Fig. 1). Traps were suspended ≈1m above the forest floor adjacent to regeneration sub-plots. Number of seeds was quantified and all seeds were identified to species or at least genera through comparison with a seed collection of reference.

SEED BANK ─ Two years after last fire (July 2012), 120 soil cores were taken from the burned treatments and the control (N = 40) using a cylinder with 20 cm diameter and 5 cm deep. The samples were collected at 0, 30, 100, 500 and 750 m from forest edge. One soil sample was composed by a mix of two cores taken from less than two meter away from the regeneration sub-plot (Fig. 1). Samples were then transported in polythene bags and stored in Styrofoam boxes in a shaded cover for one week. Afterward, the soil was spread in plastic trays up to 3 cm height, and placed in a shaded greenhouse watered twice a day. Four control trays containing only sand were randomly distributed among the samples to control potential contamination from seeds dispersed through the greenhouse. Seedlings were weekly censored for the period of one year. All individuals that emerged were counted, identified through comparison with seedlings, juveniles and adult materials previously collected during fieldwork. Non-identified seedlings were transplanted into pots and grown until a larger size to further identification. Six months after the beginning of the experiment, the soil was overturned to promote the germination of seeds that were deeply buried. This method was adapted from Roberts (1981).

RECRUITS AND RESPROUTS ─ All seedlings, saplings and resprouts of tree, shrub and liana species were recorded in 90 sub-plots (0.5 m^2) in each 50-ha plot. Sub-plots were distributed systematically adjacent to seed traps, along the cleared edge until to the forest interior (Fig. 1). All plants taller than 5 cm high and ≤ 1 cm DBH (diameter at breast height or 1.30 m above ground) were tagged and identified. The modes of regeneration (*i.e.*, individuals originating from seed germination or root resprouts) and resprouting (*i.e.*, root, basal, or epicormic) were also recorded. If the resprouts were not evident it was determined through small excavations near the plant base. Censuses were conducted annually in 2011, 2012 and 2013, when new recruits and resprouts were included. If a given individual was present in one inventory and not in the next, it was considered to be dead. Plants that were present in those inventories but lack living structures and had no resprouting were noted as dead. Plant species were identified using the botanical collection of IPAM and the Herbarium NX at Universidade do Estado de Mato Grosso at Nova Xavantina campus. Species names followed the Missouri Botanical Garden Tropicos® database (http://www.tropicos.org; Table S1).

STATISTICAL ANALYSIS ─ To evaluate the degree in which fire frequency (unburned, low- and high-frequency) affect species diversity, we analyzed patterns of species richness and abundance using individual-based species accumulation curves for seeds from seed rain (N = 90), seeds stored in the soil (N = 40), seedlings, saplings and sprouts (N = 90).

Also, structure and composition of communities (*i.e.*, seed rain, seed bank, seedling, saplings and sprouts) were analyzed using nonmetric multidimensional scaling (NMDS) ordination. The NMDS was generated from a Bray-Curtis dissimilarity matrix and *a posteriori* analysis of similarities (ANOSIM) to test whether there is a significant difference among burned plots and the control, and also to analyze whether structure and composition of seedling and sapling assemblage were similar to that in the seed rain and seed bank samples. We also analyzed species abundance by means of Whittaker plots, both for seeds and woody plant regeneration.

A generalized linear model (GLM) was used to account for differences in the species richness and abundance among edge distances (nine distances for seed rain, seedlings and saplings and sprouts; five distances for seed bank), and also among years (2011, -12, -13, except for seed bank that was collected only in 2012). GLM was performed using Poisson distribution, indicated for counts with Quasi-Poisson correction when data presented variance higher than average.

RESULTS

SEED RAIN — In the whole set of samples, we collected 39,356 seeds from 67 species (Table S1), being 15,911 (59 species; 118 seeds/m^{2}yr) in B0, 9,135 (52 species; 68 seeds/m^{2}yr) in B3, and 14,310 (52 species; 106 seeds/m^{2}yr) in B6 (Fig. 2). The total of seed rain abundance was higher in the control site when compared with both burned treatments, which presented no variations in species richness (Fig 4A). According to NMDS analysis, burned treatments were structurally similar, sharing the majority of species, presenting a slight difference when compared with unburned plot (ANOSIM: R=0.07; p = 0.001). The species *Sloanea eichleri* accounted for 50 percent of the total number of seeds in seed rain in B3 (Fig. 5).

Edge distance influenced the number of species and abundance of seeds in both burned treatments. This occurred after 50 m from extreme edge (0 m) in B6 and after 250 at B3, while in unburned plot we recorded significantly higher richness after 15 m (Fig. 6). Density of seeds became higher after 500 m from edge (0 m) in B3 and after 750 m in B6 versus 15 m in unburned plot. The number of species and density of fallen seeds were constant along the years in both burned treatments and in unburned plot (Supporting information; Fig. S1).

SEED BANK – In all soil samples we recorded 2,330 viable seeds from 34 species (Table S1), being 1,352 in B0 (30 species; 538 seeds/m²), 310 in B3 (17 species; 123 seeds/m²) and 668 in B6 (18 species; 266 seeds/m²; Fig.2). The accumulation curve showed reduction of species richness and abundance in both fire frequencies, however seed abundance was strongly reduced in B3 (Fig. 4B). The structure and composition of the seed bank community was also altered by fires, being different from the unburned plot (ANOSIM: R=0.33; p = 0.001).

Melastomataceae had five *Miconia* species among the most abundant, which contributed with 84, 92 and 95 percent of total seeds in B0, B3 and B6, respectively (Fig. 5B). Surprisingly, despite being the most abundant species in the seed bank, they were not found among the new recruits.

Edge distance influenced the number of species and abundance of seeds in both burned treatments. B3 treatment reduced species richness until 500 and 750 m from the edge (GLM, p < 0,05; Fig. 6B). While B6 treatment reduced species richness until 100 m from edge (GLM, p < 0,05; Fig. 6B). Also, B3 treatment reduced the number of seeds until 500 m from edge, and, B6 reduced the number of seeds along all distances, presenting no significant differences between 0 and 750 m (GLM, p < 0,05; Fig. S2).

Summarizing, we observed large reductions in seed availability in both fire-induced treatments. The number of seeds in the seed rain and seed bank conjointly decreased 45 and

13 percent, respectively, in B3 and B6, compared with the B0 treatment. And, the species richness of both seed sources was also reduced in B3 and in B6 compared with B0 (Fig. 2).

SEEDLINGS, SAPLINGS AND RESPROUTS ─ Overall, we registered 115 species that were counted in all or at least one inventoried category (*i.e.*, seed rain, seed bank, seedling and resprout; Table S1). Furthermore, four species were represented in all categories (*Amaioua guianensis*, *Doliocarpus spatulifolius*, *Solanum mauritianum* and *Tachigali vulgaris*); 20 species were represented in three categories; 35 in two categories; and 55 in only one category (Table S1).

The sampled recruits and resprouts included 72 species and 739 individuals across the three years after fire (65 species; 3.3 ind/m^2.yr in B0; 44 species; 1.2 ind/m^2.yr in B3; and 18 species; 0.9 ind/m^2.yr in B6; Fig. 2). Evaluating only recruits (seedlings and saplings), the species accumulation curves indicated that recruit species richness gradually decreased with increasing fire frequency (*i.e.*, 55 species in B0, 23 in B3 and 18 in B6 (Fig. 4C). However, the density of recruits was 87 percent lower in B3 (49 individuals; 0.4 ind/m^2.yr) and 73 percent lower in B6 (106 individuals; 0.8 ind/m^2.yr), compared with B0 (391 individuals; 2.9 ind/m^2.yr; Fig. 2).

One interesting result was that if we consider all seeds coming from the seed rain (2011 to 2013) along with the soil seed bank (2012) as sources for seedling regeneration density, 2.4 percent resulted in new recruits in the unburned plot versus only 0.6 percent in B3 and 0.7 percent in B6 (Fig. 2). Also, the analysis of dissimilarity between the categories showed that the seedling and sapling communities were more similar to the seed rain (ANOSIM; R = 0.35 [B3] and 0.36 [B6]) than to the seed bank (ANOSIM; R = 0.41 [B3] and 0.64 [B6]) in both burned plots (Fig. 3).

Analyzing the resprout data, we witnessed that resprouts in B3 had two times more species and a significant increase of density (≈5.5 more live stems) when compared with B6

(Fig. 2), although, both fire treatments had increased their resprout responses compared to B0. This result is important to explain why the sum of regeneration stems (counting seedlings, saplings and resprouts) presented more than twice the number of species and individuals in B3 than in B6.

Comparing the distances (10 to 750 m) with the cleared edge (0 m), both burned treatments exhibited reduced species richness and abundance of new recruits along all distances (GLM, $p > 0.05$). A different pattern was registered in the unburned plot, which increased gradually the number of species beginning at 30 m from the edge and abundance after 500 m (Fig. 6C). Sprouting species richness and abundance had no difference in unburned plot regardless of edge distance. Contrastingly, B3 increased regrowth stems density from 0 to 50 m (see graphics in supporting information; Fig. S2)

We noticed that in the second year after fires (2012) the recruited species richness increased in B3 (Fig. 7A), as well as the abundance in B3 and B6 (Fig 7B). In 2012, only two species accounted for 90 percent of total seedlings recruited bank in B6 treatment, with *Pouteria ramiflora* alone accounting for 66.5 percent of them and *Amaioua guianensis* for 23.5. In contrast, sprouts showed a gradual reduction through the years in both burned plots, losing species and individuals in the third year after fire exclusion (2013). The unburned plot had no species and abundance variations through the years for both recruits and sprouts (Fig. 7).

Finally, the rate of seedling and sapling mortality was similar among plots, around 30 percent. However, resprouts had two-fold more percent of mortality in B6 (37%) than in B3 (17.6%; Fig 2).

DISCUSSION

Overall, we observed significant reduction in seed source availability and loss of resprouts in both fire treatments, probably explaining why regeneration rates were lower in the fire treatments than the unburned control. These results suggest that fires strongly affected the main sources for understory recovery, reducing forest diversity. We also observed differences in seed sources and regeneration patterns between the two fire treatments and along the forest edges. These differences between fire treatments tell us that frequency of fires matter for regeneration processes, driving the plant community to an alternative state, which needs to be monitored for longer periods to determine whether it is stable or not.

Our results partially corroborate our prediction that fire drives reduction in forest regeneration due to reduced number of recruits and seeds. For example, we observed reduction in the density and species in the seed rain and in the viable seeds stored in the seed bank in both fire treatments (3 and 6 burns in 7 years). Contrary to our hypothesis, however, regeneration was more affected (through lower seed availability) in B3 treatment, burned every three years, than in B6, the one burned every year. The most likely explanation for this result is the difference in fire intensity between the two fire treatments. The longer fire interval in B3 led to an increase in fire intensity and thus in fire-induced tree mortality during the regional drought of 2007 (Brando *et al.* 2014, Balch *et al.* 2015). It is possible that this high-intensity fires depleted both seed sources and the pool of resprouting stems, and the associated regenerating community (Kennard *et al.* 2002, Barlow & Peres 2006, Brando *et al.* 2014, Montibeller-Santos 2014), particularly at the forest edge, where fire was more intense (Brando *et al*. 2014).

One striking analysis of this study was that surviving reproductive trees were essential to the maintenance of new recruit diversity in these fire-prone forests, given the fact that recruit assemblage was more similar with seed rain than with seed bank. Thus, fruit production is an important source of viable seeds to forest recovery, strongly increasing plant diversity in burned forests (Barlow & Peres 2006).

Our second prediction, that forest regeneration and associated processes would be lower along the forest edge than in the forest interior, was confirmed. We found that recruits and the seed sources (seed rain and seed bank) were lower at the first hundred meters from the cleared edge in both burning treatments. These results suggest that the negative effects of fires were multiplied towards the edge due to a substantial increase in dryer biomass and lower humidity, resulting fires more intense and severe (Brando *et al*. 2014) resulting a massive loss of large fruiting trees (Barlow & Peres 2006) and seeds stored in the soil (Melo *et al.* 2007). Aditionally, three interdependent processes could help to explain our results: reduced animal dispersers near the edge (Peres *et al.* 2003); increased seed predation and herbivory (Carvalho *et al.* 2012, Massad *et al.* 2013) and seed dehydration (Daws *et al.* 2005).

Our third prediction, that regeneration mode would be more dependent on resprouting than seedling germination, was partially corroborated. We noted that resprouts increased their density in the first moment (2011) in B3, particularly next to the forest edge, contributing to the species diversity increase. As reported in previous studies, vegetative growth is an adaptive trait allowing response to perturbation and, therefore, a key process for rapid forest recovery (Hoffmann *et al.* 2003, Poorter *et al.* 2010). However, we witnessed that new resprouting stem density and species richness were reduced annually in both burned treatments (2013) in B3 and in B6. Thus, we noted that even woody resprouters, from species more adapted to disturbances can also be negatively affected. The probable explanation for this pattern is that the long-time of fire degradation possibly drained root carbohydrate storage (Hoffmann *et al*. 2003), showing a limitation in the tolerance of transitional forests to fire recurrence. Also, the reduction of carbohydrate would help to explain why resprouts had two-fold more percent of mortality in B6 (37%) than in B3 (17.6%; Fig 2).

The future trajectory of this forest will depend in a great extent on how key species regenerate from the fires, for example, fours species represented in both seed sources, recruit and resprout categories. According to the theory prediction that pioneer species would prevail in the soil seed bank and in the regeneration after fires, we expected to find some similarity between them. However, *Miconia* sp., which was the most abundant genera in soil seed bank, indicating a potential of this family for early succession colonization (Dalling *et al.* 1998, Filho *et al.* (2005), showed very few species in the seedling size class in both burned treatments. Differently, seed rain guided the first pulse of regeneration, selecting some species which produced seeds that recruit quickly (*e.g.*, *Amaioua guianensis*, *Pouteria ramiflora*). We suggest that three facts would explain this result. First, species-specific traits may promote rapid post-fire germination and could be an advantage for some desiccation-sensitive species from seed rain, with higher seed nutrient reserve (*e.g.*, *Ocotea* sp., *Pouteria ramiflora*, *Mabea fistulifera*, *Virola sebifera*, *Sacoglottis guianensis*), reducing the duration of seed exposure to predation and desiccation (Daws *et al.* 2005). Second, recruits of some species, specialized for different early succession niches, may have benefited from heterogeneous understory microclimate, some under higher irradiance levels (*e.g.*, *P. venusta*, *Mabea fistulifera* and *Ocotea guianensis*). Finally, recruits from small seeds (*e.g.*, *Miconia* spp.) may be outcompeted, particularly by fast-spreading invasive grasses near to the forest edge (Snyder & Chesson 2003, Reid & Holl 2013, Silvério *et al.* 2013, Balch *et al*. 2015; Chapter 2).

Spanning the analysis along the years we noted that some tree species (*i.g.*, *Pouteria ramiflora*) recruited massively in B6 during a non-drought year (2012; 49 mm from March to August) when compared with 2011 (11 mm; Supporting information; Fig. S3), likely benefited by the local dispersal from surviving trees (Snyder & Chesson 2003) and the increased rainfall, which favored germination (Vlam *et al.* 2014). This result reinforces how harmful is the interaction between fire occurrence in Amazon Basin and the predicted increase in episodic droughts events, reducing forest resilience.

ACKNOWLEDGEMENTS

We thank IPAM and LABRE-UEL for financial support. Also, thank IPAM staff for help in fieldwork, specially, Raimundo M. Quintino, Sebastião Nascimento, Adilson R. Coelho and Darlisson N. Costa, all provided valuable field assistance. Carol C. C. Oliveira, Alba L. Cavalheiro, Renata P. Scervino, Tyler D. Lagasse, and Nicole M. S. Cury who provided helpful suggestions on earlier draft of this paper. RTSC benefited from a CNPq grant (process # 248491/2013-0) during internship term at University of Colorado-Boulder, USA, and JMDT from a CNPq research grant (process # 305854/2012-7)

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FIGURES AND LEGENDS

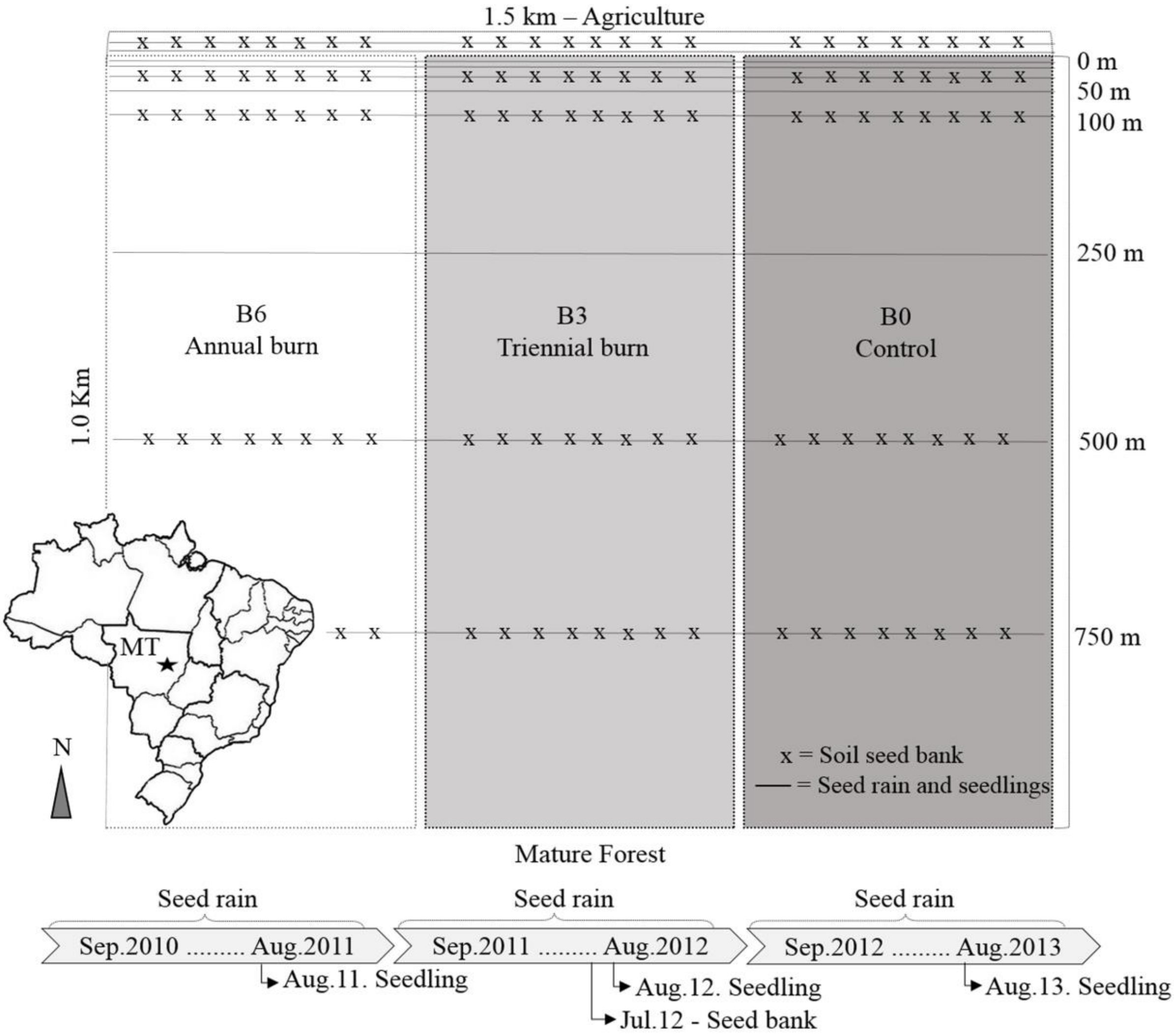

FIGURE 1. Fieldwork design of a long-term fire experiment in Mato Grosso state, southeastern Amazon Basin. Lines indicate the regeneration plots and seed rain mesh traps distributed from agriculture edge to forest interior (0-750 m). Soil seed bank plots (x). Unburned plot (B0), triennial burned plot (B3), and annual burned plot (B6).

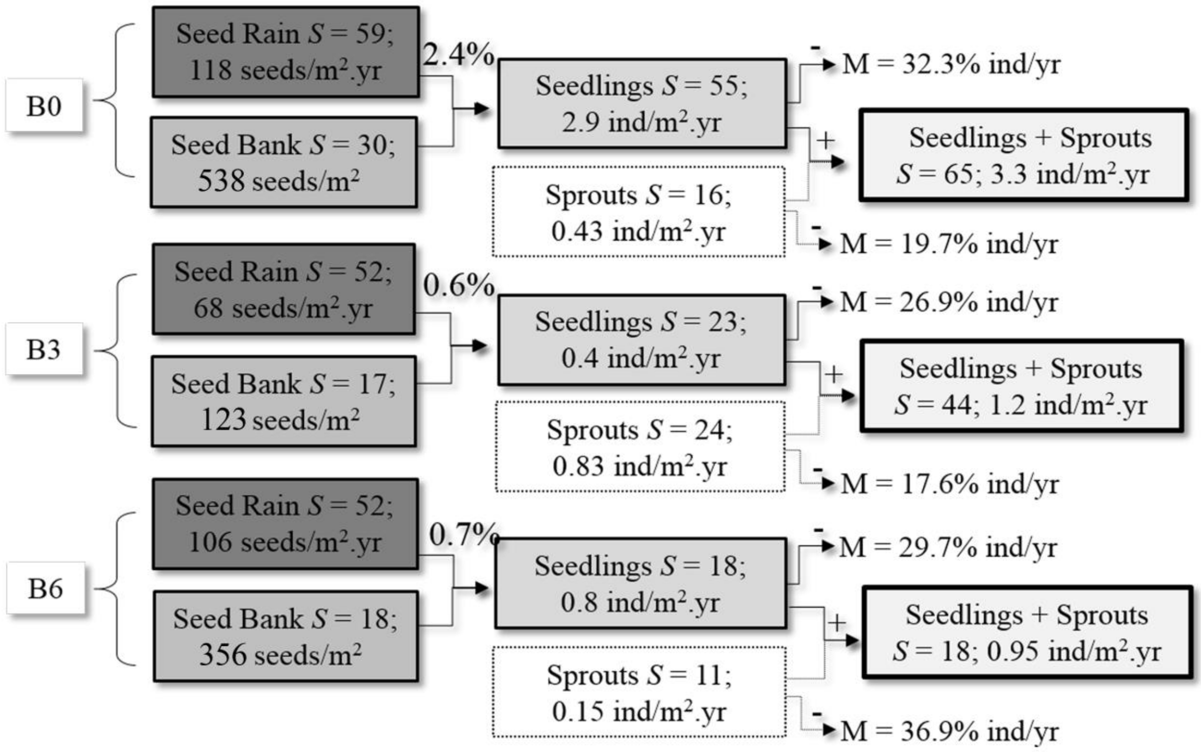

FIGURE 2. Recovery trajectory three years after fire exclusion. Richness (*S*) and density (m^2) of seeds, seedlings and sprouts. Recruit rates (% of new seedlings by total of seeds arriving). Mortality rates (%). Unburned plot (B0), triennial burned plot (B3), and annual burned plot (B6).

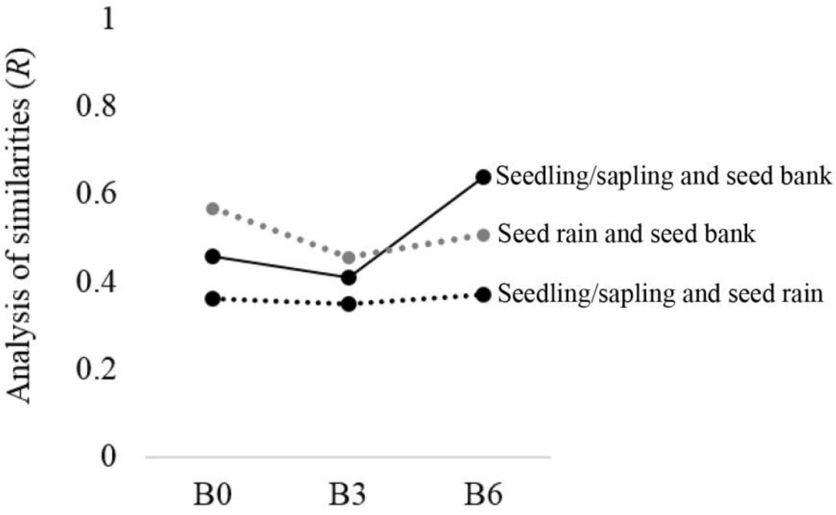

FIGURE 3. Analysis of similarities (ANOSIM) plot, based on Nonmetric multidimensional scaling (NMDS - Bray-Curtis similarity index). Unburned plot (B0), triennial burned plot (B3), and annual burned plot (B6).

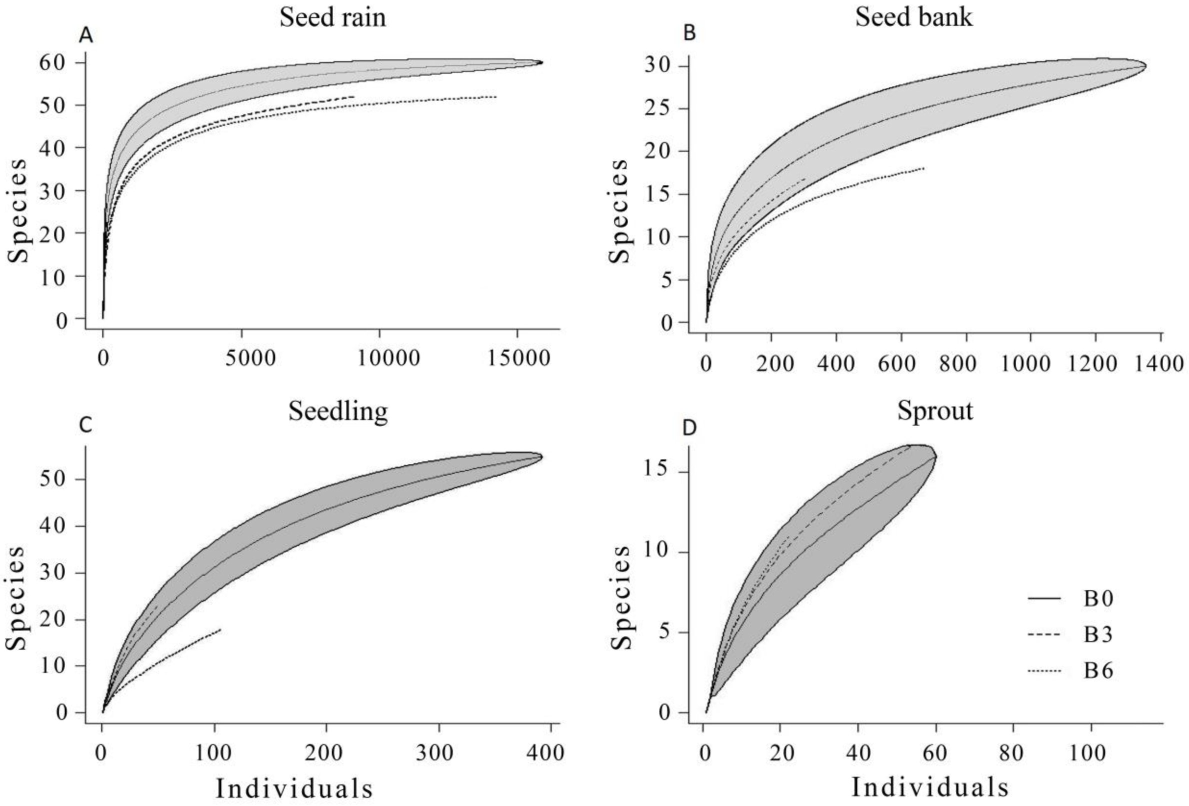

FIGURE 4. Accumulation curves for richness species by individuals of seed rain, seed bank, seedlings and sprouts. Unburned plot (B0), triennial burned plot (B3), and annual burned plot (B6). B0 shows 95% confidence interval.

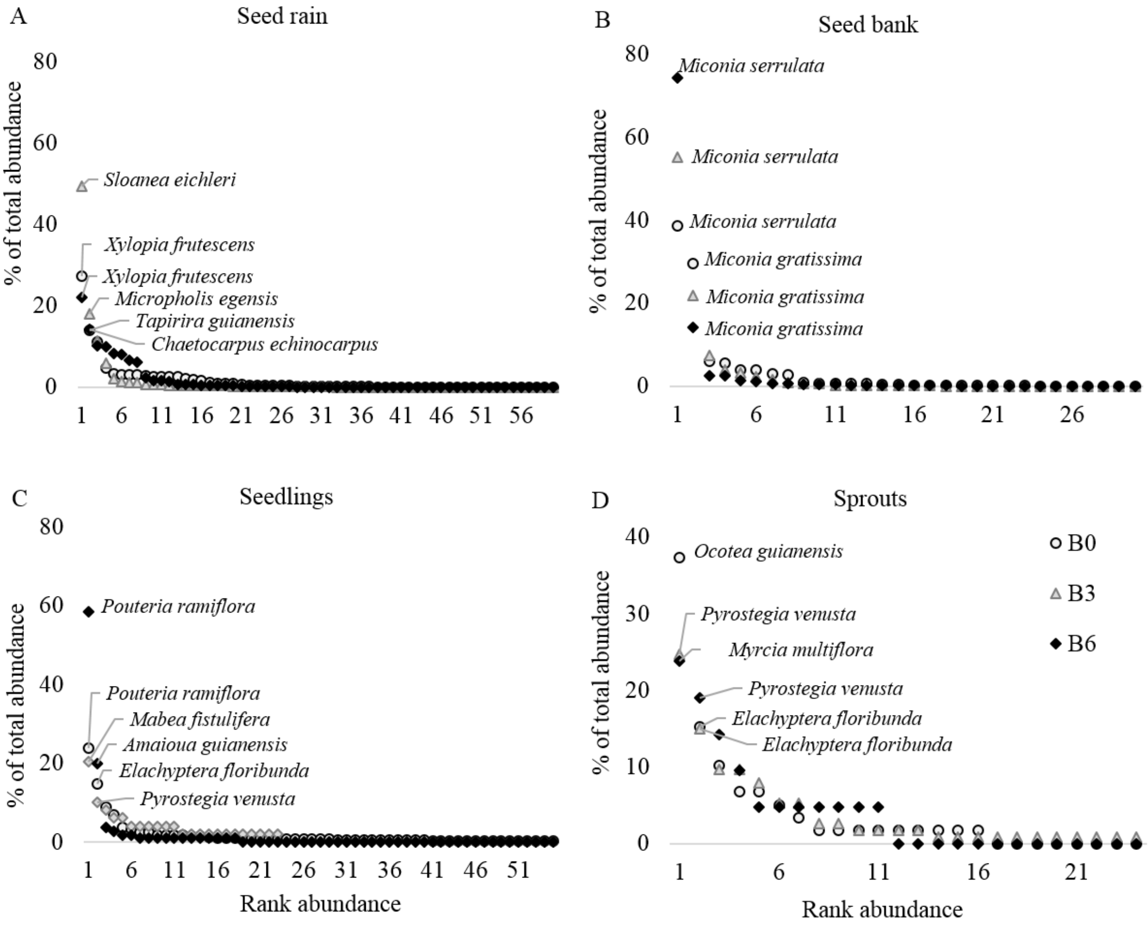

FIGURE 5. Rank abundance of seed rain (A), seed bank (B), seedlings (C) and sprouts (D). Name of species are given for the first two species more abundant by treatment in rank order. Unburned plot (B0), triennial burned plot (B3), and annual burned plot (B6).

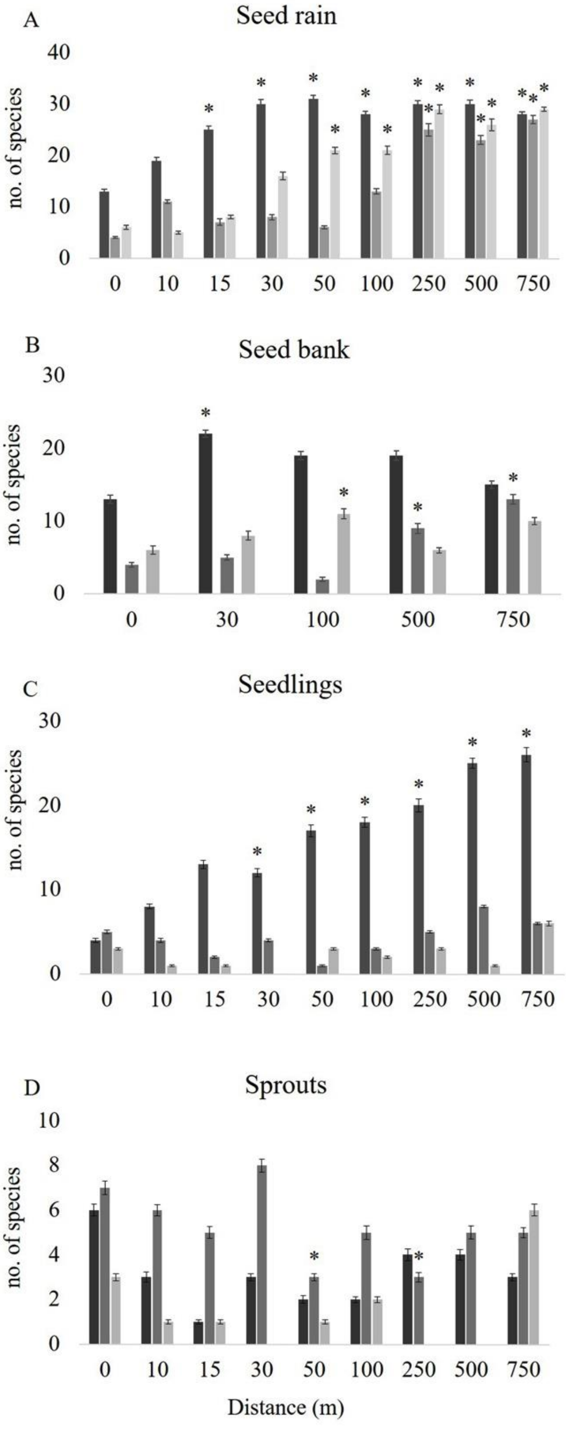

FIGURE 6. Number of species from seed rain (A), seed bank (B), seedlings (C) and sprouts (E) by distance of forest edge. Dark bars indicate the control, medium gray bars indicate burned triennially and light gray bars indicate burned annually treatment. Error bars. Asterisks indicate differences with edge (0 m) ($p < 0.05$).

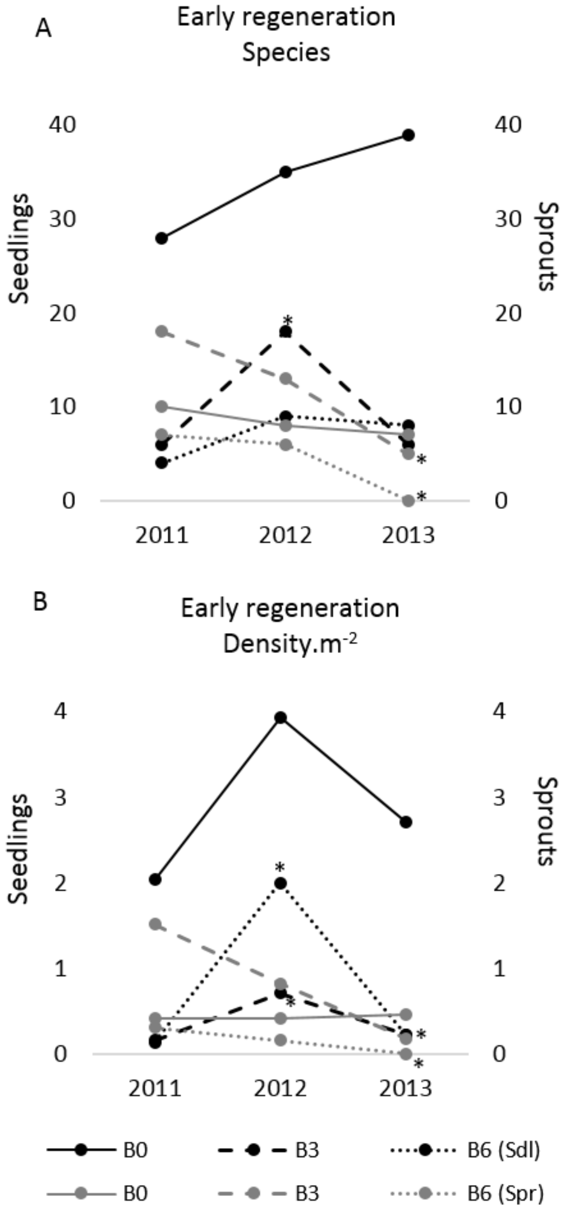

FIGURE 7. Temporal evaluation (2011, 2012, 2013) of seedlings and sprouts species (A) and density (B). Unburned plot (B0), triennial burned plot (B3), and annual burned plot (B6). Asterisks indicate differences with the first year (p < 0.05).

SUPPORTING INFORMATION

Table S1. List of species recorded in southeastern Amazon Basin in Mato Grosso state, Brazil. (x) indicate the species presence in seedlings (SD), sprouts (SP), seed rain (SR), and seed bank (SB) samples. (-) absent species by samples. Life form classification (LF).

Family/Species	**SD**	**SP**	**SR**	**SB**	**LF**
Anacardiaceae					
Tapirira guianensis Aubl.	x	x	x	-	Tree
Annonaceae					
Bocageopsis mattogrossensis (R.E. Fr.) R.E. Fr.	-	-	-	x	Tree
Guatteria blepharophylla Mart.	x	-	-	-	Tree
Guatteria schomburgkiana Mart.	-	-	x	-	Tree
Xylopia amazonica R.E. Fr.	x	-	-	x	Tree
Xylopia cayennensis Maas	-	-	x	-	Tree
Xylopia frutescens Aubl.	-	-	x	-	Tree
Apocynaceae					
Aspidosperma excelsum Benth.	-	-	x	-	Tree
Aspidosperma obscurinervium Azambuja	x	-	x	-	Tree
Forsteronia affinis Müll. Arg.	x	x	-	-	Liana
Himatanthus sucuuba (Spruce ex Müll. Arg.) Woodson	x	-	-	-	Tree
Secondatia densiflora A. DC.	x	-	-	-	Liana
Araliaceae					
Schefflera morototoni (Aubl.) Maguire, Steyerm. & Frodin	x	-	x	x	Tree
Asteraceae					
Lepidaploa gracilis (Kunth) H. Rob.	-	-	-	x	Shrub
Bignoniaceae					
Adenocalymma longilineum (A. Samp.) L.G. Lohmann	-	x	-	-	Liana
Arrabideae sp.	-	x	-	-	Liana
Cuspidaria inaequalis (DC. ex Splitg.) L.G. Lohmann	x	x	-	-	Liana
Fridericia cinnamomea (DC.) L.G. Lohmann	x	x	-	-	Liana
Indet. sp. 1	-	x	-	-	Liana
Jacaranda copaia (Aubl.) D. Don	x	-	-	x	Tree
Pleonotoma melioides (S. Moore) A.H. Gentry	x	-	-	-	Liana
Pyrostegia venusta (Ker Gawl.) Miers	x	x	-	-	Liana
Boraginaceae					
Cordia bicolor A. DC.	x	x	x	-	Tree
Burseraceae					
Dacryodes microcarpa Cuatrec.	x	-	x	-	Tree
Protium guianense (Aubl.) Marchand	x	x	x	-	Tree
Protium unifoliolatum Engl.	x	-	-	-	Tree
Trattinnickia burseraefolia Mart.	x	-	-	x	Tree
Trattinnickia glaziovii Swart	x	-	x	x	Tree
Celastraceae					
Elachyptera floribunda (Benth.) A.C. Sm.	x	x	x	-	Liana

Family/Species	SD	SP	SR	SB	LF
Hippocratea volubilis L.	x	x	-	-	Liana
Chrysobalanaceae					
Hirtella glandulosa Spreng.	x	-	x	x	Tree
Licania egleri Prance	x	-	x	-	Tree
Licania gracilipes Taub.	-	x	x	-	Tree
Combretaceae					
Buchenavia tetraphylla (Aubl.) R.A. Howard	-	-	x	-	Tree
Connaraceae					
Connarus perrottetii (DC.) Planch.	x	-	x	-	Tree
Dilleniaceae					
Davilla kunthii A. St.-Hil.	x	-	x	x	Liana
Doliocarpus spatulifolius Kubitzki	x	x	x	x	Liana
Ebenaceae					
Diospyros sericea A. DC.	-	-	x	-	Tree
Elaeocarpaceae					
Sloanea eichleri K. Schum.	x	-	x	-	Tree
Erythroxylaceae					
Erythroxylum rufum Cav.	x	-	x	-	Tree
Euphorbiaceae					
Chaetocarpus echinocarpus (Baill.) Ducke	x	x	-	x	Tree
Mabea fistulifera Mart.	x	x	x	-	Tree
Maprounea guianensis Aubl.	x	-	-	x	Tree
Pera coccinea (Benth.) Müll. Arg.	-	-	x	-	Tree
Fabaceae					
Abrus precatorius L.	x	-	-	-	Liana
Copaifera reticulata Ducke	-	-	x	-	Tree
Derris floribunda (Benth.) Ducke	x	x	x	-	Liana
Enterolobium schomburgkii (Benth.) Benth.	-	-	x	-	Tree
Inga alba (Sw.) Willd	-	-	x	-	Tree
Inga heterophylla Willd.	x	x	-	-	Tree
Machaerium myrianthum Spruce ex Benth.	x	-	-	-	Liana
Ormosia paraensis Ducke	x	-	x	-	Tree
Parkia pendula (Willd.) Benth. ex Walp.	-	-	x	-	Tree
Tachigali vulgaris L.F. Gomes da Silva & H.C. Lima	x	x	x	x	Tree
Humiriaceae					
Humiria balsamifera (Aubl.) J.St.-Hil.	-	-	x	-	Tree
Sacoglottis guianensis Benth.	x	-	x	x	Tree
Hypericaceae					
Vismia latifolia (Aubl.) Choisy	x	x	-	x	Tree
Lauraceae					
Nectandra cuspidata Nees & Mart.	x	x	x	-	Tree
Ocotea cujumary Mart.	-	-	x	-	Tree
Ocotea guianensis Aubl.	x	x	x	-	Tree
Ocotea leucoxylon (Sw.) Laness.	x	-	x	x	Tree
Ocotea sp.	-	-	x	-	Tree
Loganiaceae					
Strychnos xinguensis Krukoff	x	-	x	-	Liana

Family/Species	SD	SP	SR	SB	LF
Malpighiaceae					
Banisteriopsis malifolia (Nees & Mart.) B. Gates	x	x	-	-	Liana
Byrsonima aerugo Sagot	-	-	x	-	Tree
Tetrapterys styloptera A. Juss.	x	x	x	-	Liana
Malvaceae					
Mollia lepidota Spruce ex Benth.	-	-	x	x	Tree
Melastomataceae					
Bellucia grossularioides (L.) Triana	-	-	x	x	Tree
Miconia dichrophylla J.F. Macbr.	-	-	x	-	Tree
Miconia dispar Benth.	-	-	-	x	Tree
Miconia gratissima Benth. ex Triana	x	-	x	x	Tree
Miconia minutiflora (Bonpl.) DC.	-	-	-	x	Tree
Miconia serrulata (DC.) Naudin	-	-	-	x	Tree
Miconia sp. 1	-	-	-	x	Tree
Miconia sp. 2	-	-	-	x	Tree
Miconia sp. 3	-	-	x	-	Tree
Mouriri brachyanthera Ducke	-	-	x	-	Tree
Meliaceae					
Trichilia quadrijuga Kunth	x	-	x	-	Tree
Moraceae					
Ficus americana subsp. *guianensis* (Desv. ex Ham.) C.C. Berg	-	-	-	x	Liana
Pseudolmedia macrophylla Trécul	x	-	-	-	Tree
Myristicaceae					
Virola sebifera Aubl.	x	x	x	-	Tree
Myrtaceae					
Marlierea umbraticola (Kunth) O. Berg	-	x	x	-	Tree
Myrcia multiflora (Lam.) DC.	x	x	-	-	Tree
Myrcia sylvatica (G. Mey.) DC.	x	x	-	-	Tree
Ochnaceae					
Ouratea discophora Ducke	-	-	x	-	Tree
Polygalaceae					
Securidaca bialata Benth.	x	-	-	-	Liana
Rubiaceae					
Amaioua guianensis Aubl.	x	x	x	x	Tree
Palicourea corymbifera (Müll. Arg.) Standl.	x	-	-	x	Shrub
Psychotria prunifolia (Kunth) Steyerm.	x	-	-	x	Shrub
Psychotria sphaerocephala Müll. Arg.	x	-	-	x	Shrub
Salicaceae					
Casearia grandiflora Cambess.	x	-	-	x	Tree
Sapindaceae					
Matayba guianensis Aubl.	-	x	x	-	Tree
Matayba spruceana (Hook.) Radlk.	-	-	x	-	Tree
Paullinia pachycarpa Benth.	-	-	x	-	Liana
Paullinia sp.	-	x	-	-	Liana
Serjania membranacea Splitg.	x	-	-	-	Liana
Sapotaceae					
Micropholis egensis (A. DC.) Pierre	x	-	x	-	Tree

Family/Species	**SD**	**SP**	**SR**	**SB**	**LF**
Pouteria ramiflora (Mart.) Radlk.	x	-	x	-	Tree
Simaroubaceae					
Simarouba amara Aubl.	x	x	x	-	Tree
Siparunaceae					
Siparuna guianensis Aubl.	-	x	-	-	Tree
Solanaceae					
Solanum lycocarpum A. St.-Hil.	-			x	Shrub
Solanum mauritianum Scop.	x	x	x	x	Tree
Solanum sp. 1	-	-	-	x	Shrub
Solanum sp. 2	-	-	-	x	Shrub
Urticaceae					
Cecropia distachya Huber	-	-	-	x	Tree
Cecropia glaziovii Snethl.	x	-	-	x	Tree
Vochysiaceae					
Vochysia vismiifolia Spruce ex Warm.	-	-	x	-	Tree
Não Identificadas					
Indet. sp. 2	-	-	x	-	
Indet. sp. 3	-	-	x	-	
Indet. sp. 4	-	-	x	-	
Indet. sp. 5	-	-	x	-	
Indet. sp. 6	-	-	x	-	
Indet. sp. 7	x	x	-	-	Shrub
Indet. sp. 8	-	-	x	-	Tree

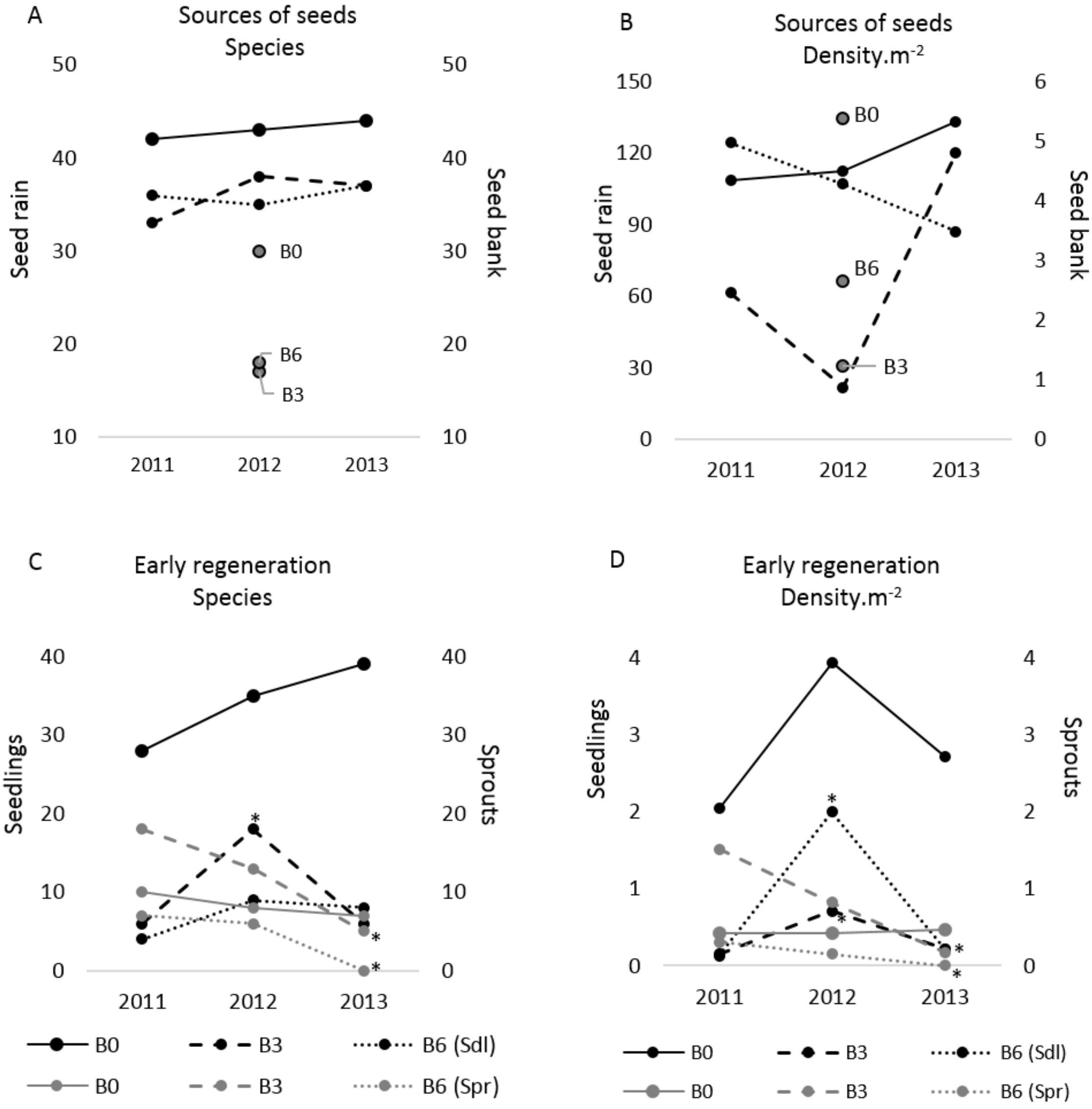

Figure S1. Temporal evaluation (2011, 2012, 2013) of seed rain, seedlings and sprouts, except seed bank that was evaluated in only 2012. Species and density measured in unburned plot (B0), triennial burned plot (B3), and annual burned plot (B6). Asterisks indicate differences with the first year ($p < 0.05$).

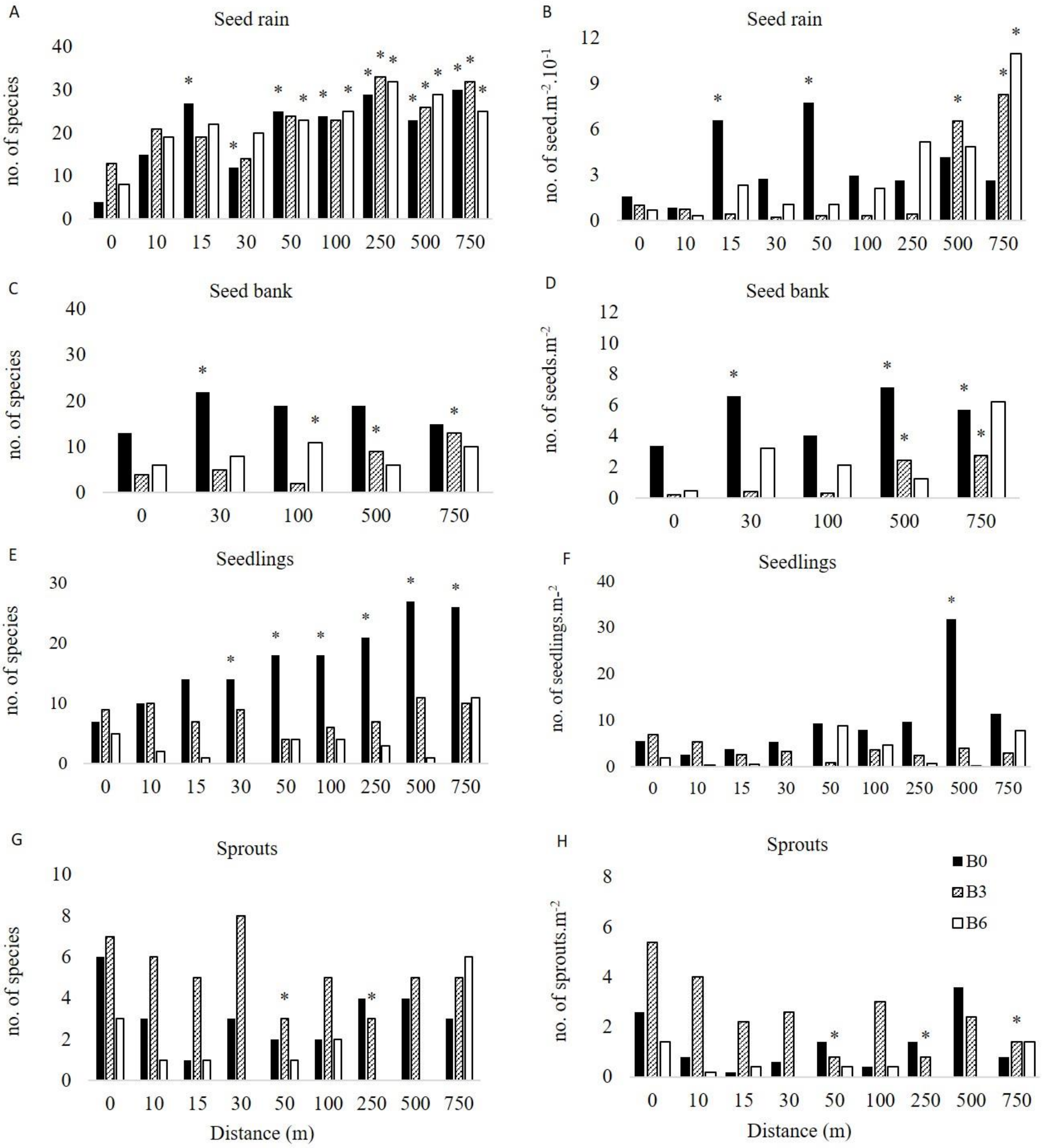

Figure S2. Number of species and density (m^2) of seed rain, seed bank, seedlings and sprouts by distance of forest edge. Unburned plot (B0), triennial burned plot (B3), and annual burned plot (B6). Asterisks indicate differences with edge (0 m) (*p* < 0.05).

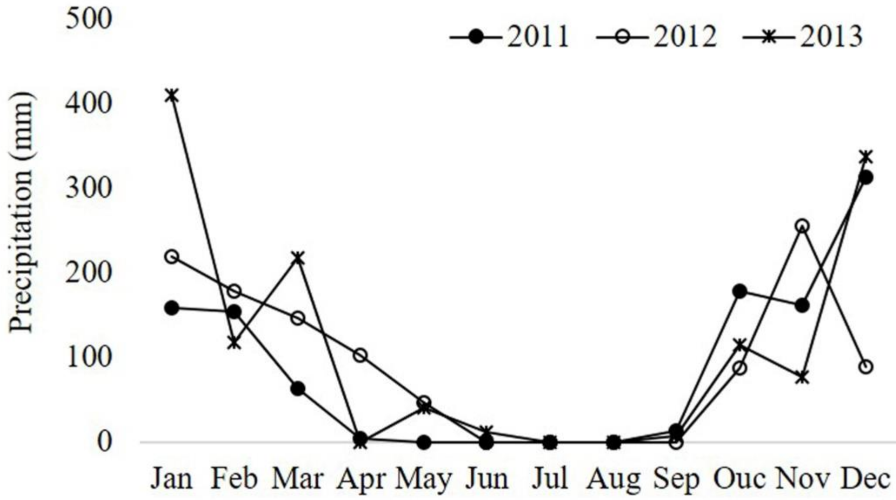

Figure S3. Monthly precipitation occurred during the experimental time registered at Tanguro’s farm in southeastern Amazon Basin in Mato Grosso state, Brazil.

ANEXO 3. NORMAS DA REVISTA BIOTROPICA

BIOTROPICA – JOURNAL OF THE ASSOCIATION FOR TROPICAL BIOLOGY AND CONSERVATION

CHECKLIST FOR PREPARATION OF MANUSCRIPTS AND ILLUSTRATIONS (updated February 2010)

Online submission and review of manuscripts is mandatory effective 01 January 2005.

Please format your paper according to these instructions and then go to the following website to submit your manuscript (http://mc.manuscriptcentral.com/bitr). Contact the BIOTROPICA Office for assistance if you are unable to submit your manuscript via Manuscript Central (biotropica@env.ethz.ch).

Authors are requested to provide a **cover letter** that details the **novelty**, **relevance** and **implications** of their work, and a brief explanation of the suitability of the work for BIOTROPICA. The number of words in the manuscript should also be given in the cover letter.

Owing to limited space within Biotropica we ask authors to place figures and tables that do not have central relevance to the manuscript as online Supporting Information (SI). SI accompanies the online version of a manuscript and will be fully accessible to everyone with electronic access to Biotropica. Authors are welcome to submit supplementary information, including photographs, for inclusion as SI, although all such material must be cited in the text of the printed manuscript. The Editor reserves the right to make decisions regarding tables, figures and other materials in SI. If authors disagree with the Editor's decision, they could ask for such tables and figures to be included in the printed article on the condition that the authors cover the additional page charges incurred at the rate of US $60 per page.

I. General Instructions

☐ Publication must be in English, but second abstract in other languages (such as Spanish, French, Portuguese, Hindi, Arabic, Chinese etc.) may be published as online Supporting Information. BIOTROPICA offers assistance in editing manuscripts if this is required (see English Editorial Assistance below). Second abstracts will **not** be copy-edited and the author(s) must take full responsibility for content and quality.

☐ Manuscripts may be submitted in the following categories, based on these suggested word limits:

Paper (up to 5000 words)
Insights (up to 2000 words)
Review (up to 8000 words)
Commentary (up to 2000 words)

Word counts exclude title page, abstract(s), literature cited, tables, figures, or appendices.

☐ Use 8.5" x 11" page size (letter size). Double space everything, including tables, figure legends, abstract, and literature cited.

☐ Use a 1" margin on all sides. Align left. Avoid hyphens or dashes at ends of lines; do not divide a word at the end of a line.

☐ Use standard 12 point type (Times New Roman).

☐ Indent all but the first paragraph of each section.

☐ Use italics instead of underline throughout. Italicize non-English words such as *e.g., i.e., et al., cf., ca, n.b., post-hoc,* and *sensu* (the exceptions being 'vs.' and 'etc.').

☐ Include page number in the centre of all pages. Do use line numbering starting on each page.

Cite each figure and table in the text. Tables and figures must be numbered in the order in which they are cited in the text.

- Use these abbreviations: yr (singular & plural), mo, wk, d, h, min, sec, diam, km, cm, mm, ha, kg, g, L, g/m^2
- For units, avoid use of negative numbers as superscripts: use the notation /m^2 rather than m^{-2}.
- Write out other abbreviations the first time they are used in the text; abbreviate thereafter: "El Niño Southern Oscillation (ENSO) . . ."
- Numbers: Write out one to ten unless a measurement (*e.g.*, four trees, 6 mm, 35 sites, 7 yr, 10 × 5 m, > 7 m, ± SE) or in combination with other numbers (*e.g.*, 5 bees and 12 wasps). Use a comma as a separator in numbers with **more than** four digits (*i.e.*, 1000, but 10,000); use decimal points as in 0.13; 21°C (no spaces); use dashes to indicate a set location of a given size (*e.g.*, 1-ha plot).
- Spell out 'percent' except when used in parentheses (20%) and for 95% CI.
- Statistical abbreviations: Use italics for P, N, t, F, R^2, r, G, U, N, χ^2 (italics, superscripts non-italics); but use roman for: df, SD, SE, SEM, CI, two-way ANOVA, ns
- Dates: 10 December 1997; Times: 0930 h, 2130 h
- Latitude and Longitude are expressed as: 10°34′21″ N, 14°26′12″ W
- Above sea level is expressed as: asl
- Regions: SE Asia, UK (no periods), but note that U.S.A. includes periods.
- Geographical place names should use the English spelling in the text (Zurich, Florence, Brazil), but authors may use their preferred spelling when listing their affiliation (Zürich, Firenze, Brasil).
- Lists in the text should follow the style: … : (1)… ; (2)…; and (3)…, as in, "The aims of the study were to: (1) evaluate pollination success in *Medusagyne oppositifolia*; (2) quantify gene flow between populations; and (3) score seed set."
- Each reference cited in text must be listed in the Literature Cited section, and vice versa. Double check for consistency, spelling and details of publication, including city and country of publisher.
- For manuscripts ACCEPTED for publication but not yet published, cite as Yaz (in press) or (Yaz, in press). Materials already published online can be cited using the digital object identifier (doi)
    - Literature citations in the text are as follows: One author: Yaz (1992) or (Yaz 1992)
      Two authors: Yaz and Ramirez (1992); (Yaz & Ramirez 1992)
      Three or more authors: Yaz *et al.* (1992), but include ALL authors in the literature cited section.
- Cite unpublished materials or papers not in press as (J. Yaz, pers. obs.) or (J. Yaz, unpubl. data). Initials and last name must be provided. 'In prep' or 'submitted' are NOT acceptable, and we encourage authors not to use 'pers. obs.' or 'unpubl. data' unless absolutely necessary. Personal communications are cited as (K. A. Liston, pers. comm.).
- Use commas (Yaz & Taz 1981, Ramirez 1983) to separate citations, BUT use semicolon for different types of citations (Fig. 4; Table 2) or with multiple dates per author (Yaz *et al.* 1982a, b; Taz 1990, 1991). Order references by year, then alphabetical (Azy 1980, Yaz 1980, Azy 1985).
- Assemble manuscripts in this order:
    Title page
    Abstract (s)
    Key words
    Text
    Acknowledgments (spelled like this)
    Literature cited
    Tables
    Appendix (when applicable)
    Figure legends (one page)
    Figures
- For the review purpose, submit the entire manuscript, with Tables, Figure legends and Figures embedded at the end of the manuscript text, as a Microsoft Word for Windows document (*.doc), or equivalent for Mac or Linux. Do NOT submit papers as pdf files.

II. Title Page

(Do not number the title page)

☐ Running heads two lines below top of page.

LRH: Yaz, Pirozki, and Peigh (may not exceed 50 characters or six author names; use Yaz *et al.*)
RRH: Seed Dispersal by Primates (use capitals; may not exceed 50 characters or six words)

☐ Complete title, flush left, near middle of page, Bold Type and Initial Caps, usually no more than 12 words.

☐ Where species names are given in the title it should be clear to general readers what type(s) of organism(s) are being referred to, either by using Family appellation or common name. For example: ‘Invasion of African Savanna Woodlands by the Jellyfish tree *Medusagyne oppositifolia*’, *or* ‘Invasion of African Savanna Woodlands by *Medusagyne oppositifolia* (Medusagynaceae)’

☐ Titles that include a geographic locality should make sure that this is clear to the general reader. For example: ‘New Species of Hummingbird Discovered on Flores, Indonesia’, and NOT ‘New Species of Hummingbird Discovered on Flores’.

☐ Below title, include author(s) name(s), affiliation(s), and unabbreviated complete address(es). Use superscript number(s) following author(s) name(s) to indicate current location(s) if different than above. In multi-authored papers, additional footnote superscripts may be used to indicate the corresponding author and e-mail address. **Please refer to a current issue**.

☐ At the bottom of the title page every article must include: Received ____; revision accepted ___ . (BIOTROPICA will fill in dates.)

III. Abstract Page

(Page 1)

☐ Abstracts should be concise (maximum of 250 words for papers and reviews; 50 words for Insights; no abstract for Commentary). Include brief statements about the intent, materials and methods, results, and significance of findings. The abstract of Insights should emphasise the novelty and impact of the paper.

☐ Do not use abbreviations in the abstract.

☐ **Authors are strongly encouraged to provide a second abstract in the language relevant to the country in which the research was conducted**, and which will be published as online Supporting Information. This second abstract should be embedded in the manuscript text following the first abstract.

☐ Provide up to eight key words after the abstract, separated by a semi-colon (;). Key words should be listed alphabetically. Include location, if not already mentioned in the title. See style below. Key words should NOT repeat words used in the title. Authors should aim to provide informative key words—avoid words that are too broad or too specific.

☐ *Key words*: Melastomataceae; *Miconia argentea*; seed dispersal; Panama; tropical wet forest.—Alphabetized and key words in English only.

IV. Text

(Page 2, etc) See General Instructions above, or recent issue of BIOTROPICA (Section I).

☐ No heading for Introduction. First line or phrase of Introduction should be SMALL CAPS.

☐ Main headings are **METHODS**, **RESULTS**, and **DISCUSSION**: All CAPITALS and **Bold**. Flush left, one line.

☐ One line space between main heading and text

☐ Second level headings: SMALL CAPS, flush left, Capitalize first letter, begin sentence with em-dash, same line (*e.g.*, INVENTORY TECHNIQUE.—The ant inventory…).

☐ Use no more than second level headings.

☐ Do not use footnotes in this section.

☐ References to figures are in the form of ‘Fig. 1’, and tables as ‘Table 1’. Reference to online Supporting Information is as ‘Fig. S1’ or ‘Table S1’.

V. Literature Cited

(Continue page numbering and double spacing)

- ☐ No ‘in prep.’ or ‘submitted’ titles are acceptable; cite only articles published or ‘in press’. ‘In press’ citations must be accepted for publication. Include journal or publisher.
- ☐ Verify all entries against original sources, especially journal titles, accents, diacritical marks, and spelling in languages other than English.
- ☐ Cite references in alphabetical order by first author's surname. References by a single author precede multi-authored works by the same senior author, regardless of date.
- ☐ List works by the same author chronologically, beginning with the earliest date of publication.
- ☐ Insert a period and space after each initial of an author's name; example: YAZ, A. B., AND B. AZY. 1980.
- ☐ Authors Names: use SMALL CAPS.
- ☐ **Every** reference should spell out author names as described above. BIOTROPICA no longer uses ‘em-dashes’ (—) to substitute previously mentioned authors.
- ☐ Use journal name abbreviations (see http://www.bioscience.org/atlases/jourabbr/list.htm). If in doubt provide full journal name.
- ☐ Double-space. Hanging indent of 0.5 inch.
- ☐ Leave a space between volume and page numbers and do not include issue numbers. 27: 3–12
- ☐ Article in books, use: AZY, B. 1982. Title of book chapter. *In* G. Yaz (Ed.). Book title, pp. 24–36. Blackwell Publications, Oxford, UK.
- ☐ Dissertations, use: ‘PhD Dissertation’ and ‘MSc Dissertation’.

VI. Tables

(Continue page numbering)

- ☐ Each table must start on a separate page, double-spaced. The Table number should be in Arabic numerals followed by a period. Capitalize first word of title, double space the table caption. Caption should be italicized, except for words and species names that are normally in italics.
- ☐ Indicate footnotes by lowercase superscript letters (^{a}, ^{b}, ^{c}, etc.).
- ☐ Do not use vertical lines in tables.
- ☐ Ensure correct alignment of numbers and headings in the table (see current issues)
- ☐ Tables must be inserted as a Word table or copy and pasted from Excel in HTML format.

VII. Figure Legends

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CONSIDERAÇÕES FINAIS

A floresta de transição Amazônica-Cerrado se mostrou extremamente sensível à ocorrência incêndios e à reincidência dos mesmos. Ao longo dos capítulos apresentamos resultados como: a mortalidade de indivíduos, troncos danificados e indicadores de resiliência florestal após incêndios recorrentes, como a chuva de sementes, o banco de sementes, o recrutamento de plântulas e a persistência das rebrotas. Como resultado geral, concluímos que todos os parâmetros analisados foram alterados negativamente nos primeiros anos após os incêndios, inclusive as rebrotas. Do mesmo modo, houve redução na diversidade da comunidade e o predomínio de poucas espécies da flora original e gramíneas.

Especificamente, no *Capítulo 1*, demonstramos que o acúmulo de combustível fino (*i.e.*, serapilheira), que ocorre durante os períodos de estiagem prolongada, tornou os incêndios mais severos, resultando em maior área queimada, maior mortalidade de indivíduos nas classes intermediárias de tamanho (1–5 cm DAP) e maior número de troncos danificados. Embora ambos os tratamentos incendiados - com e sem a adição de serapilheira – tenham resultado em valores elevados e similares na mortalidade de regenerantes (indivíduos entre 5 e 130 cm de altura ou ≤ 1 cm de DAP), o número de plântulas, rebrotas e sementes na chuva de sementes foi elevado no primeiro ano após os incêndios. Ainda, no tratamento queimado sem a adição de combustível, foi registrado 33% menor área queimada, o que contribuiu para sobrevivência de regenerantes, contribuindo para manutenção da diversidade da comunidade.

No *Capítulo 2*, observamos que o aumento na frequência de incêndios, seis incêndios os quais ocorreram anualmente, reduziu a diversidade de regenerantes, o número de rebrotas e permitiu maior invasão por gramíneas (*Aristida longifólia*) em comparação com três incêndios que ocorreram trienalmente. Embora ampla gama de espécies tenha sido perdida em ambos os tratamentos, as espécies florestais de ocorrência no Bioma de Cerrado, apresentam elevado número de rebrotas no tratamento queimado trienalmente em comparação com incêndios anuais. *Myrcia multiflora* e *Pyrostegia venusta* se mostraram abundantes em ambos os tratamentos, particularmente no tratamento com incêndios anuais, diferenciando-se do controle, onde *Pouteria ramiflora* e *Elachyptera floribunda* foram mais abundantes. *Marlierea umbraticola* e *Tachigali vulgaris* ocorreram exclusivamente no tratamento com incêndios trienais, contribuindo para maior heterogeneidade florística no tratamento.

No *Capítulo 3*, concluímos que as principais vias para recuperação florestal foram alteradas negativamente em ambas as frequências de fogo. As fontes de sementes (chuva e banco de sementes) foram reduzidas no tratamento com incêndios trienais, em comparação com incêndios anuais. As mesmas também foram reduzidas próximo à borda florestal. As plântulas foram sensíveis em ambas as frequências de incêndios. As rebrotas aumentaram no tratamento com incêndios trienais, no entanto, declinaram anualmente à níveis inferiores aos registrados no controle, não persistindo no sistema, principalmente no tratamento queimado anualmente. Os indivíduos reprodutivos sobreviventes contribuíram para a diversidade da chuva de sementes e, consequentemente, para a diversidade de recrutas em ambos os tratamentos.

RECOMENDAÇÕES PRÁTICAS

Em resposta à ampla gama de efeitos negativos decorrentes da reincidência de incêndios na floresta de transição, e da sensibilidade da mesma às mudanças climáticas atuais, recomendamos intervenções públicas de incentivo à proteção florestal, tais como:

- Incentivar financeiramente as práticas que valorizem a manutenção da floresta, coibindo o desmatamento;
- Desencorajar a extração seletiva de madeira, como manejo sustentável, nas áreas sensíveis às alterações climáticas e à pressão econômica, como é o caso da floresta de transição no estado de Mato Grosso;
- Aumentar a fiscalização e autuar as propriedades que empregam práticas agrícolas que tradicionalmente utilizam o fogo como ferramenta de manejo;
- Combater a reincidência de incêndios acidentais, por exemplo, através da manutenção de aceiros nos fragmentos florestais próximos às rodovias;
- Incentivar o plantio de cinturões verdes para controle de gramíneas nas bordas florestais;

(A e B) Queimada em um trecho preservado de floresta de transição Amazônia-Cerrado;(C) na mesma região, aspecto degradado da floresta de transição após seis queimadas que ocorreram anualmente, Estado de Mato Grosso, Brasil. Fotos: Roberta T S Cury.