UNIVERSIDADE FEDERAL DE LAVRAS

AURÉLIO DE JESUS RODRIGUES PAIS

ANTHROPOGENIC DISTURBANCES AND ECOLOGICAL MODIFICATION ON ATLANTIC FOREST TREE COMMUNITY

LAVRAS – MG
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Prof. Dr. Rubens Manoel Dos Santos
Orientador

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DISTÚRBIOS ANTROPOGÊNICOS E MODIFICAÇÕES ECOLÓGICAS EM COMUNIDADES ARBÓREAS DO DOMÍNIO ATLÂNTICO

Tese apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-Graduação em Engenharia Florestal, área de concentração em Ecologia Florestal, para obtenção do título de Doutor.

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2020

À minha Esposa Maria Luís Bracho
Aos meus filhos: Wesley Pais e Welmer Pais
Dedico

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RESUMO GERAL

Os distúrbios em florestas tropicais constituem um mecanismo fundamental para a dinâmica das comunidades arbóreas e manutenção de processos ecológicos no ecossistema. Porém quando estes são de natureza antropogênica, podem afetar negativamente a biodiversidade na sua estrutura, composição e funcionalidade. O presente estudo procurou avaliar os efeitos do histórico de distúrbios antropogênicos, suas relações com fatores abióticos na estruturação de comunidade arbóreas do Domínio Atlântico. Pra tal foram testadas duas hipóteses, nomeadamente: (i) os distúrbios antropogênicos passados alteram a funcionalidade das comunidades, sendo esperado que o aumento da sua intensidade diminuiria a estocagem de carbono, a capacidade de dispersão de sementes e a dinâmica do processo sucessional; e (ii) o histórico de distúrbios antropogênicos afetam a composição florística no tempo, sendo esperado que áreas mais impactadas tenham alteração na composição num gradiente temporal. O levantamento da comunidade arbórea consistiu numa amostragem em 12 fragmentos florestais do sul do estado de Minas Gerais, em 544 parcelas, onde foram medidos o diâmetro a altura do peito (DAP) com inclusão a partir de 5.0 cm para a vegetação, variáveis texturais e químicas para o solo e 19 váriaveis bioclimáticas do banco de dados *Worldclim* 1.4 para a caracterização climática da mesorregião. Foi também obtida a caracterização dos impactos antropogênicos pretéritos feito na região por Pereira (2003) e usando a mesma metodologia foi também feita outra caracterização por este estudo para o ano de 2019. Posteriormente, foram criados modelos lineares generalizados mistos (GLMMs) de modo a avaliar se os padrões ecológicos da comunidade respondem aos efeitos do distúrbio, com isto, o fragmento foi utilizado como fator aleatório para lidar com a pseudorreplicação. Os resultados encontraram um total de 36638 indivíduos de 550 espécies representando 76 famílias nos 12 fragmentos amostrados. Os resultados demonstraram que os distúrbios influenciaram significativamente as síndromes de dispersão de zoocoria e autocoria nos modelos, sendo que quanto maior a sua intensidade, maior a abundância de espécies autocóricas e menor das espécies zoocóricas. A produtividade respondeu de forma inversa ao distúrbio antropogênico, sendo que o aumento do distúrbio antropogênico implicou na redução da produtividade. A média ponderada da comunidade para a densidade da madeira (CWMWD) respondeu de forma significativa, sendo que o aumento do distúrbio antropogênico, também implicou no seu aumento. Por outro lado, o distúrbio antropogênico e as variáveis edáficas não tiveram efeito significativo sobre a biomassa aérea. O solo foi um preditor importante com efeito na diversidade beta temporal, na CWMWD, e na autocoria diferentemente do clima que não mostrou algum efeito nos padrões ecológicos. Portanto, nossos resultados demonstram que, de fato, os distúrbios antropogênicos podem ser um preditor importante na modificação de padrões ecológicos das comunidades arbóreas, podendo afetar serviços ecossistêmicos de que a humanidade depende.

Palavras-chave: Distúrbios antropogênicos. Fatores abióticos. Modificações ecológicas. Comunidades arbóreas.

ABSTRACT

The disturbances in tropical forests are a fundamental mechanism for tree community dynamics and the maintenance of ecosystem ecological processes. However, when these are from anthropogenic origin, they can negatively affect biodiversity on its structure, composition and functionality. The present study sought to evaluate the history effects of anthropogenic disturbances, their relationship with abiotic factors in the structuring Atlantic domain tree communities. For this purpose, two hypotheses were tested, namely: (i) the history of anthropogenic disturbances affect the floristic composition over time, and it is expected that most impacted areas will change in the temporal gradient composition, and (ii) past anthropogenic disturbances modify the communities' functionality, and increasing its intensity would decrease carbon uptake, seed dispersal capacity and successional dynamics. Tree community survey consisted of 12 forest fragments sampling in the south of Minas Gerais state, making up 544 plots, where the diameter at breast heigth (DBH) was measured from 5.0 cm for vegetation inclusion; textural and chemical variables for the soil and 19 bioclimatic variables for mesoregion climatic characterization from the Worldclim 1.4 database. The past anthropogenic impacts characterization in the region made by Pereira (2003) was also obtained, and using the same methodology, another characterization was also made by this study for the year 2019. Subsequently, mixed generalized linear models (GLMMs) were created in order to evaluate if the communities' ecological variables respond to the disturbances effects, with this, the fragment was used as a random factor to deal with pseudoreplication. A total of 36638 individuals from 550 species representing 76 families were found in the 12 fragments sampled. The results showed that anthropogenic disturbances significantly influenced the zoochory and autochory dispersion syndromes in the models, where its greater intensity results in greater autochorous species abundance and lower zoochoric species abundance. Productivity responded inversely to anthropogenic disturbances, thus its increase implied a productivity decrease. The community-weighted mean of wood density (CWMWD) responded significantly, and the anthropogenic disturbances increasing impact implied its increase. On the other hand, the anthropogenic disturbances and soil variables had no significant effect on aboveground biomass. Soil was an important driver of beta temporal diversity, CWMWD, and autochory, unlike the climate that did not show any effect on ecological variables. Therefore, our results clearly demonstrate that, in fact, anthropogenic disturbances can be an important driver in modifying the tree communities ecological parameters, and can affect ecosystem services upon which humanity depends.

Keywords: Anthropogenic disturbances. Abiotic factors. Ecological modifications. Tree communities.

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PRIMEIRA PARTE

1 INTRODUÇÃO

Desde a sua existência, o homem sempre usou os recursos naturais, em particular a biodiversidade, para sua sobrevivência. Porém, com o crescimento populacional e consequente aumento da demanda por recursos naturais, surgiu a industrialização como forma de aumento da produção e com isto a obtenção de maiores ganhos econômicos, o que levou a uma elevada sobre-exploração destes recursos. Esta pressão antropogênica tem levado à destruição, à degradação e à fragmentação dos habitats com reflexo nas mudanças da distribuição e abundância dos organismos. É fato que a biodiversidade está sendo perdida a uma taxa sem precedentes a nível global, como consequência do uso da terra, pondo em risco a integridade dos ecossistemas e seus serviços de que os seres humanos dependem para sua sobrevivência. Atualmente estima-se que a população humana seja em torno de sete bilhões de habitantes e com isto, promovendo uma perda de biodiversidade sem precedentes históricos. Tanto que os distúrbios antropogênicos são considerados como uma das principais causa de perda da biodiversidade global.

É importante que os seres humanos percebam como suas ações afetam a biodiversidade e a importância da sua conservação, pois sem ela não haveria existência humana. Portanto, compreender como as espécies e suas interações são afetadas por ações antropogênicas é crucial para a conservação das funções e serviços do ecossistema. Por outro lado, se não houver ações concretas em relação ao uso racional da biodiversidade, poderá haver uma degradação dos recursos dela provenientes, comprometendo a vida humana no planeta. A Mata Atlântica, um dos principais *hotspots* mundiais de biodiversidade não está fora desta situação. Atualmente tem a sua área reduzida entre 12 a 16% da sua extensão original e a maioria em pequenos fragmentos. O uso de terra humano, em particular a expansão agrícola, a urbanização e a sobre-exploração da biodiversidade figuram entre as principais causas da redução da extensão do Domínio Atlântico, o que resulta em elevada perda de espécies, degradação e perda de habitats.

O Laboratório de Fitogeografia e Ecologia Evolutiva, pertencente ao departamento de Ciências Florestais da Universidade Federal de Lavras liderado pelo Prof. Dr. Rubens Manoel dos Santos, vem desenvolvendo pesquisas em ecologia e dinâmica de comunidades e sobretudo como os fatores ambientais e antropogênicos influenciam a distribuição das espécies de árvores e a funcionalidade da comunidade. Com isto, surgiu o interesse em se responder à seguinte pergunta: como os fatores ambientais (solo e clima) e distúrbios antropogênicos influenciam a composição e a funcionalidade de comunidades arbóreas? Este trabalho é fruto de um banco de dados composto por 12 fragmentos de Mata Atlântica, com vários anos de inventários de dinâmica de comunidades arbóreas (desde o ano de 2003 até 2019). Adicionalmente, recorreu-se a um trabalho feito por Pereira (2003). Em uma matriz para as mesmas áreas, este autor classificou o impacto dos distúrbios humanos sobre variáveis estruturais. Com isto, fizemos modelos da dinâmica de biomassa (carbono) para estes fragmentos, associando-a aos fatores ambientais e à matriz de impactos antropogênicos elaborada por Pereira (2003). Esta associação nos permitiu inferir sobre a variação da funcionalidade da comunidade, em particular nos atributos de produtividade, síndromes de dispersão e densidade da madeira.

A presente tese foi estruturada em duas partes, na qual a primeira parte apresenta uma abordagem de revisão bibliográfica contendo conceitos, contribuições relevantes e lacunas existentes sobre o tema. A segunda parte corresponde à apresentação de um artigo científico formatado e redigido de acordo com as normas do periódico *Conservation Biology*.

2 REFERENCIAL TEÓRICO

2.1 Fatores abióticos e estruturação de comunidades arbóreas

Os fatores abióticos são fortes propulsores dos processos demográficos nas comunidades arbóreas, pois determinam a disponibilidade de recursos para o crescimento e a sobrevivência das plantas (CONDIT et al., 2013; FELDPAUSCH et al., 2011). Nos Neotrópicos, a composição das características reflete as diferenças de clima e fertilidade do solo (VAN DER SANDE et al., 2017). Em uma escala mais local, nas florestas africanas, os solos arenosos em comparação com os solos argilosos, apresentam maior abundância de espécies com alta densidade da madeira e mais tolerantes à seca. Não só, como também se adaptam melhor a ambientes com recursos bastante limitados (FAYOLLE et al., 2012; VAN DER SANDE et al., 2017). Os recursos naturais tais como a disponibilidade de água, nutrientes e luz são vitais para o crescimento das plantas (TOLEDO et al., 2011). Nas florestas tropicais, esses recursos variam em escalas espaciais e temporais e, como resultado, o crescimento das árvores varia com a disponibilidade de recursos (FELDPAUSCH et al., 2011; QUESADA et al., 2012). Geralmente, o crescimento de plantas aumenta com a precipitação e diminui com o aumento da sazonalidade (BERNARDI et al., 2016). Portanto, nestas formações o clima é tido como um dos principais preditores de produtividade das plantas (TOLEDO et al., 2011; WAGNER et al., 2012).

Independentemente da precipitação, a fertilidade do solo também pode afetar a taxa de crescimento das árvores, com melhor crescimento em solos mais ricos em nutrientes (PRADO-JUNIOR et al., 2016; VAN DER SANDE et al., 2017; VAN DER SANDE et al., 2018). Os ecossistemas tropicais são amplamente considerados como ricos em nitrogênio e relativamente pobres em nutrientes fortemente intemperizados, como é o caso do fósforo (PRADO-JUNIOR et al. 2016; QUESADA et al., 2012). Nas florestas amazônicas, o teor de fósforo no solo é considerado o melhor preditor das taxas de crescimento destas florestas (QUESADA et al., 2012). Outros macronutrientes do solo tais como cálcio, potássio e magnésio também demonstraram ser importantes na determinação das taxas de crescimento e produtividade das comunidades arbóreas de florestas tropicais (BARIBAULT et al., 2012; WRIGHT et al., 2011). Portanto, as florestas em solos mais férteis tendem a ter maiores taxas de crescimento e maior produtividade lenhosa, se comparadas às de solos pouco férteis (HEDIN et al., 2009, TOLEDO et al., 2011).

2.2 Fragmentação florestal

A fragmentação e perda de habitats são os principais processos de ameaça à biodiversidade tropical, levando à extinção de espécies em várias escalas e afetando negativamente o funcionamento do ecossistema (HADDAD et al., 2015; LIU et al., 2018). É um dos principais processos que contribuem para o declínio da população, perda de biodiversidade e alteração da estrutura da comunidade e do funcionamento do ecossistema (IBANEZ et al., 2017; TAPIA-ARMIJOS et al., 2015). É frequentemente definida como um processo durante o qual uma grande extensão de habitat é transformada em um número maior de manchas menores, isolados uns dos outros por uma matriz diferente da original (FAHRIG, 2017). A definição de fragmentação de habitat implica quatro efeitos deste processo no padrão de habitat, nomeadamente: (i) redução na quantidade de habitats, (ii) aumento no número de manchas, (iii) diminuição nos tamanhos de manchas e (iv) aumento no isolamento de manchas. Estes quatro efeitos formam a base da maioria das medidas quantitativas de fragmentação do habitat (FAHRIG, 2017; MARTIN; FAHRIG, 2012; THORNTON; BRANCH; SUNQUIST, 2011).

A fragmentação elimina árvores grandes de elevada densidade de madeira em processos sucessionais tardios (SANTO-SILVA et al., 2016). Estas árvores contribuem significativamente para a biomassa acima do solo e são vitais para o estoque de carbono, microclima, refúgio de animais entre outras funções (TABARELLI et al. 2010). Caso estas estejam nas bordas, sofrem maior efeito da temperatura que pode levar à dessecação da copa e promover elevada abundância de espécies pioneiras invasoras (FAHRIG, 2017; SANTO-SILVA et al., 2016). Quanto menor for o fragmento, mais intenso será este efeito, sendo que as espécies pioneiras e de rápido crescimento tendem a invadir o fragmento, alterando a estrutura da comunidade e o funcionamento do ecossistema (LIU et al., 2018).

Por outro lado, vários usos de terra modificados pelo homem tais como agricultura, plantações florestais, cafezais e pasto, circundam os fragmentos florestais (a matriz) nas florestas tropicais afetando sua estrutura, composição e dinâmica (RUFFELL; CLOUT; DIDHAM, 2017). A matriz pode fornecer recursos complementares que podem compensar a disponibilidade limitada de recursos nas manchas de habitat (HERNÁNDEZ-RUEDAS et al., 2018; RIES et al., 2004). Um aumento na qualidade de matriz foi associado com um aumento na riqueza e abundância de espécies nos fragmentos (OCKINGER et al., 2012; RUFFELL; CLOUT; DIDHAM, 2017).Várias evidências sugerem que a qualidade da matriz é crucialmente importante na determinação da abundância e composição de espécies dentro de fragmentos de habitat (COOK et al., 2002; HERNÁNDEZ-RUEDAS et al., 2018). Ela pode afetar a dispersão e o movimento de indivíduos entre manchas (DAVIES et al., 2001; OCKINGER et al., 2012), sendo determinantes da dinâmica de extinção e colonização dos fragmentos (BROTONS et al., 2003; KUPFER et al., 2006). Por exemplo, as florestas plantadas são usos de terra muito comuns na matriz dos biomas florestais, e elas podem ajudar a reduzir os impactos do desmatamento, aumentando a conectividade entre os fragmentos, fornecendo habitat e reduzindo o efeito de borda (PAWSON et al. 2010; RUFFELL; CLOUT; DIDHAM, 2017). Contudo, podem também trazer alguns impactos negativos principalmente para comunidades de vertebrados (ESTADES; TEMPLE, 1999). Por estas razões, o estudo da estrutura da matriz é frequentemente visto como uma das vias mais importante para se entender sobre a dinâmica das manchas na paisagem, pois a modificação da qualidade da matriz poderá afetar a dispersão, o tamanho da população e a probabilidade de persistência da população nos fragmentos florestais (DONALD; EVANS, 2006; SMITH; FAHRIG; FRANCIS, 2011).

2.3 Dinâmica de florestas tropicais

As florestas tropicais são repositórios de grande parte da biodiversidade do mundo e desempenham um papel crucial na regulação do clima global (FUJII et al., 2018; LEWIS et al., 2015). Estas formações florestais estão sob enorme pressão do desenvolvimento de atividades humanas, tais como urbanização, agricultura, mineração, entre outros (BROOKS et al., 2002; HADDAD et al. 2015). Identificar e entender as mudanças na composição e estrutura da floresta é fundamental para entender como as florestas estão respondendo à variabilidade e mudanças ambientais (NUNES et al., 2003; ROITMAN et al., 2016). Portanto, entender a dinâmica da composição da comunidade de plantas é fundamental para entender numerosos processos ecológicos em ecossistemas complexos e ricos em espécies, como as florestas tropicais (URIARTE, 2004). Pesquisadores compararam a dinâmica de comunidades de florestas tropicais de diferentes partes do mundo e encontraram taxas altamente variáveis de recrutamento, crescimento e mortalidade, destacando diferentes mecanismos para diferentes sistemas tropicais (FELFILI, 1995; SURESH; DATTARAJA; SUKUMAR, 2010; WOODS, 2000).

A mortalidade, o crescimento e o recrutamento de espécies arbóreas são fatores-chave que influenciam a estrutura, composição e sucessão das comunidades florestais (HURST, 2012; ROITMAN et al., 2016). A mortalidade das árvores é reconhecida como um dos processos mais importantes na dinâmica florestal, e é influenciada por muitos fatores (BIN et al., 2012; VINCENT et al. 2018). Pode facilitar a rotatividade na composição de espécies, afetar a estrutura da comunidade e alterar as taxas de ciclagem de nutrientes ou acumulação de biomassa (SHEN et al., 2014). Também pode determinar a dinâmica ou sucessão florestal e contribuir para a coexistência de espécies arbóreas (URIARTE, 2004). A probabilidade de mortalidade de uma árvore individual é avaliada em função de seu tamanho, crescimento e o padrão espacial das árvores circundantes, também conhecido como vizinhança competitiva (RUNKLE, 2000; VINCENT et al. 2018).

O crescimento e o recrutamento de comunidades também são processos importantes que moldam a estrutura e a dinâmica da floresta. A transição da germinação para o crescimento da regeneração é um estado crítico no estabelecimento de árvores (CONDIT et al., 1999; ROITMAN et al., 2016). O padrão espacial de recrutamento de plântulas influencia os padrões de distribuição a longo prazo das espécies e pode ter efeitos significativos na composição e abundância de espécies em comunidades vegetais. Portanto, fatores que influenciam o recrutamento de plântulas são de grande importância para ecólogos florestais e pesquisadores (MA et al., 2016; MONTES-HERNANDEZ et al., 2013; SANTOS et al., 2018). Estudos experimentais e observacionais descobriram padrões de recrutamento e mortalidade de espécies arbóreas dependentes de distância e densidade, coerentes com a hipótese de Janzen-Connell em comunidades temperadas e tropicais (HURST, 2012). Estes estudos apontam para a dependência de densidade como uma importante força estabilizadora que promove a coexistência de espécies em sistemas florestais (SHEN, 2014). A limitação de dispersão é outro mecanismo que impulsiona a diversidade de espécies, refere-se ao fenômeno do declínio da densidade de sementes com o aumento da distância em relação à árvore materna (N'DRI et al., 2014; WOODS, 2000). Sementes de plantas mais competitivas podem não chegar a micro-locais adequados e espécies menos competitivas terão mais chances de tomar seus lugares, diminuindo a exclusão competitiva e promovendo a coexistência de espécies (MONTES-HERNANDEZ et al., 2013).

MA et al. (2016) constataram que a competição é o principal fator nas mudanças de longo prazo na mortalidade, no crescimento e no recrutamento de árvores. O clima regional tem um efeito mais fraco, ainda que significativo, sobre a mortalidade, o crescimento e o recrutamento de árvores (HE; DUNCAN, 2000). Isso indica que os processos internos da comunidade, mais do que os fatores climáticos externos, impulsionam a dinâmica das florestas (MA et al., 2016; SANTOS et al., 2018). A dinâmica florestal é de ação lenta e, portanto, exige que os dados de longo prazo sejam caracterizados com precisão. Dados demográficos, como recrutamento, crescimento e mortalidade, oferecem chaves para entender as mudanças direcionais na composição das comunidades florestais (MONTES-HERNANDEZ et al., 2013; SANTOS et al., 2018).

2.4 Distúrbios antropogênicos nas florestas tropicais

Pickett & White (2013) definem distúrbios como qualquer evento no tempo que perturbe a estrutura do ecossistema, da comunidade ou da população e altera os recursos disponíveis ou o ambiente físico. Nas florestas, a perturbação (distúrbios) varia em intensidade, escala e frequência, a partir de lacunas formadas regularmente pela morte de árvores em agregado ou individuais (HILTNER et al. 2018; POWERS; MARÍN-SPIOTTA, 2017). A perturbação pode dividir-se em duas categorias: origem natural ou origem antropogênica. Distúrbios naturais, como por exemplo os deslizamentos de terra, tempestades e raios, causam a morte de organismos em seus ecossistemas (CRAUSBAY; MARTIN, 2016; MITCHELL, 2013). A morte de um indivíduo cria espaço livre no ecossistema, o que dá oportunidade a novos indivíduos para colonizarem a área (COLE; BHAGWAT; WILLIS, 2014; FOLEY et al. 2005).

As plantas se adaptaram para se recuperar de distúrbios naturais, a exemplo da densidade da madeira, uma característica funcional essencial na comunidade, que se correlaciona fortemente com as estratégias de história de vida das espécies arbóreas (FALSTER, 2006). É um indicador da resistência que demonstra a capacidade de uma árvore de resistir a danos durante distúrbios (CURRAN et al., 2008). No entanto, há uma correlação negativa entre a capacidade de resistência a distúrbios e a capacidade de recuperar a biomassa após um distúrbio (CURRAN et al., 2008; FALSTER, 2006). Tanto que o investimento em biomassa em suporte estrutural resulta em árvores com alta densidade da madeira e baixas taxas de crescimento; enquanto o baixo investimento em suporte estrutural está associado a baixa densidade da madeira e a rápidas taxas de crescimento (KING et al., 2006). No entanto, distúrbios antropogênicos podem resultar em um impacto profundo e prolongado na comunidade (BARLOW et al., 2016; TURNER et al., 2003). Os distúrbios variam em ampla escala espacial e temporal, podendo deixar legados persistentes e interações entre eles, tornando-os difíceis de avaliar (BROWN; BOUTIN, 2009; TURNER et al., 2003).

O uso da terra é uma forma de perturbação humana que cria um tipo diferente de pressão para o ecossistema em relação aos processos naturais de perturbação (DECAENS et al. 2018; MEYFROIDT et al., 2014). Segundo a FAO (2002), a agricultura e a silvicultura causam a maior pressão humana nos ecossistemas terrestres. A perturbação altera os processos do ecossistema, como estruturas tróficas, fluxo de energia, ciclagem química e outros processos (BARLOW et al., 2016; CONNELL, 1978).

De acordo com Laurance (2008), a conversão de habitats por humanos é um processo não aleatório. Acessibilidade e proximidade de estradas ou assentamentos humanos a uma área natural são questões de alta importância (LAURANCE, 2008, TOIVONEN et al. 2011). Os remanescentes florestais frequentemente persistem em áreas íngremes, em solos mais pobres, em altitudes mais elevadas e em terras parcialmente inundadas (LAURANCE, 2008). A perturbação humana altera o tamanho dos fragmentos e diminui a biodiversidade (WHITTAKER; TRIANTIS; LADLE, 2008).

As florestas tropicais de montanha remanescentes estão sob ameaça direta por causa da conversão para terras agrícolas, extração de madeira e atendimento às necessidades energéticas (ATTA-KRAH; YA, 2000; TOLEDO-ACEVES et al., 2011). Cerca de 12% da população humana global habita áreas montanhosas, a maioria em países em desenvolvimento (HUDDLESTON et al., 2003; MOWO et al., 2007; PRICE; MESSERLI, 2002). Segundo Huddleston et al. (2003), a maioria dos habitantes rurais em zonas montanhosas está ligada à atividade agrícola para sua subsistência. O pastoreio e a silvicultura são usos predominantes das terras de montanha em todas as regiões do mundo. Na América Central e do Sul, as práticas de uso misto da terra (cultivo, pastagem e exploração de recursos florestais) são típicas das comunidades em zonas montanhosas (MOWO et al., 2007).

A criação de gado, especialmente em altitudes mais elevadas nos países em desenvolvimento, é a principal forma de subsistência (BLACKHALL et al., 2008; HUDDLESTON et al., 2003). Esta atividade pode afetar a ecologia de determinada área de várias maneiras, nomeadamente: (i) alterando a riqueza e composição de espécies das comunidades, (ii) perturbando a função do ecossistema e (iii) alterando a estrutura do ecossistema (CHATURVEDI; RAGHUBANSHI; SINGH, 2012). Não só, como também vários autores demostraram que solos florestais severamente compactados pela criação de gado afetam a regeneração florestal, inibindo a germinação e crescimento de plântulas e aumentando a sua mortalidade (RATOVONAMANA et al. 2013; SCHULZ et al. 2016).

A exploração madeireira contribui significativamente para a degradação florestal, afetando a produtividade, estrutura, biomassa e composição de espécies (FOLEY et al., 2005; TOIVONEN et al., 2011). Esta atividade geralmente recorre ao abate de árvores emergentes para fins econômicos (OLIVEIRA; SANTOS; TABARELLI, 2008). Segundo De Paula (2011), as espécies de árvores emergentes geralmente representam apenas cerca de 10% da riqueza total de espécies de árvores tropicais, mas têm uma elevada influência sobre a estrutura da floresta e no funcionamento do ecossistema. As árvores emergentes armazenam grande parte da biomassa acima do solo, contribuindo decisivamente para serviços ecológicos, como ciclagem de nutrientes, captação de água, controle de erosão do solo, fornecimento de produtos florestais, entre outros (DE PAULA, 2011; OLIVEIRA; SANTOS; TABARELLI, 2008).

2.5 Síndromes de dispersão e interações ecológicas

As interações planta-animal têm um papel fundamental na manutenção da biodiversidade (VALIENTE-BANUET et al., 2014). Em particular, frugivoria e dispersão de sementes são interações importantes, pois estão envolvidas no estabelecimento de sementes e no recrutamento de plantas (GOMES et al., 2008). Pelo menos 78% das espécies lenhosas em florestas tropicais e temperadas dependem de vetores animais para dispersão primária ou secundária de sementes (AU; CORLETT; HAU, 2006; MULLER-LANDAU et al., 2008). No entanto, a perturbação do habitat afeta as populações de dispersores e as interações de dispersão de sementes, levando à redução do recrutamento de plantas e do tamanho das populações, e aumento do risco de extinção local (FONTÚRBEL et al., 2015; MARKL et al., 2012).

Em paisagens fragmentadas, a dispersão de sementes tem uma grande influência sobre a persistência das espécies de plantas, assim como na recuperação da vegetação quando a perturbação é reduzida (BOVO et al., 2018; CHAVES; BICCA-MARQUES; CHAPMAN, 2018). Poucos tipos de vegetação natural podem persistir em seu estado atual sem a dispersão de sementes mediada por animais (VALIENTE-BANUET et al., 2014). Vários autores propõem três hipóteses principais para explicar por que a dispersão de sementes em geral e em particular por animais constitui um processo crucial no ciclo de vida das plantas (CONNELL, 1971; FONTÚRBEL, 2015; HOWE; SMALLWOOD, 1982; VALIENTE-BANUET et al., 2014). Todas as três hipóteses postulam que a dispersão de sementes mediada por animais melhora o recrutamento de plantas e, mantém a diversidade genética e viabilidade populacional das plantas, a destacar: (i) hipótese de fuga, assume que fungos patogênicos e herbívoros ocorrem em alta densidade próximos às árvores progenitoras, o que aumenta a mortalidade de sementes e plântulas próxima à árvore progenitora (CONNELL, 1971; HOWE; SMALLWOOD, 1982); (ii) hipótese da colonização, propõe que a dispersão de sementes aumenta a probabilidade de as sementes atingirem novos locais onde possam germinar e se estabelecer (HOWE; SMALLWOOD, 1982; MARKL et al., 2012; VALIENTE-BANUET et al., 2014); e por último (iii) hipótese de dispersão dirigida, sugere que os agentes de dispersão de sementes depositam sementes em locais particularmente adequados para germinação e recrutamento (FONTÚRBEL, 2015; HOWE; SMALLWOOD, 1982; KUHLMANN; RIBEIRO, 2016), portanto as interações planta-frugívoro têm múltiplas implicações evolutivas e na história de vida das plantas (KUHLMANN; RIBEIRO, 2016). Estas interações envolvem benefícios recíprocos em que as plantas aumentam a sua chance de sobrevivência e persistência na paisagem, e os animais fazem o uso de frutos ou sementes carnudas como recursos alimentares (AU; CORLETT; HAU, 2006). Ademais, a dispersão a longa distância por megafauna frugívora também permite a colonização de vários fragmentos florestais isolados e a manutenção da conectividade em paisagens fragmentadas (BOVO et al., 2018; MULLER-LANDAU et al., 2008).

2.6 Síndromes de dispersão e distúrbios antropogênicos

A dispersão de sementes é um mecanismo essencial para a distribuição espacial e expansão da variabilidade genética de populações e comunidades e sua persistência nos ecossistemas (FARWIG; BERENS, 2012; HERRERA; MORALES; GARCÍA, 2011). É o único meio pelo qual as comunidades colonizam novos habitats mais favoráveis ou escapam da competição, patógenos e herbívoros associados às mães (CONNELL, 1971; HOWE; SMALLWOOD, 1982). Sendo esta por meio abiótico (vento, água, entre outros) ou por meio biótico (LEVINE; MURRELL, 2003; PEREDO et al., 2013).

A perturbação humana pode afetar a dispersão de sementes mediada por animais e a regeneração natural de populações de plantas (MARKL et al., 2012). Na matriz, os dispersores diferem em sua capacidade de se mover e na tolerância à degradação do habitat, determinando o impacto final da dispersão das sementes na paisagem (HOLBROOK; LOISELLE, 2009; SEKERCIOGLU; DAILY; EHRLICH; 2004). Portanto, a natureza da matriz circundante dos fragmentos influencia o movimento e a abundância de sementes e frugívoros (MCCONKEY et al., 2012), sendo que a abundância e diversidade de plantas e frugívoros nos fragmentos diminui ao longo de um gradiente de floresta secundária, agrossilvicultura, plantações exóticas e pastagens (FONTURBEL et al., 2015; MCCONKEY et al., 2012). A matriz circundante também influencia os padrões de circulação do vento, afetando sementes anemocóricas em habitats fragmentados (DAMSCHEN et al., 2008; MCCONKEY et al., 2012). Por exemplo, os corredores de habitat podem atuar como quebravento em matrizes abertas e levar à acumulação de sementes dispersas pelo vento (DAMSCHEN et al., 2008). Por outro lado, as matrizes de pastagem podem levar ao isolamento das manchas, uma vez que pastagens abertas não fornecem habitat adequado para o estabelecimento de sementes (PREVEDELLO; VIEIRA, 2010).

A persistência de espécies vegetais em paisagens fragmentadas também é influenciada pelas características dos frutos e sementes e pelos atributos do dispersor (MCCONKEY et al., 2012). Espécies de plantas com sementes maiores, dispersas por animais, geralmente experimentam dispersão reduzida nos fragmentos de habitat em comparação com espécies de frutos menores em paisagens tropicais e temperadas (CRAMER; MESQUITA; WILLIAMSON, 2007). Distúrbios antropogênicos como a caça e a exploração seletiva de madeira, contribuem em grande escala para redução e extinção de dispersores (FONTURBEL et al., 2015), sendo que a caça elimina diretamente o agente mamífero dispersor enquanto a exploração seletiva diminui a disponibilidade de alimento ao dispersor, o que pode levar à sua fuga (PERES; PALACIOS, 2007).

Por outro lado, a perda de frugívoros por ações antropogênicas pode limitar a capacidade das plantas de responderem aos efeitos das mudanças climáticas (CORLETT, 2009), porque a maioria das populações de plantas na Terra precisará percorrer longas distâncias nos próximos 50 a 100 anos para acompanhar as mudanças no clima (CHEN et al., 2011). Estas espécies precisarão se mover no espaço à procura de recursos e condições climáticas adequadas (CHEN et al., 2011; CORLETT, 2009). Contudo, a megafauna (herbívoros de grande porte), capaz de dispersar sementes grandes e a longas distâncias, necessárias para que as plantas mantenham o ritmo das alterações climáticas, é frequentemente ameaçada pela caça ou perda de habitat, podendo isto levar a uma extinção da biodiversidade em macroescala (FONTURBEL et al., 2015; MARKL et al., 2012).

2.7 Serviços ecossistêmicos e sequestro de carbono

As florestas cobrem cerca de um terço da superfície terrestre (4 bilhões de hectares) e desempenham um papel importante no ciclo global do carbono, representando também uma proporção substancial da biodiversidade terrestre do mundo (FAO, 2010; LINDSELL; KLOP, 2013; PARROTTA et al., 2012). Florestas armazenam enormes quantidades de carbono, o que as torna componente vital para mitigar os efeitos das mudanças climáticas globais (PARROTTA et al., 2012). Distúrbios antropogênicos, tais como exploração madeireira, incêndios, fragmentação, caça excessiva, entre outros, contribuem negativamente para a capacidade das florestas de fornecerem bens e serviços ecossistêmicos (BARLOW et al., 2016; BERENGUER, et al., 2014; LINDSELL; KLOP, 2013). Estes bens e serviços incluem a ciclagem de nutrientes, a formação de solo e produtividade primária; alimentos, água, madeira e medicamentos; serviços de regulação, como controle de erosão, regulação climática, mitigação de inundações, purificação de água e ar, polinização e serviços culturais como recreação, ecoturismo, valores educacionais, entre outros (BERENGUER, et al., 2014; MEA, 2005; PARROTTA et al., 2012). Um dos principais serviços prestados pelas florestas é a remoção de carbono da atmosfera (sequestro) e o armazenamento a longo prazo desse carbono em biomassa, matéria orgânica morta e no solo (PAN et al., 2011). LEWIS et al. (2009) estimaram em medições de longo prazo em parcelas não perturbadas que as florestas tropicais podem sequestrar anualmente cerca de 1,3 Pg de carbono.

Por outro lado, as florestas podem emitir volumes significativos de dióxido de carbono dependendo de como são manejadas, contribuindo para o agravamento dos efeitos das mudanças climáticas globais (ARAGÃO; SHIMABUKURO, 2014). Atualmente, as regiões florestadas contribuem substancialmente para emissão do dióxido de carbono atmosférico, com emissões anuais globais provenientes de desmatamento e degradação florestal estimadas em 1,2 Pg entre 1997 e 2006, equivalentes a 12% das emissões globais provocadas pelo homem (LINDSELL; KLOP, 2013; PAN et al., 2011; VAN DER WERF et al., 2009). A Convenção-Quadro das Nações Unidas sobre Mudanças Climáticas (UNFCCC) em 2007, em sua 13ª Conferência das Partes, reconheceu a degradação florestal como um dos principais fatores para as emissões globais de carbono, sendo este incorporado ao mecanismo de Redução de Emissões por Desmatamento e Degradação Florestal (REDD+) (PARROTTA et al., 2012). Nas florestas tropicais, a maioria das pesquisas ecológicas sobre estoques de carbono tem se concentrado no monitoramento de mudanças em florestas primárias relativamente não perturbadas (BERENGUER, et al., 2014; MALHI et al., 2006; PHILLIPS et al., 2008). Portanto, entender os efeitos das perturbações humanas nos estoques de carbono da floresta é crucial para avaliação de melhores práticas de manejo florestal e medidas de conservação (BERENGUER, et al., 2014).

3 CONSIDERAÇÕES FINAIS

A estrutura e composição atual das comunidades arbóreas são resultados das interações de vários processos de dinâmica florestal com os fatores ambientais, distúrbios naturais e antropogênicos passados. Muitas vezes se usa os distúrbios presentes no estudo de seus efeitos sobre a comunidade, sendo que os históricos de distúrbios passados acabam negligenciados. Neste trabalho, usamos os distúrbios passados para inferir sobre os dados atuais da comunidade,pois, acreditamos que a forma como se apresenta a comunidade arbórea hoje é reflexo dos efeitos dos distúrbios passados e suas interações. Esperamos com este trabalho contribuir com conhecimentos e abrir novos horizontes de pesquisas nesta área, de modo que estas possam ser usadas em atividades de restauração florestal e em políticas de conservação de ecossistemas.

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SEGUNDA PARTE – ARTIGO 1

(a ser submetido no periódico *Conservation Biology*)

Do abiotic factors drive ecological modifications in tropical forest fragments with a history of anthropogenic disturbances?

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Article Impact Statement: Anthropogenic disturbances can have greater effects than abiotic factors in the tree community structure and ecosystem function modification.

Abstract

Abiotic factors are important drivers of tree community structure in tropical forests, but may be minimized or hidden by the effects of anthropogenic disturbances. Here, we aimed to understand how anthropogenic disturbances affect ecological modifications in the tropical tree communities around 12 fragments of the Brazilian Atlantic Domain. We hypothesized that a history of anthropogenic disturbances would alter community temporal beta diversity and function. We found that disturbance intensity significantly influenced the abundance of zoochorous (negative effect) and autochorous (positive effect) species. Disturbance history negatively affected wood productivity in the time interval considered, but positively affected community-weighted means (CWM) of wood density. Conversely, anthropogenic disturbances and soil variables did not significantly affect aboveground woody biomass. Temporal beta diversity, wood density CWM and autochorous dispersal syndrome were significantly related to soil, whereas climate did not significantly influence any of the ecological attributes considered. Our results show that anthropogenic disturbances can be important drivers of ecological modifications in the tree communities, ultimately affecting the provision of essential ecosystem services.

Introduction

Tropical forests are highly biodiverse terrestrial systems that store large amounts of carbon and have an important role on climate change mitigation strategies (Poorter et al. 2015; Van der Sande et a. 2017; Sullivan et al. 2017; Fujii et al. 2018). Climate and soil are important drivers of tree community structure in these forests (Feldpausch et al. 2011; Condit et al. 2013; Van der Sande et al. 2016). For instance, climate factors such as precipitation directly influence tree growth and, consequently, plant productivity in forest communities (Toledo et al. 2011; Wagner et al. 2012). In addition, soil properties (e.g., fertility) can directly affect tree productivity and growth, selecting species and functional traits (Quesada et al. 2012; Prado-Junior et al. 2016; Van der sande et al. 2017, 2018). For example, although scarce in tropical formations, phosphorus is considered the main predictor of tree growth rates (Hedin et al. 2009, Quesada et al. 2012). Calcium, potassium and magnesium also seem to be important determinants of growth and productivity rates (Wright et al. 2011; Baribault et al. 2012). Another example is found in African tropical forest communities, where soil texture affects the functional characteristics displayed by the species: sandy soils harbor a larger number of dry-tolerant and high wood density species in comparison with clayey soils (Fayolle et al. 2012). Therefore, changes in climate patterns and spatial variation in the edaphic environment may entail shifts in growth rates, floristic composition and community function (Toledo et al. 2011; Wagner et al. 2012; Quesada et al. 2012). However, although the effects of past disturbances (from both natural and anthropogenic origins) may have long-lasting effects on tree community ecological processes (Burgi et al. 2017; Sfair et al. 2018), the aforementioned studies have not accounted for their influence.

Natural disturbances play an important role in community dynamics, contributing to landscape heterogeneity and determining the evolutionary history of plants (Crausbay & Martin 2016; Lewis et al., 2015; Seidl et al. 2011). Sudden disturbance events alter community structure, composition, demographic parameters (mortality and recruitment) and ecosystem function (Rodrigues et al. 2017). But human-driven disturbances, prompted by land use change and overexploitation of natural resources, currently represent the main threat to global biodiversity (Laurance et al. 2011; Simberloff et al. 2013; Giam 2017). Anthropogenic disturbances also alter the atmospheric composition and climate, posing further threats to the provision of ecosystem services (Laurance et al. 2011).

The Brazilian Atlantic Forest Domain, one of the world's biodiversity hotspots and provider of ecosystem services in the most industrialized region of Brazil (Ribeiro et al. 2009), has suffered from severe fragmentation and habitat loss. Today, only 12 to 16% of its original extent remains, mostly confined to small fragments (Ribeiro et al. 2009; SOS Mata Atlântica, 2020). The future of the Atlantic Forest and the ecosystem services it provides depend upon our ability to understand the changes and effects promoted by past anthropogenic disturbances on present-day ecosystem function (Metzger et al. 2009; Santo-Silva et al. 2016).

The dynamics of human-disturbed landscapes is a central concern of tropical forest conservation biology. Although evidence has been gathered that anthropogenic disturbances affect different ecological processes (Johnson & Miyanishi, 2010; Keane et al., 2015; Peres et al. 2016), the extent to which populations and communities are restructured by environmental change remains uncertain (Santo-Silva et al. 2016). For example, logging affects the light availability in the interior of forest fragments, promoting shifts in tree community structure, diversity, dynamics and species composition (Morris, 2010; Decaens et al. 2018; Santos et al. 2020). However, little is known about how these changes will alter long-term community dynamics, since the disturbance effects may be substantially obscured by tree longevity (Norden et al. 2015; Martínez-Ramos et al. 2016).

Data about past disturbances and their interactions with community dynamics are lacking for most tropical forests (McMichael et al. 2017). Knowledge about the history of human disturbances is an essential component of ecology, which focuses on understanding the importance and long-term effects of past events on ecosystems (Burgi et al., 2017; Szabó, 2015). Disturbance history effects can persist for a long time and influence ecosystem function and biodiversity (Szabó 2015; Perring et al., 2016). Seemingly subtle present-day human impacts may produce long-term effects on soil and vegetation, sometimes being detected only centuries later (Burgi et al., 2017).

In this study, we start from the premise that, other than the main abiotic drivers of tree community structure (i.e., climate and soil), the history of anthropogenic disturbances on the Brazilian Atlantic Domain play a key role on the functionality and temporal composition displayed by their tree communities. We expect present-day vegetation to reflect past anthropogenic disturbances undergone by the target communities. We therefore tested two hypotheses: (i) past anthropogenic disturbances alter community functional parameters, with increasing intensity predicting a decrease in carbon uptake, seed dispersal capacity and successional dynamics; and (ii) a history of anthropogenic disturbances affect floristic composition over time, in such a way that the most impacted areas tend to be more homogenized in a temporal gradient. We monitored the temporal behavior of 12 fragments of seasonal semideciduous forest fragments of the Atlantic Domain between years 2003 and 2019, accounting for the influence of past disturbances.

Material and Methods

Study site description

We gathered data about 12 seasonal semideciduous forest fragments of the Atlantic Domain in the southeast region of Brazil, in the southern portion of Minas Gerais state (Figure 1). Climate in this region falls into the Aw and Cwa categories of Köppen's classification (wet summers and dry winters) (Reboita et al. 2015). Mean annual temperature and mean annual precipitation are, respectively, 19.2°C e 1545,9 mm (Hijmans et al., 2005) (refer to Table 1 for further details).

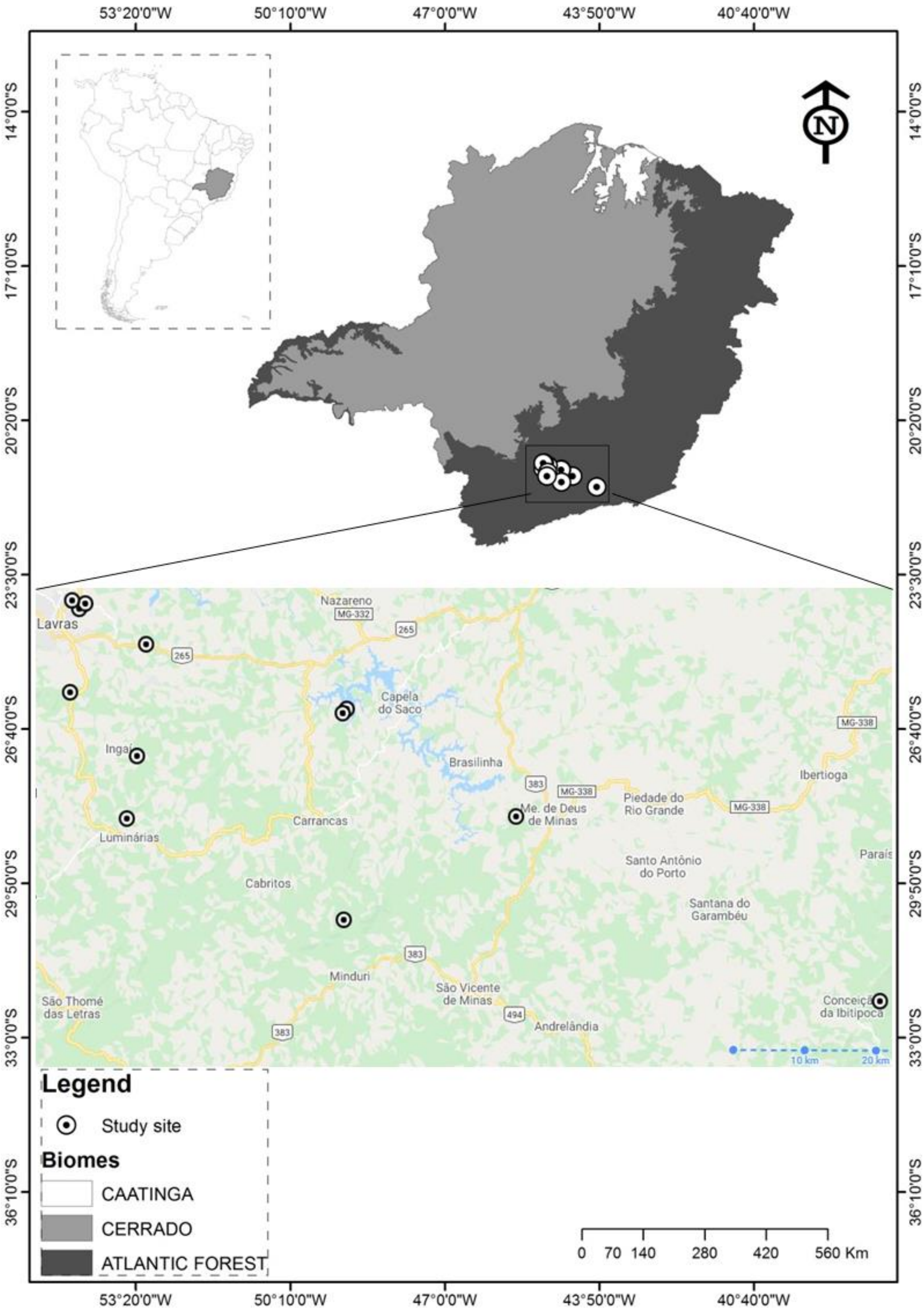

Figure 1. Location of the 12 Atlantic Domain fragments sampled in the southern portion of Minas Gerais state, Brazil

Table 1. Environmental description of the 12 Atlantic Domain fragments sampled in the southern portion of Minas Gerais state, Brazil

Id.	Fragment	Site area (ha)	Latitude (S)	Longitude (W)	MAP (mm)	MAT (^{0}C)	Altitude (m)	Inventories (years)
1	Mata da UFLA	5.72	-21.2287905°	-044.9711195°	1529.7	19.4	918-937	2006, 2010, and 2017
2	Poço Bonito	88.56	-21.3312690°	-044.9837098°	1529.7	18.6	925-1210	2006, 2011 and 2016
3	Madre de Deus	20.66	-21.4839350°	-044.3790290°	1588.5	19.4	915- 980	2006, 2009 and 2018
4	Itutinga	3.77	-21.3524520°	-044.6088975°	1514.5	19.4	913-945	2004, 2010 and 2019
5	Camargos	10.36	-21.3565432°	-044.6146468°	1514.5	19.4	913-960	2003, 2009 and 2019
6	Ibitipoca	95.05	-21.7102307°	-043.8867144°	1544.2	14.8	1150-1510	2005, 2013 and 2019
7	Capivari	9.78	-21.2729492°	-044.8810300°	1529.7	19.4	825- 875	2003, 2008 and 2017
8	Subestação	8.73	-21.2229634°	-044.9629445°	1529.7	19.4	910- 940	2005, 2010 and 2016
9	Mata da Lagoa	3.97	-21.2195251°	-044.9802359°	1529.7	19.4	855-902	2005, 2011 and 2017
10	Carrancas	35.98	-21.6105958°	-044.6131448°	1483.0	14.8	1440-1513	2005, 2010 and 2018
11	Ingaí	16.14	-21.4094428°	-044.8924867°	1529.7	19.4	860-890	2004, 2009, and 2017
12	Luminárias	77.91	-21.4857763°	-044.9061968°	1529.7	19.4	880-1000	2005, 2010 and 2018

Note: MAP – mean annual precipitation; MAT – mean annual temperature.

Data collection

Systematic sampling was employed to characterize the tree communities in the 12 study sites, totaling 544 plots of 200 m^2, 225 m^2, 300 m^2 e 400 m^2 (18.28 ha of total area sampled). All living individuals meeting the inclusion criterion of 5.0 cm of diameter at breast height (DBH, 1.30 m) were recorded. The DBH of multiple stemmed individuals was represented by the square-root of the sum of squared values of each stem's DBH (MacDicken et al. 1991). Non-arboreal life forms were not included in the dataset, and the same criteria were followed in each inventory carried out throughout the timeframe of data collection (see Table 1). We assembled data about dispersal syndromes for the species occurring in our dataset based on the literature. The dataset used herein belongs to the Laboratory of Phytogeography and Evolutionary Ecology, located in the Department of Forest Sciences at the Federal University of Lavras (UFLA), Brazil. All data are hosted in the forestplots.net system (Lopez-Gonzalez et al. 2009; Lopez-Gonzalez et al. 2011), available upon request.

To characterize the edaphic environment of each fragment, composite soil samples of 0.5 kg were collected from three points within each plot (20 cm of depth). The following chemical variables were analysed: Ca, Mg, Na, K, P, pH, cation exchange capacity, base saturation, aluminum saturation and soil organic matter. Percentages of sand, silt and clay characterized soil texture. All soil analyses were carried out in the Laboratory of Soil Analyses at Federal University of Lavras (UFLA). To characterize the climate of the study region, we extracted the 19 bioclimatic variables from WorldClim 1.4 (11 related to temperature, and 8 related to precipitation) (Hijmans et al. 2005).

To assess the influence of past anthropogenic impacts on present-day vegetation patterns, we used the data assembled by Pereira (2003), which relied upon the Leopold matrix for environmental impact assessment (Leopold et al. 1971) (Appendix S8 in the Supporting Information). The rows of this matrix list the 12 sampled fragments, whereas the columns contain environmental and disturbance-related variables, namely: (1) type of anthropogenic disturbance and (ii) surrounding matrix. Pereira (2003) attributed weights (ranging from 1 to 6) to all disturbance variables present in the columns, in order to characterize the impact’s damaging potential. Each intersection between rows and columns was divided into four quadrants, each of which aimed to characterize one of the following disturbance attributes: (i) severity (quadrant 1), (ii) spatial extent (quadrant 2), (iii) duration (quadrant 3), and (iv) magnitude of the impact (quadrant 4), representing the sum of the three former quadrants. The scores of each of these disturbance attributes varied between 0 and 4 (except for magnitude, which ranged between 0 and 12), meaning: 0 – absent disturbance, 1 – low disturbance effects, 2 – moderate disturbance effects, 3 – high disturbance effects, and 4 – very high disturbance effects. Therefore, for each fragment, the intersection between rows and columns resulted in a given score regarding each of the anthropogenic disturbance impacts assessed, which were the following: fire, logging (which received the highest impact weight), trails, cattle, internal and external roads, fence and littering (which received the lowest impact weight). We categorized the land use of the surrounding matrix as agriculture, silviculture and pasture. Finally, we also employed the same methodology as Pereira (2003) (i.e., Leopold matrix) to characterize the anthropogenic disturbance impacts underwent by the 12 fragments in the year 2019 (Appendix S7 in the Supporting Information).

Data analysis

To test for the disturbance effects on vegetation composition and function, we obtained the mean values of each vegetation variable from each inventory (structural variables) and from the intervals in-between (dynamics variables). We also extracted the following information from the Leopold matrix (i) final score, from the weighted average between the fragment’s score (impact magnitude) and impact weight, and (ii) fragment size and fragment shape index (the ratio between the fragment's perimeter and the square-root of its area).

We analyzed the following response variables: (i) average aboveground biomass recorded in the timeframe assessed (average between the multiple inventories); (ii) average productivity, (iii) mean temporal beta diversity, (iv) wood density community-weighted means (CWMWD) and (v) dispersal syndrome (percentage of individuals belonging to a given category, e.g., anemochory, zoochory, autochory). We calculated biomass values for each of the multiple inventories based on the pantropical equation by Chave et al. (2014), using package *biomass* (Rejou-Mechain et al. 2017). We averaged the plot-level values to characterize whole-fragment structure for each of the sites. The same logic was applied to calculate wood density community-weighted means (obtained with the *FD* package by Laliberté et al., 2014), and to calculate the proportion of individuals belonging to the dispersal syndromes. For each of these cases, we calculated a final fragment-level value based on the observed values across the multiple inventories. Productivity was obtained by the difference between biomass values recorded in different inventories divided by the number of years in between them, and later corrected following Talbot et al. (2014), to account for the different time intervals (in years) between the inventories. We calculated the trend of temporal biomass variation for each fragment by averaging the productivity recorded in each interval. We employed the same approach to obtain an average measure of the temporal trend in species composition variation, by calculating the mean temporal beta diversity recorded in each interval, using package *betapart* (Baselga and Orme 2012).

Due to the collinearity verified between the environmental control variables (i.e., climate and soil), we applied principal component analysis (PCA) to obtain a better depiction of their variation. We performed a PCA for climate and another for soil, separately. Adhering to the Kaiser-Guttman rule, whereby axes with eigenvalues above 1 are maintained, we used three PCA axes from each (climate and soil) analysis. We used these six axes as control variables in the models. We pre-selected the highly correlated variables (Pearson's correlation ≥ |0.95|) by choosing to maintain the higher order variables, e.g., mean annual temperature instead of mean temperature of wettest quarter (Dormann et al., 2012).

We used generalized linear mixed models to assess the effects of the environmental impacts on the vegetation variables. Fragment was added as a random factor to deal with pseudoreplication arising from the nested sampling of our data (plots within fragments). We included in the models the six PCA axes to control for the expected climate and soil effects. For each response variable, we adopted the model selection approach based on Akaike Information Criterion of second order (AICc). From the global model containing all explanatory variables, we selected the best models (ΔAICc < 4) (Burnham et al. 2011) that only contained variables with Pearson's correlation < |0.6| (Dormann et al. 2012; Burnham et al. 2011). We then applied a multimodel inference approach, obtaining the coefficients' conditional averages and confidence intervals based on the selected models. When necessary, we ensured normality of residuals through log or cube-root transformation. We also checked for spatial independence in each model's residuals (both for models of the ecological variables and the anthropogenic disturbance matrices).

We used packages lme4 and lmerTest for model fitting (Bates et al. 2015, Kuznetsova et al. 2016), MuMIn for model selection and multimodel inference (Bartón 2009), and *ncf* to test for spatial correlation (Bjørnstad 2016). All analyses were performed in the R environment (R Core Team 2018), adopting a significance level of 5%.

Results

We recorded a total of 36,638 individuals belonging to 544 species in 76 families in the 12 fragments sampled. The intensity of anthropogenic disturbances on the forest communities decreased significantly in the studied timeframe ($p < 0.05$): Pereira (2003) recorded a final score of 103.9 points of human impacts, whereas we recorded 74.1 points, all 12 fragments considered (Figure 1). In this decrease, the highlight goes to absence of clear-cutting activity in the current matrix and the selective logging that had an almost non-existent impact (**Appendices S7 and S8** in the Supporting Information).

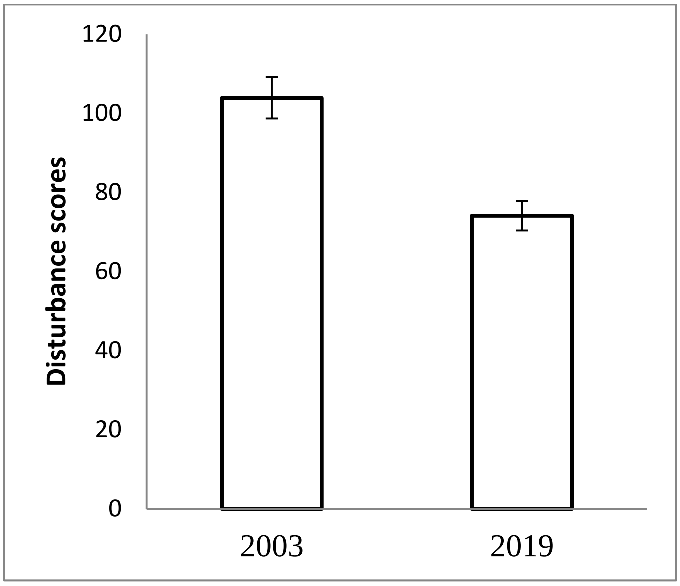

Figure 1. Temporal mean's classification of anthropogenic disturbances applied by Pereira (2003) and in 2019 (that was recently scored by this study). The bars represent the standard deviation between sample units within each category, according to the *lsmeans* contrasts applied on the model obtained in GLMM, at a significance level of 5%

Three dispersal syndromes were represented among all recorded species in the 12 fragments: anemochory (wind-dispersed species), autochory (self-dispersed species) and zoochory (animal-dispersed species) (refer to Table 2 for details). The abundance of self-dispersed species was positively and significantly affected by anthropogenic disturbances (p <

0.01), but not by soil variation. The coefficient of determination (R^2) for the self-dispersed species abundance model was 0.432, meaning that 43.2% of the variation in these species' abundances were explained by the explanatory variables. Animal-dispersed species abundances were also significantly, albeit negatively, affected by the recorded disturbances ($p < 0.001$, $R^2 = 0.408$).This syndrome also responds to soil variations, however, the soil showed a lesser effect (-1.894) than anthropogenic disturbances (-5.650). Conversely, the abundances of wind-dispersed species were not significantly affected by anthropogenic disturbances, but were significantly influenced by soil variation (Table 3).

Table 2. Generalized linear mixed model results for self-dispersal (autochory) and animal-dispersal (zoochory) syndromes as function of impact magnitude, soil, climate, fragment size and shape index. Note: (*) 5% significance level; (**) 1% significance level; (***) 0.1% significance level. ADs: Anthropogenic disturbances, FS: fragment size, FSI: fragment shape index, Est: estimate, R^2: coefficient of determination.

	Autocory			**Zoocory**		
	Est.	*p- value*	R^2	Est.	*p- value*	R^2
Intercept	1.134	<2e-16 ***	0.432	79.308	<2e-16***	0.408
ADs	0.523	7.3e-06***		-5.650	0.00644**	
FS	-0.189	0.114		3.873	0.083	
FSI	0.035	0.293		-0.922	0.073	
Soil: 1st axis	0.081	0.120		-1.894	0.013*	
Soil: 2nd axis	-0.078	0.069		-0.597	0.360	
Soil: 3rd axis	-0.015	0.790		1.532	0.075	
Climate: 1st axis	0.146	0.204		0.089	0.967	
Climate: 2nd axis	-0.121	0.231		2.963	0.128	
Climate: 3rd axis	-0.165	0.127		0.264	0.904	

Table 3. Generalized linear mixed model results for wind-dispersal syndrome (anemochory) as function of impact magnitude, soil, climate, fragment size and shape index. Note: (*) 5% significance level; (**) 1% significance level; (***) 0.1% significance level. ADs: Anthropogenic disturbances, FS: fragment size, FSI: fragment shape index, Est: estimate, R^2: coefficient of determination.

Anemocory			
	Est.	*p- value*	R^2
Intercept	2.235	<2e-16 ***	0.306
ADs	0.172	0.152	
FS	-0.117	0.395	
FSI	0.023	0.452	
Soil: 1st axis	-0.093	0.044 *	
Soil: 2nd axis	0.06	0.100	
Soil: 3rd axis	-0.089	0.800	
Climate: 1st axis	0.083	0.529	
Climate: 2nd axis	-0.017	0.884	
Climate: 3rd axis	0.094	0.449	

Wood productivity was significantly ($p < 0.05$) and negatively affected by anthropogenic disturbances, but not by the soil variables ($R^2 = 0.554$) (Table 3). Wood density community-weighted means (CWMWD), however, responded significantly and negatively to anthropogenic disturbances ($p < 0.05$, $R^2=0.128$) (Table 4). Unlike productivity, soil significantly (and negatively) influenced wood density CWM values ($p < 0.05$), with equal effect sizes to the disturbance effects.

Table 4. Generalized linear mixed model results for productivity and wood density community-weighted means (CWMWD) as function of the magnitude of impacts, soil, climate, fragment size and fragment shape index. Note: (*) 5% significance level; (**) 1% significance level; (***) 0.1% significance level. ADs: Anthropogenic disturbances, FS: fragment size, FSI: fragment shape index, Est: estimate, R^2: coefficient of determination.

	Productivity			**CWMWD**		
	Est.	*p- value*	R^2	Est.	*p- value*	R^2
Intercept	9.982	<2e-16***	0.554	0.589	<2e-16***	0.128
ADs	-1.057	0.0177*		0.008	0.018*	
FS	-0.113	0.818		0.0004	0.766	
FSI	0.113	0.685		0.0002	0.947	
Soil: 1st axis	0.046	0.893		-0.008	0.0002***	
Soil: 2nd axis	-0.296	0.346		-0.002	0.399	
Soil: 3rd axis	-0.166	0.679		-0.002	0.488	
Climate: 1st axis	0.079	0.75		0.005	0.175	
Climate: 2nd axis	0.590	0.152		0.001	0.495	
Climate: 3rd axis	0.364	0.415		-0.002	0.440	

According to the models, aboveground biomass (AGB) and temporal beta diversity were not significantly affected by anthropogenic disturbances ($p > 0.05$), although the latter had a positive, significant relationship with soil (axis 1 and axis 3). Other explanatory variables also associated with disturbance effects (i.e., fragment size and shape index) did not significantly influence any of the other response variables.

Table 5. Temporal beta diversity as function of impact magnitude, soil, climate, fragment size and shape index. Note: (*) 5% significance level; (**) 1% significance level; (***) 0.1% significance level. ADs: Anthropogenic disturbances FS: fragment size, FSI: fragment shape index, Est: estimate, R2: coefficient of determination.

	Temporal beta diversity		
	Est.	*p- value*	R^2
Intercept	0.525	<2e-16 ***	0.152
ADs	-0.006	0.456	
FS	-0.0008	0.919	
FSI	0.0008	0.837	
Soil: 1st axis	0.021	0.0002***	
Soil: 2nd axis	-0.03	0.502	
Soil: 3rd axis	0.028	3.5e-06 ***	
Climate: 1st axis	-0.001	0.894	
Climate: 2nd axis	-0.006	0.404	
Climate: 3rd axis	0.003	0.672	

Discussion

Our results supported our first hypothesis that anthropogenic disturbances significantly affect dispersal syndromes in our study areas. For instance, the animal-dispersal syndromes (zoochory) were more affected by anthropogenic disturbances than soil, in spite of soil's role as a driver of community structure. The higher the impacts, the least abundant were the animal-dispersed species in a given area. Soil also had a negative effect on the abundance of animal-dispersed species, meaning that the most fertile sites had a smaller species abundance with this syndrome. This reduction in animal-dispersed species abundances may be explained by the loss of dispersers caused by the anthropogenic disturbances. These disturbances affect dispersal in three fundamental aspects, namely: (i) by reducing the frequency of disperser visits and abundance, through local extinctions or forced migration (Markl et al. 2012; Fonturbel et al. 2015); (ii) by exposing the seed banks and increasing the likelihood of seed predation and fungi attack; and (iii) by reducing the dispersal distance by changing local biophysical characteristics coupled with the decrease in seed disperser abundance (Caves et al. 2013; Schleuning et al, 2011). These consequences are also reflected in forest regeneration, plant recruitment and other ecological processes in the community (Farwig & Berens 2012; Markl et al. 2012). Several authors highlight that the loss of dispersers alters a community's ecological functions, entailing the homogenization of floristic composition and structure, and loss of ecosystem services (García & Martínez 2012; Schleuning et al. 2015; Caughlin et al. 2015).

The reduction in seed dispersers driven by anthropogenic disturbances can lead to local extinctions and great biodiversity loss, especially for plant species dispersed by single animal species (Rodríguez-Cabal et al. 2007; Beckman & Rogers 2013; Farwig & Berens, 2012). Zoochory is the main dispersal syndrome in tropical forests, where more than 80% of tree species depend on animal dispersers (Muller-Landau et al. 2008; Au et al 2006). The breakdown in plant-animal interactions, specifically seed dispersal, enhances the chances of predator and pathogen attacks on the undispersed seeds, having profound consequences on plant recruitment, population persistence and community dynamics (Markl et al. 2012; Farwig & Berens 2012). Culot et al. (2017) found that plant recruitment decreased by 70.7 and 94.9% due to the loss of frugivore dispersers. Additionally, species that produce larger seeds are under greater threat for being usually dispersed by large sized vertebrates, given the positive relationship between seed size and frugivore disperser size (Jordano 2017; Fuzessy et al. 2018). In the case of our study sites, most are small fragments without minimum conditions or resources to support the occurrence of adequate dispersers, which can lead to a lack of recruitment and persistence of tree species dependent on them (Bueno et al. 2013; Corlett 2017).

Disturbances tend to favor autochorous (or self-dispersal) syndromes, manifested by a higher abundance of self-dispersed species in tree communities under higher disturbance impacts. This may be linked to the higher frequency of gaps in human-disturbed fragments. Several authors have found significant increases of autochorous species abundances in human-disturbed environments, especially in forest gaps resulting from selective logging, where these plants encounter suitable space and resources for colonization (Drezner et al. 2001; Kuhlmann & Ribeiro 2016). These self-dispersed species may therefore not require dispersal agents, since they usually produce dehiscent fruits that facilitate seed dispersal through gravity (Jara-Guerrero et al. 2011; Parolin et al. 2013). Conversely, although the abundance of anemochorous, or wind-dispersed, species did not respond significantly to anthropogenic disturbances, it was negatively affected by soil fertility, i.e., the lowest fertility sites had higher abundance of wind-dispersed species. This is congruent with evidence that infertile soils may promote wind-dispersal efficiency (Spasojevic et al. 2014).

The temporal beta diversity recorded in this study showed that human disturbances did not significantly affect species turnover of the studied fragments within the timeframe analysed. Based on this, we reject our second hypothesis. However, this variable was significantly and positively affected by the soil, meaning that the most fertile soils had higher species substitution in the timeframe of study. This result provides evidence of the structuring effect of soil on the tree communities of our study fragments. Other studies that analysed the effect of soils on tropical forest community structure have found similar results to us, whereby variation in soil attributes significantly influenced tree species composition (Kumar et al. 2010; Long et al. 2012 ; Baldeck et al. 2013; Prada et al. 2017; Van der Sande et a. 2018). For example, Long et al. (2012) found a positive effect of soil fertility on tree species richness.

Wood productivity was negatively affected by anthropogenic disturbances, meaning that sites more exposed to impacts had lower productivity. This finding reinforces our first hypothesis that human disturbances influence tree community productivity. This inverse relationship between productivity and anthropogenic disturbance has been explained by other authors, which state that disturbance intensity negatively influences ecosystem productivity, ecological interactions and resilience to the disturbance itself (Amiro et al. 2010; Flower et al. 2014; Flower & Gonzalez-Meler 2015; Peters et al., 2013). Gautam & Mandal (2016) found similar results when analyzing the effects of human disturbances on carbon dynamics and productivity. They found that human disturbances decreased productivity by 44%, and negatively affected ecosystem structure and functioning. Other studies have found that, the higher intensity of logging (which we also evaluated), the lower are ecosystem productivity which ultimately lead to the loss of community function (Martin et al. 2015; Mori et al. 2017; Roopsind et al. 2018). Primary productivity is a good proxy of ecosystem carbon uptake (Girardin et al. 2010). Small changes in productivity at global, regional or even local scales can therefore have substantial effects on ecosystem function and net rates of carbon sequestration (Malhi 2011; Malhi et al. 2014). This may ultimately affect the provision of ecosystem goods and services, including nutrient cycling, soil formation, food, water, medicines, erosion control, purification of water and air, polinization and carbon sequestration (Parrotta et al. 2012; Berenguer et al. 2014; Lewis et al. 2015; Shimamoto et al. 2017). The latter makes wood productivity an essential component of climate change mitigation (Parrotta et al. 2012; Kirby et al. 2017).

Concerning the community-weighted means (CWM) for wood density, the anthropogenic disturbances had a positive effect, meaning that the higher the impact, the higher the mean values of wood density in the tree community. However, during the timeframe of our study (2003-2019), the incidence of disturbances on the studied communities decreased (Figure 1), which might reflect the adoption of forest conservation policies (Pereira 2003). For instance, logging activities were almost entirely absent from all fragments in the last disturbance impact assessment, in year 2019 (Appendices S7 and S8 in the Supporting Information). The fact that human disturbances were associated with the occurrence of high wood density species may be related to their higher commercial value, which may have stimulated intense human activity in forests with high mean values of wood density in the past (Pereira et al. 2015). The presence of high wood density species today may indicate that these forests are at advanced successional stages, given that high wood density, shade-tolerant and slow-growth species are the last to emerge in the successional process (Nascimento et al. 2005; Powers & Marín-Spiotta, 2017; Hiltner et al. 2018). Moreover, several studies have shown that increases in wood density are associated with increases in the abundance of late successional species, at the expense of decreasing abundance and dominance of pioneer (fast-growing, low wood density) populations (Slik et al. 2008; Chazdon et al. 2014; Lin et al. 2015). Conversely, soil had a negative effect on wood density CWM, meaning that higher fertility predicted lower mean values of wood density. The fact that areas with low wood density species are less impacted by human diturbances may explain their higher fertility. For instance, logging intensity directly impacts soil quality, leading to decreased fertility, soil compaction and consequently the loss of ecosystem function (Singh et al. 2010; Bowd et al. 2019). In addition, the effects of anthropogenic disturbances and soil characteristics had equal effect sizes on this variable, indicating that both may be important determinants of wood density CWM in the studied communities.

The results of our study showed that, although human disturbances exert strong negative impacts on productivity and on the dispersal of zoochorous species, they were not enough to alter the advanced successional stage of the studied fragments. This may be explained by a decline in the disturbance impacts over time, recorded in the Leopold matrix of anthropogenic disturbance characterization (Figure 1). Furthermore, unlike other studies that analyzed disturbance effects on a smaller number of (or even single) forest fragments (Kleinschroth & Healey 2017; Sfair et al. 2018; Ding et al. 2019; Gaui et al. 2019), our study provides novel insight into the how the effects of anthropogenic disturbance histories, interacting with natural drivers of tree community structure (i.e., climate and soil), are manifested in tropical forest ecological patterns. Importantly, our study was performed in a highly endangered biodiversity hotspot, the Brazilian Atlantic Forest, adding further relevance to our findings, especially if taken into account that most present-day remnants are small fragments that have been exposed to human disturbances. At last, we highlight that the climate, in spite of being an important driver tree community structure on larger scales, did not produce any significant effects on the ecological variables studied, which might reflect the short climatic variation covered by the studied fragments (Schuur 2003; Adler & Levine 2007; Bai et al. 2008; Reboita et al. 2015). At last, our study shows that with exhaustive sampling, anthropogenic disturbances can be important drivers of ecological modifications in the tropical forest tree communities. These disturbances may compromise the provision of essential ecosystem goods and services, relied upon by humanity.

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Supporting information for the paper

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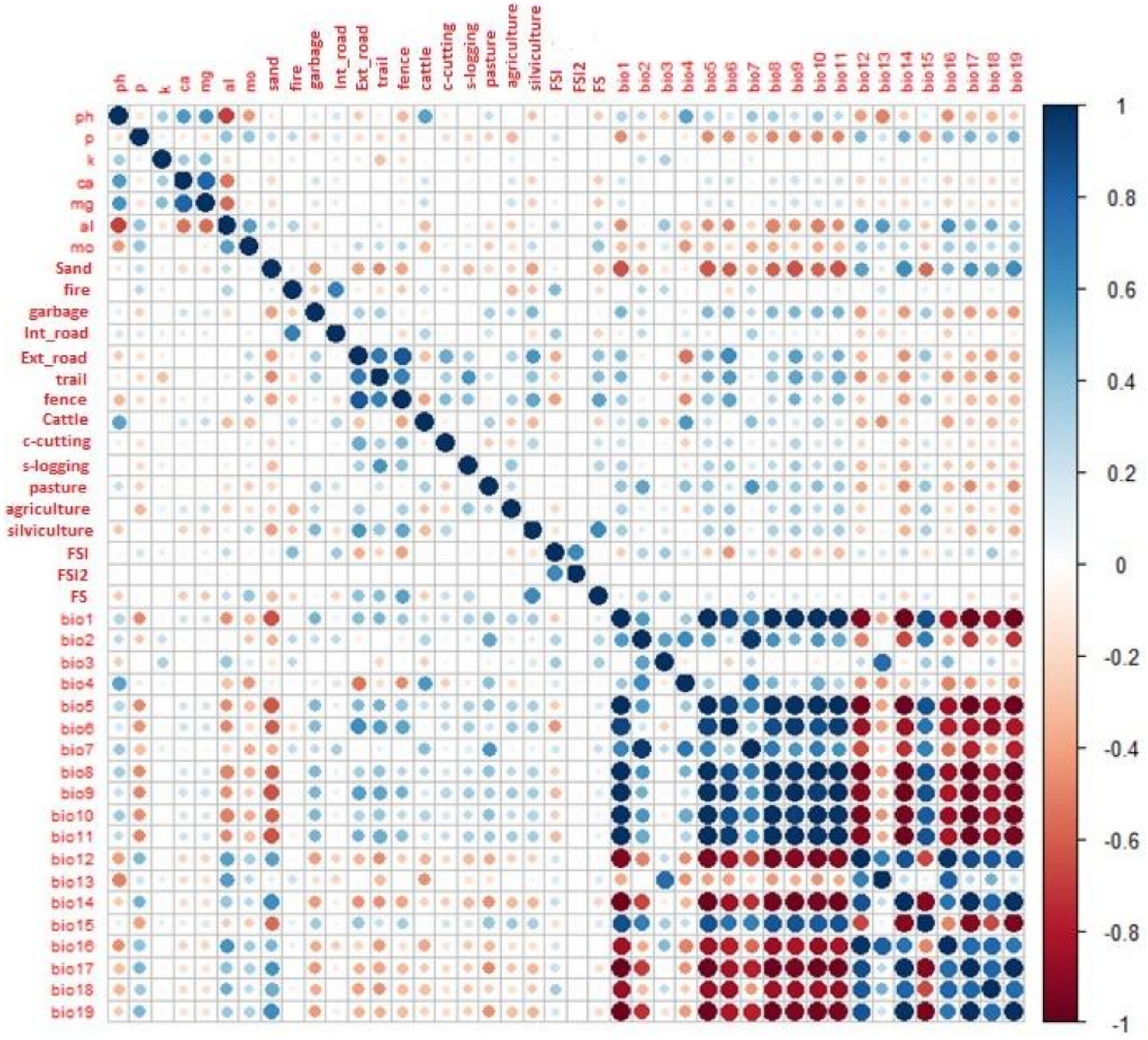
Appendix S1: Correlations among the 19 bioclimatic variables, soil and impact variables in the 12 forest fragments. Note: Note: P = phosphorus, K = potassium, Ca = calcium, Mg = magnesium, Al = aluminium, MO= organic matter; BIO1 = Annual Mean Temperature, BIO2 = Mean Diurnal Range, BIO3 = Isothermality, BIO4 = Temperature Seasonality, BIO5 = Max Temperature of Warmest Month, BIO6 = Min Temperature of Coldest Month, BIO7 = Temperature Annual Range, BIO8 = Mean Temperature of Wettest Quarter, BIO9 = Mean Temperature of Driest Quarter, BIO10 = Mean Temperature of Warmest Quarter, BIO11 = Mean Temperature of Coldest Quarter, BIO12 = Annual Precipitation, BIO13 = Precipitation of Wettest Month, BIO14 = Precipitation of Driest Month, BIO15= Precipitation Seasonality, BIO16 = Precipitation of Wettest Quarter, BIO17 = Precipitation of Driest Quarter, BIO18 = Precipitation of Warmest Quarter, BIO19 = Precipitation of Coldest Quarter; c-cutting= clear cutting; Int_road= internal road; Ext_ road= external road; s-logging= selective logging; FSI- fragment shaping index(weighted); FSI2= Fragment shaping index (simple); FS= fragment size


ph
p
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garbage
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Ext_road
trail
fence
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c-cutting
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agriculture
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bio17
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fire
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Ext_road
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bio19
1
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0.6
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-0.6
-0.8
-1

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Appendix S2: Correlations between the soil PCA axes and all soil variables (SV) included in analysis in 12 forest fragments. Note: Note: Note: P = phosphorus, K = potassium, Ca = calcium, Mg = magnesium, Al = aluminium, MO= organic matter.

SV	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
ph	20.6112	0.0033	5.9837	0.4048	11.3731	47.9130	13.2174	0.4934
p	4.0862	25.7951	13.7490	0.1887	47.5410	7.5278	1.0609	0.0513
k	5.7443	20.5127	2.0348	58.5461	10.4868	0.3478	0.7199	1.6076
ca	18.9309	7.4781	0.2155	18.1001	1.3952	7.5680	10.0133	36.298
mg	20.5787	7.2909	0.0231	7.9115	3.7403	4.3384	0.5023	55.614
al	21.4196	6.1033	0.0724	0.1688	4.0528	0.0933	63.1695	4.9203
mo	5.7456	32.6658	11.8213	7.1329	2.1782	30.2721	9.4991	0.6851
sand	2.8833	0.1507	66.1001	7.5472	19.2326	1.9397	1.8176	0.3286

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Appendix S3: Correlations between the bioclimatic PCA axes and all bioclimatic variables (BCV) included in analysis, in 12 forest fragments. Note: BIO1 = Annual Mean Temperature, BIO3 = Isothermality, BIO4 = Temperature Seasonality, BIO6 = Min Temperature of Coldest Month, BIO7 = Temperature Annual Range, BIO12 = Annual Precipitation, BIO13 = Precipitation of Wettest Month, BIO15= Precipitation Seasonality, BIO17 = Precipitation of Driest Quarter, BIO18 = Precipitation of Warmest Quarter.

BCV	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
bio1	16.0035	0.3893	1.3212	0.0862	2.33E+00	2.7375	6.7865	8.07E+00
bio3	0.2413	43.0047	0.5372	12.5981	1.36E+01	28.4676	0.0029	1.16E+00
bio4	3.9797	0.7076	49.1576	24.5496	9.95E-01	18.7089	0.0025	6.04E-01
bio6	12.4033	0.3789	16.6234	0.0094	5.68E+00	7.6201	3.8856	3.26E+00
bio7	8.7338	5.2155	23.0289	8.0761	1.21E+00	34.2186	1.3861	4.41E+00
bio12	15.3623	1.8302	0.0068	14.3199	1.31E-05	0.6318	2.9696	1.45E+01
bio13	3.9323	32.0015	2.6803	20.1406	1.64E+00	3.8616	7.6545	1.74E+01
bio15	11.1168	13.1323	1.5635	4.0707	7.38E+00	1.4225	57.8105	2.52E+00
bio17	15.5919	2.2658	0.0037	0.0689	3.05E+00	1.4249	19.4510	4.81E+01
bio18	12.6351	1.0741	5.0775	16.0805	6.42E+01	0.9059	0.0498	1.25E-06

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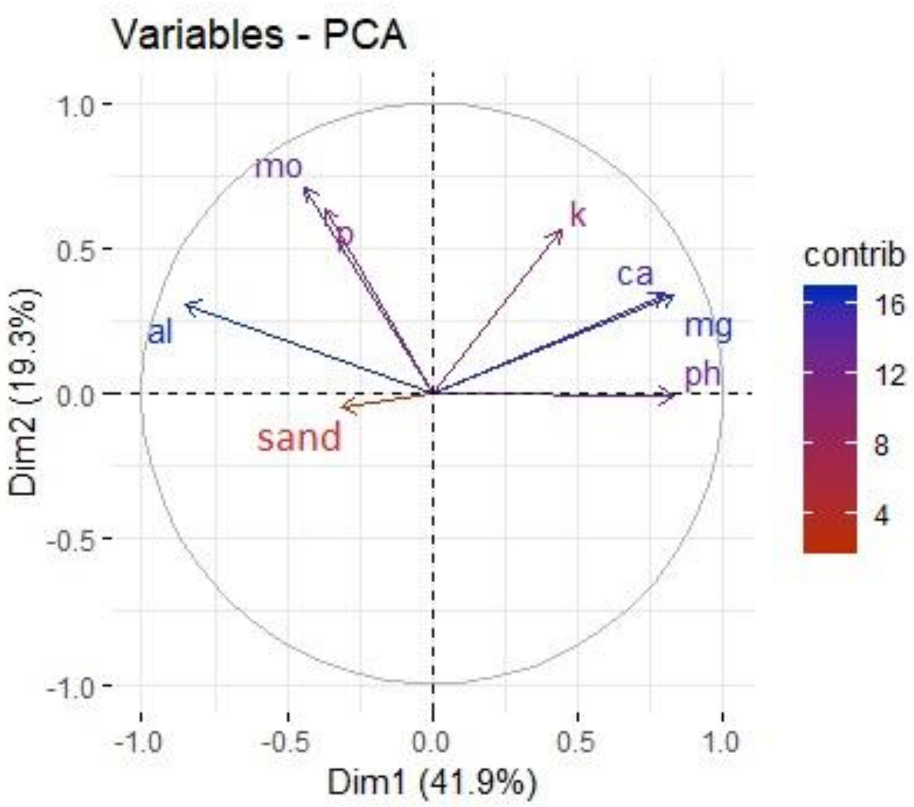
Appendix S4: Principal Component Analysis (PCA) of soil fertility, sampled in 12 forest fragments. Note: P = phosphorus, K = potassium, Ca = calcium, Mg = magnesium, Al = aluminium, MO= organic matter.



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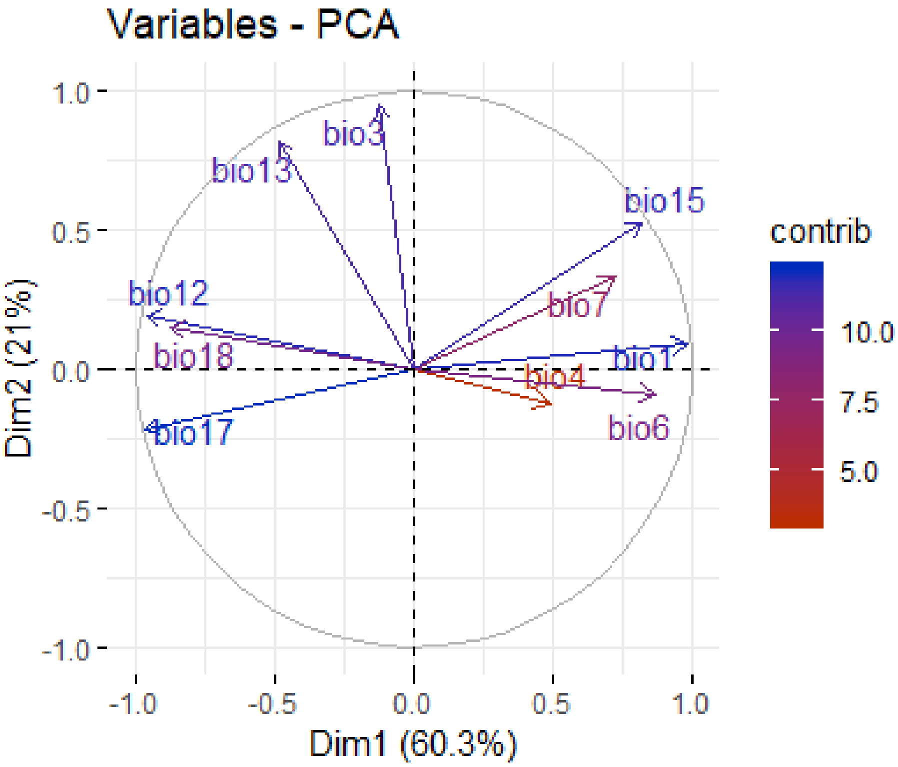
Appendix S5: Principal Component Analysis (PCA) of bioclimatic variables, sampled in 12 forest fragments. Note: BIO1 = Annual Mean Temperature, BIO3 = Isothermality, BIO4 = Temperature Seasonality, BIO6 = Min Temperature of Coldest Month, BIO7 = Temperature Annual Range, BIO12 = Annual Precipitation, BIO13 = Precipitation of Wettest Month, BIO15= Precipitation Seasonality, BIO17 = Precipitation of Driest Quarter, BIO18 = Precipitation of Warmest Quarter.



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Appendix S6: Temporal mean's classification of anthropogenic disturbances (ADs) applied by Pereira (2003) (Z) and in 2019 (that was recently scored by this study) (A), according to the obtained GLMM, at a significance level of 5%, using. Significant codes: 0.001 '***' 0.01'**' '0.05 *'

Random effects:

Groups Name	Variance	Std.Dev.
fragmento (Intercept)	3165.6	56.26
Residual	441.6	21.01

Fixed effects:

	Estimate	Std. Error	df	t value	Pr(>|t|)
(Intercept)	74.083	15.712	12.761	4.715	0.000425
Z	29.833	8.579	11.000	3.477	0.00517 **

Lsmeans of impact：

ADs	lsmean	SE	df	lower.CL	upper.CL
A	74.1	15.7	12.8	40.1	108
Z	103.9	15.7	12.8	69.9	138

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Appendix S7: Current anthropogenic disturbances characterization matrix (year 2019) on the 12 Southern Minas Gerais forest fragments, Brazil.

Note: LV= Mata da UFLA, PB= Poço Bonito, MD= Madre de Deus, IT= Itutinga, CM= Camargos, IB= Ibitipoca, CP= Capivarí, SE= Subestação, ML= Mata da lagoa, CR= Carrancas, IN= Indaí, LU= Luminárias

Fragments		**Anthropogenic disturbances**																								**Final score**
		Fire		Garbage		Internal roads		External roads		Trails		Fence		Cattle		Clear-cutting		Seletive logging		**Surrounding matrix**						
																				Pasture		agriculture		silviculture		
	weights	5		1		4		3		2		1		4		6		5		3		2		1		
1	LV	0	0	1	4	0	0	3	11	4	10	4	12	0	0	0	0	0	0	1	5	0	0	3	10	**94**
		0	0	1	2	0	0	4	4	3	3	4	4	0	0	0	0	0	0	1	3	0	0	3	4	
2	PB	2	7	1	3	1	7	1	6	1	6	0	0	2	7	0	0	0	0	3	9	0	0	1	3	**154**
		2	3	1	1	2	4	1	4	1	4	0	0	1	4	0	0	0	0	2	4	0	0	1	1	
3	MD	0	0	1	5	0	0	0	0	1	4	0	0	2	5	0	0	0	0	3	10	0	0	1	3	**66**
		0	0	2	3	0	0	0	0	1	2	0	0	1	2	0	0	0	0	3	4	0	0	1	1	
4	IT	0	0	2	9	0	0	1	5	0	0	0	0	0	0	0	0	0	0	0	0	1	3	3	10	**40**
		0	0	3	4	0	0	1	3	0	0	0	0	0	0	0	0	0	0	0	0	1	1	3	4	
5	CM	0	0	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	6	3	8	2	9	**46**
		0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	2	3	3	4	
6	IB	0	0	0	0	0	0	0	0	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**6**
		0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
7	CP	0	0	3	10	0	0	1	3	3	9	0	0	0	0	0	0	1	3	4	10	0	0	0	0	**82**
		0	0	3	4	0	0	1	1	3	3	0	0	0	0	0	0	1	1	3	3	0	0	0	0	

Continues...

Fragments		Anthropogenic disturbances																								Final scores
																				Surrounding matrix						
		Fire		Garbage		Internal roads		External roads		Trails		Fence		Cattle		Clear-cutting		Seletive logging		Pasture		agriculture		silviculture		
	weights	5		1		4		3		2		1		4		6		5		3		2		1		
8	SE	0	0	1	3	0	0	2	6	0	0	1	3	0	0	0	0	0	0	3	9	3	9	0	0	**69**
		0	0	1	1	0	0	2	2	0	0	1	1	0	0	0	0	0	0	3	3	3	3	0	0	
9	ML	0	0	2	7	0	0	2	8	3	9	3	9	4	10	0	0	1	3	3	9	2	8	0	0	**156**
		0	0	2	3	0	0	3	3	3	3	3	3	3	3	0	0	1	1	3	3	3	3	0	0	
10	CR	0	0	0	0	0	0	0	0	1	3	0	0	0	0	0	0	0	0	2	8	0	0	0	0	**30**
		0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	3	3	0	0	0	0	
11	IN	0	0	1	3	0	0	0	0	1	3	0	0	2	4	0	0	0	0	1	4	0	0	2	4	**41**
		0	0	1	1	0	0	0	0	1	1	0	0	1	1	0	0	0	0	1	2	0	0	1	1	
12	LU	0	0	2	6	1	6	0	0	2	5	0	0	1	3	0	0	0	0	3	10	3	10	1	3	**105**
		0	0	2	2	1	1	0	0	1	2	0	0	1	1	0	0	0	0	4	3	3	4	1	1	

a	**d**
b	c

Impact quadrants: a = severity, b= spatial extent, c= duration and d= magnitude (d= a+b+c); 0 – absent disturbance, 1 – low disturbance effects, 2 – moderate disturbance effects, 3 – high disturbance effects, and 4 – very high disturbance effects

Supporting information for the paper

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Appendix S8: Past anthropogenic disturbances characterization matrix from Pereira (2003) on the 12 Southern Minas Gerais forest fragments, Brazil

Fragments		**Anthropogenic disturbances**																								**Final scores**
		Fire		Garbage		Internal roads		External roads		Trails		Fence		Cattle		Clear-cutting		Seletive logging		**Surrounding matrix**						
																				Pasture		agriculture		silviculture		
	weights	5		1		4		3		2		1		4		6		5		3		2		1		
1	LV	0	0	1	3	0	0	3	9	4	11	4	12	0	0	0	0	3	10	1	6	1	6	2	6	**150**
		0	0	1	1	0	0	3	3	3	4	4	4	0	0	0	0	3	4	2	3	2	3	2	2	
2	PB	2	7	0	0	1	7	1	6	1	3	1	4	2	4	1	4	1	3	1	4	0	0	0	0	**158**
		2	3	0	0	2	4	1	4	1	1	1	2	1	1	1	2	1	1	1	2	0	0	0	0	
3	MD	0	0	0	0	0	0	0	0	2	6	0	0	4	12	0	0	1	3	2	7	0	0	0	0	**96**
		0	0	0	0	0	0	0	0	2	2	0	0	4	4	0	0	1	1	2	3	0	0	0	0	
4	IT	1	3	0	0	0	0	0	0	0	0	0	0	1	3	0	0	0	0	1	6	0	0	0	0	**45**
		1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	3	2	0	0	0	0	
5	CM	1	3	0	0	0	0	0	0	0	0	0	0	1	3	0	0	0	0	1	6	0	0	1	3	**48**
		1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	3	2	0	0	1	1	
6	IB	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**
		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	

Continues...

Fragments		Anthropogenic disturbances																								
		Fire		Garbage		Internal roads		External roads		Trails		Fence		Cattle		Clear-cutting		Seletive logging		Surrounding matrix						Final scores
																				Pasture		agriculture		silviculture		
	Peso	5		1		4		3		2		1		4		6		5		3		2		1		
7	CP	1	3	2	6	0	0	1	4	2	7	0	0	1	3	2	8	3	8	1	3	1	3	0	0	**162**
		1	1	2	2	0	0	1	2	2	3	0	0	1	1	3	3	2	3	1	1	1	1	0	0	
8	SE	0	0	0	0	0	0	2	7	1	3	3	10	0	0	2	6	1	3	1	3	2	7	0	0	**111**
		0	0	0	0	0	0	2	3	1	1	3	4	0	0	2	2	1	1	1	1	2	3	0	0	
9	ML	1	3	1	3	2	6	3	7	4	11	0	0	4	12	2	6	2	6	2	6	0	0	0	0	**217**
		1	1	1	1	2	2	2	2	3	4	0	0	4	4	2	2	2	2	2	2	0	0	0	0	
10	CR	2	5	0	0	0	0	0	0	0	0	0	0	1	3	1	4	1	3	2	6	0	0	0	0	**94**
		1	2	0	0	0	0	0	0	0	0	0	0	1	1	1	2	1	1	2	2	0	0	0	0	
11	IN	0	0	0	0	0	0	0	0	1	3	0	0	2	7	0	0	1	3	1	3	0	0	0	0	**58**
		0	0	0	0	0	0	0	0	1	1	0	0	2	3	0	0	1	1	1	1	0	0	0	0	
12	LU	1	3	0	0	1	3	0	0	1	3	1	3	1	3	2	6	1	3	1	3	0	0	0	0	**108**
		1	1	0	0	1	1	0	0	1	1	1	1	1	1	2	2	1	1	1	1	0	0	0	0	

a	**d**
b	c

Impact quadrants: a = severity, b= spatial extent, c= duration and d= magnitude (d= a+b+c); 0 – absent disturbance, 1 – low disturbance effects, 2 – moderate disturbance effects, 3 – high disturbance effects, and 4 – very high disturbance effects

Supporting information for the paper

Pais et al. Do abiotic factors drive ecological modifications in tropical forest fragments with a history of anthropogenic disturbances?

Conservation Biology

Appendix S9: Species list by dispersal syndrome, occurring in 12 forest fragments. Note: Aut- Autochory, Zoo- Zoochory, Anemo- Anemochory

Species	**Syndrome**	***Species***	**Syndrome**
Actinostemon concolor (Spreng.) Müll.Arg.	aut	*Bowdichia virgilioides* Kunth	anemo
Actinostemon klotzschii (Didr.) Pax	aut	*Byrsonima laxiflora* Griseb.	zoo
Actinostemon verticillatus (Klotzsch) Baill.	aut	*Byrsonima myricifolia G*riseb.	zoo
Aegiphila integrifólia (Jacq.) Moldenke	zoo	*Cabralea canjerana* (Vell.) Mart.	zoo
Aegiphila verticillata Vell.	zoo	*Callianthe bedfordiana* (Hook.) Donnell	anemo
Agonandra excelsa Griseb.	zoo	*Callisthene major* Mart.	anemo
Aiouea saligna Meisn.	zoo	*Calophyllum brasiliense* Cambess.	zoo
Albizia polycephala (Benth.) Killip ex Record	anemo	*Calycorectes acutatus* Cambess.	zoo
Alchornea glandulosa Poepp. & Endl.	zoo	*Calyptranthes brasiliensis* Spreng.	zoo
Alchornea triplinervia (Spreng.) Müll.Arg.	zoo	*Calyptranthes clusiifolia* O.Berg	zoo
*Allophylus edulis G*racilis Radlk.	zoo	*Calyptranthes concinna* Spreng.	zoo
Allophylus petiolulatus Radlk.	zoo	*Calyptranthes widgreniana* O.Berg	zoo
Allophylus racemosus Sw.	zoo	*Campomanesia guaviroba* (DC.) Kiaersk.	zoo
Allophylus semidentatus (Miq.) Radlk.	zoo	*Campomanesia guazumifolia* (DC.) Kiaersk.	zoo
Alseis floribunda Schott	anemo	*Campomanesia velutina (Cambess.)* O.Berg	zoo
Amaioua guianensis Aubl.	zoo	*Campomanesia xanthocarpa* O.Berg	zoo
Amaioua intermedia Mart. ex Schult.	zoo	*Cariniana estrellensis (Raddi)* Kuntze	anemo
Anadenanthera colubrina (Vell.) Brenan	anemo	*Cariniana legalis* (Mart.) Kuntze	anemo
Anadenanthera peregrina (L.) Speg.	anemo	*Carpotroche brasiliensis* (Raddi) A Gray	zoo
Andira fraxinifolia Benth.	zoo	*Casearia arbórea* (Rich.) Urb.	zoo

Aniba canelilla (Kunth) Mez	zoo	*Casearia decandra* Jacq.	zoo
Aniba firmula (Nees & Mart.) Mez	zoo	*Casearia gossypiosperma* Briq.	zoo
Annona cacans Warm.	zoo	*Casearia lasiophylla* Eichler	zoo
Annona dolabripetala Raddi	zoo	*Casearia obliqua* Briq.	zoo
Annona emarginata (Schltdl.) H.Rainer	zoo	*Casearia sylvestris* Jacq.	zoo
Annona neosericea Raddi	zoo	*Casearia ulmifolia* Vahl ex Vent.	zoo
Annona sylvatica Warm.	zoo	*Cassia ferrugínea* (Schrad.) Schrad. ex DC.	zoo
Aralia warmingiana (Marchal) J.Wen	zoo	*Cecropia glaziovii* Snethl.	zoo
Aspidosperma australe Müll.Arg.	anemo	*Cecropia pachystachya* Snethl.	zoo
Aspidosperma cylindrocarpon Müll.Arg.	anemo	*Cedrela fissilis* Vell.	anemo
Aspidosperma olivaceum Müll.Arg.	anemo	*Ceiba speciosa* Vell.	anemo
Aspidosperma parvifolium A.DC.	anemo	*Celtis brasiliensis* (Gardner) Planch.	zoo
Aspidosperma ramiflorum Müll.Arg.	anemo	*Cestrum schlechtendalii* G.Don	zoo
Aspidosperma spruceanum Benth.	anemo	*Cheiloclinium cognatum* (Miers) A.C.Sm.	zoo
Astronium fraxinifolium Schott	anemo	*Chionanthus crassifolius* (Mart.) P.S.Green	zoo
Astronium graveolens Schott	anemo	*Chomelia brasiliana* A.Rich.	zoo
Aureliana velutina Sendtn.	zoo	*Chomelia sericea* A.Rich.	zoo
Austrocritonia velutina R.M.King & H.Rob.	anemo	*Chrysophyllum gonocarpum* Mart. & Eichler	zoo
Balfourodendron molle (Miq.) Pirani	anemo	*Chrysophyllum marginatum* Mart. & Eichler	zoo
Balfourodendron riedelianum (Miq.) Pirani	anemo	*Cinnamodendron dinisii* Schwacke	zoo
Banara parviflora (A.Gray) Benth.	zoo	*Cinnamomum glaziovii* Schwacke	zoo
Bauhinia forficata Link	aut	*Cinnamomum triplinerve* Schwacke	zoo
Bauhinia longifólia Link	aut	*Citronella paniculata* (Mart.) R.A.Howard	zoo
Bauhinia rufa (Bong.) Steud.	aut	*Clethra scabra* Pers.	anemo
Beilschmiedia angustifólia Kosterm.	zoo	*Clusia criuva* Cambess.	zoo
Beilschmiedia taubertiana Kosterm.	zoo	*Clusia organensis* Planch. & Triana	zoo
Blepharocalyx salicifolius (Kunth) O.Berg	zoo	*Coccoloba alnifolia* Casar.	zoo
Boehmeria caudata Sw.	anemo	*Coccoloba warmingii* Casar.	zoo
Colubrina glandulosa Perkins	zoo	*Coffea arábica* L.	zoo
Connarus regnellii G.Schellenb.	zoo	*Endlicheria paniculata* (Spreng.) J.F.Macbr.	zoo

Copaifera langsdorffii Desf.	zoo	*Eremanthus erythropappus* (DC.) MacLeish	anemo
Cordia ecalyculata Vell.	zoo	*Eriotheca candolleana* Steud.	anemo
Cordia sellowiana Sw.	zoo	*Erythrina falcata* Benth.	zoo
Cordia trichoclada L.	zoo	*Erythroxylum citrifolium* A.St.-Hil.	zoo
Cordia trichotoma (Vell.) Arráb. ex Steud.	zoo	*Erythroxylum cuneifolium* A.St.-Hil.	zoo
Cordiera concolor Vell.	zoo	*Erythroxylum deciduum* Benth.	zoo
Cordiera elliptica (Cham.) Kuntze	zoo	*Erythroxylum gonocladum* Mart.	zoo
Cordiera myrciifolia (Cham.) Kuntze	zoo	*Erythroxylum pelleterianum* A.St.-Hil.	zoo
Cordiera sessilis (Vell.) Kuntze	zoo	*Erythroxylum suberosum* Benth.	zoo
Cordiera vinosa (Vell.) Kuntze	zoo	*Esenbeckia febrífuga* A. Juss. ex Mart.	aut
Coussapoa microcarpa (Schott) Rizzini	zoo	*Esenbeckia leiocarpa* (Cham.) Kuntze	aut
Coutarea hexandra (Jacq.) K.Schum.	anemo	*Eugenia acutata* Miq.	zoo
Croton echinocarpus Müll. Arg.	aut	*Eugenia adenantha* O.Berg	zoo
Croton erythroxyloides A.Rich.	aut	*Eugenia cerasiflora* O.Berg	zoo
Croton floribundus Müll. Arg.	aut	*Eugenia dodonaeifolia* O.Berg	zoo
Croton organensis Baill.	aut	*Eugenia florida* Miq.	zoo
Croton urucurana Baill.	aut	*Eugenia francavilleana* Miq.	zoo
Cryptocarya aschersoniana Mez	zoo	*Eugenia handroana* Meisn.	zoo
Cryptocarya micranta Meisn.	zoo	*Eugenia hiemalis* Cambess.	zoo
Cupania emarginata Cambess.	zoo	*Eugenia involucrata* DC.	zoo
Cupania ludowigii Somner & Ferrucci	zoo	*Eugenia longipedunculata* Nied.	zoo
Cupania racemosa Cambess.	zoo	*Eugenia mansoi* DC.	zoo
Cupania vernalis Cambess.	zoo	*Eugenia neomyrtifolia* Sobral	zoo
Cupania zanthoxyloides Radlk.	zoo	*Eugenia prasina* O.Berg	zoo
Cybianthus cuneifolius Mart.	zoo	*Eugenia punicifolia* (Kunth) DC.	zoo
Cybianthus detergens Müll. Arg.	zoo	*Eugenia pyriformis* Cambess.	zoo
Cybianthus peruvianus Vell.	zoo	*Eugenia sonderiana* O.Berg	zoo
Cybistax antisyphilitica (Mart.) Mart.	zoo	*Eugenia umbellata* (Kunth) DC.	zoo
Dahlstedtia muehlbergiana Hassl. M.J.Silva	aut	*Eugenia widgrenii* Sond. ex O.Berg	zoo
Dalbergia brasiliensis Vogel	anemo	*Eumachia cymuligera* (Müll. Arg.) C.M. Taylor	zoo

Dalbergia foliolosa Benth.	anemo	*Eupatorium ganophyllum* A.St.-Hil.	anemo
Dalbergia frutescens (Vell.) Britton	anemo	*Euplassa inaequalis* Mart.	zoo
Dalbergia miscolobium Vell.	anemo	*Euplassa legalis* Benth.	zoo
Dalbergia nigra (Vell.) Allemão ex Benth.	anemo	*Euplassa organensis* (Gardner) I.M.Johnst.	zoo
Dalbergia villosa Benth.	anemo	*Euplassa rufa* (Gardner) I.M.Johnst.	zoo
Daphnopsis brasiliensis Mart.	zoo	*Faramea hyacinthina* Mart.	zoo
Daphnopsis fasciculata Mart.	zoo	*Faramea latifolia* Mart.	zoo
Daphnopsis martii Mart.	zoo	*Faramea nigrescens* (Cham. & Schltdl.) DC.	zoo
Daphnopsis utilis Warm.	zoo	*Ficus adhatodifolia* Schott in Spreng.	zoo
Deguelia hatschbachii A.M.G.Azevedo	anemo	*Ficus arpazusa* Casar.	zoo
Dendropanax cuneatus (DC.) Decne. & Planch.	zoo	*Ficus enormis* Casar.	zoo
Dendrophorbium glaziovii (DC.)	anemo	*Ficus insipida* Willd.	zoo
Diatenopteryx sorbifolia Radlk.	anemo	*Ficus mexiae* Standl.	zoo
Diospyros hispida A.DC.	zoo	*Ficus obtusifolia* Kunth	zoo
Diospyros inconstans A.DC.	zoo	*Ficus pertusa* Standl.	zoo
Duguetia lanceolata A.St.-Hil.	zoo	*Galipea jasminiflora* (A.St.-Hil.) Engl.	aut
Duguetia salicifolia A.St.-Hil.	zoo	*Garcinia brasiliensis* Mart.	zoo
Geissanthus ambiguus (Mart.) G.Agostini	zoo	*Garcinia gardneriana* (Planch. & Triana) Zappi	zoo
Guapira graciliflora Mart.	zoo	*Kielmeyera lathrophyton* Saddi	anemo
Guapira hirsuta Mart.	zoo	*Lacistema hasslerianum* Kunth	zoo
Guapira opposita (Vell.) Reitz	zoo	*Lafoensia pacari* A.St.-Hil.	anemo
Guarea kunthiana Vell.	zoo	*Lamanonia ternata* Vell.	anemo
Guarea macrophylla Vahl	zoo	*Laplacea fruticosa* Mart.	anemo
Guatteria australis A.St.-Hil.	zoo	*Leandra melastomoides* Vell.	zoo
Guatteria pohliana Mart.	zoo	*Leptolobium dasycarpum* Vogel	anemo
Guatteria sellowiana A.St.-Hil.	zoo	*Leucochloron incuriale* (Vell.) Barneby	anemo
Guazuma ulmifolia Lam.	zoo	*Lithraea molleoides* (Vell.) Engl.	zoo
Guettarda uruguensis Cham. & Schltdl.	zoo	*Lonchocarpus cultratus* Vell.	anemo
Guettarda viburnoides Cham. & Schltdl.	zoo	*Luehea candicans* Mart. & Zucc.	anemo
Gymnanthes klotzschiana Müll.Arg.	zoo	*Luehea divaricata* Mart. & Zucc.	anemo

Gymnanthes schottiana Müll.Arg.	zoo	*Luehea grandiflora* Mart. & Zucc.	anemo
Handroanthus albus (Cham.) Mattos	anemo	*Machaerium acutifolium* Vogel	anemo
Handroanthus chrysotrichus (Mart. ex DC.)	anemo	*Machaerium amplum* Benth.	anemo
Handroanthus heptaphyllus (Vell.) Mattos	anemo	*Machaerium brasiliense* Vogel	anemo
Handroanthus ochraceus (Vell.) Mattos	anemo	*Machaerium debile* Benth.	anemo
Handroanthus serratifolius (Vahl) S.Grose	anemo	*Machaerium hirtum* Vogel	anemo
Handroanthus vellosoi (Mart. ex DC.)	anemo	*Machaerium isadelphum* Benth.	anemo
Heisteria silvianii Schwacke	zoo	*Machaerium lanceolatum* (Vell.) J.F.Macbr.	anemo
Helicteres brevispira A.St.-Hil.	aut	*Machaerium nyctitans* Vell.	anemo
Helicteres ovata A.St.-Hil.	aut	*Machaerium stipitatum* Benth.	anemo
Heterocondylus alatus (Vell.) R.M.King	anemo	*Machaerium villosum* Vogel	anemo
Heteropterys byrsonimifolia A.Juss.	zoo	*Machaonia acuminata* Bonpl.	aut
Hieronyma ferrugínea A.St.-Hil.	zoo	*Maclura tinctoria* (L.) D.Don ex Steud.	zoo
Hirtella glandulosa Spreng.	zoo	*Macropeplus dentatus* (Perkins) I.Santos	zoo
Hirtella hebeclada Spreng.	zoo	*Magnolia ovata* (A.St.-Hil.) Spreng.	zoo
Hyeronima alchorneoides Allemão	zoo	*Manihot grahamii* Hook.	zoo
Hymenaea courbaril L.	zoo	*Maprounea guianensis* Aubl.	aut
Ilex brevicuspis Reissek	zoo	*Marlierea gaudichaudiana* O.Berg	zoo
Ilex cerasifolia Reissek	zoo	*Marlierea obscura* O.Berg	zoo
Ilex conocarpa Reissek	zoo	*Matayba elaeagnoides* Radlk.	zoo
Ilex paraguariensis Reissek	zoo	*Matayba guianensis* Radlk.	zoo
Ilex sapotifolia Reissek	zoo	*Matayba juglandifolia* Radlk.	zoo
Ilex theezans Reissek	zoo	*Matayba marginata* Radlk.	zoo
Inga affinis DC.	zoo	*Matayba mollis* Radlk.	zoo
Inga cylindrica (Vell.) Mart.	zoo	*Maytenus glazioviana* Loes.	zoo
Inga ingoides Mart.	zoo	*Maytenus gonoclada* Mart.	zoo
Inga marginata Vell	zoo	*Maytenus salicifolia* Mart.	zoo
Inga sessilis (Vell.) Mart.	zoo	*Meliosma sellowii* Urb.	zoo
Inga striata DC.	zoo	*Meriania claussenii* (Naudin) Triana	zoo
Inga vera (Vell.) Mart.	zoo	*Metrodorea stipularis* Mart.	aut

Ixora brevifolia Benth.	zoo	*Miconia albicans* (Sw.) Triana	zoo
Ixora gardneriana Benth.	zoo	*Miconia argyrophylla* DC.	zoo
Ixora warmingii Benth.	zoo	*Miconia chartacea* Triana	zoo
Jacaranda macranta Cham.	anemo	*Miconia cinerascens* Triana	zoo
Jacaranda puberula Cham.	anemo	*Miconia cinnamomifolia* DC.	zoo
Jacaranda subalpina Cham.	anemo	*Miconia cubatanensis* Hoehne	zoo
Jacaratia spinosa (Aubl.) A.DC.	zoo	*Miconia eichleri* Triana	zoo
Miconia minutiflora (Bonpl.) DC.	zoo	*Miconia latecrenata* (DC.) Naudin	zoo
Miconia paulensis (Bonpl.) DC.	zoo	*Myroxylon balsamum* (L.) Harms	anemo
Miconia pepericarpa (Bonpl.) DC.	zoo	*Myroxylon peruiferum* L.f.	anemo
Miconia prasina (Sw.) DC.	zoo	*Myrsine coriácea* (Sw.) R.Br. ex Roem.	zoo
Miconia pusilliflora (DC.) Naudin	zoo	*Myrsine gardneriana* A.DC.	zoo
Miconia schwackei (Sw.) DC.	zoo	*Myrsine guianensis* (Aubl.) Kuntze	zoo
Miconia sellowiana Naudin	zoo	*Myrsine leuconeura* Mart.	zoo
Miconia theizans (Sw.) DC.	zoo	*Myrsine lineata* (Mez) Imkhan.	zoo
Miconia trianae Naudin	zoo	*Myrsine umbellata* (Mez) Imkhan.	zoo
Miconia tristis Spring	zoo	*Myrsine vilosíssima* Mart.	zoo
Miconia urophylla DC.	zoo	*Naucleopsis oblongifolia* (Kuhlm.) Carauta	zoo
Miconia willdenowii Spring	zoo	*Nectandra cissiflora* Nees	zoo
Mollinedia argyrogyna Perkins	zoo	*Nectandra grandiflora* Nees	zoo
Mollinedia clavigera Perkins	zoo	*Nectandra lanceolata* Nees	zoo
Mollinedia lanceolata Perkins	zoo	*Nectandra megapotamica* Nees	zoo
Mollinedia triflora (Spreng.) Tul.	zoo	*Nectandra membranácea* (Sw.) Griseb.	zoo
Mollinedia widgrenii (Spreng.) Tul.	zoo	*Nectandra nitidula* (Sw.) Griseb.	zoo
Monteverdia aquifolia (Mart.) Biral	zoo	*Nectandra oppositifolia* Nees	zoo
Monteverdia communis (Mart.) Biral	zoo	*Neocabreria pennivenia* (B.L.Rob.) R.M.King	anemo
Monteverdia evonymoides (Reissek) Biral	zoo	*Ocotea aciphylla* (Nees & Mart.) Mez	zoo
Monteverdia gonoclada (Mart.) Biral	zoo	*Ocotea bicolor* (Nees & Mart.) Mez	zoo
Monteverdia ilicifolia (Mart.) Biral	zoo	*Ocotea brachybotrya* (Meisn.) Mez	zoo
Moquiniastrum paniculatum (Less.) G. Sancho	anemo	*Ocotea corymbosa* (Meisn.) Mez	zoo

Moquiniastrum polymorphum (Less.) G. Sancho	anemo	*Ocotea diospyrifolia* (Meisn.) Mez	zoo
Mouriri glazioviana Cogn.	zoo	*Ocotea dispersa* (Nees & Mart.) Mez	zoo
Muellera campestres (Mart. ex Benth.) M.J.	aut	*Ocotea glaziovii* Mez	zoo
Myrceugenia bracteosa (DC.) D.Legrand	zoo	*Ocotea indecora* Mez	zoo
Myrceugenia miersiana (DC.) D.Legrand	zoo	*Ocotea laxa* Mez	zoo
Myrcia aethusa (O.Berg) Mattos	zoo	*Ocotea longifolia* Kunth	zoo
Myrcia amazonica DC.	zoo	*Ocotea odorifera* Kunth	zoo
Myrcia anacardiifolia (O.Berg) Mattos	zoo	*Ocotea puberula* (Rich.) Nees	zoo
Myrcia eriocalyx (O.Berg) Mattos	zoo	*Ocotea pulchella* Kunth	zoo
Myrcia eriopus DC.	zoo	*Ocotea silvestres* (Rich.) Nees	zoo
Myrcia guianensis (Aubl.) DC.	zoo	*Ocotea velloziana* (Meisn.) Mez	zoo
Myrcia hebepetala DC.	zoo	*Ocotea velutina* (Meisn.) Mez	zoo
Myrcia laruotteana DC.	zoo	*Oreopanax capitatus* (Jacq.) Decne. & Planch.	zoo
Myrcia multiflora DC.	zoo	*Ormosia arborea* (Vell.) Harms	zoo
Myrcia mutabilis (O.Berg) Mattos	zoo	*Ormosia fastigiata* (Vell.) Harms	zoo
Myrcia obovata (O.Berg) Nied.	zoo	*Ouratea salicifolia* (A.St.-Hil. & Tul.) Engl.	zoo
Myrcia pulchra (O.Berg) Nied.	zoo	*Ouratea semiserrata* Engl.	zoo
Myrcia racemosa (O.Berg) Kiaersk.	zoo	*Peltogyne angustiflora* Ducke	aut
Myrcia retorta Cambess.	zoo	*Peltophorum dubium* (Spreng.) Taub.	anemo
Myrcia retusa (O.Berg) Nied.	zoo	*Pera anisotricha* Müll. Arg.	zoo
Myrcia splendens (O.Berg) Nied.	zoo	*Pera glabrata* Müll. Arg.	zoo
Myrcia subcordata Cambess.	zoo	*Persea major* (Meisn.) L.E.Kopp	zoo
Myrcia tomentosa Cambess.	zoo	*Persea willdenovii* (Meisn.) L.E.Kopp	zoo
Myrcia vellozoi Mazine	zoo	*Picramnia ciliata* Mart.	zoo
Myrcia venulosa DC.	zoo	*Picramnia glazioviana* Engl.	zoo
Myrciaria floribunda (H.West ex Willd.)	zoo	*Picramnia parvifolia* Engl.	zoo
Myrciaria tenella (DC.) O.Berg	zoo	*Picrasma crenata* (Vell.) Engl.	zoo
Pimenta pseudocaryophyllus (Gomes) Landrum	zoo	*Pilocarpus spicatus* (Vell.) Engl.	aut
Piper aduncum (C.DC.) Yunck.	zoo	*Sacoglottis mattogrossensis* Malme	zoo
Piper arboreum L.	zoo	*Salacia elliptica* (Mart.) G. Don	zoo

Piper cernuum Vell.	zoo	*Salix humboldtiana* Willd.	anemo
Piper gaudichaudianum Vell.	zoo	*Sapium glandulosum* (L.) Morong	zoo
Piptadenia adiantoides (Spreng.) J.F.Macbr.	anemo	*Schefflera angustissima* (Marchal) Frodin	zoo
Piptadenia gonoacantha (Spreng.) J.F.Macbr.	anemo	*Schefflera calva* Marchal.	zoo
Piptocarpha axillaris (Less.) Baker	anemo	*Schinus lentiscifolia* Marchand	zoo
Piptocarpha macropoda (Less.) Baker	anemo	*Schinus terebinthifolia* Marchand	zoo
Pisonia zapallo Griseb.	zoo	*Schizolobium parahyba* (Vell.) Blake	aut
Platycyamus regnellii Benth.	anemo	*Schoepfia brasiliensis* A.DC.	zoo
Platypodium elegans Vogel	anemo	*Sebastiania brasiliensis* Spreng.	aut
Plenckia populnea Reissek	anemo	*Sebastiania commersoniana* Mull. Arg	aut
Pleroma candolleanum (Mart. ex DC.)	aut	*Seguieria langsdorffii* Moq.	anemo
Pleroma stenocarpum (Mart. ex DC.)	aut	*Senecio glaziovii* A.DC.	anemo
Plinia cauliflora (Mart.) Kausel	zoo	*Senegalia langsdorffii* (Benth.) Seigler & Ebinger	aut
Plinia grandifolia (Mart.) Kausel	zoo	*Senegalia polyphylla* Benth.	aut
Podocarpus sellowii Mart.	zoo	*Senegalia recurva* Benth.	aut
Pourouma guianensis Aubl.	zoo	*Senna macranthera* (DC. ex Collad.) H.S.Irwin	zoo
Pouteria gardneriana (A.DC.) Radlk.	zoo	*Senna multijuga* (Rich.) H.S.Irwin & Barneby	zoo
Prockia crucis P.Browne ex L.	zoo	*Senna velutina* (Rich.) H.S.Irwin & Barneby	zoo
Protium heptaphyllum (Aubl.) Marchand	zoo	*Sorocea bonplandii* (Baill.) W.C.Burger et al.	zoo
Protium spruceanum (Aubl.) Marchand	zoo	*Strychnos brasiliensis* Mart.	zoo
Protium widgrenii Aubl.	zoo	*Strychnos gardneri* Mart.	zoo
Prunus myrtifolia (L.) Urb.	zoo	*Stryphnodendron polyphyllum* Mart.	zoo
Pseudobombax grandiflorum (Cav.) A.Robyns	anemo	*Styrax acuminatus* (Seub.) Perkins	zoo
Pseudopiptadenia leptostachya Benth.	anemo	*Styrax camporum* Pohl	zoo
Psidium cattleianum Sabine	zoo	*Styrax ferrugineus* Pohl	zoo
Psidium cupreum DC.	zoo	*Styrax latifolius* Pohl	zoo
Psidium guineense Sw.	zoo	*Styrax pohlii* Pohl	zoo
Psidium rufum Mart. ex DC.	zoo	*Symplocos celastrinea* Mart.	zoo
Psychotria carthagenensis Jacq.	zoo	*Symplocos insignis* Mart.	zoo
Psychotria deflexa Jacq.	zoo	*Symplocos oblongifolia* Casar.	zoo

Psychotria suterella Müll.Arg.	zoo	*Symplocos pubescens* Klotzsch ex Benth.	zoo
Psychotria vellosiana Müll.Arg.	zoo	*Syzygium jambos* (L.) Alston	zoo
Qualea cordata Spreng.	zoo	*Tabernaemontana hystrix* Steud.	zoo
Qualea cryptantha Spreng.	zoo	*Tachigali rugosa* Müll.Arg.	anemo
Qualea grandiflora Spreng.	zoo	*Tapirira guianensis* Aubl.	zoo
Qualea multiflora Mart.	zoo	*Tapirira obtusa* Aubl.	zoo
Randia armata (Sw.) DC.	zoo	*Terminalia glabrescens* Mart.	anemo
Randia ferox (Cham. & Schltdl.) DC.	zoo	*Ternstroemia brasiliensis* Cambess.	zoo
Rhamnidium elaeocarpum Reissek	zoo	*Tibouchina sellowiana* Cogn.	anemo
Rhamnus sphaerosperma Sw.	zoo	*Toulicia subsquamulata* Radlk.	anemo
Rollinia neolaurifolia Reissek	zoo	*Tovomitopsis paniculata* (Spreng.) Planch.	zoo
Roupala longepetiolata Pohl	anemo	*Tovomitopsis saldanhae* Spreng.	zoo
Roupala montana Pohl	anemo	*Trattinnickia ferrugínea* Kuhlm.	zoo
Rudgea jasminoides (Cham.) Müll.Arg.	zoo	*Trema micranta* (L.) Blume	zoo
Rudgea triflora Müll.Arg.	zoo	*Trembleya parviflora* (D.Don) Cogn.	aut
Rudgea viburnoides Müll.Arg.	zoo	*Trichilia casaretti* C.DC.	zoo
Ruprechtia laxiflora Meisn.	anemo	*Trichilia catiguá* C.DC.	zoo
Simira pikia (K.Schum.) Steyerm.	anemo	*Trichilia pallens* Sw.	zoo
Siparuna brasiliensis (Spreng.) A.DC.	zoo	*Trichilia pallida* Sw.	zoo
Siparuna guianensis (Spreng.) A.DC.	zoo	*Urbanodendron verrucosum* (Nees) Mez	zoo
Siphoneugena crassifólia Proença & Sobral	zoo	*Urera bacífera (*L.) Gaudich. ex Wedd.	zoo
Siphoneugena densiflora O.Berg	zoo	*Vantanea compacta* (Schnizl.) Cuatrec.	zoo
Siphoneugena kiaerskoviana (Burret) Kausel	zoo	*Vernonanthura discolor* (Spreng.) H.Rob.	anemo
Siphoneugena kuhlmannii Mattos	zoo	*Vernonanthura divaricata* Spreng.	anemo
Siphoneugena reitzii D.Legrand	zoo	*Vernonanthura polyanthes* (Sprengel) Vega	anemo
Sloanea guianensis (Aubl.) Benth.	zoo	*Virola bicuhyba* (Schott ex Spreng.) Warb.	zoo
Sloanea hirsuta Aubl.	zoo	*Vismia brasiliensis* Choisy	zoo
Solanum cernuum Vell.	zoo	*Vismia guianensis* (Aubl.) Choisy	zoo
Solanum granuloso-leprosum Vell.	zoo	*Vitex agnus-castus* L.	zoo
Solanum leucodendron Vell.	zoo	*Vitex cymosa* Bertero ex Spreng.	zoo

Solanum pseudoquina A.St.-Hil.	zoo	*Vitex megapotamica* (Spreng.) Moldenke	zoo
Solanum swartzianum Roem. & Schult.	zoo	*Vitex polygama* Cham.	zoo
Vochysia magnifica Warm.	Anemo	*Xylosma prockia* (Turcz.) Turcz.	zoo
Vochysia oppugnata (Vell.) Warm.	Anemo	*Zanthoxylum fagara* (L.) Sarg.	zoo
Vochysia schwackeana Vell.	Anemo	*Zanthoxylum monogynum* A.St.-Hil.	zoo
Vochysia tucanorum Vell.	Anemo	*Zanthoxylum rhoifolium* Lam.	zoo
Xylopia aromática (Lam.) Mart.	Zoo	*Zanthoxylum riedelianum* Engl.	zoo
Xylopia brasiliensis Spreng.	Zoo	*Zeyheria tuberculosa* (Vell.) Bureau ex Verl.	anemo
Xylosma ciliatifolia (Clos) Eichler	Zoo		

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