ALEX JOSÉLIO PIRES COELHO

IMPACTOS ANTRÓPICOS NA CONSERVAÇÃO DO CERRADO E NA RESTAURAÇÃO DE BIODIVERSIDADE E CARBONO DA MATA ATLÂNTICA

Tese apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Botânica, para obtenção do título de *Doctor Scientiae*.

Orientador: João Augusto Alves Meira Neto

Coorientadores: Fabio Antônio Ribeiro Matos
Gustavo Heringer

VIÇOSA - MINAS GERAIS
2021

Ficha catalográfica elaborada pela Biblioteca Central da Universidade Federal de Viçosa - Campus Viçosa

T

C672i
2021

Coelho, Alex Josélio Pires, 1992-
Impactos antrópicos na conservação do cerrado e na restauração de biodiversidade e carbono da Mata Atlântica / Alex Josélio Pires Coelho. - Viçosa, MG, 2021.
1 tese eletrônica (144 f.): il. (algumas color.).

Texto em inglês.
Orientador: João Augusto Alves Meira Neto.
Tese (doutorado) - Universidade Federal de Viçosa.
Inclui bibliografia.
DOI: https://doi.org/10.47328/ufvbbt.2021.141
Modo de acesso: World Wide Web.

1. Florestas - Conservação. 2. Biodiversidade. 3. Créditos de carbono. 4. Solo - Uso . I. Universidade Federal de Viçosa. Departamento de Biologia Vegetal. Programa de Pós-Graduação em Botânica. II. Título.

CDD 22. ed. 634.956

ALEX JOSÉLIO PIRES COELHO

IMPACTOS ANTRÓPICOS NA CONSERVAÇÃO DO CERRADO E NA RESTAURAÇÃO DE BIODIVERSIDADE E CARBONO DA MATA ATLÂNTICA

Tese apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Botânica, para obtenção do título de *Doctor Scientiae*.

APROVADA: 17 de setembro de 2021.

Assentimento:

Alex J Coelho

Alex Josélio Pires Coelho
Autor

João Augusto Alves Meira Neto
Orientador

Dedico,

Aos meus pais, Daniel e Matildes, que me deram incondicional apoio em todas as etapas dos meus estudos.

AGRADECIMENTOS

Agradeço primeiramente aos meus pais, Daniel e Matildes, pela educação que me proporcionaram e por estarem sempre presentes dando carinho, amor e atenção. Além da vida, me deram meus maiores presentes, meu irmão Alexandre e minha irmã Aline, que vieram para aumentar nossa parceria e felicidade. Aos meus irmãos, meu muito obrigado pelo apoio diário e pela busca conjunta da realização de nossos sonhos.

Agradeço aos professores que passaram pela minha vida acadêmica, desde a Escola Estadual Barão do Rio Branco, onde concluí o ensino fundamental e o ensino médio, até o doutorado na Universidade Federal de Viçosa, onde também concluí minha graduação e mestrado. Durante todos esses anos de dedicação à minha formação foram vários os professores que me inspiraram e incentivaram minha busca pelo conhecimento. Por eles, almejo ser também um professor e contribuir para difusão do conhecimento em nosso país.

Agradeço a todos os amigos que dividiram a sala de aula, a vida universitária, ou a república, pelos bons momentos e pelas lutas que juntos vencemos. Os amigos são meu porto seguro, e foram importantes para a persistência na vida acadêmica, principalmente nos dias mais pesados e difíceis, aqueles em que sentimos vontade de desistir. Por sorte, eles são muitos, porém alguns foram essenciais neste período de doutorado: Nayara Mota, Fernando Lacerda, Flávia Ferrari, Daniela Schmitz, Josélia França, Isabella Cavallin, Herval Pinto, Larissa Miller, Alice Rodrigues, Wendelo Costa, Neil Oliveira, e outros colegas de laboratório. Não posso deixar de citar também, meu companheiro de vida, Bruno, que foi extremamente importante e presente nos últimos dois anos deste doutorado.

Meus agradecimentos a todas as pessoas que de alguma forma contribuíram para a conclusão desta tese. Ao professor João Meira por aceitar meu pedido de orientação e por me proporcionar ótimas condições de trabalho. Aos meus coorientadores Fabio Matos e Gustavo Heringer, pela atenção dispensada principalmente nas fases finais do trabalho, com muitas reuniões e ligações para aumentar a qualidade dos resultados e a aplicação destes na ciência. Ao Pedro Manuel Villa pelo apoio em todos os passos deste trabalho, desde o projeto até as versões finais dos artigos, contribuindo também como um coorientador. Ao Marcelo Leandro Bueno, Nayara Mesquita Mota, Fernando da Costa Brito Lacerda, Luiz Fernando Silva Magnago, Josiele Evaristo

Costa, Luca Aquino Costa, Victor Pinto, Flavia Ferrari, Alice Rodrigues, Nathália Silva, e Helder Nunes pelo apoio e participação nos trabalhos de campo. Ao técnico administrativo, Celso Antônio, por toda competência e dedicação na organização dos materiais de campo.

Meus agradecimentos também as instituições que possibilitaram este trabalho através de disponibilização de materiais, espaço físico, e financiamento de pesquisa: Departamento de Biologia Vegetal da Universidade Federal de Viçosa e Laboratório de Ecologia e Evolução de Plantas, Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG), Conselho Nacional de Desenvolvimento Científico e Tecnológico, e ArcelorMittal Bioflorestas Ltda.

Por fim, agradeço a Deus pela oportunidade de viver esta experiência e por poder gerar conhecimento sobre a conservação e restauração de biodiversidade no Brasil, importante para a manutenção de serviços ecossistêmicos e mitigação de mudanças climáticas.

Seria mais fácil fazer como todo mundo faz

O caminho mais curto, produto que rende mais

[...]

Mas nós vibramos em outra frequência

Sabemos que não é bem assim

.

Outras Frequências, Engenheiros do Hawaii.

RESUMO

COELHO, Alex Josélio Pires, D.Sc., Universidade Federal de Viçosa, setembro de 2021. **Impactos antrópicos na conservação do Cerrado e na restauração de biodiversidade e carbono da Mata Atlântica**. Orientador: João Augusto Alves Meira Neto. Coorientadores: Fabio Antônio Ribeiro Matos e Gustavo Heringer.

Intervenções antrópicas são consideradas como as principais ameaças à conservação de biodiversidade e de serviços ecossistêmicos prestados pelos biomas naturais. A utilização e conversão do habitat natural para sobrevivência humana causa alterações ambientais desde a escala local até a escala de paisagem. Estas alterações são responsáveis pela diminuição e o isolamento de populações de plantas, pela extinção e substituição de espécies nas comunidades remanescentes, e por alterações de funções ecossistêmicas, dentre elas o estoque de carbono, importante para a mitigação de mudanças climáticas. Entretanto, o impacto das intervenções antrópicas na conservação de biodiversidade e na restauração da Mata Atlântica, dois *hotspots* brasileiros para conservação da biodiversidade no mundo, permanecem pouco estudados. Diante disso, esta tese tem cinco objetivos principais, distribuídos em cinco capítulos: (i) avaliar se a extração de minhocoçu (*Rhinodrillus alatus* Righi) no Cerrado afeta a características do solo e a composição de espécies de plantas; (ii) entender como diversos distúrbios antropogênicos afeta a diversidade e composição funcional de plantas no cerrado; (iii) verificar se a mata atlântica recupera sua biodiversidade e estoque de carbono em áreas anteriormente ocupadas para plantio de eucalipto; (iv) avaliar qual a influência de diversos fatores na recuperação de diversidade e carbono da Mata Atlântica; e (v) entender como diversos fatores atuam na montagem de comunidades em florestas de crescimento secundário da mata atlântica. Para isso foram amostrados 12 fragmentos de Cerrado *stricto sensu* com diversos níveis de distúrbios e inseridos em diferentes paisagens e 42 áreas em regeneração natural após o último corte de eucalipto em uma região de Mata Atlântica. No primeiro capítulo encontramos alterações nas características químicas do solo e de composição de espécies de plantas em decorrer da extração de minhocoçu, que causa reviramento no solo. No segundo capítulo, vimos que a extração de minhocoçu e outros distúrbio antrópicos em escala local ou de paisagem diminuem a equitabilidade funcional e alteram a composição funcional de plantas no Cerrado. No terceiro capítulo mostramos que a mata atlântica recupera biodiversidade e carbono naturalmente após o uso da terra para plantio de eucalipto, que existe cobenefícios entre conservação de carbono e biodiversidade e que espécies tolerantes à sombra e dispersadas por animais são as mais importantes no estoque de carbono em florestas de crescimento secundário. No quarto capítulo encontramos que a intensidade de manejo e isolamento diminuem biodiversidade e carbono de florestas de crescimento secundário. Finalmente, no quinto capítulo mostramos que a as características da paisagem são principais responsáveis pela montagem de comunidades de plantas em áreas em regeneração da Mata Atlântica. Dessa forma, oferecemos conhecimento teóricos sobre impactos antrópicos na conservação do cerrado e na restauração da Mata Atlântica, que podem servir como base para inciativas que visem minimizar estes impactos e aumentar a eficiência na conservação e restauração destes biomas.

Palavras-chave: Restauração florestal. Biodiversidade. Estoque de carbono. Uso da terra.

ABSTRACT

COELHO, Alex Josélio Pires, D.Sc., Universidade Federal de Viçosa, September, 2021. **Anthropogenic impacts on Cerrado conservation and biodiversity and carbon restoration of Atlantic Forest**. Adviser: João Augusto Alves Meira Neto. Co-advisers: Fabio Antônio Ribeiro Matos and Gustavo Heringer.

Anthropogenic interventions are considered as the main threats to biodiversity conservation and ecosystem services provided by natural biomes. The land-use and conversion of these biomes for human survival causes environmental changes from the local scale to the landscape scale. These changes are responsible for the reduction and isolation of plant populations, the extinction and substitution of species in the remaining communities, and for changes in ecosystem functions, including carbon stock, which is important for mitigating climate change. However, anthropogenic impacts on biodiversity conservation of Cerrado and Atlantic Forest restoration, two Brazilian hotspots for biodiversity conservation in the world, remains poorly studied. Therefore, this thesis has five main objectives, distributed in five chapters: (i) to evaluate whether giant earthworm extraction in the Cerrado affects soil characteristics and plant species composition; (ii) to understand how chronic anthropogenic disturbances affect the diversity and functional composition of plants in the Cerrado; (iii) to verify if the Atlantic forest recovers its biodiversity and carbon stock in areas previously occupied for eucalyptus plantation; (iv) to evaluate the influence of several factors on the recovery of diversity and carbon of the Atlantic Forest; and (v) to understand how several factors act in the assembly of communities in forests of secondary growth of the Atlantic forest. For this, 12 fragments of Cerrado *stricto sensu* with different levels of disturbances and inserted in different landscapes and 42 areas in natural regeneration after the last eucalyptus cut in an Atlantic Forest region were sampled. In the first capture we found changes in soil chemical characteristics and plant species compositions because giant earthworm extraction, which causes revolving in the soil. In the second capture, we saw that the giant earthworm extraction and other chronic anthropogenic disturbances on a local or landscape scale decrease functional evenness and alter the functional composition of plants in the Cerrado. In the third capture we showed that the Atlantic Forest recovers biodiversity and carbon naturally after long-term eucalyptus plantation, that there are co-benefits between carbon conservation and biodiversity, and that shade-tolerant species and dispersed by animals are the most important in second-growth forest carbon stock. In the fourth capture we found that the management intensity and isolation decrease the second-growth biodiversity and carbon. Finally, in the fifth capture we showed that patch and landscape configuration are main responsible for the assembly of plant communities in areas in regeneration of the Atlantic Forest. Thus, we offer theoretical knowledge about anthropic impacts on the conservation of the Cerrado and in the restoration of the Atlantic Forest, which can serve as a basis for initiatives aimed at minimizing these impacts and increasing the efficiency in the conservation and restoration of these biomes.

Keywords: Forest restoration. Biodiversity. Carbon stock. Land-use.

SUMÁRIO

INTRODUÇÃO GERAL

O uso da terra causa diversos tipos de distúrbios em seus ecossistemas além de provocar a fragmentação de habitats naturais (MELO et al., 2013; NAZARENO et al., 2012; RATTER; RIBEIRO; S., 1997). Além da exploração de recursos madeireiros e não madeireiros nos remanescentes naturais, esses biomas são diariamente convertidos em áreas de pastagens, agricultura, florestas plantadas, e áreas de mineração que intensificam a fragmentação dos habitats e os distúrbios sofridos por estes ecossistemas (GIROLDO; SCARIOT, 2015; LAURANCE et al., 2011; RIBEIRO et al., 2016; SCHMIDT; TICKTIN, 2012). Essas intervenções humanas influenciam diretamente e indiretamente a biodiversidade e o funcionamento destes ecossistemas, importantes para a manutenção de serviços ambientais (ARROYO-RODRÍGUEZ et al., 2016; FAHRIG, 2003; MAGNAGO et al., 2014; RIBEIRO et al., 2016; TSCHARNTKE et al., 2012). Além disso, no contexto de mudanças climáticas, existe uma demanda mundial pelo aumento de áreas cobertas por vegetação nativa, visando aumento no sequestro de carbono e recuperação de biodiversidade (URIARTE; CHAZDON, 2016). Entretanto, áreas disponíveis para restauração passaram por distúrbios prévios, e estão inseridos em paisagens altamente modificadas, o que também compromete o sequestro de carbono e a recuperação da biodiversidade (ARROYO-RODRÍGUEZ et al., 2017).

O Cerrado e a Mata Atlântica, são dois *hotspots* brasileiros para conservação da biodiversidade altamente ameaçados por atividades antrópicas (MYERS et al., 2000). A influência antrópica no Cerrado é mais recente, após políticas de colonização do interior do Brasil, como a transferência da capital para Brasília (AB'SÁBER, 2003; BEUCHLE et al., 2015; MACHADO et al., 2004; RATTER; RIBEIRO; S., 1997). Entretanto, este bioma vem perdendo sua cobertura original em uma taxa muito rápida: entre 1990 e 2010 a cobertura vegetal nas áreas de Cerrado reduziu em média 0,6% ao ano, totalizando 265.595 Km² de área perdida para ocupação humana (BEUCHLE et al., 2015). Já a Mata Atlântica, apresenta um histórico de degradação mais antigo, desde a colonização do país, no século XVI, até o presente (NAZARENO et al., 2012; TABARELLI et al., 2010). A intensidade de exploração resultou na redução drástica de sua cobertura florestal com apenas 12,5% dos remanescentes florestais considerando áreas com mais de 3 hectares, ou 8,5% dos fragmentos nativos quando consideradas apenas áreas maiores que 100 hectares (Fundação SOS Mata Atlântica, 2014). Devido à alta influencia antrópica nestes biomas, é necessário acúmulo de estudos que auxiliem a tomada de decisões eficientes na conservação destes biomas. Além disso, pela alta taxa de perda de cobertura vegetal, estes biomas apresentam alta demanda de restauração, principalmente a Mata Atlântica, sendo necessário entender como distúrbios e modificações na paisagem influenciam a restauração deste bioma.

Os distúrbios alteram inicialmente condições ambientas em escala local podendo eliminar populações de plantas e animais sensíveis à estas variações (CARRARA et al., 2015; RIBEIRO-NETO et al., 2016; ROCHA-SANTOS et al., 2016; SOLAR et al., 2016). Um dos distúrbios frequentes no Cerrado é a extração de minhocoçu (*Rhinodrillus alatus* Righi) para venda a pescadores nas rodovias com destino ao pantanal. A atividade dos extratores causa revolvimento do solo e aplicação de fogo no local de coleta, o que pode afetar as características do solo e a conservação de biodiversidade deste bioma (DRUMOND et al., 2013). Por isso, no capítulo 1, investigamos o efeito destas atividades nas características do solo e na composição de espécies de plantas do cerrado.

As influências antrópicas também alteram a configuração e composição da paisagem, diminuindo o habitat natural e provocando o isolamento entre fragmentos de um mesmo bioma (EWERS; DIDHAM, 2006; FAHRIG, 2003; LAURANCE et al., 2011; MAGNAGO et al., 2014, 2016; MELO et al., 2010). As alterações em escala local e de paisagem afetam a biodiversidade selecionando espécies capazes de sobreviver às novas condições ambientais (GÁMEZ-VIRUÉS et al., 2015). Dessa forma, distúrbios antropogênicos crônicos podem causar perda de diversidade funcional no Cerrado, selecionando traços funcionais que conferem adaptabilidade as novas características ambientais, o que pode causar também perda de serviços ecossistêmicos. Assim, no capítulo 2, avaliamos o efeito de distúrbios antrópicos na diversidade e composição funcional. Os efeitos foram divididos em escala local como a extração de minhocoçu, extração de pequi (*Caryocar brasiliense* Camb.), queimadas, circulação de gado, e tamanho do fragmento, e em escala de paisagem como densidade de fragmentos, conectividade, perda de habitat, cobertura de silvicultura, e cobertura de terras em uso para pastagem ou agricultura na paisagem na diversidade e composição funcional de plantas do Cerrado.

As áreas disponíveis para restauração também passam por distúrbio prévios, o que pode diminuir a capacidade de recuperação natural dos biomas (JAKOVAC et al., 2015; VILLA et al., 2018). Na Mata Atlântica, por exemplo, um dos principais uso da terra é para o plantio de eucalipto (*Eucalyptus* sp.), sendo parte das áreas disponíveis para restauração anteriormente utilizadas para essa atividade (BRANCALION et al., 2019; GONÇALVEZ et al., 2013). Sendo a restauração passiva (regeneração natural) a de melhor custo-benefício (URIARTE; CHAZDON, 2016), é importante avaliar se a Mata Atlântica recupera naturalmente sua diversidade e estoque de carbono em áreas anteriormente utilizadas para o plantio de eucalipto. Assim, no capítulo 3, avaliamos a recuperação de espécies de plantas e estoque de carbono com passar do tempo em áreas da Mata Atlântica anteriormente usadas para plantio de eucalipto. Para isso, comparamos a riqueza de espécies e de estoque de carbono de florestas de crescimento secundário amostradas com os índices de florestas de crescimento antigo da mesma região. Além disso, analisamos se existe cobeneficios entre o estoque de carbono e a biodiversidade nessas florestas de crescimento secundário.

A recuperação das florestas secundárias em paisagens antropizadas é dependente de múltiplos fatores (bióticos e abióticos) como, fertilidade do solo, intensidade de manejo, montante de florestas na paisagem, isolamento entre florestas remanescentes, e contraste entre a matriz e o fragmento em sucessão secundária (ARROYO-RODRÍGUEZ et al., 2017; EWERS; DIDHAM, 2006; SLOAN; GOOSEM; LAURANCE, 2015). A sucessão destas florestas é altamente dependente da fertilidade e do banco de sementes disponível no solo após o uso da terra (GUARIGUATA; OSTERTAG, 2001). Com maior intensidade, frequência e duração do manejo, o solo de áreas em regeneração tendem a ter menor fertilidade e diversidade de sementes (JAKOVAC et al., 2015; VILLA et al., 2018). Além disso, fatores de composição e configuração da paisagem podem limitar processos de dispersão e polinização, necessários para a recuperação florestal de áreas em regeneração (MATOS et al., 2020; PÉREZ-CÁRDENAS et al., 2021). A influência de múltiplos fatores é importante para escolha de áreas mais eficientes e com melhor custo-benefício para restauração na Mata Atlântica. Dessa forma, no capítulo 4, investigamos como estes múltiplos fatores, desde a escala local até a escala de paisagem, afetam a diversidades o estoque de carbono de florestas secundárias. Enquanto no capítulo 5, avaliamos a influência destes fatores na montagem de comunidades de florestas de crescimento secundário por meio da seleção de traços funcionais, possibilitando estratégias de intervenção na regeneração natural da Mata Atlântica que visem aumentar a eficiência na recuperação de biodiversidade.

Referências

AB’SÁBER, A. **Os Domínios de Natureza no Brasil: Potencialidades Paisagísticas**, 2003.

ARROYO-RODRÍGUEZ, V. et al. Landscape composition is more important than landscape configuration for phyllostomid bat assemblages in a fragmented biodiversity hotspot. **Biological Conservation**, v. 198, n. May, p. 84–92, 2016.

ARROYO-RODRÍGUEZ, V. et al. Multiple successional pathways in human-modified tropical landscapes: new insights from forest succession, forest fragmentation and landscape ecology research. **Biological Reviews**, v. 92, n. 1, p. 326–340, 2017.

BEUCHLE, R. et al. Land cover changes in the Brazilian Cerrado and Caatinga biomes from 1990 to 2010 based on a systematic remote sensing sampling approach. **Applied Geography**, v. 58, p. 116–127, 2015.

BRANCALION, P. H. S. et al. Intensive silviculture enhances biomass accumulation and tree diversity recovery in tropical forest restoration. **Ecological Applications**, v. 29, n. 2, p. 1–12, 2019.

CARRARA, E. et al. Impact of landscape composition and configuration on forest specialist and generalist bird species in the fragmented Lacandona rainforest, Mexico. **Biological Conservation**, v. 184, p. 117–126, 2015.

CHAZDON, R. L. et al. Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics. n. ii, 2016.

DRUMOND, M. A. et al. História de vida, distribuição e abundância do minhocuçu Rhinodrilus alatus RIGHI 1971: Implicações para sua conservação e manejo. **Brazilian Journal of Biology**, v. 73, n. 4, p. 699–708, 2013.

EWERS, R.; DIDHAM, R. Confounding factors in the detection of species responses to habitat fragmentation. **Biological Reviews of the Cambridge Philosophical Society**, v. 81, n. 1, p. 117–142, 2006.

FAHRIG, L. Effects of Habitat Fragmentation on Biodiversity. **Annual Review of Ecological and Environmental Systems**, v. 34, n. May, p. 487–515, 2003.

GÁMEZ-VIRUÉS, S. et al. Landscape simplification filters species traits and drives biotic homogenization. **Nature Communications**, v. 6, p. 8568, 2015.

GIROLDO, A. B.; SCARIOT, A. Land use and management affects the demography and conservation of an intensively harvested Cerrado fruit tree species. **Biological Conservation**, v. 191, p. 150–158, 2015.

GONÇALVEZ, J. L. DE M. et al. Forest Ecology and Management Integrating genetic and silvicultural strategies to minimize abiotic and biotic constraints in Brazilian eucalypt plantations. **Forest Ecology and Management**, v. 301, p. 6–27, 2013.

GUARIGUATA, M. R.; OSTERTAG, R. Neotropical secondary forest succession : changes in structural and functional characteristics. **Forest Ecology and Management**, v. 148, p. 185–206, 2001.

JAKOVAC, C. C. et al. Loss of secondary-forest resilience by land-use intensification in the Amazon. **Journal of Ecology**, v. 103, n. 1, p. 67–77, 2015.

LAURANCE, W. F. et al. The fate of Amazonian forest fragments: A 32-year investigation. **Biological Conservation**, v. 144, n. 1, p. 56–67, 2011.

MACHADO, R. B. et al. Análise de lacunas de proteção da biodiversidade no Cerrado. **Anais do IV Congresso Brasileiro de Unidades de Conservação. Volumen II**, 2004.

MAGNAGO, L. F. S. et al. Functional attributes change but functional richness is unchanged after fragmentation of Brazilian Atlantic forests. **Journal of Ecology**, v. 102, n. 2, p. 475–485, 2014.

MAGNAGO, L. F. S. et al. Do fragment size and edge effects predict carbon stocks in trees and lianas in tropical forests? **Functional Ecology**, 2016.

MATOS, F. A. R. et al. Secondary forest fragments offer important carbon and biodiversity cobenefits. **Global Change Biology**, v. 26, n. 2, p. 509–522, 2020.

MELO, F. P. L. et al. Forest fragmentation reduces recruitment of large-seeded tree species in a semi-deciduous tropical forest of southern Mexico. **Journal of Tropical Ecology**, v. 26, n. 01, p. 35, 2010.

MELO, F. P. L. et al. On the hope for biodiversity-friendly tropical landscapes. **Trends in Ecology**

and Evolution, v. 28, n. 8, p. 461–468, 2013.

MYERS, N. et al. Biodiversity hotspots for conservation priorities. **Nature**, v. 403, n. February, p. 853–858, 2000.

NAZARENO, A. G. et al. Serious New Threat to Brazilian Forests. **Conservation Biology**, v. 26, n. 1, p. 5–6, 2012.

PÉREZ-CÁRDENAS, N. et al. Effects of landscape composition and site land-use intensity on secondary succession in a tropical dry forest. **Forest Ecology and Management**, v. 482, p. 118818, 2021.

RATTER, J. A.; RIBEIRO, J. F.; S., B. The Brazilian Cerrado Vegetation and Threats to its Biodiversity. **Annals of Botany**, v. 80, p. 223–230, 1997.

RIBEIRO-NETO, J. D. et al. Chronic anthropogenic disturbance causes homogenization of plant and ant communities in the Brazilian Caatinga. **Biodiversity and Conservation**, v. 25, n. 5, p. 943–956, 2016.

RIBEIRO, E. M. S. et al. Phylogenetic impoverishment of plant communities following chronic human disturbances in the Brazilian Caatinga. **Ecology**, v. 97, n. 6, p. 1583–1592, 2016.

ROCHA-SANTOS, L. et al. The shrinkage of a forest: Landscape-scale deforestation leading to overall changes in local forest structure. **Biological Conservation**, v. 196, p. 1–9, 2016.

SCHMIDT, I. B.; TICKTIN, T. When lessons from population models and local ecological knowledge coincide - Effects of flower stalk harvesting in the Brazilian savanna. **Biological Conservation**, v. 152, n. November, p. 187–195, 2012.

SLOAN, S.; GOOSEM, M.; LAURANCE, S. G. Tropical forest regeneration following land abandonment is driven by primary rainforest distribution in an old pastoral region. **Landscape Ecology**, 2015.

SOLAR, R. R. DE C. et al. Biodiversity consequences of land-use change and forest disturbance in the Amazon: A multi-scale assessment using ant communities. **Biological Conservation**, v. 197,

p. 98–107, 2016.

TABARELLI, M. et al. Effects of pioneer tree species hyperabundance on forest fragments in Northeastern Brazil. **Conservation Biology**, v. 24, n. 6, p. 1654–1663, 2010.

TSCHARNTKE, T. et al. Global food security, biodiversity conservation and the future of agricultural intensification. **Biological Conservation**, v. 151, n. 1, p. 53–59, 2012.

URIARTE, M.; CHAZDON, R. L. Incorporating natural regeneration in forest landscape restoration in tropical regions: synthesis and key research gaps. **Biotropica**, v. 48, n. 6, p. 915–924, 2016.

VILLA, P. M. et al. Intensification of shifting cultivation reduces forest resilience in the northern Amazon. **Forest Ecology and Management**, v. 430, n. August, p. 312–320, 2018.

VILLA, P. M. et al. Policy forum: Shifting cultivation and agroforestry in the Amazon: Premises for REDD+. **Forest Policy and Economics**, v. 118, n. September 2019, 2020.

CHAPTER 1: The extraction of the giant earthworm alters the soil chemical characteristics and tree composition in the Cerrado

Abstract: Anthropic disturbances are one of the main causes of loss of biodiversity and alteration in natural ecosystems. By resources exploitation humans alter the environmental conditions of a given location and make it inhospitable for some species. The giant earthworm (*Rhinodrilus alatus*, Righi) extraction in the Cerrado biome for sale to fishermen generates the revolving of the soil in addition to burning caused by extractors to facilitate the location of these animals. Thus, to evaluate the impacts of this activity on soil characteristics and composition of the Cerrado woody plant species is important to the conservation of this biome. For this we used 12 areas of Cerrado *stricto sensu* with different intensities of giant earthworm extraction and sampled the soil, tree plants, and the intensity of fire in a plot of 20 x 50 m. Our results showed that in the areas with higher intensity of giant earthworm extraction there is a change in soil chemical composition, mainly due to the increase in aluminum (Al3+) and phosphorus concentrations as well as the increasing in cation exchange capacities (CEC). In addition, the intensity of giant earthworm extraction also influenced the woody species composition, probably due to the influence of Al3+ and CEC on the species composition showed by this work. The intensity of fire was not changed by the extraction of giant earthworm. Thus, we suggest that soil revolving by earthworm extractors generates soil chemical changes that alters the composition of species of the Cerrado *stricto sensu*.

Keywords: Giant earthworm extraction, anthropogenic disturbances, Cerrado stricto sensu, soil disturbances, Cerrado plants.

Introduction

Nowadays, with the increasing human population and therefore the demand for raw materials and food, many natural biomes face an increase in the exploitation of their resources (Williams et al. 2015). These activities may alter the natural conditions of the ecosystem and cause the loss of some specialist species (Gámez-Virués et al. 2015; Ribeiro et al. 2015). However, most of these activities are not supervised by environmental agencies and little has been studied about their consequences for biodiversity conservation, especially in non-forest biomes (Overbeck et al. 2015). In the Cerrado, one hotspot for conservation in the word (Myers et al. 2000), some of the main anthropic activities are the extraction of giant earthworms, *Rhinodrillus alatus* Righi (Oligochaeta), widely used for sport fishing (Drumond et al. 2012). This activity, in addition to increasing human circulation in fragments of the Cerrado, generates intense soil revolving and application of fire to vegetation to facilitate collection (Drumond et al. 2013). Thus, the extractivism of giant earthworms can have an impact on the natural characteristics of the soil and vegetation of the Cerrado.

The extractivism of one species decreases the size of its population and can have an effect on the size of populations of other species and the entire ecosystem (Schmidt and Ticktin 2012; Poisot et al. 2013). For instance, selective cut of large canopy trees can cause more light to enter the vegetation and thus alter environmental conditions such as irradiation, average temperature, and soil characteristics (Rocha-Santos et al. 2016). Thus, anthropogenic disturbances can act as environmental filters leaving only species capable of surviving the new conditions, generally generalist species that have a broader ecological niche (Lôbo et al. 2011; Gámez-Virués et al. 2015; Carrié et al. 2017). Among these, some species have strong invasive potential and may dominate some areas after disturbances and change the structure and composition of the vegetation (Heringer and Thiele 2019).

The giant earthworm species is endemic to the Cerrado, restrict to the central region of the state of Minas Gerais and with an extension of its occurrence limited to approximately 20,000 km² (Drumond 2008). The extraction of these giant earthworms in the Cerrado is done by traditional extractors who sell them on Brazilian highways to fishermen, most of whom are destined for the Pantanal biome (Drumond et al. 2013). The extractors, remove this earthworms from their own areas of Cerrado vegetation, or invade private reserves and conservation units (Drumond et al. 2015a). In addition to causing the soil revolving inside the Cerrado phytophysiognomies, they set fire to the soil to facilitate visualization of *R. alatus* feces and locate individuals (Drumond et al. 2015b). Thus, the activity of extractors, in addition to endangering the population density of these giant earthworms, may be altering soil characteristics and increasing the occurrence of fire in the biome.

One of the determining characteristics for the Cerrado vegetation is the composition of the soil and the fire regime (Gottsberger and Silberbauer-Gottsberger 2006). The soils of the Cerrado are naturally dystrophic, acidic and alic, which is related to the constitution of its source material and to its high weathering process (Fageria and Gheyi 1999; Silveira et al. 2000). Under these conditions, calcium, magnesium, and phosphorus deficiency and high aluminum concentration are often reported as a limiting factor in the structure, composition and productivity of this ecosystem (Goodland and Pollard 1973; Lloyd et al. 2008; Neri et al. 2012a, 2013; Vourlitis et al. 2013, 2014). Likewise, the natural fire regime is essential for the nutrient cycling in the Cerrado, and many species have become dependent on the natural frequency of fire for the maintenance of their life cycles due to reproductive strategies obtained throughout evolution (Durigan and Ratter 2016). As a result, possible changes caused by earthworm extraction in soil characteristics and fire frequency can be prejudicial to the conservation of the Cerrado's natural vegetation.

Considering these risks caused by giant earthworm extraction in the Cerrado in the conservation of natural characteristics and its biodiversity, our objective in this study was: (1) to evaluate if there are changes in soil characteristics in areas with intense giant earthworm extraction; (2) if the earthworm extraction activities increase the intensity of the fire; and (3) whether this disturbance alters plant composition and species richness in remnants of Cerrrado *stricto sensu*. For this we quantified the intensity of the earthworm extractivism during the last 10 years and the local fire intensity, and we sampled soil characteristics and floristic composition of 12 fragments of Cerrado. Our hypothesis is that the disturbance generated by giant earthworm extraction causes: (1) changes in soil chemical and physical characteristics; (2) increase the intensity of fire in the Cerrado; and (3) thus also changes the woody floristic composition and the number of endemic species of the fragments.

Materials e Methods

Study area

The study was conducted in three municipalities of the state of Minas Gerais, Paraopeba, Caetanópolis and Curvelo, within the Cerrado *lato sensu* domain. Twelve Cerrado *stricto sensu* fragments were selected under different disturbance intensities and a 20x50m plot was installed inside each fragment. Cerrado *stricto sensu*, most characteristic phytophysiognomy of the Cerrado, occupies approximately 70% of the Cerrado biome, and it is characterized by prominent herbaceous dominated by grasses, and cover of trees and shrubs varying between 10 to 60 % (Eiten 1972; Ribeiro and Walter 1998). Of these, only one remnant is included in a conservation unit, Paraopeba National Forest, coordinated by the Chico Mendes Institute for Biodiversity Conservation (ICMBio). The remaining 11 fragments are legal reserves, inserted in pasture, agricultures and eucalyptus plantations. The Cerrado fragments of the region suffer daily disturbances generated by the extraction of *R. alatus*. The climate of the region is characterized as humid subtropical, Aw type in the Köppen system, with an extensive dry season from April to September and usually less than 1400 mm of annual precipitation with concentrated rainfall during summers (Neri et al. 2012b). Data collections were carried out between September 2015 and January 2016.

Giant earthworm extraction intensity

To estimate the intensity of giant earthworm extraction in the Cerrado areas studied, we interviewed the area owners or administrators regarding the performance of extractors in the last ten years. Giant earthworm extraction foci within the sampled plots were also quantified. Thus, we ranked the intensity of giant earthworm extraction from 0 to 3: “0”, there was no focus of earthworms extraction in the plot nor record of performance of extractors in the fragment during the last 10 years; “1”, there was no focus of earthworm extraction in the plot, but there was sporadic performance of extractors in the fragment during the determined period; “2”, there was a focus of earthworm extraction in the plot and frequent records of the extractors performance in the fragment during the determined period; “3”, there were two or more focus of earthworm extraction in the plot and records intense performance of earthworm extractors in the fragment during the last 10 years.

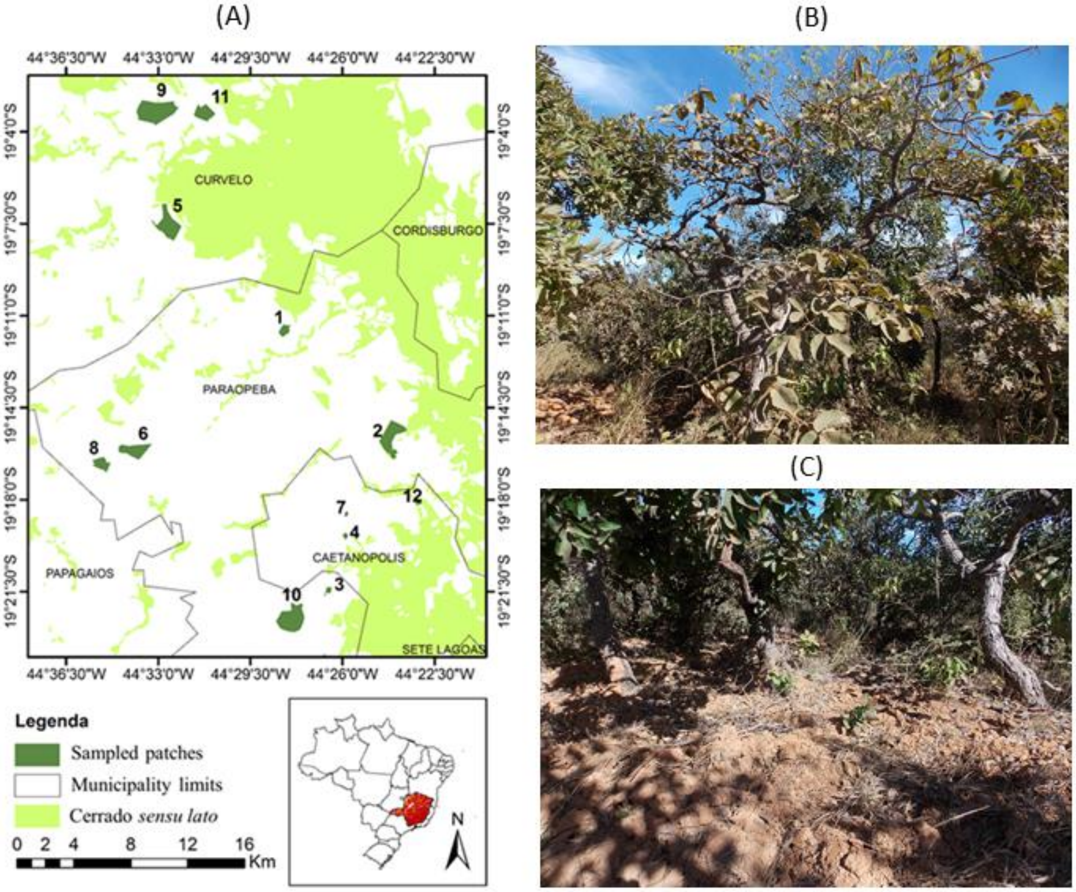


Figure 1. Map of study area (A), Cerrado *stricto sensu* physiognomy (C) and soil of Cerrado *strito sensu* after revolving by giant earthworm extractors.

Soil variables

Three random soil samples of 0-15 cm depth were collected from each plot, then homogenized, air dried and sieved (Giroldo and Scariot 2015), for subsequent chemical analysis at the UFV Soil Department. Important soil chemical constituents were considered as pH, exchangeable base sum, cation exchange capacity, aluminum saturation index and concentrations of aluminum (Al^{3+}), potassium (K), calcium (Ca^{2+}), phosphorus (P), and magnesium (Mg^{3+}) according to protocol described by EMBRAPA (2011). For the physical characteristics, we calculated the proportion of fine sand, coarse sand, silt, and clay in the samples, also following the protocol of EMBRAPA.

Plant community sampling

For sampling we installed a permanent plot (20 x 50 m) inside each fragment of Cerrado *stricto sensu*, considering only living woody individuals in which at least one stem had a circumference at ground height greater than 10 cm (CGH ≥ 10cm). Thus, we recorded CGH, the individual's height, and height reached by fire in individuals with carbonization marks. The species were collected and later identified according to APG IV (2014). Every species was classified as endemic or not according to the list of flora in Brazil (Reflora).

Burning intensity

Burning intensity was measured by the number of sampled individuals that were affected by fire, based on the observation of carbonization marks, and by the calculation of the biomass volume affected by fire. For volume affected by fire we used the equation obtained by Cetec (1995) to calculate the total volume of the stem with the bark in woody individuals of Cerrado *stricto sensu*:

$$\textit{Individual volume of tree} = (0.000038857 \times \textit{Diameter}^{1.70764} \times \textit{Height}^{1.32032});$$

however, for height we only considered the height at which carbonization marks were observed.

Statistical analysis

To analyze the effect of giant earthworm extraction on soil chemical characteristics we summarize the soil variables using the first two axes of a principal component analyses (PCA). We used linear regression to evaluate the relationship between earthworm extraction and soil PCA axes 1 and 2. Subsequently, we repeated the linear regression separately for all chemical and physical soil variables considered. Linear regression analysis was also used to evaluate the relationship between giant earthworm extraction intensity and fire intensity (individuals and volume affected by fire) in the studied areas. To obtain vegetation composition data we used an ordination analysis, the non-metric multidimensional scaling (NMDS) method, using “Bray-Curtis” as a measure of similarity and species abundance data in the sampled plots. Subsequently, we used linear regression to assess the influence of extraction of giant earthworms and soil characteristics with the two axes of NMDS, species richness and number of endemic species. We tested data normality with Shapiro Wilk test. All statistical analyses were performed in R software version 3.2.1 (R Developement Core Team 2015).

Results

The first axis of soil chemical PCA explained 45% of the variation of the soil variables, while the second axis explained 38%. Only the first axis of soil chemical PCA was related to the extraction of giant earthworms by increasing their values ($t = 2{,}404$; $p = 0.037$; Fig. 2). In addition, cation exchange capacity (t = 3.441; p = 0.006), phosphorus concentration (t = 3,016; p = 0.013), and aluminum concentration (t = 6,369; p = 0.000) were also positively influenced by the intensity of earthworm extraction. The soil variables pH, exchangeable base sum, aluminum saturation index, potassium, and magnesium were not directly related to the intensity of extraction of giant earthworms. No soil physics variable was significantly influenced by the activity of extracting giant earthworms. Regarding the fire intensity variables, none showed a significant relationship with the extraction of giant earthworms.

Were sampled 2,837 individuals of woody plants belonging to 102 species, 71 genera and 37 families. The species composition had a significant relationship with the giant earthworm extraction demonstrated by the alteration of second axis of the NMDS (t = -2,519; p = 0.030; Fig.3) but did not change the number of endemic species. The second axis of NMDS also had a negative relationship with the cation exchange capacity (t = -2.345; p = 0.041) and with the aluminum concentration (t = -3,067; p = 0.011).

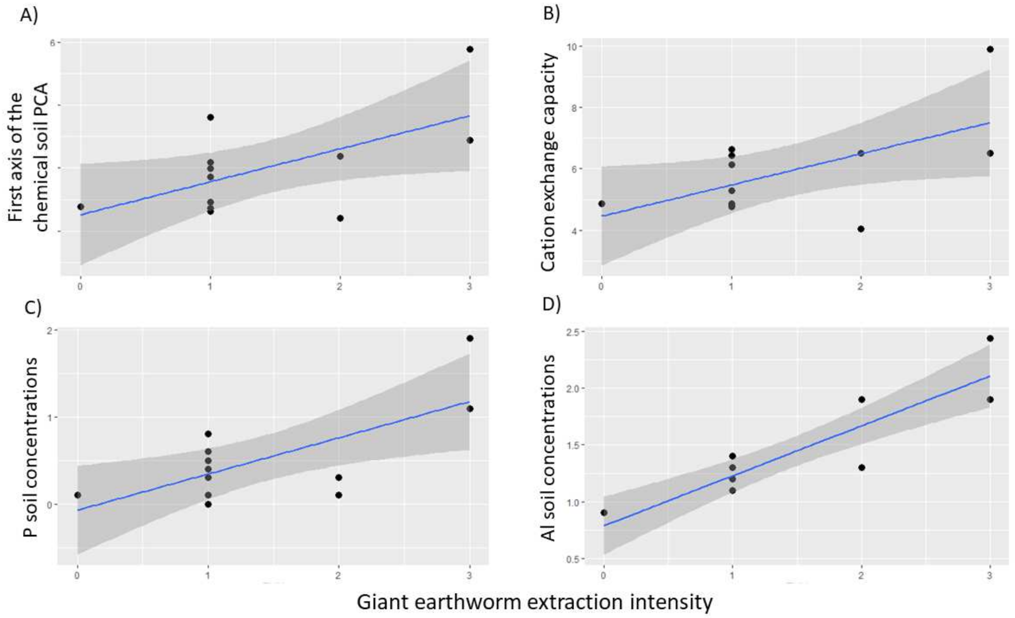


Figure 2. Relationship between the intensity of giant earthworm extraction and the chemical characteristics of the soil in the Cerrado *stricto sensu*: (A) axis 1 of the PCA of chemical characteristics of the soil; (B) effective cation exchange capacity; (C) phosphorus concentration; and (D) aluminum concentrations.

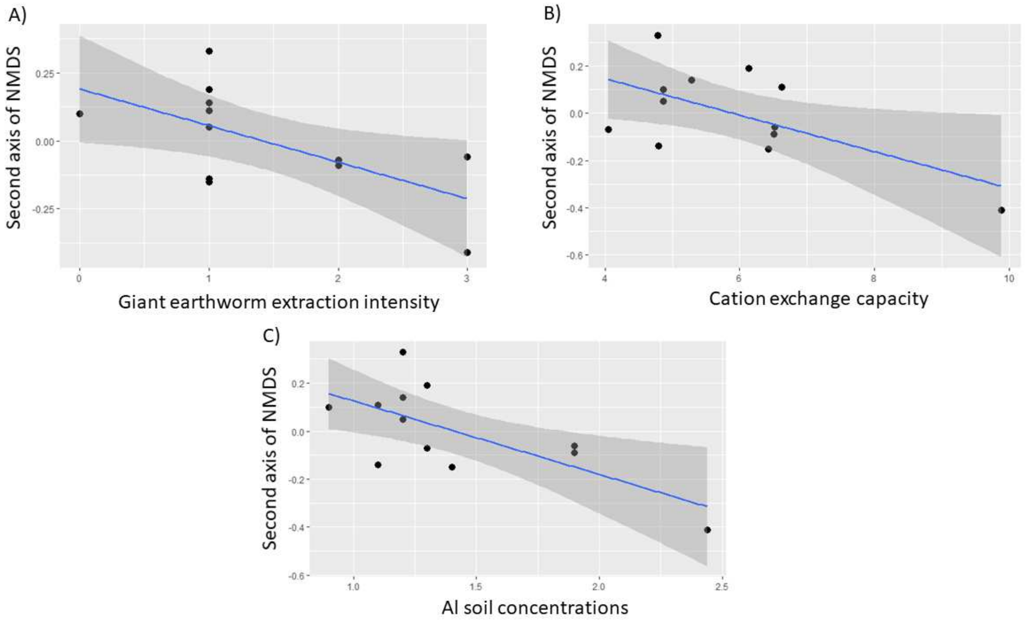


Figure 3. Relationship between the intensity of giant earthworm extraction (A), soil cation exchange capacity (B) and soil aluminum concentrations (C) with the second axis of NMDS of vegetation composition of Cerrado *stricto sensu.*

Discussion

Our results suggest that the giant earthworm extraction results in changes of the chemical characteristics of the soil and the woody floristic composition of the Cerrado *stricto sensu*. This activity increases the soil cation exchange capacity, phosphorus concentrations and aluminum concentrations. Likewise, the increased capacity for cationic exchanges and increased aluminum concentrations alongside with the disturbance of earthworm extraction alters the floristic composition of the remnants possibly allowing establishment of species intolerant to low nutrients generally found in Cerrado *stricto sensu*. However, the activity of extractivists does not affect the physical characteristics of the soil. In addition, fire intensity did not increase which earthworm extraction. Thus, our results show that the giant earthworm extraction activity threatens the conservation of specific characteristics of the soil and vegetation of the Cerrado *stricto sensu*.

The influence of giant earthworm extraction on soil chemical composition can be explained by the consequent soil revolving, a practice used in agriculture that increases the rate of mineralization of organic matter, and thus the cationic exchange capacity and phosphorus concentration in the soil (Ciotta et al. 2003; Santana et al. 2018). Similarly, soil revolving increases clay decomposition, especially in latosols, which generates an increase in Al3+ concentration (Ronquim 2010). Another effect can be that the aluminum concentration is greater at 15 cm depth than on the surface (Pavinato et al. 2009) which may explain the increase in aluminum in the uppermost layers soil of Cerrado with higher earthworm extraction intensity. Thus, the increase in Al^{3+} might be an effect of homogenization of the chemical characteristics between the soil surface and deeper layers but without the most of the root biomass that usually chelate Al^{3+} (Delhaize et al. 1993; Hocking 2001; Kochian et al. 2004). However, by accelerating mineralization processes, the intensity of this long-term disturbance can result in a rapid depletion of soil carbon and nutrient reserves in giant earthworm extraction areas.

As predicted, the giant earthworm extraction has significantly influenced the composition of tree species, and different factors may be behind it. First, the greater availability of nutrients and their ease of uptake (higher CTC) in areas with high intensity of extraction of giant earthworms may have favored a greater diversification of species. It is remarkable that the aluminum saturation does not vary (data not shown) with the increasing extraction and shows that the increased CEC means more nutrient availability for plants. In the Cerrado *stricto sensu*, stress factors such as the low availability of soil nutrients act filtering in lower-sized tree species, with slow growth and reduced specific leaf area (Westoby et al. 2002; Hoffmann et al. 2012; Bueno et al. 2013b). In this way, improvements in soil nutritional quality in these areas, even if transient, may have allowed the establishment of other species typical of less dystrophic formations of the Cerrado, such as Cerrado woodland (Cerradão) and seasonal forests (Bueno et al. 2013a; Neri et al. 2013; Meira-Neto et al. 2017). Secondly, the increase in aluminum concentrations may also have acted as an environmental filter, filtering out intolerant species and filtering in tolerant species to high aluminum concentrations. According to Neri et al. (2013), tree species of forest physiognomies have higher tolerance to high concentrations of aluminum, which corroborates the feasible occurrence of these species in the altered areas of Cerrado *stricto sensu*. Finally, it is important to mention that, to facilitate the search and capture of minhococu, part of the vegetation that makes up the lower stratum of the vegetation is disturbed or totally removed during the extraction (Paro 2013). In addition to threatening the survival of herbaceous plants, this impact can delay the regeneration process of the plant community, mainly because this activity has occurred in the region for more than fifty years, which reinforces the influence of extraction on the composition of tree species.

The fire set by earthworm extractors is not increasing the frequency of fire, demonstrated by the lack of significative influence of earthworm extraction intensity in these variables. The occurrence of natural burning is essential for maintaining diversity and structure of Cerrado, especially the Cerrado *stricto sensu* (Lehmann et al. 2014; Pellegrini et al. 2016). However, fire-handling practices in the conservation of APPs and Cerrado conservation units are not yet adopted (Durigan and Ratter 2016). In addition, biome fragmentation may be hindering the natural spread of fire in this biome (Abreu et al. 2017). In this sense, the extraction would be contributing to the maintenance of the natural frequency of fire in this biome.

Thus, in addition to the impacts of the conservation of giant earthworms, the extractivism of this species can cause loss of important ecosystem functions performed by this biome (i.e. storage of subsoil water favored by the long roots of characteristic plants) due to change in species composition sensitive to soil chemical alterations. Thus, the regulation and management of giant earthworm extraction might be necessary in order to mitigate the effects on the soil chemical and plant composition of the Cerrado *stricto sensu*. However, further studies are needed to evaluate the effects of the giant earthworm extraction on functional aspects of this ecosystem. For now, it would be necessary rotation between areas to mitigate the extraction intensity in Cerrado and increase environmental supervision mainly in legal preservation areas.

References

Abreu RCR, Hoffmann WA, Vasconcelos HL, et al (2017) The biodiversity cost of carbon sequestration in tropical savanna. Science Advances 3:e1701284. https://doi.org/10.1126/sciadv.1701284

Bueno ML, Neves DR, Oliveira Filho AT, et al (2013a) A study in an area of transition between seasonally dry tropical forest and mesotrophic cerradão, in mato grosso do sul, southwestern Brazil. Edinburgh Journal of Botany 70:469–486. https://doi.org/10.1017/S0960428613000164

Bueno ML, Neves DRM, Souza AF, et al (2013b) Influence of edaphic factors on the floristic composition of an area of cerradão in the brazilian central-west. Acta Botanica Brasilica 27:445–455. https://doi.org/10.1590/S0102-33062013000200017

Carrié R, Andrieu E, Cunningham SA, et al (2017) Relationships among ecological traits of wild bee communities along gradients of habitat amount and fragmentation. 85–97. https://doi.org/10.1111/ecog.02632

Ciotta MN, Bayer C, Fontoura SMV, et al (2003) Matéria orgânica e aumento da capacidade de troca de cátions em solo com argila de atividade baixa sob plantio direto. Ciência Rural 33:1161–1164. https://doi.org/10.1590/s0103-84782003000600026

Delhaize E, Ryan PR, Randall PJ (1993) Aluminum Tolerance in Wheat (Triticum aestivum L.) (II. Aluminum-Stimulated Excretion of Malic Acid from Root Apices). Plant Physiol 103:695–702

Drumond MA (2008) Manejo adaptativo do minhocuçu Rhinodrilus alatus. Universidade Federal de Minas Gerais

Drumond MA, Brown GG, Marini-filho OJ (2012) Rhinodrilus alatus. 2:125–130

Drumond MA, Guimarães AQ, Da Silva RHP (2015a) The role of local knowledge and traditional extraction practices in the management of giant earthworms in Brazil. PLoS ONE 10:1–19. https://doi.org/10.1371/journal.pone.0123913

Drumond MA, Guimarães AQ, El Bizri HR, et al (2013) Life history , distribution and abundance of the giant earthworm Rhinodrilus alatus RIGHI 1971 : conservation and management implications. 73:699–708. https://doi.org/10.1590/S1519-69842013000400004

Drumond MA, Queiroz A, Hosken R (2015b) The Role of Local Knowledge and Traditional Extraction Practices in the Management of Giant Earthworms in Brazil. 1–19. https://doi.org/10.1371/journal.pone.0123913

Durigan G, Ratter JA (2016) The need for a consistent fire policy for Cerrado conservation. Journal of Applied Ecology 53:11–15. https://doi.org/10.1111/1365-2664.12559

Eiten G (1972) The Cerrado Vegetation Of Brazil. The Botanical Review. 38:201–327

Fageria NK;, Gheyi HR (1999) Efficient crop production. UFPB, Capina Grande, Brazil

Gámez-Virués S, Perović DJ, Gossner MM, et al (2015) Landscape simplification filters species traits and drives biotic homogenization. Nature Communications 6:8568. https://doi.org/10.1038/ncomms9568

Giroldo AB, Scariot A (2015) Land use and management affects the demography and conservation of an intensively harvested Cerrado fruit tree species. Biological Conservation 191:150–158. https://doi.org/10.1016/j.biocon.2015.06.020

Goodland R, Pollard R (1973) The Brazilian Cerrado Vegetation: A Fertility Gradient. J Ecol 61:219–224

Gottsberger G, Silberbauer-Gottsberger (2006) Life in the Cerrado: a South American Tropical Seasonal Ecosystem. Vol. II. Pollination and Seed Dispersal. Reta, Ulm

Heringer G, Thiele J (2019) Biological invasion threatens the sandy-savanna Mussununga ecosystem in the Brazilian Atlantic Forest. 5:2045–2057. https://doi.org/10.1007/s10530-019-01955-5

Hocking PJ (2001) Organic acids exuded from roots in phosphorus uptake and aluminum tolerance of plants in acid soils. In: Advances in Agronomy. Academic Press, pp 63–97

Hoffmann WA, Geiger EL, Gotsch SG, et al (2012) Ecological thresholds at the savanna-forest boundary: How plant traits, resources and fire govern the distribution of tropical biomes. Ecology Letters 15:759–768. https://doi.org/10.1111/j.1461-0248.2012.01789.x

Kochian LV, Hoekenga OA, Piñeros MA (2004) How do crop plants tolerate acid soils? Mechanisms of aluminum tolerance and phosphorous efficiency. Annual Review of Plant Biology 55:459–493. https://doi.org/10.1146/annurev.arplant.55.031903.141655

Lehmann CER, Anderson TM, Sankaran M, et al (2014) Savanna Vegetation-Fire-Climate Relationships Differ Among Continents. Science 343:548–553. https://doi.org/10.1126/science.1247355

Lloyd J, Bird MI, Vellen L, et al (2008) Contributions of woody and herbaceous vegetation to tropical savanna ecosystem productivity: A quasi-global estimate. Tree Physiology 28:451–468. https://doi.org/10.1093/treephys/28.3.451

Lôbo D, Leão T, Melo FPL, et al (2011) Forest fragmentation drives Atlantic forest of northeastern Brazil to biotic homogenization. Diversity and Distributions 17:287–296. https://doi.org/10.1111/j.1472-4642.2010.00739.x

Meira-Neto JAA, Tolentino GS, da Silva MCNA, et al (2017) Functional antagonism between nitrogen-fixing leguminous trees and calcicole-drought-tolerant trees in the Cerrado. Acta Botanica Brasilica 31:11–18. https://doi.org/10.1590/0102-33062016abb0380

Myers N, Mittermeier RA, Mittermeier CG, et al (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858

Neri A V., Schaefer CEGR, Silva AF, et al (2012a) the Influence of Soils on the Floristic Composition and Community Structure of an Area of Brazilian Cerrado Vegetation. Edinburgh Journal of Botany 69:1–27. https://doi.org/10.1017/S0960428611000382

Neri A V., Schaefer CEGR, Silva AF, et al (2012b) THE INFLUENCE OF SOILS ON THE FLORISTIC COMPOSITION AND COMMUNITY STRUCTURE OF AN AREA OF BRAZILIAN CERRADO VEGETATION. Edinburgh Journal of Botany 69:1–27. https://doi.org/10.1017/S0960428611000382

Neri A V., Schaefer CEGR, Souza AL, et al (2013) Pedology and plant physiognomies in the cerrado, Brazil. Anais da Academia Brasileira de Ciencias 85:87–102. https://doi.org/10.1590/S0001-37652013000100007

Overbeck GE, Vélez-Martin E, Scarano FR, et al (2015) Conservation in Brazil needs to include non-forest ecosystems. Diversity and Distributions 21:1455–1460. https://doi.org/10.1111/ddi.12380

Paro SP (2013) Influência de fatores abióticos na diversidade de espécies do estrato herbáceo-subarbustivo em cerrado, FLONA de Paraopeba, MG

Pavinato PS, Merlin A, Rosolem CA (2009) Soil cation availability as affected by the tillage system. Revista Brasileira de Ciencia do Solo 33:1031–1040. https://doi.org/10.1590/s0100-06832009000400027

Pellegrini AFA, Socolar JB, Elsen PR, Giam X (2016) Trade-offs between savanna woody plant diversity and carbon storage in the Brazilian Cerrado. Global Change Biology 1–10. https://doi.org/10.1111/gcb.13259

Poisot T, Mouquet N, Gravel D (2013) Trophic complementarity drives the biodiversity-ecosystem functioning relationship in food webs. Ecology Letters 16:853–861. https://doi.org/10.1111/ele.12118

Ribeiro EMS, Arroyo-Rodri´guez V, Santos BA, et al (2015) Chronic anthropogenic disturbance drives the biological impoverishment of the Brazilian Caatinga vegetation. Journal of Applied Ecology 52:611–620. https://doi.org/10.1111/1365-2664.12420

Ribeiro JF, Walter BMT (1998) Fitofisionomias do Bioma Cerrado. In: Sano SM, Almeida SP (eds) Cerrado: ambiente e flora, ed. Empraba Cerrados, Brasiília, pp 89–166

Rocha-Santos L, Pessoa MS, Cassano CR, et al (2016) The shrinkage of a forest: Landscape-scale deforestation leading to overall changes in local forest structure. Biological Conservation 196:1–9. https://doi.org/10.1016/j.biocon.2016.01.028

Ronquim CC (2010) Conceitos de fertilidade do solo e manejo adequado para as regiões tropicais. Boletim de Pesquisa e Desenvolvimento - Embrapa Monitoramento por Satélite 351:139–140. https://doi.org/10.1016/S0140-6736(05)78120-4

Santana JS, Lima EF, Komatsu RS, et al (2018) CARACTERIZAÇÃO FÍSICA E QUÍMICA DE SOLO EM SISTEMAS DE MANEJO PLANTIO DIRETO E CONVENCIONAL. Enciclopedia Biosfera 15:22. https://doi.org/10.18677/EnciBio

Schmidt IB, Ticktin T (2012) When lessons from population models and local ecological knowledge coincide - Effects of flower stalk harvesting in the Brazilian savanna. Biological Conservation 152:187–195. https://doi.org/10.1016/j.biocon.2012.03.018

Silveira PM;, Zimmermann FJP;, Silva SC da;, Cunha AA da; (2000) Amostragem e variabilidade espacial de características químicas de um latossolo submetido a diferentes sistema de preparo. Pesquisa Agropecuária Brasileira 35:2057–2064

Vegetação DA, Caatinga DA, Castellanos J, et al (2011) Uma Classificação Morfo-Estrutural Para Descrição E a Morpho-Structural Classification for Description and Evaluation of the Biomass of the Caatinga Vegetation. Revista Brasileira de Geografia Física 06:225–228. https://doi.org/10.1007/BF00009452

Vourlitis GL, de Almeida Lobo F, Lawrence S, et al (2014) Nutrient resorption in tropical savanna forests and woodlands of central Brazil. Plant Ecology 215:963–975. https://doi.org/10.1007/s11258-014-0348-5

Vourlitis GL, de Almeida Lobo F, Lawrence S, et al (2013) Variations in Stand Structure and Diversity along a Soil Fertility Gradient in a Brazilian Savanna (Cerrado) in Southern Mato

Grosso. Soil Science Society of America Journal 77:1370–1379. https://doi.org/10.2136/sssaj2012.0336

Westoby M, Falster DS, Moles AT, et al (2002) Plant ecological strategies: Some leading dimensions of variation between species. Annual Review of Ecology and Systematics 33:125–159. https://doi.org/10.1146/annurev.ecolsys.33.010802.150452

Williams M, Zalasiewicz J, Haff PK, et al (2015) The anthropocene biosphere. Anthropocene Review 2:196–219. https://doi.org/10.1177/2053019615591020

CHAPTER 2: The role of chronic anthropogenic disturbances on functional diversity and composition in the Brazilian Cerrado

Abstract: The Cerrado is one of the main biodiversity hotspots for conservation in the world, playing important ecosystem functions, but it is threatened by chronic anthropogenic disturbances (CADs). Thus, it is necessary to assess how CADs influences the functional diversity and composition of Cerrado remnants. For this, we sampled the vegetation of 12 fragments of Cerrado and the intensity of CADs on a local (burning intensity, cattle grazing, earthworm extraction, caryocar fruit extraction, and fragment size) and landscape scale (Cerrado cover, patch density, connectivity, silviculture cover, and land covered by mosaic of pastures, agriculture, and urbanized areas). To calculate the functional diversity and composition, we used 8 functional traits: wood density, maximum height, maximum diameter, fruit length, fruit width, seed length, seed width, and dispersal syndrome. As functional diversity index we used functional richness (FRiC), functional evenness (FEve), and functional dispersion (FDis). For functional composition, we calculated the community-weighted mean (CWM) for each trait evaluated. Cattle grazing increased the CWM of wood density, fruit width, and seed length and width. In contrast, earthworm extraction decreased FEve and the CWM of the length and width of the fruit and increased the CWM of maximum height. Fragment size increased the CWM of fruit and seed width, while patch density increased the CWM of seed length and maximum diameter and decreased dispersal syndrome, indicating a decrease in zoochoric dispersion. Finally, silviculture cover negatively influenced FEve. Therefore, CADs on a local and landscape scale decreased the functional diversity and changed functional composition of the Cerrado. This puts the maintenance of ecosystem functions at risk and shows the need for conservation initiatives aimed at minimizing this CADs effects in the Cerrado biome.

Keywords: chronic anthropogenic disturbances, fragmentation, land use, cattle grazing, earthworm extraction, Brazilian Cerrado, savanna, functional diversity.

Introduction

Chronic anthropogenic disturbances (CADs) are the main threats to biodiversity and ecosystems functioning in the world (Ratter et al. 1997; Nazareno et al. 2012; Melo et al. 2013). Thus, land-use change through CADs by intensive farming systems, logging, forest fires, and exploitation of non-timber forest products can simultaneously induce forest fragmentation and loss of habitats (Laurance et al. 2011; Schmidt and Ticktin 2012; Lima et al. 2013; Giroldo and Scariot 2015; Ribeiro et al. 2016), which are the main drivers that causes loss of biodiversity and ecosystem functioning (Lewis et al. 2015; Edwards et al. 2019). These drivers can affect negatively multiple diversity dimensions (taxonomic, functional, and phylogenetic diversity) of plant communities (Magnago et al. 2014; Villa et al. 2020), and consequently multiple ecosystem services, which are crucial to human well-being (Lewis et al. 2015; Walker et al. 2020). CADs can induce biotic and abiotic changes in ecosystems at multiple scales, from the local scale to the landscape scale (Metzger 1997; Fahrig 2003). However, understanding of the effects of these factors on the diversity and function of tropical ecosystems has been limited for forests (Chapin 2003; Gardner et al. 2009) and is much more particularly for savannas, such as the Cerrado in Brazil.

CADs on a local scale initially change the structure of communities by removing plant biomass by selective logging can change environmental conditions (i.e. Ribeiro-Neto et al. 2016; Ribeiro et al. 2019, 2016); For example, clearings generated in forest fragments, increases the light incidence on the understory and change plant community composition (Carrara et al. 2015; Rocha-Santos et al. 2016; Solar et al. 2016). On a landscape scale, CADs, mainly dominated by human-induced land-use change and loss of habitats in tropical ecosystems, can also result in: (i) a reduction in the probability of survival of plant populations; (ii) enlargement of the edge effect, where most of the natural habitat is under stressful environmental conditions; (iii) an increase in the isolation between fragments, limiting seed dispersal; and (iv) increased isolation between fragments, can also increase the occurrence of disturbances, such as fire and biological invasion (Ewers and Didham 2006; Laurance et al. 2011; Fahrig 2013; Magnago et al. 2014; Carrié et al. 2017; Heringer et al. 2020b).

The CADs influence on plant communities can be understood as habitat filtering of species with similar functional traits growing on functionally similar new environmental conditions, which can generate floristic homogenisation (Gámez-Virués et al. 2015; Solar et al. 2015). Thus, if the species coexisting in the local communities are functionally more similar than expected based on functional traits, this would suggest the occurrence of environmental filtering or limitation of dispersion are dominant processes (Cavender-Bares et al. 2009). For example, when habitat filtering selects plant species based on resource availability (i.e., nutrients, water, light), can reduce the trait ranges within the community (Gámez-Virués et al. 2015; Villa et al. 2020). However, when this filtering is related to CADs, could also promote a high dispersion and divergence of functional traits, mainly those related to colonization and regeneration (Ackerly and Cornwell 2007; Villa et al. 2021). The most specialist species usually are affected to environmental changes by disturbances, reducing their populations or causing local extinction (Carrara et al. 2015; Carrié et al. 2017). Thus, species loss and their associated functional traits can cause the loss of ecosystem functioning and affect species complementarity (Poisot et al. 2013; Liu et al. 2018). For example, in Caatinga dry forests, CADs increase the dominance of plant species with a greater capacity to capture resources, decrease the abundance of plants pollinated by specialised insects, and negatively affect seed dispersal by specialised ants (Machado and Lopes 2004; Lopes et al. 2009; Ribeiro et al. 2019; Oliveira et al. 2019). Therefore, to maintain multiple ecosystem functions, it is necessary to maintain an equilibrium between generalised and specialised functional values in a community (Gámez-Virués et al. 2015).

The most common measurements of functional diversity allow hierarchical grouping of species at a more specific level with respect to an ecosystem function, analysing the impact of species that have similar responses to environmental or habitat filtering (Villéger et al. 2008; Mouchet et al. 2010). Thus, functional diversity and composition indices are estimated to discriminate two main generic properties of plant communities, such as the community-weighted mean (CWM) and functional diversity (i.e. divergence and dispersion) of traits (Conti and Díaz 2013). The community-weighted mean (CWM) shows the trait values variability and thus the functional composition of the community are altered by different constraints (e.g., Ali et al., 2017; Conti and Díaz, 2013; Poorter et al., 2019). Meanwhile, functional diversity of multivariate-trait, explain complementarity in resource use and ecological niches in forests (Ali et al. 2017; Villa et al. 2020).

In this context, due to the area of 2 million squared kilometres and the largest biodiversity among tropical savannas, studies on trait-based approach in the Cerrado are fundamental for the conservation and maintenance of ecosystem services (Miranda et al. 1997; Santos et al. 2004; Grace et al. 2006). Despite this, more than half of the original Cerrado vegetation has already been converted into croplands and pastures, with 42% of these areas dominated by exotic grasses, 11.35% by agriculture, and 0.07% by planted forests (Klink and Machado 2005). Of the remaining natural areas, only 8.3% are protected areas, while the rest are strongly threatened (Ganem et al. 2013; Françoso et al. 2015). In contrast to the need to increase the protected area network (Heringer et al. 2020a), the new forest code in Brazil, established in 2012 by law nº 12.651, allowed the deforestation of an average of 88 million hectares and granted amnesty to 58% of the private reserve areas that should be recovered (i.e., legal reserves) being the Cerrado the most affected biome by this legal change (Soares-filho et al. 2014). However, there are few studies on the anthropogenic impacts on Cerrado diversity, and those are mostly concerned with taxonomic diversity (i.e., Carmo et al. 2011; Dodonov et al. 2013; Mendonça et al. 2015; Vanmelis et al. 2020). Thus, the need to assess the CADs effects on the functional diversity of woody communities in the Cerrado is urgent to propose initiatives that minimize possible impacts on ecosystem functioning.

Functional diversity indices make it possible to measure the variation in the morphophysiological traits of individuals in a community and to evaluate how these traits are distributed (Villéger et al. 2008; Magnago et al. 2014). In this study, we sought to evaluate the effects of CADs on the functional diversity of woody plants communities in the Cerrado. Considering that CADs filter species by selecting functional traits (Tscharntke et al. 2012; Gámez-Virués et al. 2015; Ribeiro et al. 2019), we expected that CADs intensification (i) decreases the functional diversity in Cerrado vegetation; and (ii) and select functional attributes more related to resistance, acquisitive capacity and ability to colonise.

Materials and Methods

Study area

The study area is in a region of humid tropical climate, type Aw in the Köppen system, with a dry season from April to September and 1300 mm of mean annual precipitation with rains concentrated during the summer (Neri et al. 2013). The soils are Oxisols, Argisols and Cambisols generally well drained and with high levels of exchangeable aluminum (Oliveira-

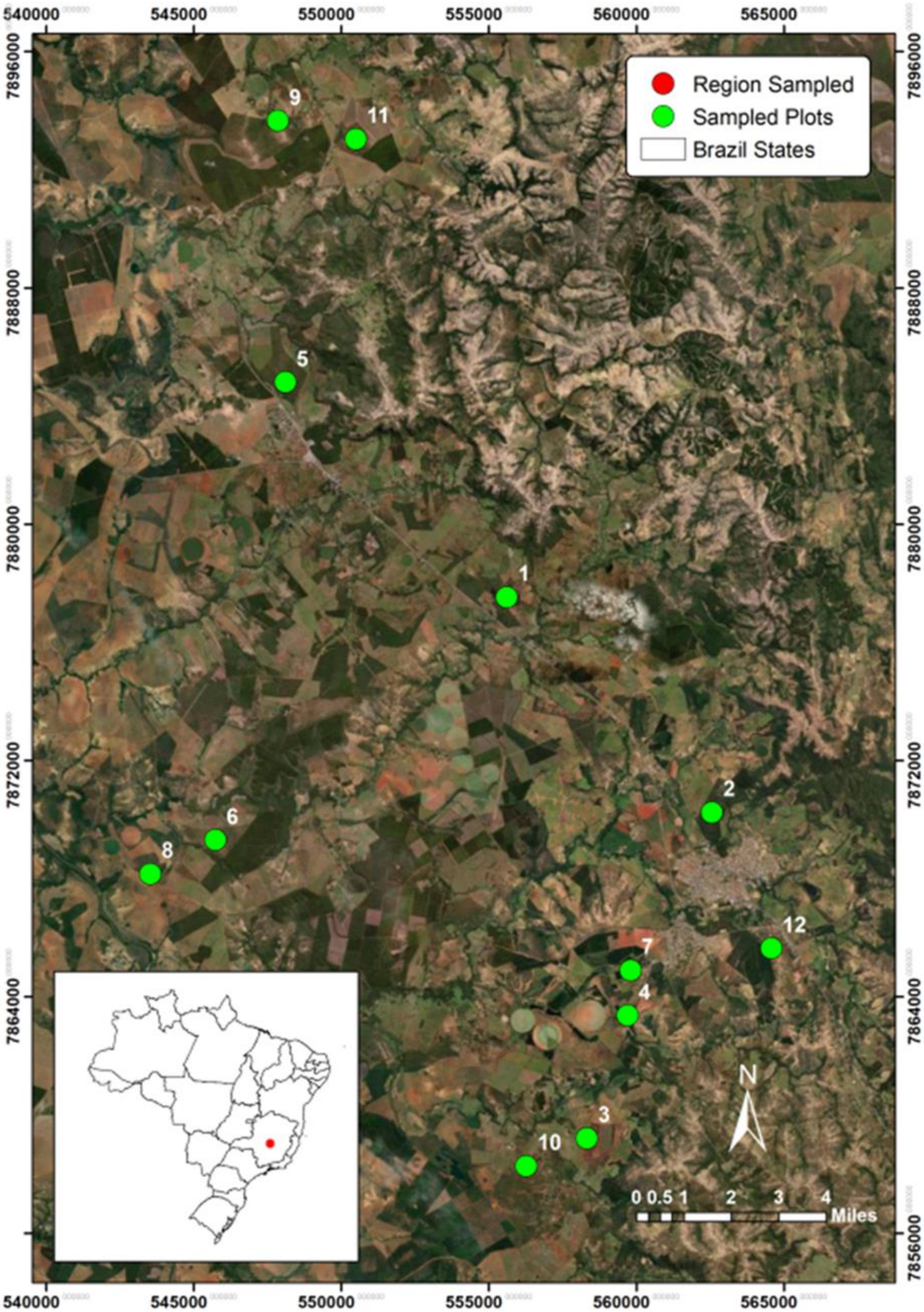


Figure 1. Map of the Cerrado region where the 12 fragments sampled in this work are inserted.

Filho and Ratter 2002; Walter et al. 2008; Neri et al. 2013). The study area is in the Brazilian Cerrado biome, a global hotspot for biodiversity conservation (Myers et al. 2000) and presents a range of vegetation types that vary between grasslands and woodlands dominated by tree species (Oliveira-Filho and Ratter 2002; Coutinho 2006). The study was carried out on twelve fragments of different sizes of the Cerrado *sensu stricto*, the intermediate physiognomy inserted in different landscape conditions and under different intensities of CADs (Figure 1). The fragments are distributed in three municipalities in the state of Minas Gerais (southeastern Brazil): Paraopeba, Caetanópolis and Curvelo (Figure 1). Among the fragments, only one is insert in a protected area, within the Paraopeba National Forest, coordinated by the Chico Mendes Institute for Biodiversity Conservation (ICMBio).

Sampling of woody communities

For sampling, we installed a permanent plot (20-m x 50-m) inside each fragment, at least 30 meters away from the edge, and we sampled live woody species with circumference at ground level greater than 10 cm (CAS ≥ 10 cm). In addition, we estimated the height of each plant. Sampling was carried out between September 2015 and January 2016. The botanical collections were identified through literature, specialists or by comparisons with Herbarium VIC (UFV) specimens and virtual herbarium. The classification followed the Angiosperm Phylogeny Group (APG IV 2016).

Chronic anthropogenic disturbances

We considered for CAD measurements the most common disturbances in the Brazilian Cerrado and the most frequent in the study area at local and landscape scales. On a local scale, we evaluated the following anthropic disturbances: burning (BUR), cattle grazing (CG), caryocar (*Caryocar brasiliense* Camb.) fruit extraction (CE) and earthworm (*Rhinodrilus alatus* Righi) extraction (EE). Burning is necessary in Cerrado conservation, however CADs can change its natural frequency. Thus, the burning intensity was measured by calculating the volume of biomass reached by fire in the fragments. For this, we collected the height reached by the fire in all individuals sampled based on the burn marks. For the other CADs on a local scale, we ranked the intensity from “0” to “3” in the last 10 years, with “0” being the absence of the disturbance in a particular fragment and “3” the maximum intensity found. For the ranking, we collected data from landowners and collected traces inside the fragments such as cattle spoors, earthworm extraction focus, and remains of caryocar fruits left by collectors (see table 1 in supplementary information and Coelho et al. 2020). In addition, we consider the fragment size (FS) as a proxy for local habitat loss.

For landscape-scale CADs, we consider the percentage Cerrado stricto sensu cover in the landscape (CC) as a proxy for landscape habitat loss, the patch density of Cerrado fragments in the landscapes (PD) and connectivity between patches (CON), as proxies for habitat fragmentation, and the percentage of adjacent land cover and use (USE; mosaics of agriculture, pastures, and urbanized areas) and silviculture (SI, monoculture of *Eucalyptus* sp.) as proxies of adjacent land use. For CON were considered mean euclidean nearest-neighbor distance of Cerrado *stricto sensu* patches. To calculate these metrics, we performed the classification of land use and cover in the study area, considering the following elements in the landscape: Cerrado *sensu stricto*; areas used for human occupation agriculture, pasture, urbanized areas and exposed land; areas of use for silviculture; natural forests; and bodies of water. The classification was carried out using 30-m spatial resolution images from the Operational Land Imager sensor (LandSat 8 satellite), with atmospheric correction, performed with supervised classification process using ArcGis software (Esri, Redlands, California, USA). A total of 110 points distributed throughout the region with the studied fragments were sampled for further validation of the landscape classification that obtained more than 75% accuracy. After landscape classification, we created a 2 km circular buffer around each sampled plot (Matos et al. 2016) and we calculated CC, PD, CON, USE, and SI inside the 2 km buffers using Fragstats software (McGarial et al. 2012).

Functional traits

To assess the functional diversity of each fragment we consider all species identified at least to the family level and consider the following traits: wood density, maximum height, maximum diameter at ground level, fruit length and width, seed length and width, and dispersal syndrome (0, not zoochoric; 1, zoochoric). Wood density was selected mainly due to mechanical resistance; height and diameter were selected because they are indicators of competitive strength and capacity of establishments after disturbances; and, width and length of the fruit and seed and dispersal syndrome because they say, mainly, on the dispersal and colonization capacity (Chave et al. 2009; Pérez-Harguindeguy et al. 2013; Meira-Neto et al. 2019; Ribeiro et al. 2019). The density of the wood retrieved from the database The Global Wood Density (GWD; Zanne et al., 2009); the plant height and diameter data were collected in the field; and the functional traits of fruits and seeds were consulted in the literature (Silva-Júnior and Santos 2005; Sano et al. 2008; Kuhlmann and

Ribeiro 2016). In the case of wood density, all species of the same genus were averaged for species that were not in the GWD.

Functional diversity

Using the functional traits mentioned above, we calculated three functional diversity indices: Functional Richness (FRic); Functional Evenness (FEve); and Functional Dispersion (FDis). According to Villéger et al. (2008), FRic represents the amount of functional space filled by the community, while FEve quantifies the regularity that the functional space is filled by species, weighing their abundances. Low values of FRic and FEve indicate that the performance of environmental filters reducing the richness of traits in the community and the abundance of these traits, respectively (Mouchet et al. 2010; Mason et al. 2013). On the other hand, FDis refers to the mean distance of a species in the multidimensional functional space to the centroid of all species (Laliberte and Legendre 2010). FDis is recommended to assess patterns of divergence and convergence of traits and low values also indicate the presence of environmental filters (Ricotta and Moretti 2011; Ribeiro et al. 2019). All functional diversity indices were calculated in R version 3.1.2 (R Development Core Team 2019), using the methods and scripts of (Villéger et al. 2008) and functions of the FD package (Laliberte and Legendre 2010).

Functional composition

Finally, we calculated the weighted average of the values of traits assessed in the communities (community-weighted mean - CWM). This metric is a measure of functional composition weighed by the abundance of species and indicates dominance of values of functional traits (Ribeiro et al. 2019). Thus, we calculate the CWM for wood density, maximum height, maximum diameter, fruit length, fruit width, seed length, seed width and dispersal syndrome. This analysis was performed in R version 3.1.2 using functions from the *Tidyverse* package (Tidyverse Team 2020). Some community weighted mean measures of the traits evaluated in this work showed a significant correlation (see Table 1).

Table 1. Spearman's correlation between the community weighted mean of the considered functional traits: wood density (WD); maximum height (Hmax); maximum diameter (Dmax); fruit length (FL); fruit width (FW); seed length (SL); seed width (SW); and dispersal syndrome (DS).

CWM	WD	Hmax	Dmax	FL	FW	SL	SW	DS
WD	-	0.15	0.02	0.37*	0.64*	0.09	0.63*	0.37
Hmax	-	-	0.15	0.36	0.4	0.08	0.28	0.13
Dmax	-	-	-	0.65*	0.31	0.70*	0.16	0.7
FL	-	-	-	-	0.80**	0.56	0.58*	-0.46
FW	-	-	-	-	-	0.49	0.88**	0.12
SL	-	-	-	-	-	-	0.48	-0.80**
SW	-	-	-	-	-	-	-	0.002
DS	-	-	-	-	-	-	-	-

(Significant correlations: * $p < 0.05$); ** $p < 0.01$)

Statistical analysis

To test the consequences of local and landscapes CADs on the functional diversity and composition of Cerrado *stricto sensu*, we developed two Global Generalized Linear Models (GLM; local and landscape scales) for the functional diversity indices (FRic, FEve, and FDis) and for functional composition indices of each considered trait using the Gaussian family. The local global models contained as possible explanatory variables burning, cattle grazing, caryocar extraction, earthworm extraction, and fragment size. In the other hand, the landscape global models contained as possible explanatory variables cerrado cover, patch density, connectivity, silviculture cover, and others land-use cover. Subsequently, we used the multi-model inference approach to generate a set of models with all combinations of possible explanatory variables using the *dredge* function (Barton 2017). However, we restricted the function so that models with explanatory variables that are highly correlated (Spearman's correlation > 0.7) were not generated. Thus, as earthworm extraction was negatively correlated with fragment size (s = -0.73; p = 0.02) and patch density negatively correlated with Cerrado cover (s = -0.83; p = 0.01), these variables were not included in the same models. The generated models were hierarchical based on the second order Akaike Information Criterion (AICc) in order to identify the models that best explain the data variation (Whittingham et al. 2005; Burnham et al. 2011; Carrara et al. 2015). We considered those with ΔAICc < 5 to be the best models, as they have greater explanatory power (Burnham et al. 2011). Finally, we calculated the average of the coefficients of all the explanatory variables present in any of the models with ΔAICc < 5, using the function *model.avg* (Mazerolle 2019). The assumptions of linearity and normality of the selected models (ΔAICc < 5) were tested using visual inspection by applying the plot function on the model and from the Shapiro Wilk test using the *shapiro.test* function (R Development Core Team 2019).

Results

Local chronic anthropogenic disturbances influences

The local CADs influenced functional evenness and community weighted means of wood density, maximum height, fruit length, fruit width, seed length and seed width (Fig. 2). Earthworm extraction negatively influenced functional evenness ($\beta = -0.06 \pm 0.25$ SE, $z = 2.19$, $p = 0.02$), fruit length ($\beta = -0.58 \pm 0.25$ SE, $z = 1.99$, $p = 0.04$), fruit width ($\beta = 0.46 \pm 0.18$ SE, $z = 2.22$, $p = 0.02$) and positively influenced maximum height ($\beta = 0.72 \pm 0.22$ SE, $z = 2.86$, $p = 0.005$). Cattle grazing positively influenced wood density ($\beta = 0.63 \pm 0.25$ SE, $z = 2.18$, $p = 0.02$), fruit width ($\beta = 0.91 \pm 0.17$ SE, $z = 4.53$, $p = 0.000$), seed length ($\beta = 0.52 \pm 0.27$ SE, $z = 2.10$, $p = 0.03$), and seed width ($\beta = 0.81 \pm 0.21$ SE, $z = 3.31$, $p = 0.000$). Finally, fragment size positively influenced fruit width ($\beta = 0.60 \pm 0.16$ SE, $z = 3.25$, $p = 0.001$) and seed width ($\beta = 0.63 \pm 0.19$ SE, $z = 2.86$, $p = 0.004$). Functional richness, functional dispersion, maximum diameter, and dispersal syndrome were not directly influenced by local CADs variables.

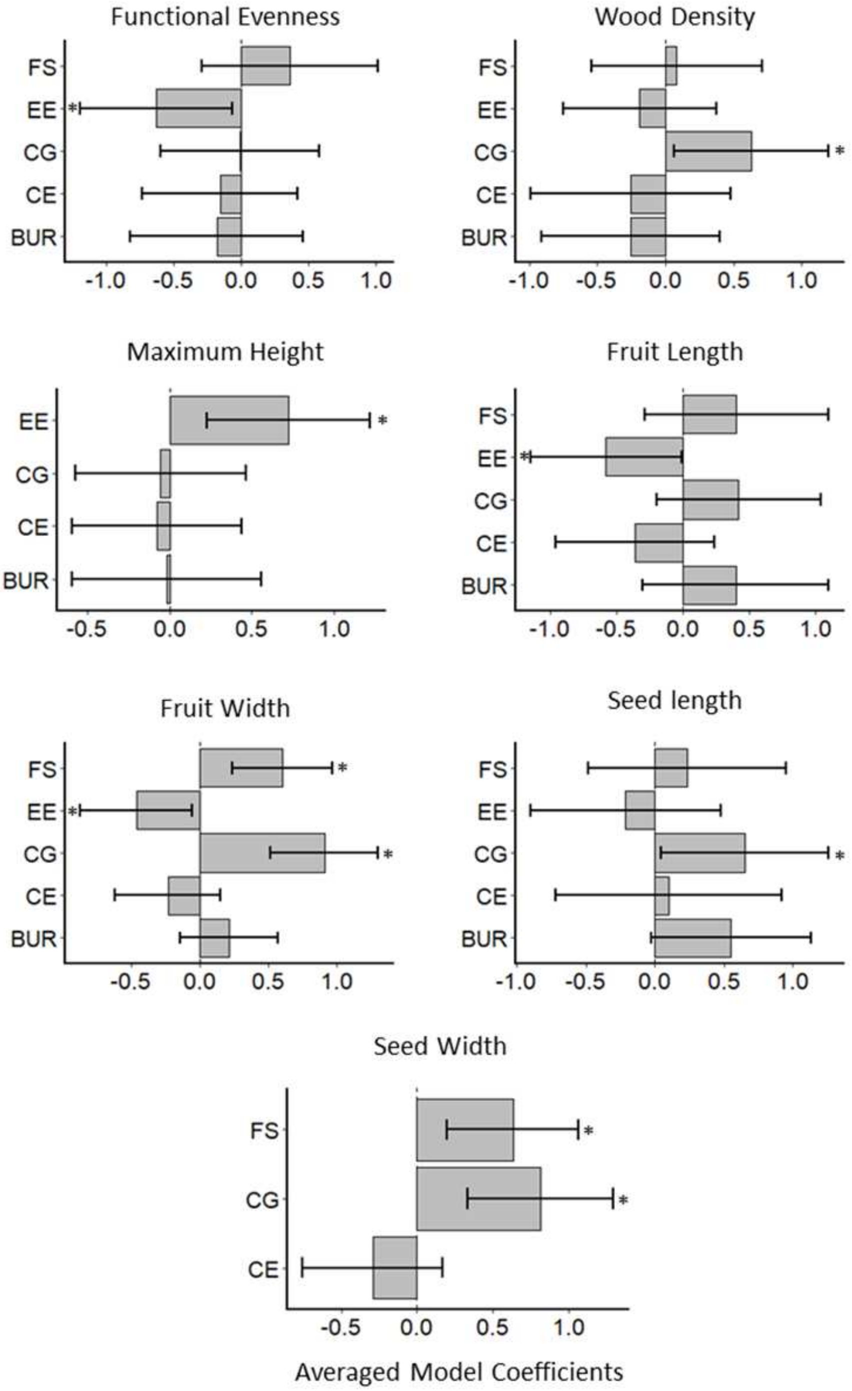


Figure 2. Averaged model coefficients of the main Generalized Linear Models (ΔAICc < 5) to tested the influence of local chronic anthropogenic disturbances (CADs) variables on functional diversity and community weighted means of evaluated traits. The different local scale CADs are indicated: BUR, burning intensity; CG, cattle grazing intensity; CE, *Caryocar brasiliense* fruit extraction intensity; and EE, earthworm (Rhinodrilus alatus) extraction intensity (EE). Only functional diversity e trait community weighted means significatively influenced are indicated and the significant effects are indicated by (*).

Landscape chronic anthropogenic disturbances influences

The landscape CADs influenced functional eveness, maximum diameter, seed length, and dispersal syndrome (Fig.3). The silviculture cover had a negative influence on FEve (β = -0.68 ± 0.23 SE, z = 2.54, p = 0.01). Patch density positively influenced maximum diameter (β = 0.60 ± 0.26 SE, z = 2.00, p =0.04), and seed length (β = 0.73 ± 0.22 SE, z = 2.90, p = 0.003) and negatively influenced dispersal syndrome (β = 0.76 ± 0.20 SE, z = 3.19, p = 0.001). Functional richness, functional dispersion, wood density, maximum height, fruit length, fruit width, and seed width were not directly influenced by landscape CADs variables.

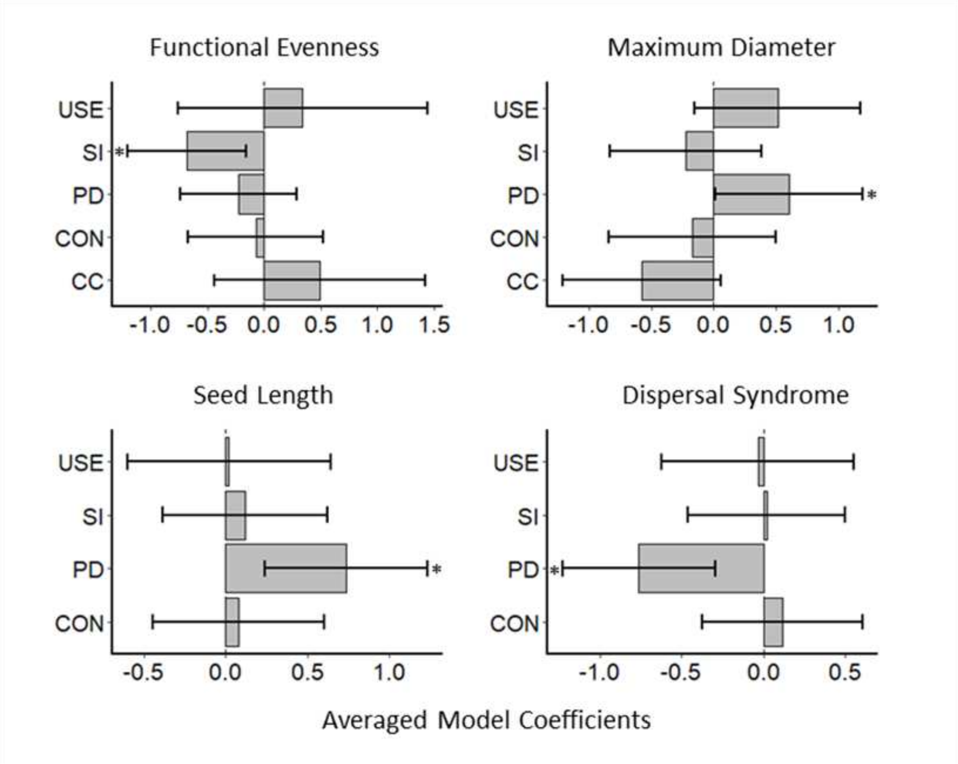


Figure 3. Averaged model coefficients of the main Generalized Linear Models (ΔAICc < 5) used to test the influence of landscape chronic anthropogenic disturbances (CADs) variables on functional diversity and community weighted means of evaluated traits. The different landscape-scale CADs are indicated: CC, Cerrado stricto sensu cover in the landscape; PD, patch density of Cerrado stricto sensu in the landscapes; CON, connectivity of Cerrado stricto sensu patches in the landscape; USE; cover of mosaics between agriculture, pastures, and urbanized areas in the landscape; and SI, silviculture cover (Eucalyptus sp.) in the landscape. Only functional diversity e trait community weighted means significatively influenced are indicated and the significant effects are indicated by (*).

Discussion

We found that local and landscape chronic anthropogenic disturbances cause the loss of functional diversity in the Cerrado *stricto sensu*, as well as change functional composition, increasing the dominance of some functional attributes. These effects are due to favoring of species with greater competitive ability and a greater capacity to colonise environments with CADs (Tabarelli et al. 2010; Sfair et al. 2018; Meira-Neto et al. 2019). Thus, this ecosystem undergoes a process of biotic homogenisation, where most of the woody community has similar functional characteristics (Gámez-Virués et al. 2015; Solar et al. 2015). The results are congruent with studies that evaluated the effect of CADs on the functional diversity of plants and animals in other tropical ecosystems (Magnago et al. 2014; Carrié et al. 2017; Ribeiro et al. 2019) and with expected losses of functional diversity in birds (Batalha et al. 2010) and plants (Rosatti et al. 2015) in the Cerrado.

Local chronic anthropogenic disturbances influence

The effects of CADs on a local scale are evidenced by the influence of cattle grazing, earthworm extraction, and fragment size on functional diversity and composition. These local disturbances directly shift habitat conditions, such as soil characteristics and vegetation structure (Rocha-Santos et al. 2016; Sfair et al. 2018; Sá et al. 2020). Cattle grazing, for example, decreased the density of young individuals and increased the occurrence of plants that are more resistant to trampling, less palatable, and with shorter life cycles (Souza et al. 2010; Giroldo and Scariot 2015; Carlos et al. 2018). In addition, cattle grazing caused the loss of phylogenetic structure in our fragments, possibly due to favoring of plant species with wood density values that are more resistant to trampling, which are phylogenetically conserved in the community (Coelho et al. 2020). The positive influence of CG on wood density community-weighted means corroborates this knowledge. Generally, plants with higher wood densities have larger fruit and seed sizes (Meira-Neto et al. 2019), as shown here by the positive correlation of wood density with fruit length, fruit width, and seed width community-weighted means. Thus, the selection of higher wood densities by cattle grazing may indirectly generate the dominance of larger fruits and seeds in Cerrado communities. However, seed length weighted-community means was positively influenced by cattle grazing but was not correlated with wood density. Another possible explanation for the influence of cattle grazing on the dominance of larger fruits and seeds is that trampling by cattle generates soil compaction and limits the germination of the soil seed bank, which is usually composed of small seeds (Pérez-Harguindeguy et al. 2013).

On the other hand, earthworm extraction may act in contrast to the trampling of cattle, unpacking the soil and allowing the germination of species of smaller seed and fruit sizes. This is corroborated in this study by the negative influence of earthworm extraction on fruit width and fruit length community-weighted means. In addition, this activity can accelerate the soil nutrient cycling allowing the establishment of more characteristic species of woodland physiognomy, which have greater nutrient cycling (Ciotta et al. 2003; Bueno et al. 2013; Neri et al. 2013; Meira-Neto et al. 2017; Santana et al. 2018; Tolentino et al. 2020). In this way, the negative influence of earthworm extraction on functional evenness indicates that earthworm extraction acts as an environmental filter (Villéger et al. 2008; Mouillot et al. 2013) changing the regularity of distribution of some traits evaluated in our community.

The effect of habitat loss can be seen by the positive influence of fragment size on fruit width and seed width community-weighted means. Thus, the smaller the habitat, the smaller the fruit and seed width in the community. One of the biggest problems with smaller fragments is that much of its area is in edge conditions (Ewers and Didham 2006; Zambrano et al. 2019). Thus, these areas are more subject to CADs (Pivello et al. 1999; Mendonça et al. 2015), such as cattle grazing and earthworm extraction. In fact, earthworm extraction intensity was negatively correlated with fragment size in our study area and negatively influenced seed and fruit sizes. In addition, there is less zoochoric species in the edge than on the interior in the Cerrado *stricto sensu* (Jardim and Batalha 2009; Christianini and Oliveira 2013; Mendonça et al. 2015). The edges are inhospitable environments for several dispersers, mainly those of larger sizes that disperse fruits and seeds of larger sizes. Thus, larger fragments, with a smaller part of their areas in edge conditions, tend to have more fruit and seeds of greater width.

Landscape chronic anthropogenic disturbances influence

One of the influences of CADs on a landscape scale was evidenced by the patch density in dispersal syndrome community-weighted means, meaning that in landscapes with many fragments of Cerrado *stricto sensu*, there is a lower abundance of zoochoric individuals. There is a tendency to have smaller fragments and less natural habitats in very fragmented landscapes (Fahrig 2013; Zambrano et al. 2019). Because this, there is a decrease or extinction of animals that need larger habitat sizes for their survival and reproduction (Batalha et al. 2010; Vynne et al. 2011). The exclusion of these animals, like birds and mammals, decreases the zoochoric species dispersion, generally with bigger fruits and seeds (Vynne et al. 2011; Jacoboski et al. 2016; Meira-Neto et al.

2019). This is reinforced by the negative correlation between Cerrado cover in the landscape and patch density and by the positive influences of fragment size on fruit and seed widths. In this way, the positive influence of patch density on seed length community-weighted means was unexpected. In addition, we found a negative correlation between dispersal syndrome and seed length community-weighted means. This can be explained because there is an increase in species dispersed by the wind in very fragmented landscapes (Collevatti et al. 2010; Cote et al. 2017). These species can present adaptations to flight, i.e., increased length, with a smaller width and seed mass.

The positive influence of patch density on maximum diameter community-weighted means showed an opposite pattern found in tropical forests: in less fragmented landscapes the forests have trees of greater diameter and height, with greater capacity to stock biomass. However, in the Cerrado *stricto sensu*, more fragmented landscapes present fragments with a greater above-ground biomass stock (Coelho et al. 2020). This is because the fragmentation can prevent the natural spread of the fire in Cerrado remnants (Abreu et al. 2017). The decrease in the natural frequency of burnings in this biome makes it difficult for endemic species dependent on fire to reproduce and favours the establishment of species intolerant to fire, generally of forest physiognomies, of larger diameter and greater biomass stock capacity (Lehmann et al. 2014; Pellegrini et al. 2016; Abreu et al. 2017).

Finally, the silviculture cover negative influence on functional evenness indicates that monoculture forests function as an environmental filter in the Cerrado, probably selecting characteristics linked to dispersal abilities (Neri et al., 2005). The more different the matrix and fragments, the smaller the movement of animals between fragments, causing reduced dispersal of zoochoric species between them (Haddad et al., 2017). In planted forests, as well as natural forests, there is a greater density of woody individuals, the crown of the trees touch and are also higher when compared to the vegetation of the Cerrado *stricto sensu*. In this way, even-aged eucalyptus plantations, in our case study, in addition to acting as a barrier in the dispersal of zoochoric species, are also barriers to dispersal by wind, decreasing functional trait distribution evenness in Cerrado *stricto sensu* communities.

Conclusions

Our results show that actions to mitigate the impacts of CADs on the functional diversity and composition are needed to maintain biodiversity and ecosystem services in the Cerrado. The CADs evaluated decreased functional evenness and changed functional composition of Cerrado *stricto sensu* patches. Some action, such as the rotation of time and place in earthworm extraction and cattle grazing, can mitigate the intensity with which these disturbances affect the functional diversity and composition of Cerrado communities. Likewise, rotations in land use, alternating between pastures, silviculture, and possibly fallow time, would decrease the negative influences of anthropogenic pressures, such as the intensity of cattle grazing and percentage of eucalyptus plantations in the landscape. It is even more urgent to create policies that aim to reduce the impacts of human exploitation in the Cerrado, considering that the new Brazilian forest code facilitates deforestation in this biome. This may make it even more fragmented, with less coverage of natural habitats, exposing it to CADs and isolation.

References

Abreu RCR, Hoffmann WA, Vasconcelos HL, et al (2017) The biodiversity cost of carbon sequestration in tropical savanna. Sci Adv 3:e1701284. https://doi.org/10.1126/sciadv.1701284

Ackerly DD, Cornwell WK (2007) A trait-based approach to community assembly: Partitioning of species trait values into within- and among-community components. Ecol Lett 10:135–145. https://doi.org/10.1111/j.1461-0248.2006.01006.x

Ali A, Yan ER, Chang SX, et al (2017) Community-weighted mean of leaf traits and divergence of wood traits predict aboveground biomass in secondary subtropical forests. Sci Total Environ 574:654–662. https://doi.org/10.1016/j.scitotenv.2016.09.022

APG IV (2016) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Bot J Linn Soc 181:1–20

Barton K (2017) ‘MuMIn’: Multi-Model Inference.

Batalha MA, Cianciaruso MV, Motta-Junior J carlos (2010) Consequences of simulated loss of open cerrado areas to bird functional diversity. 2010 / 8 1 - 5 Nat e Conserv. https://doi.org/10.1111/j.1365-2699.2012.02715.x

Bueno ML, Neves DRM, Souza AF, et al (2013) Influence of edaphic factors on the floristic composition of an area of cerradão in the brazilian central-west. Acta Bot Brasilica 27:445–455. https://doi.org/10.1590/S0102-33062013000200017

Burnham KP, Anderson DR, Huyvaert KP (2011) AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. Behav Ecol Sociobiol 65:23–35. https://doi.org/10.1007/s00265-010-1029-6

Carlos J, Sá DM, Ruiz D, et al (2018) Soil carbon fractions and biological activity based indices can be used to study the impact of land management and ecological successions. Ecol Indic 84:96–105. https://doi.org/10.1016/j.ecolind.2017.08.029

Carmo AB, Vasconcelos HL, Araújo GM (2011) Estrutura da comunidade de plantas lenhosas em fragmentos de cerrado: relação com o tamanho do fragmento e seu nível de perturbação. Rev Bras Botânica 34:31–38. https://doi.org/10.1590/S0100-84042011000100004

Carrara E, Arroyo-Rodríguez V, Vega-Rivera JH, et al (2015) Impact of landscape composition and configuration on forest specialist and generalist bird species in the fragmented Lacandona rainforest, Mexico. Biol Conserv 184:117–126. https://doi.org/10.1016/j.biocon.2015.01.014

Carrié R, Andrieu E, Cunningham SA, et al (2017) Relationships among ecological traits of wild bee communities along gradients of habitat amount and fragmentation. 85–97. https://doi.org/10.1111/ecog.02632

Cavender-Bares J, Kozak KH, Fine PVA, Kembel SW (2009) The merging of community ecology and phylogenetic biology. Ecol Lett 12:693–715. https://doi.org/10.1111/j.1461-0248.2009.01314.x

Chapin FS (2003) Effects of plant traits on ecosystem and regional processes: A conceptual framework for predicting the consequences of global change. Ann Bot 91:455–463. https://doi.org/10.1093/aob/mcg041

Chave J, Coomes D, Jansen S, et al (2009) Towards a worldwide wood economics spectrum. Ecol Lett 12:351–366. https://doi.org/10.1111/j.1461-0248.2009.01285.x

Christianini A V., Oliveira PS (2013) Edge effects decrease ant-derived benefits to seedlings in a neotropical savanna. Arthropod Plant Interact 7:191–199. https://doi.org/10.1007/s11829-

012-9229-9

Ciotta MN, Bayer C, Fontoura SMV, et al (2003) Matéria orgânica e aumento da capacidade de troca de cátions em solo com argila de atividade baixa sob plantio direto. Ciência Rural 33:1161–1164. https://doi.org/10.1590/s0103-84782003000600026

Coelho AJP, Magnago LFS, Matos FAR, et al (2020) Effects of anthropogenic disturbances on biodiversity and biomass stock of Cerrado, the Brazilian savanna. Biodivers Conserv 0123456789: https://doi.org/10.1007/s10531-020-02013-6

Collevatti RG, Lima JS, Soares TN, Telles MP de C (2010) Spatial genetic structure and life history traits in cerrado tree species: Inferences for conservation. Nat a Conserv 8:54–59. https://doi.org/10.4322/natcon.00801008

Conti G, Díaz S (2013) Plant functional diversity and carbon storage - an empirical test in semi-arid forest ecosystems. J Ecol 101:18–28. https://doi.org/10.1111/1365-2745.12012

Cote J, Bestion E, Jacob S, et al (2017) Evolution of dispersal strategies and dispersal syndromes in fragmented landscapes. 56–73. https://doi.org/10.1111/ecog.02538

Coutinho LM (2006) O conceito de bioma_Biomas brasileiros.pdf. Acta Botânica Bras 20:13–23. https://doi.org/10.1590/S0102-33062006000100002

Dodonov P, Harper KA, Silva-Matos DM (2013) The role of edge contrast and forest structure in edge influence: Vegetation and microclimate at edges in the Brazilian cerrado. Plant Ecol 214:1345–1359. https://doi.org/10.1007/s11258-013-0256-0

Edwards DP, Socolar JB, Mills SC, et al (2019) Conservation of Tropical Forests in the Anthropocene. Curr Biol 29:R1008–R1020. https://doi.org/10.1016/j.cub.2019.08.026

Ewers R, Didham R (2006) Confounding factors in the detection of species responses to habitat fragmentation. Biol Rev Camb Philos Soc 81:117–142. https://doi.org/10.1017/s1464793105006949

Fahrig L (2003) Effects of Habitat Fragmentation on Biodiversity. Annu Rev Ecol Environ Syst 34:487–515. https://doi.org/10.1146/132419

Fahrig L (2013) Rethinking patch size and isolation effects: The habitat amount hypothesis. J Biogeogr 40:1649–1663. https://doi.org/10.1111/jbi.12130

Françoso RD, Brandão R, Nogueira CC, et al (2015) Habitat loss and the effectiveness of protected areas in the Cerrado Biodiversity Hotspot. Nat e Conserv 13:35–40. https://doi.org/10.1016/j.ncon.2015.04.001

Gámez-Virués S, Perović DJ, Gossner MM, et al (2015) Landscape simplification filters species traits and drives biotic homogenization. Nat Commun 6:8568. https://doi.org/10.1038/ncomms9568

Ganem RS, Drummond J a, Franco JL a (2013) Conservation polices and control of habitat fragmentation in the brazilian Cerrado Biome. Ambient Soc 16:99–118. https://doi.org/10.1590/S1414-753X2013000300007

Gardner TA, Barlow J, Chazdon R, et al (2009) Prospects for tropical forest biodiversity in a human-modified world. Ecol Lett 12:561–582. https://doi.org/10.1111/j.1461-0248.2009.01294.x

Giroldo AB, Scariot A (2015) Land use and management affects the demography and conservation of an intensively harvested Cerrado fruit tree species. Biol Conserv 191:150–158. https://doi.org/10.1016/j.biocon.2015.06.020

Grace J, José JS, Meir P, et al (2006) Productivity and carbon fluxes of tropical savannas. J Biogeogr 33:387–400. https://doi.org/10.1111/j.1365-2699.2005.01448.x

Heringer G, Almeida TE, Dittrich VA de O, Salino A (2020a) Assessing the effectiveness of protected areas for the conservation of ferns and lycophytes in the Brazilian state of Minas Gerais. J Nat Conserv 53:. https://doi.org/10.1016/j.jnc.2019.125775

Heringer G, Thiele J, do Amaral CH, et al (2020b) Acacia invasion is facilitated by landscape permeability: The role of habitat degradation and road networks. Appl Veg Sci. https://doi.org/10.1111/avsc.12520

Jacoboski LI, De Mendonça-Lima A, Hartz SM (2016) Structure of bird communities in eucalyptus plantations: nestedness as a pattern of species distribution. J Biol Braz J Biol 76:583–591.

https://doi.org/10.1590/1519-6984.18614

Jardim AVF, Batalha MA (2009) Dispersal syndromes related to edge distance in cerrado sensu stricto fragments of central-western Brazil. Brazilian Arch Biol Technol 52:1167–1177. https://doi.org/10.1590/S1516-89132009000500014

Klink CA, Machado RB (2005) Conservation of the Brazilian Cerrado. Conserv Biol 19:707–713. https://doi.org/10.1111/j.1523-1739.2005.00702.x

Kuhlmann M, Ribeiro JF (2016) Fruits and frugivores of the Brazilian Cerrado: ecological and phylogenetic considerations. Acta Bot Brasilica 30:271–282. https://doi.org/10.1590/0102-33062015abb0331

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

Laurance WF, Camargo JLC, Luizão RCC, et al (2011) The fate of Amazonian forest fragments: A 32-year investigation. Biol Conserv 144:56–67. https://doi.org/10.1016/j.biocon.2010.09.021

Lehmann CER, Anderson TM, Sankaran M, et al (2014) Savanna Vegetation-Fire-Climate Relationships Differ Among Continents. Science (80-) 343:548–553. https://doi.org/10.1126/science.1247355

Lewis SL, Edwards DP, Galbraith D (2015) Increasing human dominance of tropical forests. Science (80-) 349:

Lima ILP, Scariot A, Giroldo AB (2013) Sustainable Harvest of Mangaba (Hancornia speciosa) Fruits in Northern Minas Gerais, Brazil. Econ Bot 67:234–243. https://doi.org/10.1007/s12231-013-9244-5

Liu J, Wilson M, Hu G, et al (2018) How does habitat fragmentation affect the biodiversity and ecosystem functioning relationship? Landsc Ecol 33:341–352. https://doi.org/10.1007/s10980-018-0620-5

Lopes AV, Girão LC, Santos BA, et al (2009) Long-term erosion of tree reproductive trait diversity in edge-dominated Atlantic forest fragments. Biol Conserv 142:1154–1165. https://doi.org/10.1016/j.biocon.2009.01.007

Machado IC, Lopes AV (2004) Floral traits and pollination systems in the Caatinga, a Brazilian tropical dry forest. Ann Bot 94:365–376. https://doi.org/10.1093/aob/mch152

Magnago LFS, Edwards DP, Edwards FA, et al (2014) Functional attributes change but functional richness is unchanged after fragmentation of Brazilian Atlantic forests. J Ecol 102:475–485. https://doi.org/10.1111/1365-2745.12206

Mason NWH, De Bello F, Mouillot D, et al (2013) A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. J Veg Sci 24:794–806. https://doi.org/10.1111/jvs.12013

Matos FAR, Magnago LFS, Gastauer M, et al (2016) Effects of landscape configuration and composition on phylogenetic diversity of trees in a highly fragmented tropical forest. J Ecol. https://doi.org/10.1111/1365-2745.12661

McGarial K, Cushman SA, Ene E (2012) FRAGSTATS v4: spatial patern analysis program for categorical and continuous maps

Meira-Neto JAA, Nunes Cândido HM, Miazaki Â, et al (2019) Drivers of the growth–survival trade-off in a tropical forest. J Veg Sci 30:1184–1194. https://doi.org/10.1111/jvs.12810

Meira-Neto JAA, Tolentino GS, da Silva MCNA, et al (2017) Functional antagonism between nitrogen-fixing leguminous trees and calcicole-drought-tolerant trees in the Cerrado. Acta Bot Brasilica 31:11–18. https://doi.org/10.1590/0102-33062016abb0380

Melo FPL, Arroyo-Rodríguez V, Fahrig L, et al (2013) On the hope for biodiversity-friendly tropical landscapes. Trends Ecol Evol 28:461–468. https://doi.org/10.1016/j.tree.2013.01.001

Mendonça AH, Russo C, Melo ACG, Durigan G (2015) Edge effects in savanna fragments: a case study in the cerrado. Plant Ecol Divers 0874:1–11. https://doi.org/10.1080/17550874.2015.1014068

Metzger JP (1997) Relationships between landscape structure and tree species diversity in tropical forests of South-East Brazil. 35:29–35

Miranda a C, Miranda a C, Miranda HS, et al (1997) Fluxes of carbon, water and energy over Brazilian cerrado: an analysis using eddy covariance and stable isotopes. Plant, Cell Environ 20:315–328. https://doi.org/10.1046/j.1365-3040.1997.d01-80.x

Mouchet MA, Villéger S, Mason NWH, Mouillot D (2010) Functional diversity measures: An overview of their redundancy and their ability to discriminate community assembly rules. Funct Ecol 24:867–876. https://doi.org/10.1111/j.1365-2435.2010.01695.x

Mouillot, Graham, Villéger, et al (2013) A functional approach reveals community responses to disturbances. Trends Ecol Evol 28:167–177. https://doi.org/10.1016/j.tree.2012.10.004

Myers N, Mittermeier RA, Mittermeier CG, et al (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858

Nazareno AG, Feres JM, de Carvalho D, et al (2012) Serious New Threat to Brazilian Forests. Conserv Biol 26:5–6. https://doi.org/10.1111/j.1523-1739.2011.01798.x

Neri A V., Schaefer CEGR, Souza AL, et al (2013) Pedology and plant physiognomies in the cerrado, Brazil. An Acad Bras Cienc 85:87–102. https://doi.org/10.1590/S0001-37652013000100007

Oliveira-Filho AT, Ratter JA (2002) Vegetation Physiognomies and Woody Flora of the Cerrado Biome. In: The Cerrados of Brazil. pp 91–120

Oliveira FMP, Andersen AN, Arnan X, et al (2019) Effects of increasing aridity and chronic anthropogenic disturbance on seed dispersal by ants in Brazilian Caatinga. J Anim Ecol 88:870–880. https://doi.org/10.1111/1365-2656.12979

Pellegrini AFA, Socolar JB, Elsen PR, Giam X (2016) Trade-offs between savanna woody plant diversity and carbon storage in the Brazilian Cerrado. Glob Chang Biol 1–10. https://doi.org/10.1111/gcb.13259

Pérez-Harguindeguy N, Díaz S, Lavorel S, et al (2013) New Handbook for standardized measurment of plant functional traits worldwide. Aust J Bot 23:167–234.

https://doi.org/http://dx.doi.org/10.1071/BT12225

Pivello V, Carvalho V, Lopes P (1999) Abundance and distribution of native and alien grasses in a "Cerrado"(Brazilian Savanna) biological reserve. Biotropica 31:71–82. https://doi.org/10.1111/j.1744-7429.1999.tb00117.x

Poisot T, Mouquet N, Gravel D (2013) Trophic complementarity drives the biodiversity-ecosystem functioning relationship in food webs. Ecol Lett 16:853–861. https://doi.org/10.1111/ele.12118

Poorter L, Rozendaal DMA, Bongers F, et al (2019) Wet and dry tropical forests show opposite successional pathways in wood density but converge over time. Nat Ecol Evol 3:928–934. https://doi.org/10.1038/s41559-019-0882-6

Ratter J a., Ribeiro JF, S. B (1997) The Brazilian Cerrado Vegetation and Threats to its Biodiversity. Ann Bot 80:223–230. https://doi.org/10.1006/anbo.1997.0469

Ribeiro-Neto JD, Arnan X, Tabarelli M, Leal IR (2016) Chronic anthropogenic disturbance causes homogenization of plant and ant communities in the Brazilian Caatinga. Biodivers Conserv 25:943–956. https://doi.org/10.1007/s10531-016-1099-5

Ribeiro EMS, Lohbeck M, Santos BA, et al (2019) Functional diversity and composition of Caatinga woody flora are negatively impacted by chronic anthropogenic disturbance. J Ecol 107:2291–2302. https://doi.org/10.1111/1365-2745.13177

Ribeiro EMS, Santos BA, Arroyo-Rodr??guez V, et al (2016) Phylogenetic impoverishment of plant communities following chronic human disturbances in the Brazilian Caatinga. Ecology 97:1583–1592. https://doi.org/10.1890/15-1122.1

Ricotta C, Moretti M (2011) CWM and Rao's quadratic diversity: A unified framework for functional ecology. Oecologia 167:181–188. https://doi.org/10.1007/s00442-011-1965-5

Rocha-Santos L, Pessoa MS, Cassano CR, et al (2016) The shrinkage of a forest: Landscape-scale deforestation leading to overall changes in local forest structure. Biol Conserv 196:1–9. https://doi.org/10.1016/j.biocon.2016.01.028

Rosatti NB, Silva DM, Batalha MA (2015) Loss of phylogenetic and functional originalities of woody cerrado species in simulated extinction scenarios. Austral Ecol 40:267–274. https://doi.org/10.1111/aec.12210

Sá D, Scariot A, Ferreira JB (2020) Effects of ecological and anthropogenic factors on population demography of the harvested Butia capitata palm in the Brazilian Cerrado. Biodivers Conserv 29:1571–1588. https://doi.org/10.1007/s10531-018-1669-9

Sano SM, Semíramis A, Ribeiro JF (2008) Cerrado: ecologia e flora

Santana JS, Lima EF, Komatsu RS, et al (2018) CARACTERIZAÇÃO FÍSICA E QUÍMICA DE SOLO EM SISTEMAS DE MANEJO PLANTIO DIRETO E CONVENCIONAL. Encicl Biosf 15:22. https://doi.org/10.18677/EnciBio

Santos AJB, Quesada CA, Da Silva GT, et al (2004) High rates of net ecosystem carbon assimilation by Brachiara pasture in the Brazilian Cerrado. Glob Chang Biol 10:877–885. https://doi.org/10.1111/j.1529-8817.2003.00777.x

Schmidt IB, Ticktin T (2012) When lessons from population models and local ecological knowledge coincide - Effects of flower stalk harvesting in the Brazilian savanna. Biol Conserv 152:187–195. https://doi.org/10.1016/j.biocon.2012.03.018

Sfair JC, De Bello F, De Frana TQ, et al (2018) Chronic human disturbance affects plant trait distribution in a seasonally dry tropical forest. Environ Res Lett 13:. https://doi.org/10.1088/1748-9326/aa9f5e

Silva-Júnior MC, Santos GC (2005) 100 Árvores do Cerrado: Guia de Campo. Rede de Sementes do Cerrado

Soares-filho B, Rajão R, Macedo M, et al (2014) Cracking Brazil ’ s Forest Code. 363–364

Solar R, Barlow J, Ferreira J, et al (2015) How pervasive is biotic homogenization in human-modified tropical forest landscapes? Ecol Lett 18:1108–1118. https://doi.org/10.1111/ele.12494

Solar RR de C, Barlow J, Andersen AN, et al (2016) Biodiversity consequences of land-use change and forest disturbance in the Amazon: A multi-scale assessment using ant communities. Biol Conserv 197:98–107. https://doi.org/10.1016/j.biocon.2016.03.005

Souza IF, Souza AF, Pizo MA, Ganade G (2010) Using tree population size structures to assess the impacts of cattle grazing and eucalypts plantations in subtropical South America. Biodivers Conserv 19:1683–1698. https://doi.org/10.1007/s10531-010-9796-y

Tabarelli M, Aguiar A V., Girão LC, et al (2010) Effects of pioneer tree species hyperabundance on forest fragments in Northeastern Brazil. Conserv Biol 24:1654–1663. https://doi.org/10.1111/j.1523-1739.2010.01529.x

Tolentino G, Maguas C, Magnago L, et al (2020) Groups Of Species Responding To Soil And Light In The Cerrado. https://doi.org/10.1101/2020.02.20.955955

Tscharntke T, Clough Y, Wanger TC, et al (2012) Global food security, biodiversity conservation and the future of agricultural intensification. Biol Conserv 151:53–59. https://doi.org/10.1016/j.biocon.2012.01.068

Vanmelis J, Camargo MGG, Carvalho PG, et al (2020) Contrasting edge effect on lianas and trees in a cerrado savanna remnant. Austral Ecol 1–12. https://doi.org/10.1111/aec.12968

Villa PM, Ali A, Venâncio Martins S, et al (2020) Stand structural attributes and functional trait composition overrule the effects of functional divergence on aboveground biomass during Amazon forest succession. For Ecol Manage 477:118481. https://doi.org/10.1016/j.foreco.2020.118481

Villa PM, Martins SV, Diniz ÉS, et al (2021) Taxonomic and functional beta diversity of woody communities along Amazon forest succession: The relative importance of stand age, soil properties and spatial factor. For Ecol Manage 482:118885. https://doi.org/https://doi.org/10.1016/j.foreco.2020.118885

Villéger S, Mason NWH, Mouillot D (2008) New multidimensional functional diversity indices for a multifaceted framwork in functional ecology. Ecology 89:2290–2301. https://doi.org/10.1890/07-1206.1

Vynne C, Keim JL, Machado RB, et al (2011) Resource selection and its implications for wide-ranging mammals of the Brazilian Cerrado. PLoS One 6:. https://doi.org/10.1371/journal.pone.0028939

Walker WS, Gorelik SR, Baccini A, et al (2020) The role of forest conversion, degradation, and disturbance in the carbon dynamics of Amazon indigenous territories and protected areas. Proc Natl Acad Sci U S A 117:3015–3025. https://doi.org/10.1073/pnas.1913321117

Walter BMT, Carvalho A, Ribeiro JF (2008) O conceito de Savana e de seu componente Cerrado. In: Cerrado: ecologia e flora. pp 21–45

Whittingham MJ, Swetnam RD, Wilson JD, et al (2005) Habitat selection by yellowhammers Emberiza citrinella on lowland farmland at two spatial scales: Implications for conservation management. J Appl Ecol 42:270–280. https://doi.org/10.1111/j.1365-2664.2005.01007.x

Zambrano J, Garzon-Lopez CX, Yeager L, et al (2019) The effects of habitat loss and fragmentation on plant functional traits and functional diversity: what do we know so far? Oecologia 191:505–518

Zanne AE, Lopez-Gonzalez, G., Coomes DA, Ilic J, et al (2009) Data from: Towards a worldwide wood economics spectrum, Dryad

Supplementary Material

Table 1. Details of sampling and calculations of the intensity of chronic anthropogenic disorders on a local scale.

Disturbance	Code	Scale	Sampling Methods
Burning	BUR	Intensity	Total volume of biomass reached by burning within the plot in individuals with CAS≥10cm. The equation obtained by Cetec (1995) was used to calculate the total volume of the stem with the bark in woody individuals: Total volume = (0.000038857 x Diameter^1.70764 x Height reached by fire^1.32032).
Cattle Grazing	CG	Intensity (0-3)	Interviews with the owners regarding the circulation of cattle inside the fragments in the last 10 years and observation of traces (feces and footprints) within the plots: "0", there were no traces or records of cattle circulation in the given period; "1", there were no traces, but in the last 10 years there has been frequent cattle grazing in the fragment; "2", there were traces in the plot and records of frequent cattle grazing in the given period; "3" there were traces in the plot and records of intense cattle circulation in the fragment in the last 10 years.
Earthworm Extraction	EE	Intensity (0-3)	Interview with the owners regarding the performance of extractors in the last 10 years besides the quantification of focus of earthworm extraction within the plots: "0", there was no focus of earthworm extraction in the plot or record of the performance of extractors in the fragment during the last 10 years; "1", there was no focus of earthworm extraction in the plot, but sporadic action of extractors was recorded in the fragment during the given period; "2", there was a focus of earthworm extraction in the plot and frequent records of the performance of extractors in the fragment during the given period; "3", there were two or more focus of earthworm extraction in the plot and records of annual and intense

			performance of extractors in the fragment during the last 10 years.
Caryocar Extraction	CE	Intensity (0-3)	Observation in the plot of traces of caryocar collection (organic bark and fruit remains abandoned in the plot) and interviews with the owners of the fragments and residents of the region regarding the extraction of caryocar in the last 10 years: "0", there was no trace or record of caryocar extraction in the fragment during the given period; "1" did not present traces of caryocar collection, but there were records of collection during the last 10 years for family consumption; "2", there were traces or frequent records of collection for family consumption and/or commercialization in the community in the given period; "3", there was a large accumulation of traces near the plot and records of intense collection of caryocar for commercialization beyond the community.

CHAPTER 3*: Atlantic Forest recovery after long-term eucalyptus plantations: the role of zoochoric and shade-tolerant tree species on carbon stock

Abstract: Currently, about a third of the world's forest areas that have been deforested are regrowing. These second-growth forests (SGF) promote carbon stocks and tree species richness recovery (co-benefits recovery), which is central to mitigating the negative impact of climate change and loss of biodiversity. In Brazil's Atlantic Forest, second-growth forests that are regrowing after eucalyptus (Eucalyptus sp.) plantations can have important carbon-tree diversity co-benefits. Thus, we evaluate the recovery of tree species richness and above-ground carbon stock (AGC) in second-growth forests that are regrowing after a long-period of eucalyptus plantations. For this we sampled 43 SGF with stand ages varying from 1 - 32 years after eucalyptus plantations cutting and three reference old-growth forests (OGF). We considered all individuals with more than 15 cm of circumference at breast height in one 20×50m plot by patch. We identified all tree species, which were categorized into functional attributes, such as zoochoric and non-zoochoric, pioneer and shade-tolerant, and fleshy and dry fruits species. There were marked differences in species richness and AGC between OGF and SGF, but SGFs were not different between then. However, in 32 years these second-growth forests recovered ~38% of species richness and ~14% of carbon stock of old-growth forests. In addition, there was a carbon-biodiversity co-benefits mainly between zoochoric and shade-tolerant species richness. These results showed that these second-growth forests could naturally recover biodiversity and AGC. Possibly, this is due to the connectivity provided by land-use for eucalyptus plantations that induces favorable conditions to zoochoric and shade-tolerant species recruitment and thus recovery of biodiversity and AGC after eucalyptus cutting. Thus, this second-growth forest management can contribute to Atlantic Forest biodiversity conservation and carbon stock initiatives.

Keywords: Forest recovery, secondary succession, eucalyptus plantations, passive restoration, carbon-biodiversity co-benefits.

---

* This chapter are submitted in Forest Ecology and Management.

Introduction

Currently, about a third of the world's forest areas have been deforested are second-growth forests (SGF) with different successional stages (Hansen et al., 2013; Arroyo-Rodríguez et al., 2017). These SGF are important reservoir of biodiversity which provides multiples ecosystem services, such as carbon dynamic and stock, , and non-timber forestry resources (food, medicines, fibers) as a sustainable livelihood (Chazdon et al., 2016; Klemick, 2011; Roberts et al., 2018). Furthermore, SGF can promote carbon-biodiversity co-benefits, i.e., carbon stock recovery along with a positive relationship with tree species richness (Liang et al., 2016; Matos et al., 2020; Osuri et al., 2020). Thus, SGF become central to mitigate the impact of climate change and biodiversity loss on a global scale (Gellie et al., 2018; Hansen et al., 2020). However, anthropogenic disturbances (i.e., land-use change for logging, agriculture, pasture) can affect negatively the recovery of biodiversity, carbon stock and ecosystems services along tropical forest (Fernandes Neto et al., 2019; Jakovac et al., 2015; Sloan et al., 2015; Villa et al., 2018). In this context, understanding how these SGF can contribute to biodiversity and carbon stock recovery under different forest types and land-use is an scenarios important issues in tropical forest ecology management and conservation (e.g., Matos et al., 2020; Rozendaal et al., 2019).

Studies on SGF in different ecological contexts have been compared mainly changes in tree community diversity and structure using as reference the old-growth forests (OGF) and estimating the recovery rate (e.g., Rozendaal et al., 2019; Poorter et al., 2019; Villa et al., 2020b). Furthermore, beyond these stand-age dependent forest attributes, the variation in the relative importance of functional attributes (i.e., seed dispersal syndrome, fruit types, regeneration strategies) on carbon during natural regeneration of SGF (Jakovac et al., 2015; Poorter et al., 2016; Pyles et al., 2018; Rodrigues et al., 2019; Santo-Silva et al., 2016, 2013), can also be important to estimate the recovery rate. However, the few studies that analyze the contribution of different functional attributes on carbon recovery are based on a community scale (considering all tree species). For example, early successional stages of SGF that are re-growing after disturbances harbor predominantly fast-growth and light-demanding pioneer species with short life cycles between 10 and 15 years (Chazdon, 2014; Guariguata and Ostertag, 2001; Chazdon 2014; Villa et al., 2018, 2019) along with dominance of anemochoric and autochoric (non-zoochoric) pioneer species (Chazdon 2014; Santo-Silva et al., 2016). Then, shade-tolerant and long-lived species gradually dominate the forest canopy, along late-successional stages and OGF (Chazdon, 2014; Poorter et al., 2019). The non-zoochoric species occurrence also decreases during late-successional stages, while the dominance of zoochoric species increases in OGF (e.g. Santo-Silva et al., 2016). Thus, these changes in tree species richness consequently influences the carbon stock (Osuri et al., 2014; Safar et al., 2020) and possibly carbon-biodiversity co-benefits.

In this context, as one of Earth's most biodiverse regions, Brazilian Atlantic Forest is an important to investigate carbon-biodiversity co-benefits changes along forest succession. This ecological region is one of the world's hotspots for biodiversity conservation (Myers et al., 2000) and suffered a drastic reduction in forest cover with only 12.5% of forest remnants (considering areas with more than 3 hectares; Scarano and Ceotto 2015). A recent study showed that after 20 years of regeneration, the second-growth forests on Atlantic Forest have recovered on average 52% of total species richness and 16% of carbon stock compared to old-growth forests (Safar et al., 2020). Moreover, co-benefit between above-ground carbon stock and biodiversity has been found after 30 years of Atlantic Forest succession, which recovered an average of 76% of species richness and 20% of carbon stock of the old-growth forest (Matos et al., 2020). Although carbon recovery is slow in these second-growth forests, there is a high positive relationship between carbon and biodiversity, which can be an important strategy to reducing emissions from deforestation and forest degradation, and conserve biodiversity (Matos et al., 2020; McCarthy et al., 2012). However, evaluating the forest recovery and carbon-biodiversity co-benefits after a specific land-use type of eucalyptus plantations and the relative contribution of functional attributes in the Atlantic Forest are still necessary to improve management and conservation criteria.

Here, we evaluated the tree species richness and carbon stock recovery and the carbon-tree species richness co-benefits along Atlantic Forest succession after a long-term of eucalyptus plantation. Thus, we postulate three main research questions: (i) What is the difference in tree species richness and above-ground carbon stock (AGC) between secondary forests growing after a long-term of eucalyptus plantation and nearby old-growth forests? (ii) Are these second-growth forests recovering tree species richness and AGC along stand age? and (iii) Is there co-benefit between tree species richness (total and by functional attributes) and AGC in these second-growth forests?

Material and Methods

Study area

This study was carried out in a semideciduous seasonal Atlantic Forest in the Rio Doce Basin (19°48'29"S; 42°37'40"W), beside to Rio Doce State Park in Minas Gerais State, Brazil (Fig. 1A). The study area is specifically between Dionísio, São José do Goiabal, São Pedro dos Ferros, and Timóteo, municipalities of the Minas Gerais state (Fig. 1B). This region has a long land-use history which consisted mainly in converting natural habitat to agriculture, livestock and planted forests (Oliveira-Junior et al., 2020; Scarano and Ceotto, 2015). Thus, these forests are found mainly as SGFs (i.e., forests that are regrowing after anthropogenic disturbance) in small remnant fragments representing less than 12% of the original forest (Scarano and Ceotto, 2015). The regional climate, according to Köppen classification is Aw with mean annual precipitation of 1450 mm and mean temperature ranging between 20 and 23 °C (Alvares et al., 2013). The study area presents two dominant soil classes, a Red-Yellow Latosol covers hilltops and mountainsides (Santos et al., 2018).

Specifically, our study area has a complex landscape configuration represented mainly by second-growth forests patches with different stand age (3 to 32 years old), and old-growth forest patches (Fig. 1C, and Table A1 from Appendices). The second-growth forests sampled were inserted in areas previously occupied by eucalyptus plantation with at least 30 years of land-use. The OGF remnants in the study area occur inside the Rio Doce State Park that is protected since 1962 by Forest Institute of Minas Gerais State.

Sampling design and tree inventory

We sampled 43 forest patches of second-growth forests at different stand ages after eucalyptus cutting and three old-growth forest patches in the study area. At each forest patch (SGF and OGF), from January to March 2018, one plot of 20×50 m (0.1 ha) was randomly installed. Then, all tree individuals with a diameter at breast height (DBH) $\geq$ 4.8 cm and 1.30 m above ground height were sampled (Magnago et al., 2014; Matos et al., 2016). We sampled a total of 4.6 ha of second-growth forests and 0.3 ha of old-growth forests. For those species difficult to identify in the field, their specimens were collected and identified at the Herbarium of the Federal University of Viçosa (VIC) according to Angiosperm Phylogeny Group IV (APG IV, 2016).

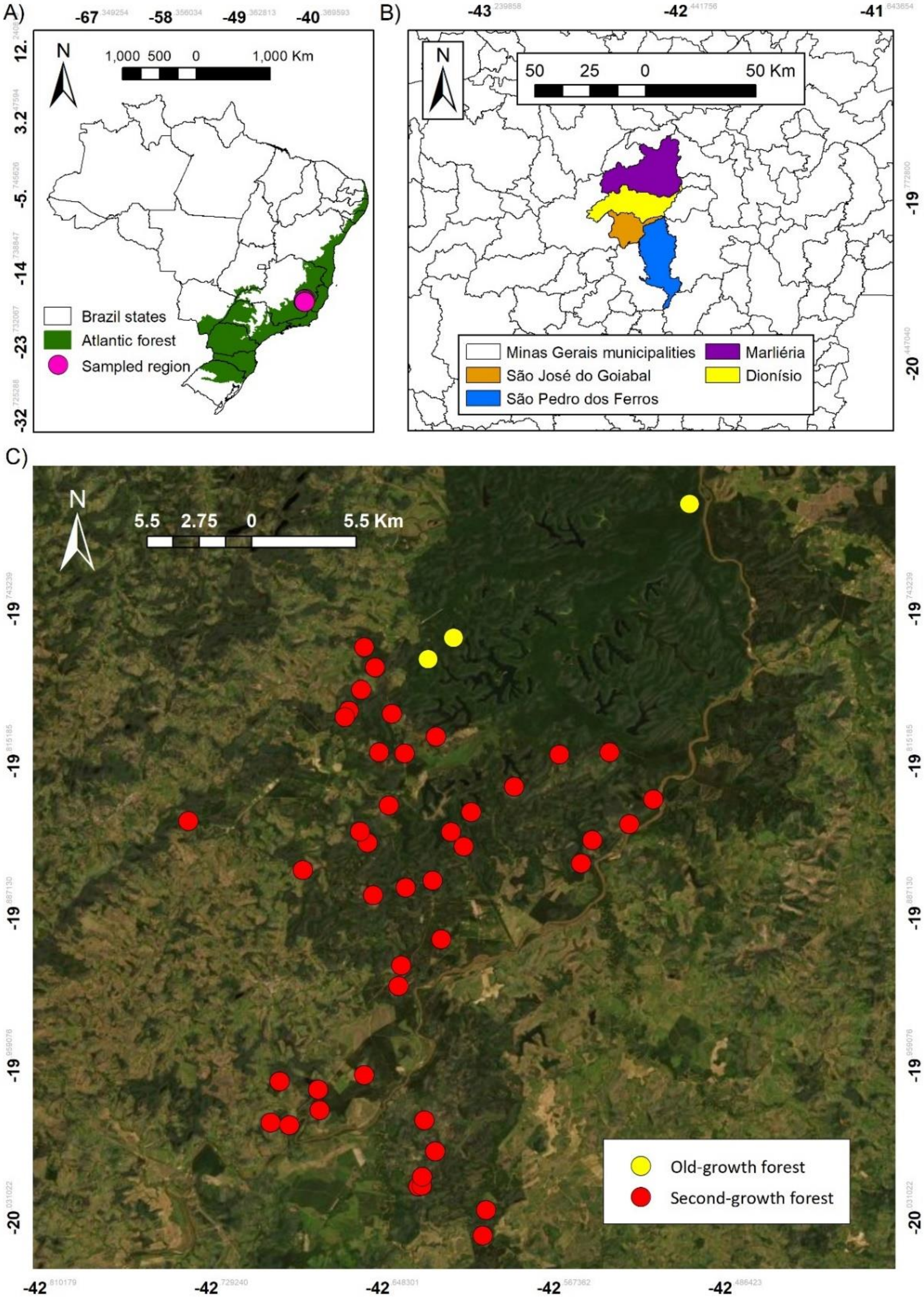


Fig. 1. Localization of the study area and sampling plots in relation to Brazil states (A), Minas Gerais state (B), and forest landscape sampled (C). SGF and OGF sampled plots are indicated with red and yellow dots respectively.

Above-ground carbon quantification

We calculated the biomass of each individual sampled using the equation suggested by Chave et al. (2014):

$$\text{AGBest} = \exp[-1.803 - 0.976E + 0.976\ln(\rho) + 2.673\ln(D) - 0.0299[\ln(D)]^2]$$

where AGBest is the estimated above-ground biomass (Mg), E is a measure of environmental stress; ρ is wood density (g/cm^3) and D (cm) is the diameter of the tree at breast height. This analysis were carried out using the "BIOMASS" package for R (Réjou-Méchain et al., 2017).The environmental stress was obtained in this package using geographic coordinate of each patch. The value for wood density (g/cm^3) was obtained from Global Wood Density database (GWD; Zanne et al., 2009). For species that were not included in the GWD or when they were identified only at the genus level, we used the average density of wood for all species of the same genus included in the database (see Magnago et al., 2014; Matos et al., 2020). Finally, we obtained the carbon stock value for each second-growth forest and old-growth forest assuming as 50% of AGBest of each tree individual sampled (Malhi et al., 2004).

Functional attributes classification

Each sampled tree species was classified into three functional attributes, such as successional strategy, fruit type and dispersal syndrome. Each functional attributes were divided into two categories, for example the successional strategy was categorized into pioneer or shade-tolerant species (Bongers et al., 2009; Magnago et al., 2014). The fruit type was categorized into fleshy fruit or dry fruit. We consider fleshy fruit when accumulate water and many other organic compounds and dry fruit those that do not have these characteristics (Coombe, 1976; Matos et al., 2020). The dispersal syndrome was categorized into zoochoric and non-zoochoric (Magnago et al., 2014; Santo-Silva et al., 2016). The zoochoric species were trees dispersed by animals and non-zoochoric species dispersed by anemochory and autochory. These functional attributes mainly represent the ability to colonize different types of habitats, resist disturbances, and store carbon (Matos et al., 2020; Pérez-Harguindeguy et al., 2013). These traits were obtained for each species from consulting in the data available in the SpeciesLink (for more details see: http://splink.cria.org.br/), by Maganago et al. (2014), and by the database of Matos et al. (2020).

Data analyses

All analyses were run in R 3.6.0 (R Development Core Team, 2019) and to draw the graphs illustration in this study, we used the "ggplot2" package (Hadley, 2015).

Species Richness and Carbon Stock Along Second-Growth Forests and Old-Growth Forests

To compare the species richness and AGC between forest stand ages we divided then in five stand age categories: i) SGF_5yr - 14 second-growth forests which comprises areas between three and seven years of succession; ii) SGF_10yr - 16 second-growth forest which comprises between 8 and 11 years of succession; iii) SGF_18yr - 6 second-growth forests areas with 18 years of regeneration; iv) SGF_30yr - 7 second-growth forests which covers areas between 27 and 32 years of regeneration; vi) and OGF – three protected old-growth forest patches.

Them, to compare species richness between stand age categories we used an individual-based approach to estimate rarefaction and extrapolation curves using the first ($q = 0$) Hill number (Chao et al., 2014). Extrapolations were made based on presence/absence in the plots data of species (Colwell et al., 2012), using the "iNEXT" package (Hsieh et al., 2016). The Hill number was estimated as the mean of 100 replicate bootstrapping runs to estimate 95% confidence intervals. Whenever the 95% confidence intervals did not overlap, species numbers differed significantly at $p < 0.05$ (Colwell et al., 2012).

To compare AGC between stand-age categories we tested the normal distribution of all variables using the Shapiro-Wilk test and the Q-Q graph, and the homogeneity of the variations was evaluated by the Bartlett test (Crawley, 2013). We used Kruskal-Wallis's test followed by a posterior Dunn's test performed with the "dunn.test" package (Dinno, 2017).

Forest Recovery Analysis

We calculated the recovery ratio (Rc) of the species richness, species richness by categorical functional attributes, and of the AGC in each tree community. The forest recovery of each community was based on the equation (2) proposed by Liu et al. (2019):

$$Rc = \frac{SGF}{OGF} \qquad (2)$$

where SGF is the value found in second-growth forests and OGF the average values found of the same variable in the three areas of old-growth forest sampled. Then we used Linear Regression from "stats" package to evaluate the relationship of the species richness recovery, species richness recovery by categorical functional attributes, and aboveground carbon stock recovery rate along the stand age.

Carbon-biodiversity Co-benefits

We applied generalized linear mixed-effects models (GLMMs, with random and fixed effects) to evaluate co-benefits between the aboveground carbon stock and species richness of second-growth forest by categorical functional attributes. Species richness was the response variable (data count), and predictors with fixed effects were carbon stock (continuous explanatory variable) and functional attributes (three discrete explanatory variable). These discrete variables were dispersal syndrome (two levels, zoochoric and non-zoochoric groups), regeneration strategy (two levels, pioneer and shade-tolerant groups), and fruit types (two levels, fleshy and dry groups). The stand age, forest patch and plots were considered as a random effect in all models (Rozendaal et al., 2019). The previous data analysis distribution, the Poisson error distribution was tested after checking the most suitable distribution and link function (Fig S4 from SM) (Crawley, 2013; Zuur et al., 2009). We constructed a separate model for each categorical functional attribute (i.e., dispersal syndrome, regeneration strategy, fruit types). All models were calculated using the package "lme4" (Bates et al., 2019).

Results

Species richness and carbon stock along second-growth forests and old-growth forests

In the rarefaction and extrapolation curves we found higher species richness in old-growth forests (OGF) than in second-growth forests (SGF) (Fig 2). However, we did not observe differences between SGFs richness (Fig. 2). In the same way, OGF had higher carbon stock than all the SGF, but all SGF had similar carbon stock values (Fig. 3). Thus, there were differences in carbon stock only between OGF (~130.78 Mg ha^{-1}) and SGF_5yr (~7.08 Mg ha^{-1}; $p < 0.01$), SGF_10yr (~8.73 Mg ha^{-1}; $p < 0.01$), SGF_18yr (~13.64 Mg ha^{-1}; $p < 0.01$), and SGF_30yr (~18.20 Mg ha^{-1}; $p < 0.01$).

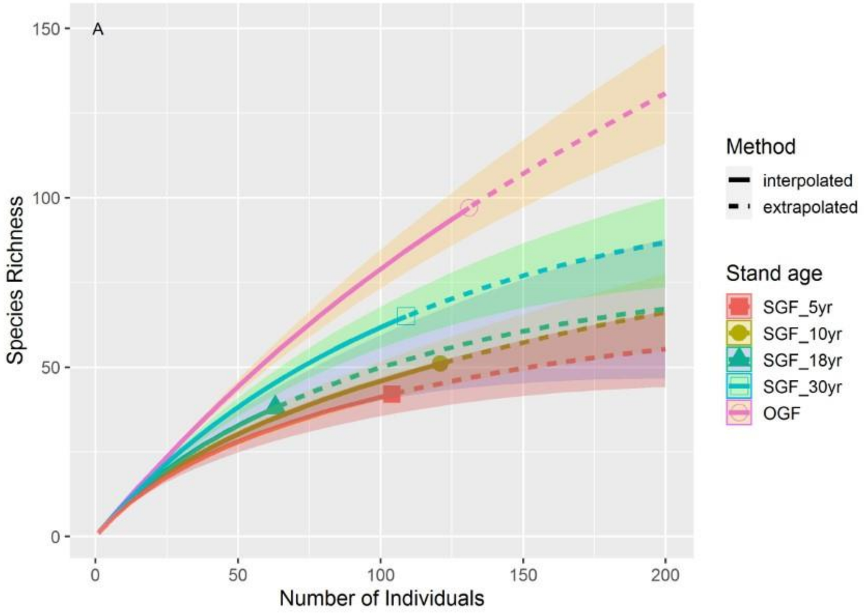


Fig. 2. Rarefaction (solid lines) and extrapolation curves (dashed lines) of woody species diversity based on the first Hill numbers (q = 0) at different stand ages categories (5, 10, 18, and 30 years old) of second-growth forests (SGF) and old-growth forest (OGF).

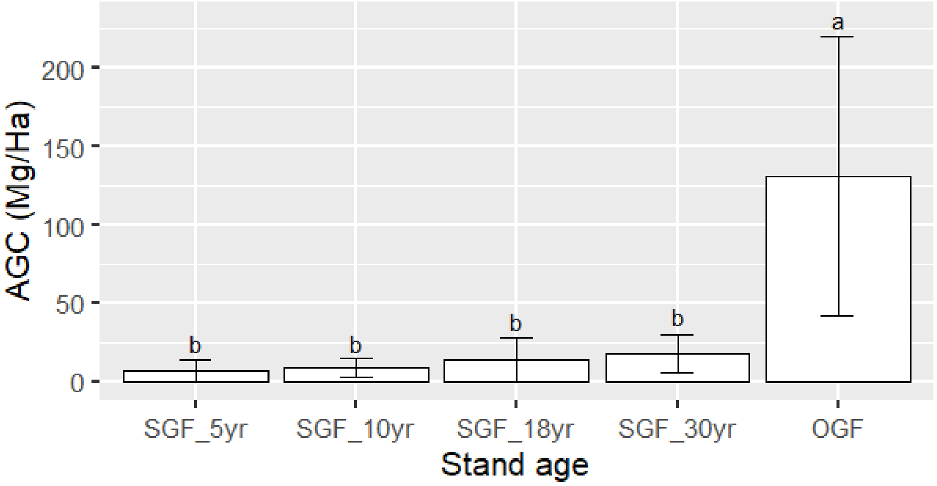


Fig. 3. Differences in aboveground carbon stock (AGC) between second-growth forests (SGF) and old-growth forest patch (OGF). The AGC median value is presented for stand age categories (5, 10, 18, and 30 years old) of second-growth forests and for old-growth forests (OGF). Different letters indicate significant differences (Dunn's test, $p < 0.05$) between stand ages categories.

Species richness and carbon recovery

In 32 years, the evaluated SGFs areas recovered on average 38% of the species richness ($t = 3.585$; $p = 0.0008$), and 14% of carbon stock ($t = 3.059$; $p = 0.0039$) of the OGFs (Fig. 4). The species richness recovery according to successional strategy in these 32 years was ~28% for shade-tolerant species ($t = 3.228$; $p = 0.002$) and ~60% for pioneer species ($t = 2.143$; $p = 0.038$) of the OGF (Fig. 5). The species richness according to of fruit types, showed a recovery rate of ~34% for fleshy fruit species ($t = 3.221$; $p = 0.002$) and ~32% for dry fruit species ($t = 2.495$; $p = 0.016$). By dispersal syndrome, the recovery was ~35% for zoochoric species richness ($t = 3.382$; $p = 0.001$) but the richness recovery of non-zoochoric species did not change (Fig. 5). The AGC relative recovery according to successional strategy was ~42% ($t = 3.822$; $p = 0.0004$) for pioneer species but the carbon recovery of shade-tolerant species did not change along SGF stand age (Fig. 5). The relative carbon recovery was ~7% ($t = 2.988$; $p = 0.004$) for fresh fruit species and ~20% ($t = 2.314$; $p = 0.025$) for dry fruit species. Finally, the carbon relative recovery was ~12% ($t = 2.444$; $p = 0.018$) for zoochoric species but the carbon recovery of non-zoochoric species did not change across the stand age (Fig. 5).

Carbon-biodiversity co-benefits

Our tested models showed a significant positive relationship between AGC and species richness of evaluated SGFs in all categorical functional attributes (Fig. 6). Thus, the variation in aboveground carbon stock had the strongest positive effect on the variation of species richness of dispersal syndromes (Est. = 0.09, $z = 3.03$, $p < 0.002$, $R^2 = 0.71$), fruit types (Est. = 0.01, $z = 0.16$, $p < 0.001$, $R^2 = 0.64$) and regeneration strategy (Est. = 0.08, $z = 3.23$, $p < 0.001$, $R^2 = 0.73$). When analyzed by categorical functional attributes, we observed that zoochoric species (Est. = 1.01, $z = 8.6$, $p < 0.001$, $R^2 = 0.54$) and shade-tolerant species (Est. = 0.96, $z = 8.82$, $p < 0.001$, $R^2 = 0.73$) have a strong and positive relationship between AGC and species richness, but fleshy fruits species do not have this relationship (Est. = 0.01, $z = 0.16$, $p = 0.87$, $R^2 = 0.14$).

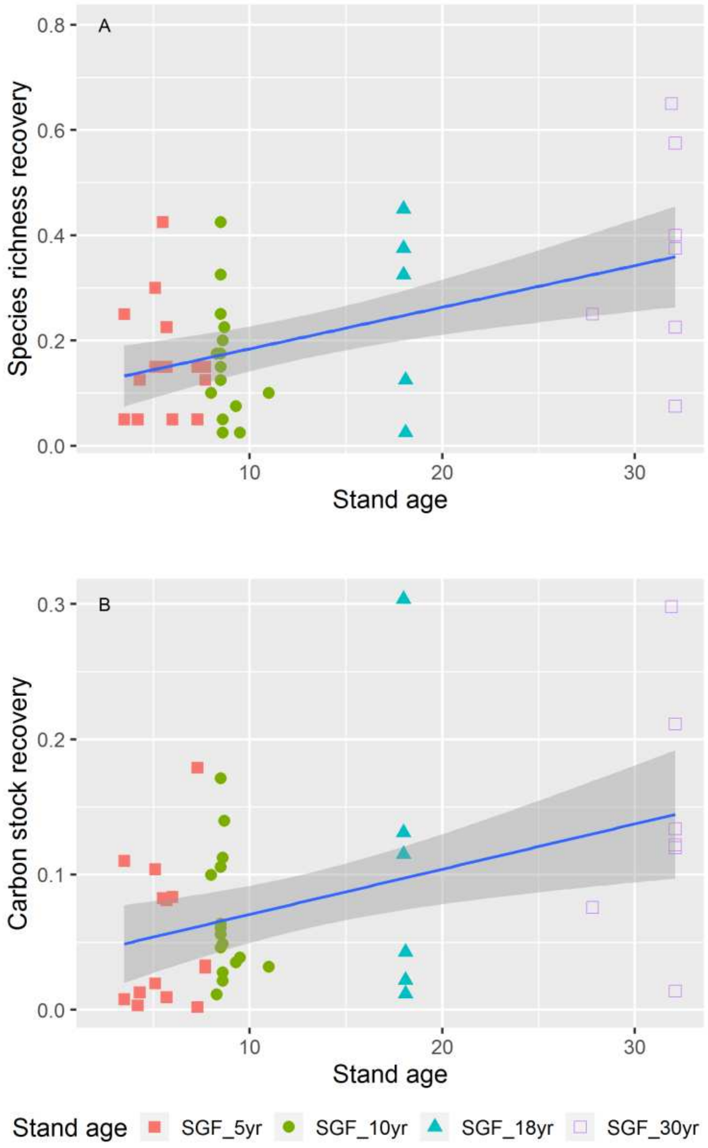


Fig. 4. Relationships between species richness relative recovery (A) and aboveground carbon relative recovery (B) with second-growth forests stand age. The dots are the observed data, the lines are the predictions from the model, and the shaded area is the 95% confidence interval.

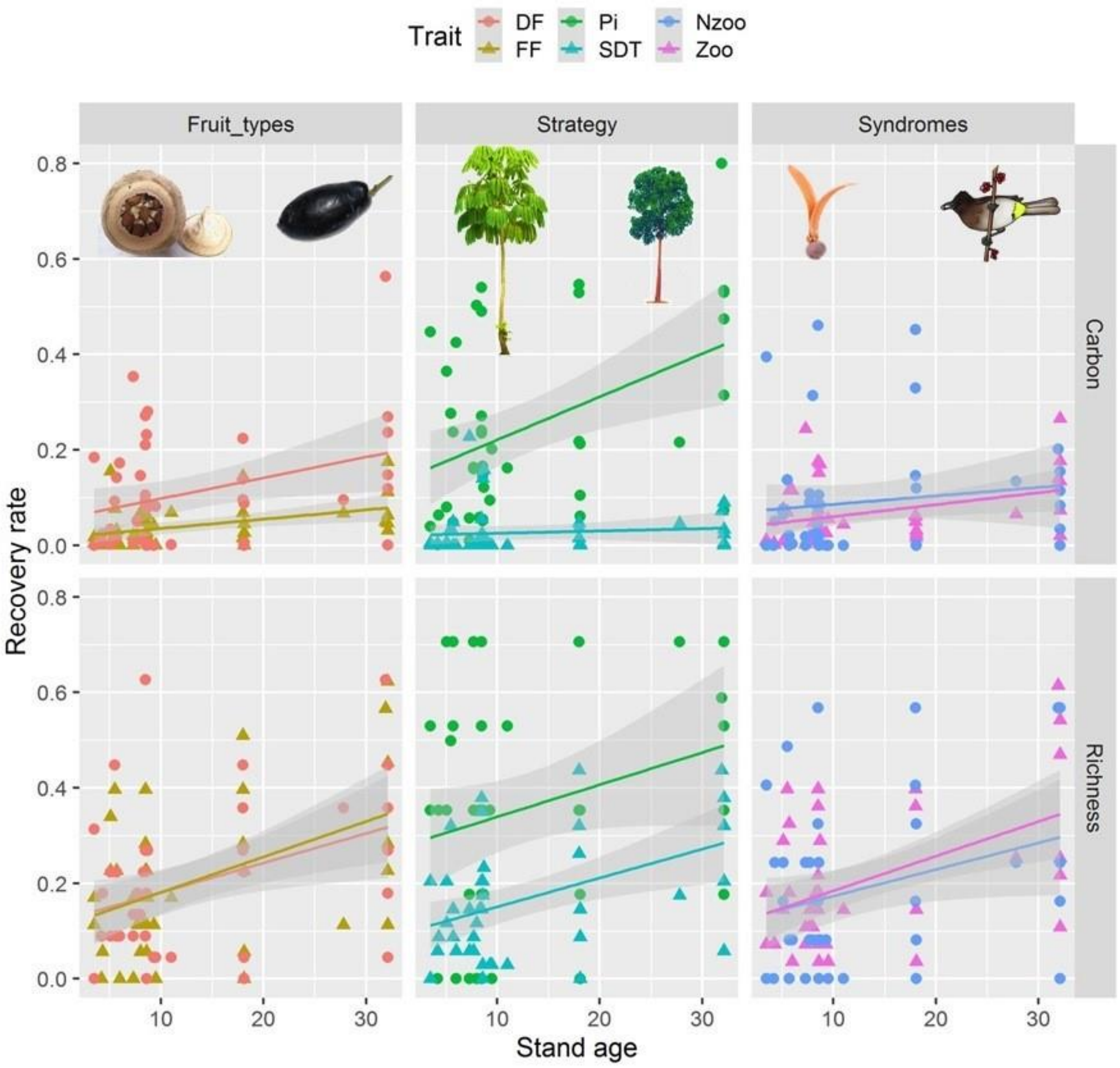


Fig. 5. Relationships between species richness and aboveground carbon relative recovery by functional attributes along second-growth forest stand age. We considered three functional attributes: fruit types, fleshy fruits (FF) or dry fruits (DF); regeneration strategy, pioneer (Pi) or shade-tolerant (SDT); and dispersal syndromes, zoochoric (Zoo) and non-zoochoric (Nzoo). The dots are the observed data, the lines are the predictions from the model, and the shaded area is the 95% confidence interval.

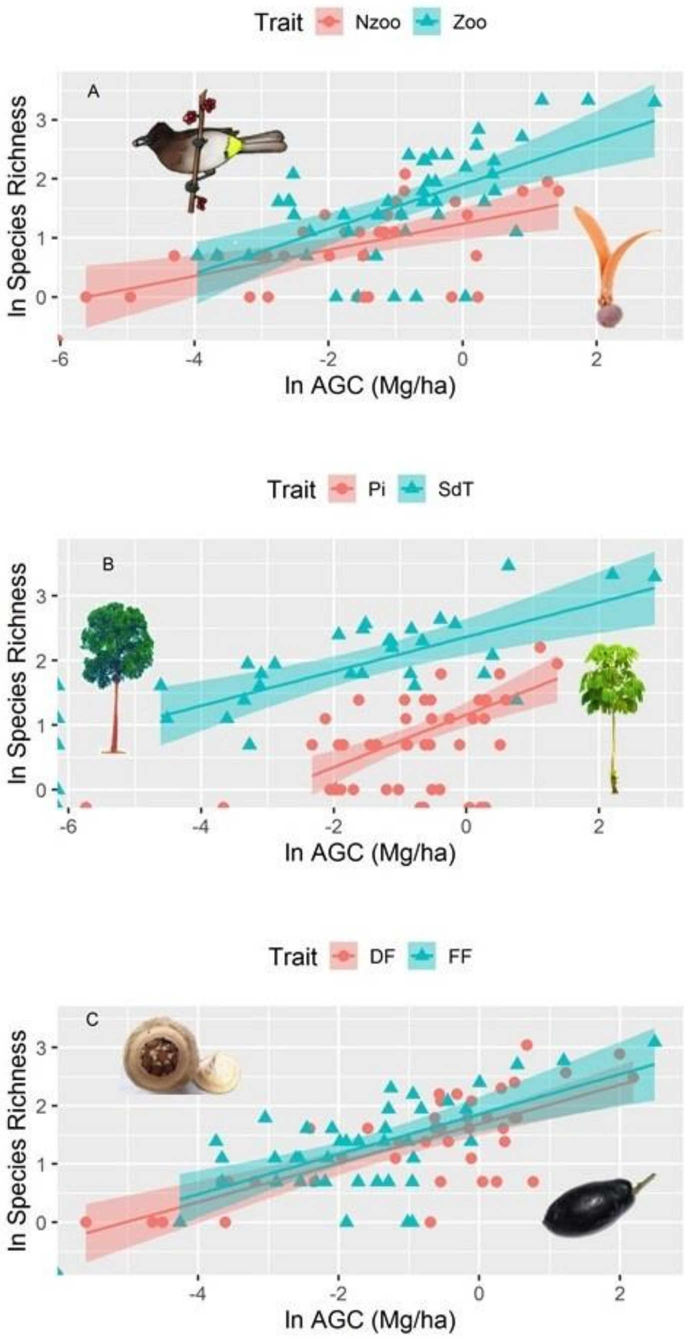


Fig 6. Relationships between aboveground carbon stock (AGC) and species richness of the evaluated second-growth forests by categorical functional attributes: A) dispersal syndromes, zoochoric (Zoo) or non-zoochoric (Nzoo) tree species); B) regeneration strategy, pioneer (Pi) or shade-tolerant (SdT); and C) fruit types, fleshy fruits (FF) or dry fruits (DF). Solid lines represent fitted (predicted) values of the models, and the shaded polygons the 95 % associated with the modeled predictions.

Discussion

Our results demonstrate significant rates of Atlantic Forest recovery after a long period of eucalyptus plantation management and highlight the implications for carbon-biodiversity co-benefits. Furthermore, we revealed the relationship between stand age-dependent functional attributes and ecosystem functioning based on carbon stock (e.g., co-benefits) along forest succession. Previous studies in Atlantic Forest have found that deforestation, disturbance, and edge effect promote a replacement of shade tolerant tree species by pioneer species (Pütz et al., 2011; Tabarelli et al., 2010). These species replacement could negatively affect the species richness and AGC (Paula et al., 2011; Pütz et al., 2014). Here, even after a long-term eucalyptus plantation, we found a significant forest recovery, but at a slower rate than the rates found in other Atlantic Forest recovery studies. Similarly, the relationship between specific functional attributes (i.e., successional strategy, fruit type, dispersal syndrome) and ecosystem functioning based on co-benefits approach tend to reach the values observed in old-growth forest fragments. Thus, here we discuss the recovery rate and the differences in functional attribute responses along with forest succession, suggesting that these SGF are recovering species richness and AGC; and that zoochoric and shade-tolerant tree species are responsible for a strong and positive relationship between AGC and species richness in these fragmented forest patches.

There were marked differences in species richness and carbon stock between OGF and SGFs. However, we did not find differences between stand age categories of SGFs. OGFs have greater species richness and AGC because they had a long time to grow and to gain shade-tolerant species. This is an expected result due the early successional stages are dominated by fast-growth and light-demanding pioneer species with short life cycles and less carbon stock (Guariguata and Ostertag, 2001; Villa et al., 2019). These results highlight the importance of OGFs for species conservation and carbon storage. Furthermore, they show that SGFs growing after long-term eucalyptus plantations at the same age can have very distinct indexes of species richness and AGC.

The recovery of species richness and carbon stock was demonstrated along stand age, where second-growth forests recovered 38% of species richness and 14% of AGC in three decades. The recovery of carbon stock is generally slower than the recovery of tree species richness (Bello et al., 2015; Matos et al., 2020; Safar et al., 2020) explaining the marked AGC difference between OGFs and SGFs found here. Neotropical forests take a median time of two decades to recover 80% of species richness (Rozendaal et al., 2019), and little more than 50% of carbon stock of old-growth forest (Oberleitner et al., 2021; Poorter et al., 2016). However, specifically in the Atlantic Forest, some studies have found a lower recovery rate: 52% of species richness and 16% of carbon stock in 20 years (Safar et al., 2020) and 76% of species richness and 20% of carbon stock in 30 years (Matos et al., 2020). Here, we found even slower recovery rates. These different recovery rates can be explained because Atlantic Forest biome are highly fragmented and both studies (Safar et al., 2020 and Matos et al., 2020) were carried out in secondary forests on different land-use type and history, including second-growth forests growing after the clear cut of native forests. The secondary succession process may be slower depending on the frequency, intensification and duration of the land use, because these factors affect seed bank and soil fertility (Jakovac et al., 2015; Pyles et al., 2018; Villa et al., 2018). In the case of the land-use history for eucalyptus plantations, we know that the longer the time of use and the number of plantation cycles there is a soil nutrient decreasing and less understory plant species diversity in SGF that are regrowing after eucalyptus cutting (Cook et al., 2016; Zhou et al., 2020).

We presume that factor related to habitat filtering and spatial factor related to dispersal limitation (e.g., van Breugel et al., 2019; Villa et al., 2021) can be stronger drivers of forest recovery (Pérez-Cardenas et al., 2021) and should be better explored in landscapes with eucalyptus plantations. Probably, some eucalyptus plantations were distributed nearby OGF patches, increasing the forest patch connectivity through eucalyptus plantation by the canopy strata (Brancalion et al., 2020). This connectivity can induce favorable conditions to animal movement attracting more seed dispersing fauna (Barlow et al., 2007; Bertacchi et al., 2016; Brancalion et al., 2019; Carrilho et al., 2017) and for recruitment of shade-tolerant species that become common in late-successional stages (Poorter et al., 2019; Rozendaal et al., 2019; Santo-Silva et al., 2016; Villa et al., 2021). These conditions maintain part of species richness of OGFs in eucalyptus plantations' seed bank (Brockerhoff et al., 2013; Gabriel et al., 2013; Zhang et al., 2014) witch can explain similar species richness in SGFs with distinct age categories and the significant species richness relative recovery after eucalyptus cutting.

The spatial factor can also explain the same AGC pattern between stand age categories of second-growth forests. Probably, there is a functional attributes convergence, where light-demanding pioneer and shade-tolerant species or non-zoochoric and zoochoric species can coexist since the beginning of succession, in areas previously occupied by eucalyptus plantations. Previous studies have reported a tendency for large shade-tolerant and zoochoric tree species to have larger fruits and seeds, which have a positive relationship to aboveground carbon stock (Bello et al., 2015; Peres et al., 2016). This tendency has been observed mainly in old-growth forests where carbon stocks are greatest due to shade-tolerant and zoochoric tree species (Stephenson et al., 2014). Thus, the presence of these species since de beginning of succession allows higher carbon indexes in some areas, preventing the differentiation of carbon stock between SGF categories. Curiously, for shade-tolerant species, there was no significant recovery in the SGF in terms of carbon stock and only 28% in terms of species richness in 32 years. This result reinforces the coexistence of pioneer and shade-tolerant species since the beginning of the succession and explains the greater carbon stock in the evaluated OGFs.

The co-benefit relationship between aboveground carbon stock and tree species richness along with Atlantic Forest succession highlights the importance of zoochoric and shade-tolerant tree species on carbon stock. These results are congruent with other results found for the Atlantic Forest (Magnago et al., 2015; Matos et al., 2020) and Amazon forest (Lennox et al., 2018), indicating that the recovery of carbon stock along succession also recover the tree species richness. In addition, our results indicate that carbon and species richness recovery in these forest patches are following patterns found in OGF that are dominated by larger sized species with larger seeds, which are dispersed by vertebrates (Tabarelli et al., 2010; Tabarelli and Peres, 2002) and have higher carbon stock potential (Bello et al., 2015). These species become less abundant in fragmented and SGF causing a decrease in carbon stock (Magnago et al., 2016, 2015; Pyles et al., 2018), but they remain the main species responsible for carbon stock along secondary succession as showed here by the stronger positive relationship between zoochoric and shade-tolerant species richness with AGC.

Our results suggest that the long-term eucalyptus plantation can probably reduce forest recovery as other land-use types, such as logging and shifting cultivation intensification in tropical forest (de Avila et al., 2018; Jakovac et al., 2015; Villa et al., 2018; Xu et al., 2015). However, we show here that areas previously occupied by eucalyptus plantations can be considered for passive restoration methods based on co-benefits, and actions to reduce carbon emissions due to forest degradation. Furthermore, evidence shows that eucalyptus did not negatively affect the natural regeneration of native woody species before or after eucalyptus cutting: the natural regeneration species richness and planted non-pioneer growth were similar across treatments in the post-logging period (Brancalion et al., 2020). In the same way, another study showed that there is not a trade-off between above-ground carbon accumulation by planted trees and the spontaneous regeneration of tree species (Brancalion et al., 2019). In addition, our study demonstrated that the stronger co-benefits between zoochoric and shade-tolerant species and AGC can be a basis for applied forest management, which can be used for the identification of key species that promote the recovery of aboveground carbon stock along active and passive restoration in human-modified tropical landscapes.

Conclusions

Our study demonstrated that after long-term eucalyptus plantations the second-growth forests have much less species richness and carbon stock than nearby old-growth forests, and they cannot be differentiated in species richness and AGC by stand age categories. However, there is a significant but slower relative recovery rate of richness and carbon stock when compared with other studies in neotropical second-growth forests. In addition, we showed that there is a co-benefit between above-ground carbon stock and species richness, mainly zoochoric and shade-tolerant species. The slower recovery rate can be explained by low fertility of areas after intensive land use. However, probably the connectivity provided by eucalyptus plantations between forest fragments and the canopy strata allow the establishment of the OGF species in the soil seed bank during land-use time. Thus, zoochoric and shade-tolerant species can coexist in this second-growth forests since the beginning of succession, allowing similar species richness and above-ground carbon stock in different stand age categories, and a significant recovery of these attributes along stand age. Thus, our study indicates that passive restoration may be applicable on areas previously used for eucalyptus plantation to recover the tree species richness and above-ground carbon stock. Furthermore, the occurrence of zoochoric and shade-tolerant species can be key species to increase carbon stock along forest recovery process.

References

Alvares, C.A., Stape, J.L., Sentelhas, P.C., De Moraes Gonçalves, J.L., Sparovek, G., 2013. K??ppen’s climate classification map for Brazil. Meteorol. Zeitschrift 22, 711–728. https://doi.org/10.1127/0941-2948/2013/0507

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

Barlow, J., Gardner, T.A., Araujo, I.S., Ávila-Pires, T.C., Bonaldo, A.B., Costa, J.E., Esposito, M.C., Ferreira, L. V., Hawes, J., Hernandez, M.I.M., Hoogmoed, M.S., Leite, R.N., Lo-Man-Hung, N.F., Malcolm, J.R., Martins, M.B., Mestre, L.A.M., Miranda-Santos, R., Nunes-Gutjahr, A.L., Overal, W.L., Parry, L., Peters, S.L., Ribeiro, M.A., Da Silva, M.N.F., Da Silva Motta, C., Peres, C.A., 2007. Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. Proc. Natl. Acad. Sci. U. S. A. 104, 18555–18560. https://doi.org/10.1073/pnas.0703333104

Bates, D., Maechler, M., Ben Bolker, B., Walker, S., Christensen, R.H.B., Singmann, H., Dai, B., Scheipl, F., Grothendieck, G., Green, P., Fox, J., 2019. ‘lme4’: Linear Mixed-Effects Models using “Eigen” and S4.

Bello, C., Galetti, M., Pizo, M.A., Magnago, L.F.S., Rocha, M.F., Lima, R.A.F., Peres, C.A., Ovaskainen, O., Jordano, P., 2015. Defaunation affects carbon storage in tropical forests. Sci. Adv. 1, 1–11. https://doi.org/10.1126/sciadv.1501105

Bertacchi, M.I.F., Amazonas, N.T., Brancalion, P.H.S., Brondani, G.E., de Oliveira, A.C.S., de Pascoa, M.A.R., Rodrigues, R.R., 2016. Establishment of tree seedlings in the understory of restoration plantations: Natural regeneration and enrichment plantings. Restor. Ecol. 24, 100–108. https://doi.org/10.1111/rec.12290

Bongers, F., Poorter, L., Hawthorne, W.D., Sheil, D., 2009. The intermediate disturbance hypothesis applies to tropical forests, but disturbance contributes little to tree diversity. Ecol. Lett. 12, 798–805. https://doi.org/10.1111/j.1461-0248.2009.01329.x

Brancalion, P.H.S., Amazonas, N.T., Chazdon, R.L., van Melis, J., Rodrigues, R.R., Silva, C.C., Sorrini, T.B., Holl, K.D., 2020. Exotic eucalypts: From demonized trees to allies of tropical forest restoration? J. Appl. Ecol. 57, 55–66. https://doi.org/10.1111/1365-2664.13513

Brancalion, P.H.S., Campoe, O., Mendes, J.C.T., Noel, C., Moreira, G.G., van Melis, J., Stape, J.L., Guillemot, J., 2019. Intensive silviculture enhances biomass accumulation and tree diversity recovery in tropical forest restoration. Ecol. Appl. 29, 1–12. https://doi.org/10.1002/eap.1847

Brockerhoff, E.G., Jactel, H., Parrotta, J.A., Ferraz, S.F.B., 2013. Role of eucalypt and other planted forests in biodiversity conservation and the provision of biodiversity-related ecosystem services. For. Ecol. Manage. 301, 43–50. https://doi.org/10.1016/j.foreco.2012.09.018

Carrilho, M., Teixeira, D., Santos-Reis, M., Rosalino, L.M., 2017. Small mammal abundance in Mediterranean Eucalyptus plantations: how shrub cover can really make a difference. For. Ecol. Manage. 391, 256–263. https://doi.org/10.1016/j.foreco.2017.01.032

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

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B.C., Duque, A., Eid, T., Fearnside, P.M., Goodman, R.C., Henry, M., Martínez-Yrízar, A., Mugasha, W.A., Muller-Landau, H.C., Mencuccini, M., Nelson, B.W., Ngomanda, A., Nogueira, E.M., Ortiz-Malavassi, E., Pélissier, R., Ploton, P., Ryan, C.M., Saldarriaga, J.G., Vieilledent, G., 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. Glob. Chang. Biol. 20, 3177–3190. https://doi.org/10.1111/gcb.12629

Chazdon, R.L., 2014. Second growth: the promise of tropical forest regeneration in an age of deforestation. University of Chicago Press.

Chazdon, R.L., Broadbent, E.N., Rozendaal, D.M.A., Bongers, F., María, A., Zambrano, A., Aide, T.M., Balvanera, P., Becknell, J.M., Boukili, V., Brancalion, P.H.S., Craven, D., Almeida-cortez, J.S., Cabral, G.A.L., Jong, B. De, Denslow, J.S., Dent, D.H., Dewalt, S.J., Dupuy, J.M., Durán, S.M., Jakovac, C.C., Junqueira, A.B., Kennard, D., Letcher, S.G., Lohbeck, M., Muscarella, R., Nunes, Y.R.F., Ochoa-gaona, S., Orihuela-belmonte, E., Peña-claros, M., Ruíz, J., Saldarriaga, J.G., Sanchez-azofeifa, A., Schwartz, N.B., Steininger, M.K., 2016. Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics.

Colwell, R.K., Chao, A., Gotelli, N.J., Lin, S.Y., Mao, C.X., Chazdon, R.L., Longino, J.T., 2012. Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. J. Plant Ecol. 5, 3–21. https://doi.org/10.1093/jpe/rtr044

Cook, R.L., Binkley, D., Luiz, J., 2016. Forest Ecology and Management Eucalyptus plantation effects on soil carbon after 20 years and three rotations in Brazil. For. Ecol. Manage. 359, 92–98. https://doi.org/10.1016/j.foreco.2015.09.035

Coombe, B.G., 1976. The Development of Fleshy Fruits. Annu. Rev. Plant Physiol. 27, 207–228.

Crawley, M.J., 2013. The R Book, 2nd ed. Wiley, London.

de Avila, A.L., van der Sande, M.T., Dormann, C.F., Peña-Claros, M., Poorter, L., Mazzei, L., Ruschel, A.R., Silva, J.N.M., de Carvalho, J.O.P., Bauhus, J., 2018. Disturbance intensity is a stronger driver of biomass recovery than remaining tree-community attributes in a managed Amazonian forest. J. Appl. Ecol. 55, 1647–1657. https://doi.org/10.1111/1365-2664.13134

Dinno, A., 2017. Dunn's Test of Multiple Comparisons Using Rank Sums.

Fernandes Neto, J.G., Costa, F.R.C., Williamson, G.B., Mesquita, R.C.G., 2019. Alternative functional trajectories along succession after different land uses in central Amazonia, Journal of Applied Ecology. https://doi.org/10.1111/1365-2664.13484

Gabriel, V. de A., Vasconcelos, A.A., Lima, E.F. de, Cassola, H., Barretto, K.D., Brito, M.C. de, 2013. A importância das plantações de eucalipto na conservação da biodiversidade. Pesqui. Florest. Bras. 33, 203–213. https://doi.org/10.4336/2013.pfb.33.74.435

Gellie, N.J.C., Breed, M.F., Mortimer, P.E., Harrison, R.D., Xu, J., Lowe, A.J., 2018. Networked and embedded scientific experiments will improve restoration outcomes. Front. Ecol. Environ. 16, 288–294. https://doi.org/10.1002/fee.1810

Guariguata, M.R., Ostertag, R., 2001. Neotropical secondary forest succession : changes in structural and functional characteristics. For. Ecol. Manage. 148, 185–206. https://doi.org/10.1016/S0378-1127(00)00535-1

Hadley, W., 2015. R ggplot2 package: An implementation of the grammar of graphics.

Hansen, A.J., Burns, P., Ervin, J., Goetz, S.J., Hansen, M., Venter, O., Watson, J.E.M., Jantz, P.A., Virnig, A.L.S., Barnett, K., Pillay, R., Atkinson, S., Supples, C., Rodríguez-Buritica, S., Armenteras, D., 2020. A policy-driven framework for conserving the best of Earth's remaining moist tropical forests. Nat. Ecol. Evol. https://doi.org/10.1038/s41559-020-1274-7

Hansen, M.C., Potapov, P. V, Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., 2013. High-Resolution Global Maps of 134, 850–854.

Hsieh, T.C., Ma, K.H., Chao, A., 2016., 2016. iNEXT: iNterpolation and EXTrapolation for species diversity.

Jakovac, C.C., Peña-Claros, M., Kuyper, T.W., Bongers, F., 2015. Loss of secondary-forest resilience by land-use intensification in the Amazon. J. Ecol. 103, 67–77. https://doi.org/10.1111/1365-2745.12298

Klemick, H., 2011. Shifting cultivation , forest fallow , and externalities in ecosystem services : Evidence from the Eastern Amazon. J. Environ. Econ. Manage. 61, 95–106. https://doi.org/10.1016/j.jeem.2010.07.003

Lennox, G.D., Gardner, T.A., Thomson, J.R., Ferreira, J., Berenguer, E., Lees, A.C., Mac Nally, R., Aragão, L.E.O.C., Ferraz, S.F.B., Louzada, J., Moura, N.G., Oliveira, V.H.F., Pardini, R., Solar, R.R.C., Vaz-de Mello, F.Z., Vieira, I.C.G., Barlow, J., 2018. Second rate or a second chance? Assessing biomass and biodiversity recovery in regenerating Amazonian forests. Glob. Chang. Biol. 24, 5680–5694. https://doi.org/10.1111/gcb.14443

Liang, J., Crowther, T.W., Picard, N., Wiser, S., Zhou, M., Alberti, G., Schulze, E.D., McGuire, A.D., Bozzato, F., Pretzsch, H., De-Miguel, S., Paquette, A., Hérault, B., Scherer-Lorenzen, M., Barrett, C.B., Glick, H.B., Hengeveld, G.M., Nabuurs, G.J., Pfautsch, S., Viana, H., Vibrans, A.C., Ammer, C., Schall, P., Verbyla, D., Tchebakova, N., Fischer, M., Watson, J. V., Chen, H.Y.H., Lei, X., Schelhaas, M.J., Lu, H., Gianelle, D., Parfenova, E.I., Salas, C., Lee, E., Lee, B., Kim, H.S., Bruelheide, H., Coomes, D.A., Piotto, D., Sunderland, T., Schmid, B., Gourlet-Fleury, S., Sonké, B., Tavani, R., Zhu, J., Brandl, S., Vayreda, J., Kitahara, F., Searle, E.B., Neldner, V.J., Ngugi, M.R., Baraloto, C., Frizzera, L., Bałazy, R., Oleksyn, J., Zawiła-Niedźwiecki, T., Bouriaud, O., Bussotti, F., Finér, L., Jaroszewicz, B., Jucker, T., Valladares, F., Jagodzinski, A.M., Peri, P.L., Gonmadje, C., Marthy, W., O’Brien, T., Martin, E.H., Marshall, A.R., Rovero, F., Bitariho, R., Niklaus, P.A., Alvarez-Loayza, P., Chamuya, N., Valencia, R., Mortier, F., Wortel, V., Engone-Obiang, N.L., Ferreira, L. V., Odeke, D.E., Vasquez, R.M., Lewis, S.L., Reich, P.B., 2016. Positive biodiversity-productivity relationship predominant in global forests. Science (80-.). 354. https://doi.org/10.1126/science.aaf8957

Liu, Xiaofei, Garcia-Ulloa, J., Cornioley, T., Liu, Xuehua, Wang, Z., Garcia, C., 2019. Main ecological drivers of woody plant species richness recovery in secondary forests in China. Sci. Rep. 9, 1–8. https://doi.org/10.1038/s41598-018-35963-7

Magnago, L.F.S., Edwards, D.P., Edwards, F.A., Magrach, A., Martins, S. V., Laurance, W.F., 2014. Functional attributes change but functional richness is unchanged after fragmentation of Brazilian Atlantic forests. J. Ecol. 102, 475–485. https://doi.org/10.1111/1365-2745.12206

Magnago, L.F.S., Magrach, A., Barlow, J., Schaefer, C.E.G.R., Laurance, W.F., Martins, S.V., Edwards, D.P., 2016. Do fragment size and edge effects predict carbon stocks in trees and lianas in tropical forests? Funct. Ecol. https://doi.org/10.1111/1365-2435.12752

Magnago, L.F.S., Magrach, A., Laurance, W.F., Martins, S. V., Meira-Neto, J.A.A., Simonelli, M., Edwards, D.P., 2015. Would protecting tropical forest fragments provide carbon and biodiversity cobenefits under REDD+? Glob. Chang. Biol. 21, 3455–3468. https://doi.org/10.1111/gcb.12937

Malhi, Y., Baker, T.R., Phillips, O.L., Almeida, S., Alvarez, E., Arroyo, L., Chave, J., Czimczik, C.I., Di Fiore, A., Higuchi, N., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Montoya, L.M.M., Monteagudo, A., Neill, D.A., Vargas, P.N., Patino, S., Pitman, N.C.A., Quesada, C.A., Salomao, R., Silva, J.N.M., Lezama, A.T., Martínez, R.V., Terborgh, J., Vinceti, B., Lloyd, J., 2004. The above-ground coarse wood productivity of 104 Neotropical forest plots. Glob. Chang. Biol. 10, 563–591. https://doi.org/10.1111/j.1529-8817.2003.00778.x

Matos, F.A.R., Magnago, L.F.S., Aquila Chan Miranda, C., de Menezes, L.F.T., Gastauer, M., Safar, N.V.H., Schaefer, C.E.G.R., da Silva, M.P., Simonelli, M., Edwards, F.A., Martins, S. V., Meira-Neto, J.A.A., Edwards, D.P., 2020. Secondary forest fragments offer important carbon and biodiversity cobenefits. Glob. Chang. Biol. 26, 509–522. https://doi.org/10.1111/gcb.14824

Matos, F.A.R., Magnago, L.F.S., Gastauer, M., Carreiras, J.M.B., Simonelli, M., Meira-Neto, J.A.A., Edwards, D.P., 2016. Effects of landscape configuration and composition on phylogenetic diversity of trees in a highly fragmented tropical forest. J. Ecol. https://doi.org/10.1111/1365-2745.12661

McCarthy, D.P., Donald, P.F., Scharlemann, J.P.W., Buchanan, G.M., Balmford, A., Green, J.M.H., Bennum, L.A., Burgess, N.D., Fishpool, L.D.C., Garnett, S.T., Leonard, D.L., Maloney, R.F., Morling, P., Schaefer, H.M., Symes, A., Wiedenfeld, D.A., Butchart, S.H.M., 2012. Financial Costs of Meeting Global Biodiversity Conservation Targets: Current Spending and Unmet Needs. Science (80-.). 1. https://doi.org/10.1126/sciense.1229803

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fronseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.

Oberleitner, F., Egger, C., Oberdorfer, S., Dullinger, S., Wanek, W., Hietz, P., 2021. Recovery of aboveground biomass, species richness and composition in tropical secondary forests in SW Costa Rica. For. Ecol. Manage. 479, 118580. https://doi.org/https://doi.org/10.1016/j.foreco.2020.118580

Oliveira-Junior, N.D. de, Heringer, G., Bueno, M.L., Pontara, V., Meira-Neto, J.A.A., 2020. Prioritizing landscape connectivity of a tropical forest biodiversity hotspot in global change scenario. For. Ecol. Manage. 472. https://doi.org/10.1016/j.foreco.2020.118247

Osuri, A.M., Kumar, V.S., Sankaran, M., 2014. Altered stand structure and tree allometry reduce carbon storage in evergreen forest fragments in India’s Western Ghats. For. Ecol. Manage. 329, 375–383. https://doi.org/10.1016/j.foreco.2014.01.039

Osuri, A.M., Machado, S., Ratnam, J., Sankaran, M., Ayyappan, N., Muthuramkumar, S., Parthasarathy, N., Pélissier, R., Ramesh, B.R., DeFries, R., Naeem, S., 2020. Tree diversity and carbon storage cobenefits in tropical human-dominated landscapes. Conserv. Lett. 1–9. https://doi.org/10.1111/conl.12699

Paula, M.D. de, Costa, C.P.A., Tabarelli, M., 2011. Carbon storage in a fragmented landscape of Atlantic forest: The role played by edge-affected habitats and emergent trees. Trop. Conserv. Sci. 4, 349–358. https://doi.org/10.1177/194008291100400310

Peres, C.A., Emilio, T., Schietti, J., Desmoulière, S.J.M., Levi, T., 2016. Dispersal limitation induces long-term biomass collapse in overhunted Amazonian forests. Proc. Natl. Acad. Sci. 113, 892–897. https://doi.org/10.1073/pnas.1516525113

Pérez-Harguindeguy, N., Díaz, S., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S., Cornwell, W.K., Craine, J.M., Gurvich, D.E., Urcelay, C., Veneklaas, E.J., Reich, P.B., Poorter, L., Wright, I.J., Ray, P., Enrico, L., Pausas, J.G., Vos, A.C. de, Buchmann, N., Funes, G., Quétier, F., Hodgson, J.G., Thompson, K., Morgan, H.D., Steege, H. ter, Heijden, M.G.A. van der, Sack, L., Blonder, B., Poschlod, P., Vaieretti, M. V., Conti, G., Staver, A.C., Aquino, S., Cornelissen, J.H.C., 2013. New Handbook for standardized measurment of plant functional traits worldwide. Aust. J. Bot. 23, 167–234. https://doi.org/http://dx.doi.org/10.1071/BT12225

Poorter, L., Bongers, F., Aide, T.M., Almeyda Zambrano, A.M., Balvanera, P., Becknell, J.M., Boukili, V., Brancalion, P.H.S., Broadbent, E.N., Chazdon, R.L., Craven, D., De Almeida-Cortez, J.S., Cabral, G.A.L., De Jong, B.H.J., Denslow, J.S., Dent, D.H., DeWalt, S.J., Dupuy, J.M., Durán, S.M., Espírito-Santo, M.M., Fandino, M.C., César, R.G., Hall, J.S., Hernandez-Stefanoni, J.L., Jakovac, C.C., Junqueira, A.B., Kennard, D., Letcher, S.G., Licona, J.C., Lohbeck, M., Marín-Spiotta, E., Martínez-Ramos, M., Massoca, P., Meave, J.A., Mesquita, R., Mora, F., Munõz, R., Muscarella, R., Nunes, Y.R.F., Ochoa-Gaona, S., De Oliveira, A.A., Orihuela-Belmonte, E., Penã-Claros, M., Pérez-Garciá, E.A., Piotto, D., Powers, J.S., Rodríguez-Velázquez, J., Romero-Pérez, I.E., Ruíz, J., Saldarriaga, J.G., Sanchez-Azofeifa, A., Schwartz, N.B., Steininger, M.K., Swenson, N.G., Toledo, M., Uriarte, M., Van Breugel, M., Van Der Wal, H., Veloso, M.D.M., Vester, H.F.M., Vicentini, A., Vieira, I.C.G., Bentos, T.V., Williamson, G.B., Rozendaal, D.M.A., 2016. Biomass resilience of Neotropical secondary forests. Nature 530, 211–214. https://doi.org/10.1038/nature16512

Poorter, L., Rozendaal, D.M.A., Bongers, F., de Almeida-Cortez, J.S., Almeyda Zambrano, A.M., Álvarez, F.S., Andrade, J.L., Villa, L.F.A., Balvanera, P., Becknell, J.M., Bentos, T. V, Bhaskar, R., Boukili, V., Brancalion, P.H.S., Broadbent, E.N., César, R.G., Chave, J., Chazdon, R.L., Colletta, G.D., Craven, D., de Jong, B.H.J., Denslow, J.S., Dent, D.H., DeWalt, S.J., García, E.D., Dupuy, J.M., Durán, S.M., Espírito Santo, M.M., Fandiño, M.C., Fernandes, G.W., Finegan, B., Moser, V.G., Hall, J.S., Hernández-Stefanoni, J.L., Jakovac, C.C., Junqueira, A.B., Kennard, D., Lebrija-Trejos, E., Letcher, S.G., Lohbeck, M., Lopez, O.R., Marín-Spiotta, E., Martínez-Ramos, M., Martins, S. V, Massoca, P.E.S., Meave, J.A., Mesquita, R., Mora, F., de Souza Moreno, V., Müller, S.C., Muñoz, R., Muscarella, R., de Oliveira Neto, S.N., Nunes, Y.R.F., Ochoa-Gaona, S., Paz, H., Peña-Claros, M., Piotto, D., Ruíz, J., Sanaphre-Villanueva, L., Sanchez-Azofeifa, A., Schwartz, N.B., Steininger, M.K., Thomas, W.W., Toledo, M., Uriarte, M., Utrera, L.P., van Breugel, M., van der Sande, M.T., van der Wal, H., Veloso, M.D.M., Vester, H.F.M., Vieira, I.C.G., Villa, P.M., Williamson, G.B., Wright, S.J., Zanini, K.J., Zimmerman, J.K., Westoby, M., 2019. Wet and dry tropical forests show opposite successional pathways in wood density but converge over time. Nat. Ecol. Evol. 3, 928–934. https://doi.org/10.1038/s41559-019-0882-6

Pütz, S., Groeneveld, J., Alves, L.F., Metzger, J.P., Huth, A., 2011. Fragmentation drives tropical forest fragments to early successional states: A modelling study for Brazilian Atlantic forests. Ecol. Modell. 222, 1986–1997. https://doi.org/10.1016/j.ecolmodel.2011.03.038

Pütz, S., Groeneveld, J., Henle, K., Knogge, C., Martensen, A.C., Metz, M., Metzger, J.P., Ribeiro, M.C., De Paula, M.D., Huth, A., 2014. Long-term carbon loss in fragmented Neotropical forests. Nat. Commun. 5, 1–8. https://doi.org/10.1038/ncomms6037

Pyles, M. V., Prado-Junior, J.A., Magnago, L.F.S., de Paula, A., Meira-Neto, J.A.A., 2018. Loss of biodiversity and shifts in aboveground biomass drivers in tropical rainforests with different disturbance histories. Biodivers. Conserv. 27, 3215–3231. https://doi.org/10.1007/s10531-018-1598-7

R Development Core Team, 2019. R version 3.6.0.

Réjou-Méchain, M., Tanguy, A., Piponiot, C., Chave, J., Hérault, B., 2017. Biomass: an R Package for Estimating Above-Ground Biomass and Its Uncertainty in Tropical Forests. Methods Ecol. Evol. 8, 1163–1167. https://doi.org/10.1111/2041-210X.12753

Roberts, P., Boivin, N., Kaplan, J.O., 2018. Finding the anthropocene in tropical forests. Anthropocene 23, 5–16. https://doi.org/10.1016/j.ancene.2018.07.002

Rodrigues, A.C., Villa, P.M., Neri, A.V., 2019. Fine-scale topography shape richness, community composition, stem and biomass hyperdominant species in Brazilian Atlantic forest. Ecol. Indic. 102, 208–217. https://doi.org/10.1016/j.ecolind.2019.02.033

Rozendaal, D.M.A., Bongers, F., Aide, T.M., Alvarez-Dávila, E., Ascarrunz, N., Balvanera, P., Becknell, J.M., Bentos, T. V., Brancalion, P.H.S., Cabral, G.A.L., Calvo-Rodriguez, S., Chave, J., César, R.G., Chazdon, R.L., Condit, R., Dallinga, J.S., De Almeida-Cortez, J.S., De Jong, B., De Oliveira, A., Denslow, J.S., Dent, D.H., DeWalt, S.J., Dupuy, J.M., Durán, S.M., Dutrieux, L.P., Espírito-Santo, M.M., Fandino, M.C., Fernandes, G.W., Finegan, B., García, H., Gonzalez, N., Moser, V.G., Hall, J.S., Hernández-Stefanoni, J.L., Hubbell, S., Jakovac, C.C., Hernández, A.J., Junqueira, A.B., Kennard, D., Larpin, D., Letcher, S.G., Licona, J.C., Lebrija-Trejos, E., Marín-Spiotta, E., Martínez-Ramos, M., Massoca, P.E.S., Meave, J.A., Mesquita, R.C.G., Mora, F., Müller, S.C., Muñoz, R., De Oliveira Neto, S.N., Norden, N., Nunes, Y.R.F., Ochoa-Gaona, S., Ortiz-Malavassi, E., Ostertag, R., Peña-Claros, M., Pérez-García, E.A., Piotto, D., Powers, J.S., Aguilar-Cano, J., Rodriguez-Buritica, S., Rodríguez-Velázquez, J., Romero-Romero, M.A., Ruíz, J., Sanchez-Azofeifa, A., De Almeida, A.S., Silver, W.L., Schwartz, N.B., Thomas, W.W., Toledo, M., Uriarte, M., De Sá Sampaio, E.V., Van Breugel, M., Van Der Wal, H., Martins, S.V., Veloso, M.D.M., Vester, H.F.M., Vicentini, A., Vieira, I.C.G., Villa, P., Williamson, G.B., Zanini, K.J., Zimmerman, J., Poorter, L., 2019. Biodiversity recovery of Neotropical secondary forests. Sci. Adv. 5. https://doi.org/10.1126/sciadv.aau3114

Safar, N.V.H., Magnago, L.F.S., Schaefer, C.E.G.R., 2020. Resilience of lowland Atlantic forests in a highly fragmented landscape: Insights on the temporal scale of landscape restoration. For. Ecol. Manage. 470–471, 118183. https://doi.org/10.1016/j.foreco.2020.118183

Santo-Silva, E.E., Almeida, W.R., Melo, F.P.L., Zickel, C.S., Tabarelli, M., 2013. The nature of seedling assemblages in a fragmented tropical landscape: Implications for forest regeneration. Biotropica 45, 386–394. https://doi.org/10.1111/btp.12013

Santo-Silva, E.E., Almeida, W.R., Tabarelli, M., Peres, C.A., 2016. Habitat fragmentation and the future structure of tree assemblages in a fragmented Atlantic forest landscape. Plant Ecol. 217, 1129–1140. https://doi.org/10.1007/s11258-016-0638-1

Santos, H.G. dos, Jacomine, P.K.T., Anjos, L.H.C. dos, Oliveira, V.A. de, Lumbreras, J.F., Coelho, M.R., Almeida, J.A. de, Araújo-Filho, J.C. de, Oliveira, J.B. de, Cunha, T.J.F., 2018. Sistema brasileiro de classificação de solos, 5. ed. rev. ed, Embrapa Solos.

Scarano, F.R., Ceotto, P., 2015. Brazilian Atlantic forest: impact, vulnerability, and adaptation to climate change. Biodivers. Conserv. 24, 2319–2331. https://doi.org/10.1007/s10531-015-0972-y

Sloan, S., Goosem, M., Laurance, S.G., 2015. Tropical forest regeneration following land abandonment is driven by primary rainforest distribution in an old pastoral region. Landsc. Ecol. https://doi.org/10.1007/s10980-015-0267-4

Stephenson, N.L., Das, A.J., Condit, R., Russo, S.E., Baker, P.J., Beckman, N.G., Coomes, D.A., Lines, E.R., Morris, W.K., Rüger, N., Álvarez, E., Blundo, C., Bunyavejchewin, S., Chuyong, G., Davies, S.J., Duque, Á., Ewango, C.N., Flores, O., Franklin, J.F., Grau, H.R., Hao, Z., Harmon, M.E., Hubbell, S.P., Kenfack, D., Lin, Y., Makana, J.R., Malizia, A., Malizia, L.R., Pabst, R.J., Pongpattananurak, N., Su, S.H., Sun, I.F., Tan, S., Thomas, D., Van Mantgem, P.J., Wang, X., Wiser, S.K., Zavala, M.A., 2014. Rate of tree carbon accumulation increases continuously with tree size. Nature 507, 90–93. https://doi.org/10.1038/nature12914

Tabarelli, M., Aguiar, A. V., Girão, L.C., Peres, C.A., Lopes, A. V., 2010. Effects of pioneer tree species hyperabundance on forest fragments in Northeastern Brazil. Conserv. Biol. 24, 1654–1663. https://doi.org/10.1111/j.1523-1739.2010.01529.x

Tabarelli, M., Peres, C.A., 2002. Abiotic and vertebrate seed dispersal in the Brazilian Atlantic forest: Implications for forest regeneration. Biol. Conserv. 106, 165–176. https://doi.org/10.1016/S0006-3207(01)00243-9

Villa, P.M., Martins, S.V., Diniz, É.S., Nolasco de Oliveira Neto, S., Neri, A.V., Pinto-Junior, H., Nunes, J.A., Bueno, M.L., Ali, A., 2021. Taxonomic and functional beta diversity of woody communities along Amazon forest succession: The relative importance of stand age, soil properties and spatial factor. For. Ecol. Manage. 482, 118885. https://doi.org/https://doi.org/10.1016/j.foreco.2020.118885

Villa, P.M., Martins, S.V., Rodrigues, A.C., Safar, N.V.H., Bonilla, M.A.C., Ali, A., 2019. Testing species abundance distribution models in tropical forest successions: Implications for fine-scale passive restoration. Ecol. Eng. 135, 28–35. https://doi.org/10.1016/j.ecoleng.2019.05.015

Villa, P.M., Venâncio, S., Nolasco, S., Neto, D.O., Cristina, A., Guerreiro, L., Delgado, L., Mota, N., Gastauer, M., 2018. Intensification of shifting cultivation reduces forest resilience in the northern Amazon. For. Ecol. Manage. 430, 312–320. https://doi.org/10.1016/j.foreco.2018.08.014

Xu, L., Marinova, D., Guo, X., 2015. Resilience thinking: a renewed system approach for sustainability science. Sustain. Sci. 10, 123–138. https://doi.org/10.1007/s11625-014-0274-4

Zanne, A.E., Lopez-Gonzalez, G., Coomes, D.A., Ilic, J., Jansen, S., Lewis, S.L., Miller, R.B., Swenson, N.G., Wiemann, M.C., Chave, J., 2009. Data from: Towards a worldwide wood economics spectrum, Dryad.

Zhang, D., Zhang, J., Yang, W., Wu, F., Huang, Y., 2014. Plant and soil seed bank diversity across a range of ages of Eucalyptus grandis plantations afforested on arable lands. Plant Soil 376, 307–325. https://doi.org/10.1007/s11104-013-1954-z

Zhou, X., Zhu, H., Wen, Y., Goodale, U.M., Zhu, Y., Yu, S., Li, C., Li, X., 2020. Intensive management and declines in soil nutrients lead to serious exotic plant invasion in Eucalyptus plantations under successive short-rotation regimes. L. Degrad. Dev. 31, 297–310. https://doi.org/10.1002/ldr.3449

Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed effects models and extensions in ecology with R. Springer, New York.

Appendices

Table A.1 – Localization and description of second-growth forests and old-growth forests sampled.

Code	City	Region	Stand Age	Latitude	Longitude
CD1	São José do Goiabal	Cachoeira D'Dantas	8.6	19°58'5.00"S	42°39'42.40"O

CD2	São José do Goiabal	Cachoeira D'Dantas	8.6	19°59'5.30"S	42°40'57.80"O
CD3	São José do Goiabal	Cachoeira D'Dantas	8.6	19°58'29.50"S	42°41'0.30"O
CD4	São José do Goiabal	Cachoeira D'Dantas	5.1	19°59'27.30"S	42°42'21.70"O
CD5	São José do Goiabal	Cachoeira D'Dantas	5.1	19°59'30.30"S	42°41'49.50"O
CD6	São José do Goiabal	Cachoeira D'Dantas	5.5	19°58'16.10"S	42°42'6.40"O
M1	Dionísio	Mumbaça	9.5	19°48'55.00"S	42°32'44.30"O
M10	Dionísio	Mumbaça	5.7	19°49'53.30"S	42°35'25.00"O
M3	Dionísio	Mumbaça	8.5	19°50'59.00"S	42°32'11.10"O
M4	Dionísio	Mumbaça	8.3	19°50'38.50"S	42°36'40.30"O
M5	Dionísio	Mumbaça	8	19°51'10.90"S	42°37'15.70"O
M6	Dionísio	Mumbaça	8.5	19°52'4.60"S	42°33'32.40"O
M7	Dionísio	Mumbaça	8.5	19°51'25.90"S	42°33'14.30"O
M8	Dionísio	Mumbaça	8.5	19°50'16.20"S	42°31'30.50"O
M9	Dionísio	Mumbaça	7.3	19°48'59.00"S	42°34'10.40"O
R1	Dionísio	Requerente	9.3	19°55'32.80"S	42°38'43.60"O
R10	Dionísio	Requerente	18.1	19°54'14.00"S	42°37'30.70"O
R11	Dionísio	Requerente	18.1	19°51'36.80"S	42°36'52.80"O
R2	Dionísio	Requerente	8.5	19°55'0.30"S	42°38'40.00"O
R3	Dionísio	Requerente	4.3	19°52'59.40"S	42°39'27.00"O
R4	Dionísio	Requerente	7.3	19°52'17.50"S	42°41'26.10"O
R5	Dionísio	Requerente	4.2	19°52'48.50"S	42°38'29.30"O
R6	Dionísio	Requerente	18	19°52'34.00"S	42°37'45.20"O
R7	Dionísio	Requerente	18	19°51'30.70"S	42°39'36.50"O
R8	Dionísio	Requerente	18	19°51'11.30"S	42°39'49.70"O
R9	Dionísio	Requerente	18.1	19°50'27.00"S	42°39'0.30"O
SC1	Dionísio	Santa Cruz	8.6	19°48'29.70"S	42°37'40.40"O
SC11	Dionísio	Santa Cruz	31.9	19°46'32.40"S	42°39'24.10"O
SC2	Dionísio	Santa Cruz	8.5	19°48'58.80"S	42°38'33.20"O
SC3	Dionísio	Santa Cruz	8.7	19°47'50.00"S	42°38'53.80"O
SC4	Dionísio	Santa Cruz	7.7	19°47'45.00"S	42°40'7.70"O
SC5	Dionísio	Santa Cruz	3.5	19°47'57.20"S	42°40'15.90"O
SC6	Dionísio	Santa Cruz	7.7	19°47'10.20"S	42°39'47.60"O

SC7	Dionísio	Santa Cruz	3.5	19°50'52.30"S	42°44'39.70"O
SC8	Dionísio	Santa Cruz	5.7	19°48'56.50"S	42°39'17.10"O
SC9	Dionísio	Santa Cruz	27.8	19°45'57.90"S	42°39'42.00"O
SPF1	São Pedro dos Ferros	São Pedro dos Ferros	32.1	20° 1'15.10"S	42°38'10.20"O
SPF2 - B	São Pedro dos Ferros	São Pedro dos Ferros	32.1	20° 1'14.50"S	42°38'4.90"O
SPF3 - A	São Pedro dos Ferros	São Pedro dos Ferros	6	19°59'22.50"S	42°38'0.60"O
SPF3 - B	São Pedro dos Ferros	São Pedro dos Ferros	32.1	20° 0'59.10"S	42°38'3.10"O
SPF4	São Pedro dos Ferros	São Pedro dos Ferros	32.1	20° 0'14.40"S	42°37'42.10"O
SPF5 - B	São Pedro dos Ferros	São Pedro dos Ferros	32.1	20° 2'38.70"S	42°36'20.00"O
SPF6	São Pedro dos Ferros	São Pedro dos Ferros	11	20° 1'53.20"S	42°36'15.06"O
PERD1	Parque Estadual do Rio Doce	Parque Estadual do Rio Doce	-	19°46'18.09"S	42°37'53.56"O
PERD2	Parque Estadual do Rio Doce	Parque Estadual do Rio Doce	-	19°45'41.59"S	42°37'10.60"O
PERD3	Parque Estadual do Rio Doce	Parque Estadual do Rio Doce	-	19°41'53.87"S	42°30'28.97"O

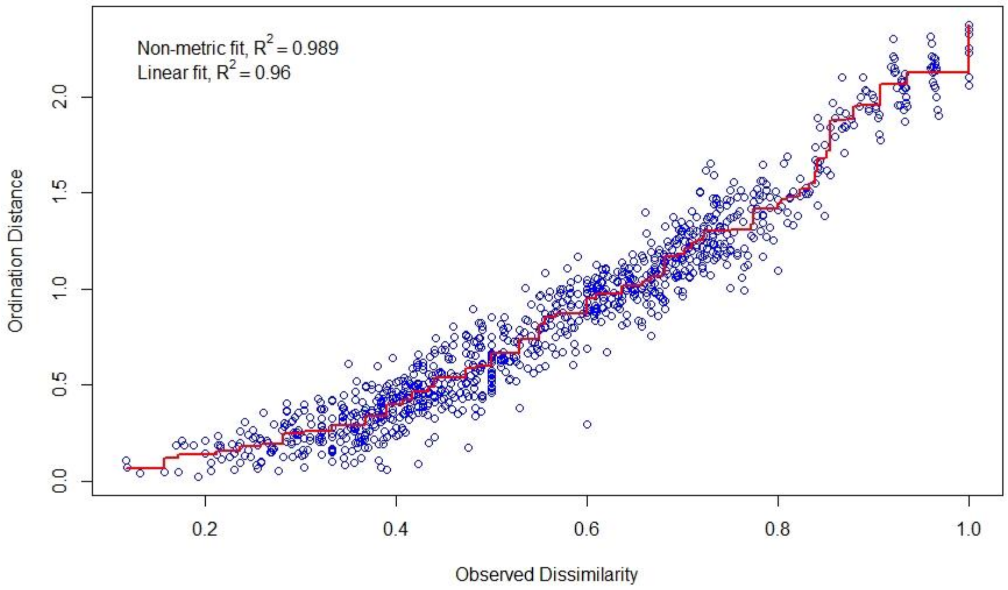


Fig.A.1. Shepard plot showing the nonmetric fit based on stress using linear regression between Euclidean distance in reduced space and the Jaccard dissimilarities.

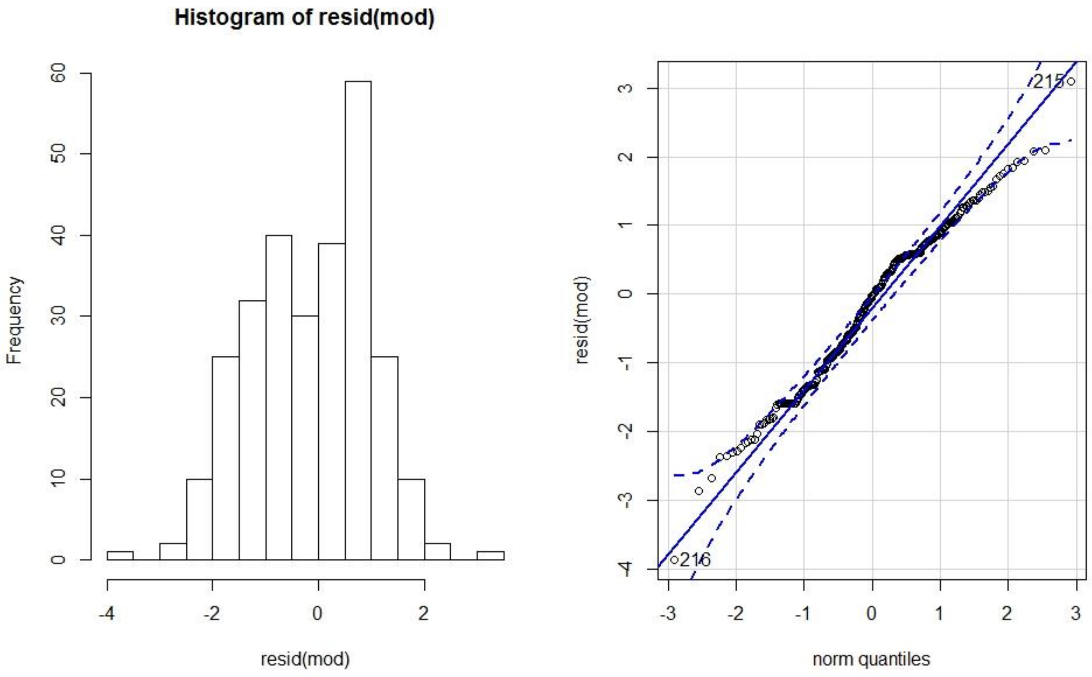


Fig.A.2. Example to test the most suitable distribution and link function using histogram and Q-Q graph.

CHAPTER 4: Multiple drivers influence Atlantic Forest secondary succession: implications for the passive restoration in human-modified landscape

Abstract: Second-growth forests (SGF) are ac-have piece for biodiversity recovery and climate change mitigation in the world. However, these forests are established after anthropic disturbances such as land use for planting, and in highly human-modified landscapes. These interventions can decrease the ability of biomes to recover naturally, and it is necessary to understand how multiple drivers, from local scale to landscape scale, influence the diversity and carbon stock of these forests in natural regeneration. For this, we used data from 35 SGF growing on areas previously used for eucalyptus plantation in Brazilian Atlantic Forest, one of the hotspots for biodiversity conservation in the world. For each SGF, the diversity of species was calculated based on the Hills number and the above-ground carbon stock. Then, we evaluated the influence of multiple environmental factors in these indexes: soil properties, management intensity, patch configuration, and landscape composition. Little influence of soil properties was found, only soil fertility negatively influenced in above-ground carbon stock. However, management intensity negatively influenced species diversity and carbon stock. The isolation of other forests, and a source fragment of propagules (>500ha) also negatively influenced the diversity of species. This is probably due to the favoring of pioneer species in highly human-modified landscapes because they are more tolerant of environmental changes, less dependent on animal dispersal, and with low carbon stock capacity. Thus, areas with higher previous management intensity and more isolated are less effective for passive restoration and may require intervention to recover diversity and carbon stock in the Atlantic Forest.

Keywords: Second-growth forests; biodiversity recovery; carbon stock recovery; climate change mitigation; management intensity; human-modified landscapes.

Introduction

The rapid growth of the world's population and the demand for natural resources has led to the worldwide replacement of old-growth forests for agricultural systems, mining, and other human occupations (Nazareno et al. 2012). Currently, about one-third of the deforested areas undergoes regeneration processes and develop, for a period (i.e. due to following time on plantations) or permanently (i.e. because of land abandonment or due to restoration initiatives), into second-growth forests (Hansen et al. 2013; Arroyo-Rodríguez et al. 2017). These forests are important because they protect soils from erosive processes, provide products to local populations, and contribute to the maintenance of biodiversity and ecosystem services, such as carbon sequestration (Klemick 2011; Chazdon et al. 2016; Villa et al. 2020). Thus, the world's main initiatives for biodiversity conservation and climate change mitigation aim to reforestation of converted areas. However, these areas are usually located in landscapes with strong anthropic influences and the regeneration depends, among other factors, on the management intensity and the landscape configuration (Sloan et al. 2015; Jakovac et al. 2015; Arroyo-Rodríguez et al. 2017). Thus, it is important to know how multiple drives influence the regeneration in human-modified landscapes of tropical forests to choose priority areas for forest restoration.

Global initiatives foresee the deployment of large-scale second-growth forests worldwide. These initiatives were discussed at the Paris Climate Agreement and recently reinforced at the 2014 United Nations Climate Summit in New York, when more than 130 governments, private companies, civil society and indigenous peoples pledged to restore more than 350 million hectares of forests globally by 2030 (Uriarte and Chazdon 2016; Brancalion et al. 2019; Ivanova et al. 2020). Thus, the United Nations' Decade on Ecosystem Restoration (2021–2030) was established. This ambitious goal would be met primarily by the forest planting methods that could cost up to US$ 837 billion over 15 years. However, natural or assisted regeneration (both passive restoration methods) can make this goal possible on a large scale by offering better cost benefits (Uriarte and Chazdon 2016).

Along tropical forest regeneration, there is an increase in species richness, crown height, stem density and basal area of the trees, meanwhile the canopy opening and abundance of herbs, shrubs and lianas decrease (Finegan 1996; Chazdon 2014). The neotropical second-growth forests take an average of 20 years to recover 80% of species richness and 50% of above-ground carbon stock (AGC) of old-growth forests (Rozendaal et al. 2019; Oberleitner et al. 2021). These forest recovery rates depend mainly on climatic conditions and soil properties (Guariguata and Ostertag 2001; Rozendaal et al. 2019). However, in a scenario of human-modified landscapes the previous management intensity can decrease the recovery rate and successional trajectories, because the disturbance can alter local environment conditions (Guariguata and Ostertag 2001; Jakovac et al. 2015; Villa et al. 2018). In addition, the landscape configuration (e.g., patch size and isolation) and composition of these SGFs can also induce dispersal limitation, due to distance to old-growth forests and matrix dissimilarity, slowing down the forest recovery (Matos et al. 2020; Pérez-Cárdenas et al. 2020). Thus, the recovery of species and AGC during regeneration in human-modified landscapes may be slower or does not happen naturally.

The Atlantic Forest is the second-largest tropical forest in America and represents one of the world's hotspots for biodiversity conservation (Myers et al. 2000). This forest has a long history of deforestation and land use from the country´s colonization in the 16th century to the present, resulting in a highly fragmented biome (Tabarelli et al. 2010a; Nazareno et al. 2012). Therefore, the Atlantic Forest has many areas to be restored with different soil properties, management intensity and landscape configurations. There are pacts aimed at recovering millions of hectares of Atlantic Forest, such as the Pact for the Restoration of the Atlantic Forest (15 Mha until 2050) and Brazil's Determined National Contribution to the Paris Climate Agreement (12 Mha until 2030), which includes the Atlantic Forest (Rosa et al. 2021). Part of these areas have been used for eucalyptus (*Eucalyptus* sp.) plantations, one of the main land uses in the Atlantic Forest region (Gonçalvez et al. 2013). It is known that after eucalyptus cutting these areas regenerate naturally (Brancalion et al. 2019, 2020) and can recover in 32 years 38% of species richness and 14% of the AGC of nearby old-growth forests (unpublished data). Due to the structural similarity of eucalyptus planting with natural forests, there is a movement of seed-dispersing animals and similar environmental conditions during the land use, which allows the regeneration of old-growth forest species as well as the establishment of these in the soil seed bank (Barlow et al. 2007; Zhang et al. 2014; Bertacchi et al. 2016; Carrilho et al. 2017). Thus, these areas can be considered for passive restoration, but we do not know how multiple drivers affect species richness and aboveground carbon stock after long-term eucalyptus plantations in the Atlantic Forest biome.

In this context, considering the demand for restoration of Brazil's Atlantic Forests, we investigate how multiple drivers influence stand age dependent forest attributes in a in human-modified Atlantic Forest landscape. Specifically, were to evaluate how soil properties, management intensity, local configuration and landscape composition influence tree diversity and AGC. We hypothesized that after long-term eucalyptus plantations: (i) soil properties would have an influence on tree diversity and AGC recovery; (ii) the management intensity would negatively affect the species diversity and AGC; (iii) patch size would positively affect while patch isolation and source distance would negatively affect the recovery; and that (iv) forest and silviculture cover in the landscape would positively affect regeneration. In addition, we suggested how choose priority areas for passive restoration in the Atlantic Forest domain after long-term land use. For this we used 35 second-growth forests of different regeneration ages (3-32 years) after at least 30 years of use for eucalyptus plantations with different, soil properties, management intensity, patch characteristics and landscape composition.

Material and Methods

Study area

The study area was near the largest fragment of the Atlantic Forest in the state of Minas Gerais, Rio Doce State Park, between the municipalities of São José do Goiabal, Dionísio and Timóteo (Fig. 1a). The region are included in the Atlantic Forest domain, and according to the Brazilian vegetation classification, are submontane semideciduous seasonal forests (Veloso et al. 1991). The region have mean annual precipitation of 1450 mm, mean temperature ranging between 20 and 23 °C with well-defined periods of rain and drought, and two dominant soil classes: Red-Yellow Latosol in hilltops and mountainsides and Red-Yellow Podosol upper fluvial terraces (Lopes et al. 2002; Alvares et al. 2013; Santos et al. 2018). This region is very developed e economically important, mainly by land use for agriculture, livestock, and eucalyptus plantation (Scarano and Ceotto 2015; Oliveira-Junior et al. 2020).

Were randomly selected 43 second-growth forest patches previously used for eucalyptus planting in fallow age after the last cutting. The land-use history of these patches was made available by the landowner company. Thus, we excluded 7 patches with different land-use before eucalyptus planting, like by livestock and coffee planting. All the other patches were primary forest cleared for charcoal production and later used for eucalyptus planting. The first eucalyptus planting cycle in these areas was soon after the primary forest clearing. The fallow age times range from 3 - 32 years after the last cutting cycle (see Fig. 1e an example of a second-growth forest with 8 years of fallow age). We avoided patches with more than four eucalyptus regenerating individuals.

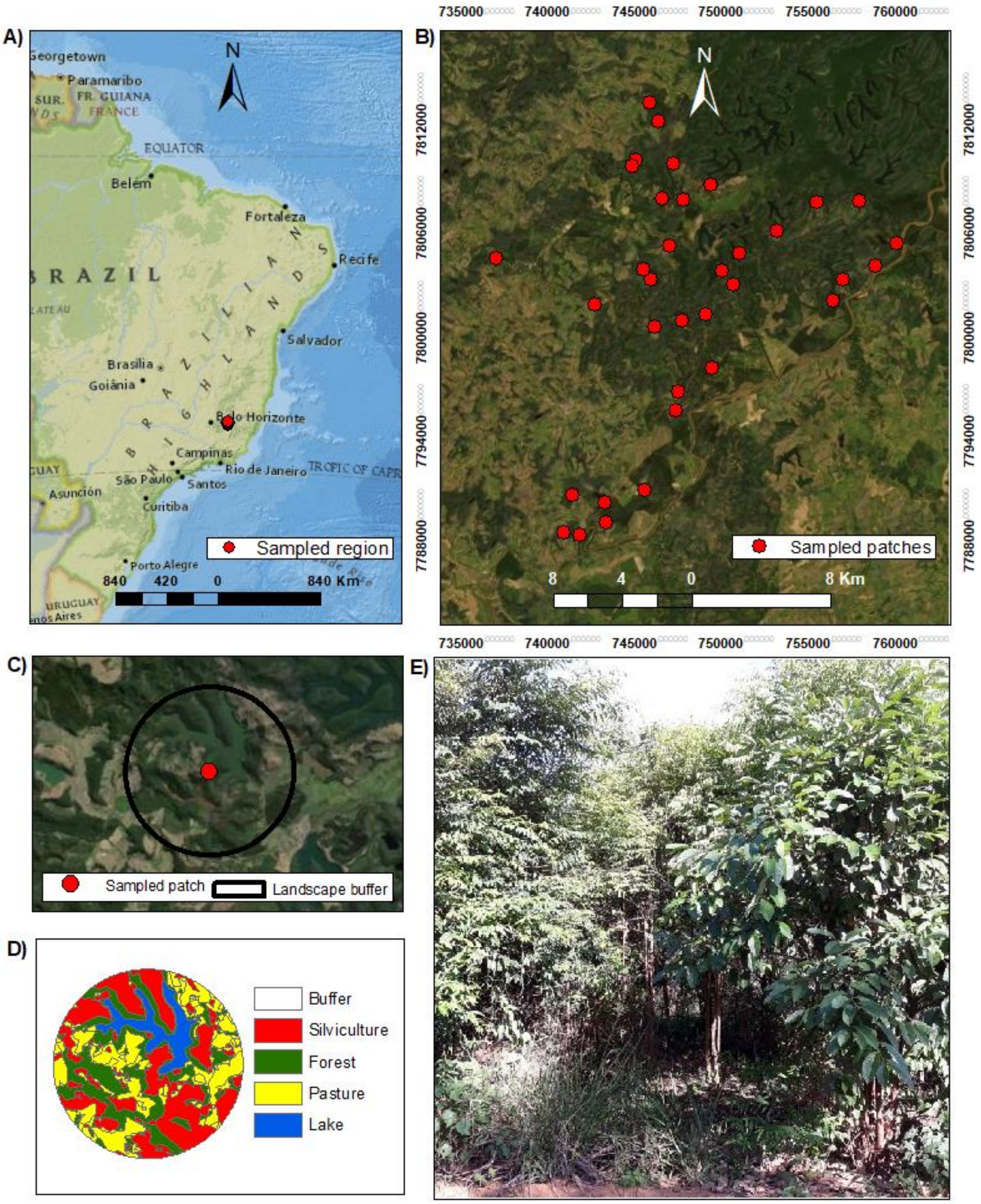


Figure 1. Map of location and characteristics of the sampled patches. A) Region sampled in the state of Minas Gerais, Brazil; B) Second-growth forests sampled near to the state park of Rio Doce; C) Example of the 2km buffer created from each sampling point for collecting landscape composition variables; D) Example of the 2km buffer cutout on the classified image of MapBiomas collection 5 of 2018 for the quantification of forest and silviculture cover; E) second-growth forest sampled at the point represented in C) and D) with 8 years-old of fallow.

Tree sampling

We sampled 35 second-growth forests (Fig. 1b). In each second-growth forest, we sampled one plot of 20x50 meters (0.1 ha). Within each plot, both the shrub and arboreal strata were sampled, including all individuals rooted within our plots ≥4.8 cm in diameter at breast height (1.30 m above ground height) following Matos *et al*., (2020). For tree individuals that were not identified at the site, we collected leaves and any reproductive parts, and these were then classified into morphospecies and subsequently identified by morphological comparison in the Herbarium of Viçosa (VIC) or by botanical experts for their families following APG IV (2016). The botanical material collected in the reproductive stage was deposited in the Herbarium of the Federal University of Viçosa, Minas Gerais (VIC).

Tree diversity

To measure the woody species diversity we used three Hill numbers (effective number of species) based on species relative abundances (Hsieh et al. 2016; Rother et al. 2019). These diversity indexes are parameterized in three orders of q: i) q=0 - number of species richness, measure rare species with the same weight of dominant species; ii) q=1 - exponential form of Shannon entropy, measure species diversity giving less weight to rare species; and iii) q=2 - inverse of Simpson diversity, measure the relative abundance distribution of species giving even less weight to rare species than Shannon, where higher values indicate evenness on abundance distribution (Hill 1973; Jost 2006; Gotelli and Chao 2013). These indexes were calculated in “iNEXT” package (Hsieh et al. 2016) and the equations are described in Jost (2006).

Above-ground carbon stock

First, we calculated the above-ground biomass of each individual with the allometric equation improved by Chave *et al* (2014) in equation 1:

$$AGB = \exp[-1.803 - 0.976E + 0.976\ln(\rho) + 2.673\ln(D) - 0.0299[\ln(D)]^2] \quad \text{(Eq. 1)}$$

where AGB is the estimated above-ground biomass, E is a measure of environmental stress; ρ is wood density (g/cm3) and D (cm) is the tree´s diameter at breast height. The value of E was obtained according to the geographic coordinates of each area using the “BIOMASS” package where we calculated AGBest (Réjou-Méchain et al. 2017). The total AGB per patch was the sum of the AGBs of all trees having DBH ≥ 5 cm, which was then converted to megagrams per hectare (Mg ha^{-1}). The value for wood density (g/cm3) was obtained from Global Wood Density database

(GWD; Zanne et al. 2009). For species with wood density that have not been recorded in GWD we made an average with the species of de same genus recorded (Magnago et al. 2014; Matos et al. 2020). Second, we obtained the carbon stock assuming that the carbon concentration of a tree's different organs is assumed to be approximately 50% of the biomass (Malhi et al. 2004).

Drivers of second-growth forest recovery

Plot scale drivers

Plot drivers were grouped into two categories, such as soil properties and management intensity. We considered ten properties-related soil: i) P - phosphorus concentration; ii) Mg^{2+} - magnesium concentration; iii) Ca^{2+} - calcium concentration; iv) K - potassium concentration; v) Fe - iron concentration; vi) Al^{3+} - aluminum concentration; vii) pH - measure of hydrogen ion concentration; viii) clay - percentage of clay; ix) sand - percentage of sand; and x) silt - percentage of silt in the soil sample. For this, three random samples of 0-20 cm depth were taken in each patch. The three samples were later homogenized and analyzed by Soil Department of Federal University of Viçosa, following the protocol of Santos *et al* (2018).

For management intensity were considered the data of land-use history of the patches improved by the landowner company: i) planting cycle - numbers of times that each patch was used by eucalyptus plantation; ii) cutting cycle - number of times that the eucalyptus plantation was cutting in each patch; iii) use time - time between de first cycle planting and last cycle cutting; and iv) fallow age - time between the last cutting cycle and the tree sampling along secondary succession. These variables-related management intensity and land-use history have been used in previous studies (Jakovac et al. 2015; Villa et al. 2018; Pérez-Cárdenas et al. 2020).

We summarized the soil properties variables and management intensity performing two principal component analyses (PCA) based on correlation matrix separately using "FactorMiner" package (Husson et al. 2020). The soil properties PCA was composed by concentrations of phosphorus, magnesium, calcium, potassium, iron, aluminum, pH, and percentages of clay, sand, and silt. Meanwhile, the management intensity PCA was composed by planting cycle, cutting cycle, use time, and fallow age. Then, we analyzed how many axes of PCA we needed to retain for both variables sets applying the Horn's parallel analysis with 600 iterations and retaining the axes with an adjusted eigenvalue > 1. These parallel analyses were processed using "Paran" package (Dinno 2018). Thus, were retained only one axis as proxy for management intensity and two axes as proxy for soil properties. We called the first PCA axis of the soil properties as soil fertility and the second PCA axis as soil texture because strong correlation with chemical and physical properties, respectively (see more information in the results topic).

Patch and landscape scale drivers

For patch configuration and landscape composition characteristics we used patch-scale and patch-landscape approaches, respectively (Matos et al. 2020; Pérez-Cárdenas et al. 2021). Thus, we measured three patch-scale variables in independent patches: i) patch size - area in hectares (ha); ii) patch isolation - the minor linear distance in meters between the patch sampled and another natural forest patch; and iii) source distance - the minor linear distance between each patch sampled and some natural forest patch ≥ 500 ha. We collected two patch-landscape metrics for landscape composition: i) forest cover - percentage of forest cover in the landscape; and ii) silviculture cover - percentage of planted forests in the landscape. Patch configuration and landscape composition metrics were obtained by classified images improved by Brazilian Annual Land Use and Land Cover Mapping Project (MapBiomas Collection 5) referent to 2018. The patch isolation and source distance were measured in ArcGis software (Environmental Systems Research Institute, Redlands, CA, USA). The patch area, forest cover and silviculture cover were calculated in "FRAGSTAT 4.2" software (McGarial et al. 2012) in a buffer of 2 km of radius since the center of each transect (Matos et al. 2016; Coelho et al. 2020) was extracted from "ArcGis" software (Fig 1c and 1d).

Statistical analyses

We applied the Moran's I test to check for the potential influence of spatial autocorrelation in diversity and carbon stock of the sampled transects. For this, we used the "spdep" package (Bivand and Piras 2015) and the significance was determined by the Monte-Carlo permutation test (1000 permutations). Thus, we did not find a geographical correlation between our sampled transects. To evaluate the influences of management intensity, soil properties, local configuration and landscape composition on diversity and carbon stock (response variables) we used generalized linear models (GLM) based on equation 2:

$$\text{Diversity or AGC} \sim \text{Soil fertility} + \text{Soil texture} + \text{Management intensity} + \text{Patch area} + \text{Patch isolation} + \text{Source distance} + \text{Forest cover} + \text{Silviculture cover} \quad \text{(Eq. 2)}$$

where soil fertility was the first PCA axis of soil properties, soil texture the second PCA axis of soil properties, and management intensity was the first PCA axis of management intensity PCA.

Using an information-theoretic approach and multi-model inference (Burnham et al. 2011) in the "MuMIn" package (Barton 2017) we calculated Akaike's information criterion (AICc, indicated for small samples), by the combination of all candidate models. Were applied Spearman correlation analyses to avoid variables with correlations > 0.6 in the same candidate models. We considered the models with $\Delta AICc \leq 5$ as the best models to explain the variation of variables responses and calculated the average models (Burnham and Anderson 2002; Matos et al. 2020). In addition, we obtained the independent contribution of each environmental predictor from the sum of Akaike weights of average models (Burnham et al. 2011).

Results

Drivers of second-growth forests

In this study, 3.5 ha of sampled secondary forest area were included. A total of 1,103 individuals were sampled, distributed among 84 species. The sampled soils were generally acidic pH, with very varied chemical and physical characteristics (Tab. 1). In the soil properties PCA was retained two axes: the first axis (adjusted eigenvalue = 5.293; explained 64.2% of the variation) was positively correlated with pH, Mg^{2+}, Ca^{2+}, K, P, and silt percentage, and negatively correlated with Fe, Al^{3+}, and clay percentage; and the second axis (adjusted eigenvalue = 1.144; explained 17.6% of the variation) was positively correlated with P, silt and clay percentages, e negatively correlated with sand percentage. Thus, we called the first axis of soil fertility, because strong correlation with nutrient contents, and the second axis of soil texture, because strong correlation with physical characteristics (see Tab.1).

The fallow age of our second-growth forests varies between 3 and 32 years and the use time for eucalyptus plantation varied between 16 and 50 years. During the time of use these areas had 1 to 3 planting cycles, and 2 to 4 cutting cycles. Only the first axis of management intensity PCA was retained in the Horn's parallel analyses (adjusted eigenvalue = 2.170). This axis was positively correlated with cutting cycle and use time, and negatively correlated with follow age.

The patch configuration and landscape composition were also quite varied among the secondary forests sampled. The area of forests ranged from 13.4 to 199 ha, and the isolation from 25 to 698 meters. The source patch larger than 500 ha was the same for all SGFs, the Rio do Doce state park, ranging source distance from 25 to 21,632 meters. The landscape composition varied between 5 and 54% of forest cover and 9 to 62% of eucalyptus cover.

Effects of multiple drivers

The diversity parameters and above-ground carbon stock were influenced by the environmental variables (Fig 2). Species richness (q = 0) was negatively influenced by management intensity (β = -1.495 ± 0.536 *SE*, z = 2.679, p = 0.007) and patch isolation (β = -0.011 ± 0.004 *SE*, z = 2.618, p = 0.009). The exponential Shannon (q = 1) was negatively influenced by management intensity (-0.993 ± 0.375 *SE*, z = 2.554, p = 0.011) and patch isolation (β = -0.006 ± 0.003, z = 2.05, p = 0.040), and positively influenced by source distance (β = 0.0002 ± 0.00009 *SE*, z = 1.96, p = 0.05). The inverse of Simpson was also negatively influenced by management intensity (q=2; β -0.676 ± 0.284 *SE*, z = 2.296, p = 0.021) and by source distance (β = -0.003 ± 0.002 *SE*, z = 1.76, p = 0.078). Finally, above-ground carbon stock was negatively influenced by management intensity (β = -2.066 ± 0.913 *SE*, z = 2.175, p = 0.029) and soil fertility (β = -1.511 ± 0.583 *SE*, z = 2.49, p = 0.012).

In all diversity parameters, management intensity was the most important variable. The other two variables more important for species richness were patch isolation and soil fertility. For exponential Shannon were patch isolation and source distance, and for inverse of Simpson were source distance and patch isolation, in this order. For above-ground carbon stock, soil fertility was the variable with higher independent contribution, followed by management intensity and forest cover.

Table 1. Environmental variables used to evaluate influences in secondary succession in this work. The management intensity and soil properties were summarized into PCA axis. Parallel Horn's analyses retained only one axis for management intensity and two for soil properties. Because strong correlations between chemical characteristics and the first axis and between the second axis and physical characteristics we called these axes of soil fertility and soil texture, respectively. Local configuration and landscape composition variables were directed inserted in the models.

Variable sets	*Unit*	*Minimum*	*Maximum*	*PCA axis 1*	*PCA axis 2*
Soil Properties					
pH	(H2O)	3.48	6.41	0.968*	-0.0531
Mg^{2+}	cmol/dm³	0.05	1.23	0.9268*	0.1509
Ca^{2+}	cmol/dm³	0.32	6.36	0.9127*	0.1074
K	mg/dm³	11	195	0.8503*	0.1087
P	mg/dm³	1.3	9.9	0.5122*	0.4112*
Fe	mg/dm³	17.4	104.4	-0.8115*	0.2475
Al^{3+}	cmol/dm³	2.2	8.7	-0.8994*	0.0563
Silt	%	0.006	0.341	0.688*	0.6258*
Clay	%	0.295	0.757	-0.7823*	0.4947*
Sand	%	0.104	0.632	0.3066	-0.9184*
Explained variation by PCA	*%*	-	-	*62.6*	*17.6*
Management Intensity					
Planting cycle	Number	1	3	-0.0900	0.9921*
Cutting cycle	Number	2	4	0.9376*	-0.05
Use time	Years	16	50	0.8691*	0.15
Fallow age	Years	3	32	-0.9626*	-0.01
Explained variation by PCA	*%*	-	-	*64.2*	*25.2*
Patch Configuration					
Patch area	ha	13.4	199	-	-
Patch isolation	m	25	698	-	-
Source distance	m	25	21632	-	-
Landscape composition					
Forest cover	%	5.011	54.610	-	-
Silviculture Cover	%	9.746	62.156	-	-

* Significance values of correlation ($p < 0.05$).

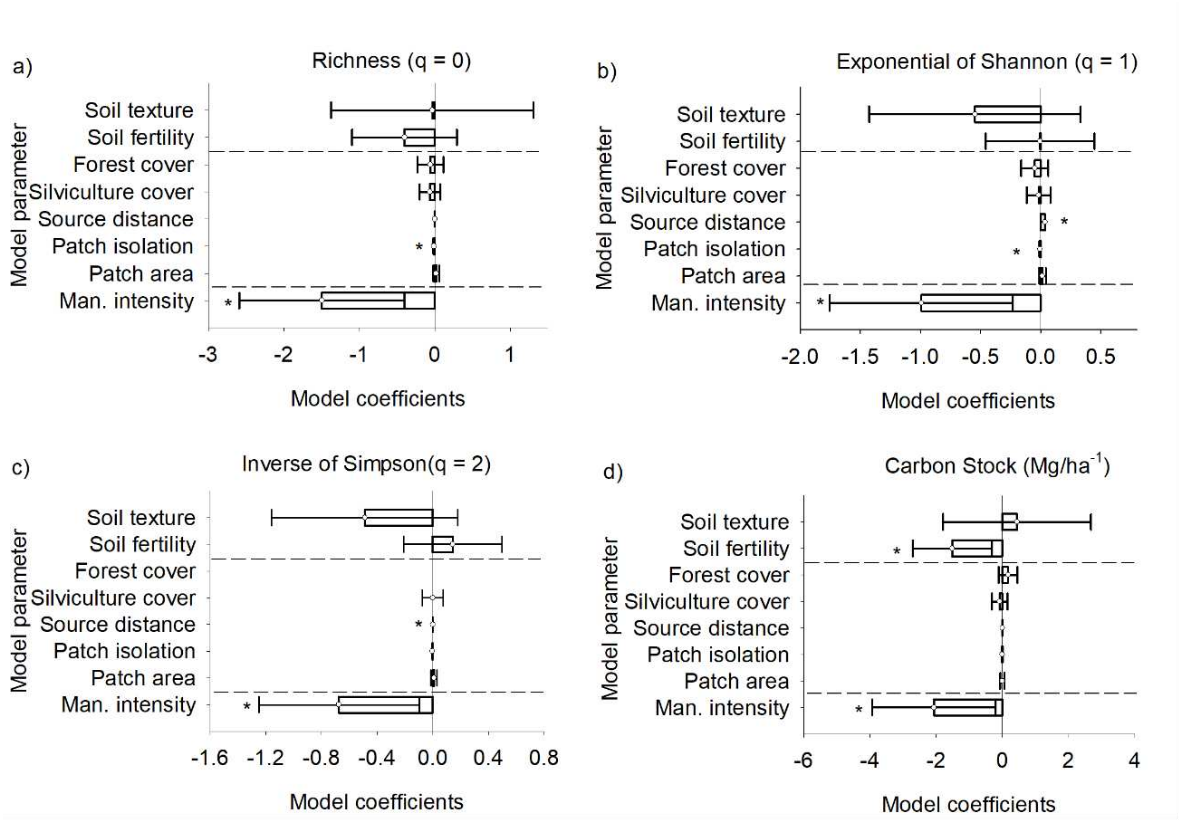


Figure 2. Multiple drivers influence species richness (q=0), exponential Shannon diversity (q=1), inverse of Simpson diversity (q=2), and above-ground carbon stock considering models with values of ΔAICc ≤ 5. The position of the bars represents positive or negative effect and error bars represent the (±) adjusted standard errors obtained after average models analysis. If the error bar is crossing the line of zero the variable is not significant. The significant influences are shown by (*).

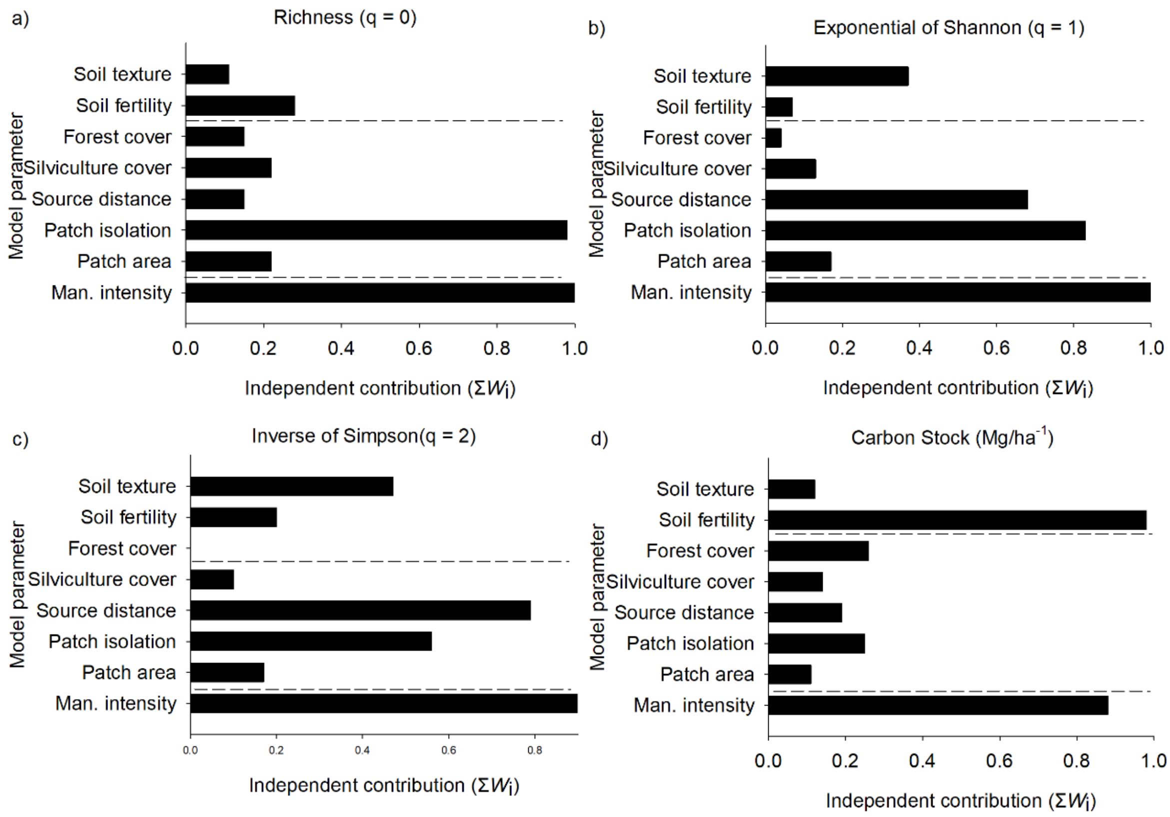


Figure 3. Sum of independent contribution of each environmental variable on species richness (q=0), exponential Shannon diversity (q=1), inverse of Simpson diversity (q=2), and above-ground carbon stock considering models with values of ΔAICc ≤ 5.

Discussion

Our study indicates how multiple drivers influence the above-ground carbon stock and diversity after long-term land use history in human-modified Atlantic Forest landscape. We found a limited effect of soil properties in the evaluated parameters: soil fertility negatively influenced the AGC, but soil properties did not influence the diversity parameters. However, as expected, we found a negative effect of management intensity, isolation, and source distance on forest recovery. These factors probably favor pioneer species, which are more tolerant to environmental changes, little dependent on animal dispersal, and low AGC capacity (Villa et al. 2018; Pérez-Cárdenas et al. 2021). Thus, we discuss these effects and suggest that priority areas for passive restoration are those as lower management intensities and with lower isolation and source distance.

Plot driver effects on diversity and AGC

Soil properties are important predictors that explain diversity and carbon stock variation in the most ecosystems including the Atlantic Forest (Neri et al. 2013; Punchi-Manage et al. 2013; Rodrigues et al. 2018; Cantidio and Souza 2019). Generally, the less soil acidity (i.e. the higher pH), the higher the concentration of nutrients, the greater the fertility, and thus the greater the diversity and AGC (Gastauer and Meira-Neto 2014). In this study, the soil acidity axis value is positively correlated with pH, Mg^{2+}, Ca^{2+}, K, P, and negatively correlated with Fe and Al^{3+} concentrations, confirming soil fertility patterns. However, soil properties, specifically soil fertility, influenced only AGC in our study in a negative way: the higher nutrients concentrations, the lower the carbon stock. This result was also found by another study in the Amazon domain and can be explained by the high level of potassium in the soil, responsible for the increasing of exchanging cations concentrations and for selection of species with lower wood density, with lower carbon stock (Quesada et al. 2012). The limited effect of soil properties diversity regeneration was also found for Amazon domain, indicating more importance of management intensity and landscape configurations after long-term land use (Jakovac et al. 2015).

The disturbances caused by the management of several land uses (e.g., soil revolving before planting and harvesting after crop growth) cause changes in soil properties, in its seed bank, and thus in the resilience of ecosystems (Lawrence et al. 2007; Randriamalala et al. 2015; Jakovac et al. 2016; de Avila et al. 2018). In our study, the management intensity did not affect soil properties (there was no significant correlation between soil acidity or soil texture with management intensity) but affected diversity and carbon stock. This is because disturbances generate drastic changes in the environment favoring pioneer species, which survive on various environmental conditions, with faster life cycles, and lower carbon stocks (Tabarelli et al. 2010b; Villa et al. 2018). The successive planting and cutting cycles more often expose the soil seed bank to high solar irradiation and temperatures, making it difficult to establish species sensitive to these factors (Holp 1999), the so-called shade-tolerant species. The decrease of shade-tolerant species can explain loss of species richness, which are the main responsible for AGC in old-growth forests (Stephenson et al. 2014; Bello et al. 2015) and increasing AGC during secondary succession (unpublished data). These favoring of pioneer species may also explain the decrease in exponential Shannon and inverse of Simpson, showing increase of dominance of some species.

Patch and landscape driver effects on diversity and AGC

The isolation of regenerating areas is a limiting factor for the tree species recolonization. The distance between forest fragments can prevent seed-dispersing animals through the regenerating areas (Ewers and Didham 2006; Arroyo-Rodríguez et al. 2017). This depends on the survival home range of an animal population: smaller species typically have a smaller home range and circulate for short distances (Jetz et al. 2004; Pardini 2004). Isolation also forces animal populations to move through inhospitable environments (e.g., pastures), making the movement of some species even more difficult because of matrix contrasts (Antongiovanni and Metzger 2005; Zambrano et al. 2019). Furthermore, seeds dispersed by wind also have their dispersal range limited by seed shape and mass: seeds of larger masses and less aerodynamics reach shorter distances (Collevatti et al. 2010; Cote et al. 2017). Thus, isolation decreases the recolonization chance of some species affecting the diversity in areas during regeneration.

The source patches are important in fragmented landscapes, because they are larger sizes, and capable of housing greater diversity and populations of plants and dispersing animals (Fahrig 2003, 2007). Thus, these fragments are sources of propagules for the maintenance of diversity in smaller fragments where there is a decrease in populations size and species extinctions (Ewers and Didham 2006; Pardini et al. 2010; Bello et al. 2015; Magnago et al. 2015a), as well as for areas in regeneration. Our results showed that the increase in the distance of the source patch increases the exponential Shannon and decreases the inverse of Simpson. This means that the increase in the source distance generates a decrease in rare species, but still allows some species dominance. Rare species are generally more present in larger fragments because they are more sensitive to variations in environmental conditions (Gámez-Virués et al. 2015; Magnago et al. 2015a; Solar et al. 2015). For example, some shade-tolerant species that may not survive or germinate in environments with high solar irradiations, common conditions in smaller fragments that have most of the habitat under edge influences, and areas in early stages of regeneration (Paula et al. 2011; Magnago et al. 2015b; Villa et al. 2018). Thus, the farther from large patches (source distance), the lower the chance of recolonization by rare species in small patches and consequently in the areas under regeneration, which can explain de positive effect in exponential Shannon diversity. However, the farther away from source fragments, the lower the chance of recolonization by species dispersed by animals that are concentrated in nuclear areas of large fragments, decreasing the abundance of species dispersed by animals (Magnago et al. 2014; Lino et al. 2019; Zambrano et al. 2019; Chase et al. 2020), which can explain the negative influence of source distance in inverse of Simpson concentration.

We expected that the patch area, as well as the composition of the landscape, would influence regeneration after the long-term eucalyptus planting. Matos et al (2020) found a positive effect of patch area on diversity and AGC recovery. Similarly, Pérez-Cárdenas et al (2021) and Jakovac et al (2015) found greater diversity in areas with greater forest cover and lower AGC in areas with higher pasture cover. The higher natural habitat amount in the landscape, greater connectivity between the patches and the capacity to conserve populations in the landscape, maintaining seed dispersal patterns (Tscharntke et al. 2012; Fahrig 2013). We also expected positive effects on silviculture cover, since eucalyptus is a matrix more similar to tropical forests and allows fauna movement between plantations, increasing connectivity between forest fragments (Barlow et al. 2007; Carrilho et al. 2017; Brancalion et al. 2019). However, our data show that these factors do not significantly affect and have little importance in the regeneration of diversity and carbon stock in regenerating areas after long-term eucalyptus planting.

Implication on passive restoration priority areas

There is a great demand for ecosystems restoration in the world and in Brazil, either for carbon emission reduction targets or even environmental legislation of the countries (Soares-filho et al. 2014; Uriarte and Chazdon 2016; Strassburg et al. 2020). Considering the expressive land use for different activities in the Atlantic Forest and its high degree of fragmentation, part of the priority areas and available areas for restoration in Brazil is in this biome (Nazareno et al. 2012; Scarano and Ceotto 2015). In this sense, our study provides scientific bases on the choice of areas with higher potential for diversity and AGC recovery, mainly for areas used for a long time by eucalyptus planting. It is known that these areas regenerate naturally, but we indicate that areas with lower previously management intensity and less isolated from other forest patches, have greater capacity to regenerate species diversity and carbon stock. Thus, these areas reduce the costs of forest restoration, reducing the need for human interventions. Similarly, we indicate that the more previously management intensity and patch isolation, the more intense restoration monitoring should be, thus evaluating the need for intervention, such as the inclusion of disperser attraction methods.

References

Alvares CA, Stape JL, Sentelhas PC, et al (2013) K??ppen's climate classification map for Brazil. Meteorol Zeitschrift 22:711–728. https://doi.org/10.1127/0941-2948/2013/0507

Antongiovanni M, Metzger JP (2005) Influence of matrix habitats on the occurrence of insectivorous bird species in Amazonian forest fragments. Biol Conserv 122:441–451. https://doi.org/10.1016/j.biocon.2004.09.005

APG IV (2016) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Bot J Linn Soc 181:1–20

Arroyo-Rodríguez V, Melo FPL, Martínez-Ramos M, et al (2017) Multiple successional pathways in human-modified tropical landscapes: new insights from forest succession, forest fragmentation and landscape ecology research. Biol Rev 92:326–340. https://doi.org/10.1111/brv.12231

Barlow J, Gardner TA, Araujo IS, et al (2007) Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. Proc Natl Acad Sci U S A 104:18555–18560. https://doi.org/10.1073/pnas.0703333104

Barton K (2017) 'MuMIn': Multi-Model Inference.

Bello C, Galetti M, Pizo MA, et al (2015) Defaunation affects carbon storage in tropical forests. Sci Adv 1:1–11. https://doi.org/10.1126/sciadv.1501105

Bertacchi MIF, Amazonas NT, Brancalion PHS, et al (2016) Establishment of tree seedlings in the understory of restoration plantations: Natural regeneration and enrichment plantings. Restor Ecol 24:100–108. https://doi.org/10.1111/rec.12290

Bivand R, Piras G (2015) Comparing implementations of estimation methods for spatial econometrics. J Stat Softw 63:1–36. https://doi.org/10.18637/jss.v063.i18

Brancalion PHS, Amazonas NT, Chazdon RL, et al (2020) Exotic eucalypts: From demonized trees to allies of tropical forest restoration? J Appl Ecol 57:55–66. https://doi.org/10.1111/1365-2664.13513

Brancalion PHS, Campoe O, Mendes JCT, et al (2019) Intensive silviculture enhances biomass accumulation and tree diversity recovery in tropical forest restoration. Ecol Appl 29:1–12. https://doi.org/10.1002/eap.1847

Burnham KP, Anderson DR (2002) Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach (2nd ed)

Burnham KP, Anderson DR, Huyvaert KP (2011) AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. Behav Ecol Sociobiol 65:23–35. https://doi.org/10.1007/s00265-010-1029-6

Cantidio LS, Souza AF (2019) Aridity, soil and biome stability influence plant ecoregions in the Atlantic Forest, a biodiversity hotspot in South America. Ecography (Cop) 42:1887–1898. https://doi.org/10.1111/ecog.04564

Carrilho M, Teixeira D, Santos-Reis M, Rosalino LM (2017) Small mammal abundance in Mediterranean Eucalyptus plantations: how shrub cover can really make a difference. For Ecol Manage 391:256–263. https://doi.org/10.1016/j.foreco.2017.01.032

Chase JM, Blowes SA, Knight TM, et al (2020) Ecosystem decay exacerbates biodiversity loss with habitat loss. Nature 584:238–243. https://doi.org/10.1038/s41586-020-2531-2

Chave J, Réjou-Méchain M, Búrquez A, et al (2014) Improved allometric models to estimate the aboveground biomass of tropical trees. Glob Chang Biol 20:3177–3190. https://doi.org/10.1111/gcb.12629

Chazdon RL (2014) Second growth: the promise of tropical forest regeneration in an age of deforestation. University of Chicago Press

Chazdon RL, Broadbent EN, Rozendaal DMA, et al (2016) Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics

Coelho AJP, Magnago LFS, Matos FAR, et al (2020) Effects of anthropogenic disturbances on biodiversity and biomass stock of Cerrado, the Brazilian savanna. Biodivers Conserv 0123456789: https://doi.org/10.1007/s10531-020-02013-6

Collevatti RG, Lima JS, Soares TN, Telles MP de C (2010) Spatial genetic structure and life history traits in cerrado tree species: Inferences for conservation. Nat a Conserv 8:54–59. https://doi.org/10.4322/natcon.00801008

Cote J, Bestion E, Jacob S, et al (2017) Evolution of dispersal strategies and dispersal syndromes in fragmented landscapes. 56–73. https://doi.org/10.1111/ecog.02538

de Avila AL, van der Sande MT, Dormann CF, et al (2018) Disturbance intensity is a stronger driver of biomass recovery than remaining tree-community attributes in a managed Amazonian forest. J Appl Ecol 55:1647–1657. https://doi.org/10.1111/1365-2664.13134

Dinno A (2018) Paran: Horn's test of principal components/factors. 1–6

Ewers R, Didham R (2006) Confounding factors in the detection of species responses to habitat fragmentation. Biol Rev Camb Philos Soc 81:117–142. https://doi.org/10.1017/s1464793105006949

Fahrig L (2003) Effects of Habitat Fragmentation on Biodiversity. Annu Rev Ecol Environ Syst 34:487–515. https://doi.org/10.1146/132419

Fahrig L (2007) Non-optimal animal movement in human-altered landscapes. Funct Ecol 21:1003–1015. https://doi.org/10.1111/j.1365-2435.2007.01326.x

Fahrig L (2013) Rethinking patch size and isolation effects: The habitat amount hypothesis. J Biogeogr 40:1649–1663. https://doi.org/10.1111/jbi.12130

Finegan B (1996) Pattern and process In neotropical secondary rain forests: the first 100 years of succession. 793–796

Gámez-Virués S, Perović DJ, Gossner MM, et al (2015) Landscape simplification filters species traits and drives biotic homogenization. Nat Commun 6:8568. https://doi.org/10.1038/ncomms9568

Gastauer M, Meira-Neto JAA (2014) Interactions, Environmental Sorting and Chance: Phylostructure of a Tropical Forest Assembly. Folia Geobot 49:443–459.

https://doi.org/10.1007/s12224-013-9181-1

Gonçalvez JL de M, Alvares CA, Higa AR, et al (2013) Forest Ecology and Management Integrating genetic and silvicultural strategies to minimize abiotic and biotic constraints in Brazilian eucalypt plantations. For Ecol Manage 301:6–27. https://doi.org/10.1016/j.foreco.2012.12.030

Gotelli NJ, Chao A (2013) Measuring and Estimating Species Richness, Species Diversity, and Biotic Similarity from Sampling Data. Elsevier Ltd.

Guariguata MR, Ostertag R (2001) Neotropical secondary forest succession : changes in structural and functional characteristics. For Ecol Manage 148:185–206. https://doi.org/10.1016/S0378-1127(00)00535-1

Hansen MC, Potapov P V, Moore R, et al (2013) High-Resolution Global Maps of. 134:850–854

Hill MO (1973) Diversity and Evenness: A Unifying Notation and Its Consequences. Ecology 54:427–432. https://doi.org/10.2307/1934352

Holp KD (1999) Factors Limiting Tropical Rain Forest Regeneration in Abandoned Pasture : Seed Rain , Seed Germination , Microclimate , and Soil ’. Biotropica 31:229–242

Hsieh TC, Ma KH, Chao, A. 2016. (2016) iNEXT: iNterpolation and EXTrapolation for species diversity.

Husson AF, Josse J, Le S, et al (2020) Package ‘ FactoMineR ’

Ivanova A, Zia A, Ahmad P, Bastos-Lima M (2020) Climate mitigation policies and actions: access and allocation issues. Int Environ Agreements Polit Law Econ 20:287–301. https://doi.org/10.1007/s10784-020-09483-7

Jakovac CC, Bongers F, Kuyper TW, et al (2016) Land use as a filter for species composition in Amazonian secondary forests. J Veg Sci 27:1104–1116. https://doi.org/10.1111/jvs.12457

Jakovac CC, Peña-Claros M, Kuyper TW, Bongers F (2015) Loss of secondary-forest resilience by land-use intensification in the Amazon. J Ecol 103:67–77. https://doi.org/10.1111/1365-

2745.12298

Jetz W, Carbone C, Fulford J, Brown JH (2004) The scaling of animal space use. Science (80-) 306:266–268. https://doi.org/10.1126/science.1102138

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

Klemick H (2011) Shifting cultivation , forest fallow , and externalities in ecosystem services : Evidence from the Eastern Amazon. J Environ Econ Manage 61:95–106. https://doi.org/10.1016/j.jeem.2010.07.003

Lawrence D, D'Odorico P, Diekmann L, et al (2007) Ecological feedbacks following deforestation create the potential for a catastrophic ecosystem shift in tropical dry forest. Proc Natl Acad Sci U S A 104:20696–20701. https://doi.org/10.1073/pnas.0705005104

Lino A, Fonseca C, Rojas D, et al (2019) A meta-analysis of the effects of habitat loss and fragmentation on genetic diversity in mammals. Mamm Biol 94:69–76. https://doi.org/10.1016/j.mambio.2018.09.006

Lopes W de P, Silva AF da, Souza AL de, Meira Neto JAA (2002) Estrutura fitossociólога de um trecho de vegetação arbórea no Parque Estadual do Rio Doce - Minas Gerais , Brasil. Acta Bot Brasilica 16:443–456. https://doi.org/10.1590/s0102-33062002000400007

Magnago LFS, Edwards DP, Edwards FA, et al (2014) Functional attributes change but functional richness is unchanged after fragmentation of Brazilian Atlantic forests. J Ecol 102:475–485. https://doi.org/10.1111/1365-2745.12206

Magnago LFS, Magrach A, Laurance WF, et al (2015a) Would protecting tropical forest fragments provide carbon and biodiversity cobenefits under REDD+? Glob Chang Biol 21:3455–3468. https://doi.org/10.1111/gcb.12937

Magnago LFS, Rocha MF, Meyer L, et al (2015b) Microclimatic conditions at forest edges have significant impacts on vegetation structure in large Atlantic forest fragments. Biodivers Conserv 24:2305–2318. https://doi.org/10.1007/s10531-015-0961-1

Malhi Y, Baker TR, Phillips OL, et al (2004) The above-ground coarse wood productivity of 104 Neotropical forest plots. Glob Chang Biol 10:563–591. https://doi.org/10.1111/j.1529-8817.2003.00778.x

Matos FAR, Magnago LFS, Aquila Chan Miranda C, et al (2020) Secondary forest fragments offer important carbon and biodiversity cobenefits. Glob Chang Biol 26:509–522. https://doi.org/10.1111/gcb.14824

Matos FAR, Magnago LFS, Gastauer M, et al (2016) Effects of landscape configuration and composition on phylogenetic diversity of trees in a highly fragmented tropical forest. J Ecol. https://doi.org/10.1111/1365-2745.12661

McGarial K, Cushman SA, Ene E (2012) FRAGSTATS v4: spatial patern analysis program for categorical and continuous maps

Myers N, Mittermeier RA, Mittermeier CG, et al (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858

Nazareno AG, Feres JM, de Carvalho D, et al (2012) Serious New Threat to Brazilian Forests. Conserv Biol 26:5–6. https://doi.org/10.1111/j.1523-1739.2011.01798.x

Neri A V., Schaefer CEGR, Souza AL, et al (2013) Pedology and plant physiognomies in the cerrado, Brazil. An Acad Bras Cienc 85:87–102. https://doi.org/10.1590/S0001-37652013000100007

Oberleitner F, Egger C, Oberdorfer S, et al (2021) Recovery of aboveground biomass, species richness and composition in tropical secondary forests in SW Costa Rica. For Ecol Manage 479:118580. https://doi.org/https://doi.org/10.1016/j.foreco.2020.118580

Oliveira-Junior ND de, Heringer G, Bueno ML, et al (2020) Prioritizing landscape connectivity of a tropical forest biodiversity hotspot in global change scenario. For Ecol Manage 472:. https://doi.org/10.1016/j.foreco.2020.118247

Pardini R (2004) Effects of forest fragmentation on small mammals. Biodivers Conserv 13:2567–2586

Pardini R, de Bueno AA, Gardner TA, et al (2010) Beyond the fragmentation threshold hypothesis: Regime shifts in biodiversity across fragmented landscapes. PLoS One 5:. https://doi.org/10.1371/journal.pone.0013666

Paula MD de, Costa CPA, Tabarelli M (2011) Carbon storage in a fragmented landscape of Atlantic forest: The role played by edge-affected habitats and emergent trees. Trop Conserv Sci 4:349–358. https://doi.org/10.1177/194008291100400310

Pérez-Cárdenas N, Mora F, Arreola-Villa F, et al (2021) Effects of landscape composition and site land-use intensity on secondary succession in a tropical dry forest. For Ecol Manage 482:118818. https://doi.org/https://doi.org/10.1016/j.foreco.2020.118818

Pérez-Cárdenas N, Mora F, Arreola F, et al (2020) Effects of landscape composition and land use intensity on secondary succession in a Mexican tropical dry forest. For Ecol Manage

Punchi-Manage R, Getzin S, Wiegand T, et al (2013) Effects of topography on structuring local species assemblages in a Sri Lankan mixed dipterocarp forest. J Ecol 101:149–160. https://doi.org/10.1111/1365-2745.12017

Quesada CA, Phillips OL, Schwarz M, et al (2012) Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. Biogeosciences 9:2203–2246. https://doi.org/10.5194/bg-9-2203-2012

Randriamalala JR, Hervé D, Letourmy P, Carrière SM (2015) Effects of slash-and-burn practices on soil seed banks in secondary forest successions in Madagascar. Agric Ecosyst Environ 199:312–319. https://doi.org/10.1016/j.agee.2014.09.010

Réjou-Méchain M, Tanguy A, Piponiot C, et al (2017) Biomass: an R Package for Estimating Above-Ground Biomass and Its Uncertainty in Tropical Forests. Methods Ecol Evol 8:1163–1167. https://doi.org/10.1111/2041-210X.12753

Rodrigues PMS, Schaefer CEGR, De Oliveira Silva J, et al (2018) The influence of soil on vegetation structure and plant diversity in different tropical savannic and forest habitats. J Plant Ecol 11:226–236. https://doi.org/10.1093/jpe/rtw135

Rosa MR, Brancalion PHS, Crouzeilles R, et al (2021) Hidden destruction of older forests threatens Brazil's Atlantic Forest and challenges restoration programs. Sci Adv 7:1–9. https://doi.org/10.1126/sciadv.abc4547

Rother DC, Liboni AP, Magnago LFS, et al (2019) Ecological restoration increases conservation of taxonomic and functional beta diversity of woody plants in a tropical fragmented landscape. For Ecol Manage 451:117538. https://doi.org/10.1016/j.foreco.2019.117538

Rozendaal DMA, Bongers F, Aide TM, et al (2019) Biodiversity recovery of Neotropical secondary forests. Sci Adv 5:. https://doi.org/10.1126/sciadv.aau3114

Santos HG dos, Jacomine PKT, Anjos LHC dos, et al (2018) Sistema brasileiro de classificação de solos, 5. ed. rev

Scarano FR, Ceotto P (2015) Brazilian Atlantic forest: impact, vulnerability, and adaptation to climate change. Biodivers Conserv 24:2319–2331. https://doi.org/10.1007/s10531-015-0972-y

Sloan S, Goosem M, Laurance SG (2015) Tropical forest regeneration following land abandonment is driven by primary rainforest distribution in an old pastoral region. Landsc Ecol. https://doi.org/10.1007/s10980-015-0267-4

Soares-filho B, Rajão R, Macedo M, et al (2014) Cracking Brazil ' s Forest Code. 363–364

Solar R, Barlow J, Ferreira J, et al (2015) How pervasive is biotic homogenization in human-modified tropical forest landscapes? Ecol Lett 18:1108–1118. https://doi.org/10.1111/ele.12494

Stephenson NL, Das AJ, Condit R, et al (2014) Rate of tree carbon accumulation increases continuously with tree size. Nature 507:90–93. https://doi.org/10.1038/nature12914

Strassburg BBN, Iribarrem A, Beyer HL, et al (2020) Global priority areas for ecosystem restoration. Nature 586:724–729. https://doi.org/10.1038/s41586-020-2784-9

Tabarelli M, Aguiar A V., Girão LC, et al (2010a) Effects of pioneer tree species hyperabundance on forest fragments in Northeastern Brazil. Conserv Biol 24:1654–1663. https://doi.org/10.1111/j.1523-1739.2010.01529.x

Tabarelli M, Aguiar A V., Girão LC, et al (2010b) Effects of pioneer tree species hyperabundance on forest fragments in Northeastern Brazil. Conserv Biol 24:1654–1663. https://doi.org/10.1111/j.1523-1739.2010.01529.x

Tscharntke T, Tylianakis JM, Rand TA, et al (2012) Landscape moderation of biodiversity patterns and processes - eight hypotheses. Biol Rev 87:661–685. https://doi.org/10.1111/j.1469-185X.2011.00216.x

Uriarte M, Chazdon RL (2016) Incorporating natural regeneration in forest landscape restoration in tropical regions: synthesis and key research gaps. Biotropica 48:915–924. https://doi.org/10.1111/btp.12411

Veloso HP, Rangel Filho ALR, Lima JCA (1991) Classificação da Vegetação Brasileira Adaptada a um Sistema Universal

Villa PM, Martins SV, de Oliveira Neto SN, et al (2020) Policy forum: Shifting cultivation and agroforestry in the Amazon: Premises for REDD+. For Policy Econ 118:. https://doi.org/10.1016/j.forpol.2020.102217

Villa PM, Venâncio S, Nolasco S, et al (2018) Intensification of shifting cultivation reduces forest resilience in the northern Amazon. For Ecol Manage 430:312–320. https://doi.org/10.1016/j.foreco.2018.08.014

Zambrano J, Garzon-Lopez CX, Yeager L, et al (2019) The effects of habitat loss and fragmentation on plant functional traits and functional diversity: what do we know so far? Oecologia 191:505–518

Zanne AE, Lopez-Gonzalez, G., Coomes DA, Ilic J, et al (2009) Data from: Towards a worldwide wood economics spectrum, Dryad

Zhang D, Zhang J, Yang W, et al (2014) Plant and soil seed bank diversity across a range of ages of Eucalyptus grandis plantations afforested on arable lands. Plant Soil 376:307–325.

https://doi.org/10.1007/s11104-013-1954-z

CHAPTER 5: Multiple drivers influence the tree functional composition of second-growth Atlantic Forests

Abstract: Second-growth forests (SGF) are important for biodiversity conservation and climate change mitigation. These forests are regenerating after disturbances caused by land use, and generally in highly human-modified landscapes. These changes can influence the community assembly in SGFs and decrease the capacity to recover biodiversity and ecosystem functions. However, the effect of anthropic disturbances and other environmental factors in the community assemblages of regenerating forests remains poorly studied, including for the Atlantic Forest, a highly threatened Brazilian biome with high demands for forest restoration. Thus, in this study, were evaluated how multiple environmental factors (i.e. soil properties, management intensity, patch area, patch isolation, source distance, forest cover and silviculture cover) influence the community assembly of SGF of the Atlantic Forest through functional traits. For this, we used data from 36 SGF, regenerating naturally after a long-term eucalyptus planting. All tree individuals, with at least 4.8 cm of diameter at breast height, were included in a plot of 20x50 meters in each SGF. Then, were calculated the community weighted means (CWM) of 12 traits in these communities: wood density, maximum height, maximum diameter, leaf length, leaf width, shade tolerance, seed length, seed width, fruit length, fruit width, fruit type and dispersion type. Soil fertility negatively influenced wood density and management intensity did not influence the functional composition of the areas under regeneration. However, patch isolation and source distance decrease the occurrence of species with larger fruits and seeds, while the forest cover is important for maintaining species with larger seed widths and shade-tolerant species. Silviculture cover also positively influences fruit size. Thus, patch configuration and landscape composition are more important in the community assemblages and shows the necessity for intervention in passive restoration in very isolated areas with little forest coverage in order to increase efficiency in biodiversity recovery.

Key Words: community assemblages; forest regeneration; second-growth forests; functional traits; trait selection; forest restauration.

Introduction

World's tropical forests have been deforested due to different land uses. These deforested areas, after used or abandoned, begin a natural regeneration process that characterizes second growth tropical forests (SGF) (Hansen et al. 2013; Rozendaal et al. 2019). SGF are very important in mitigating climate change, as they are potential carbon sinks, which cause the greenhouse effect (Gellie et al. 2018). In addition, SGF are also essential for biodiversity conservation, as they increase the amount of natural habitat and, consequently, the size of populations, reducing the chance of species extinctions (Fahrig 2003; Magnago et al. 2015; Matos et al. 2020). However, SGF are forest established after disturbances and in landscapes highly modified by humans, which can drive community assembly in these regenerating forests and ecosystem functions, through the selection of plant traits that confer adaptability to these environment (Boukili and Chazdon 2017; de Avila et al. 2018; Villa et al. 2021). Thus, it is necessary studies that evaluate the influence of these factors on functional attributes to understand the diversity patterns and functionality of SGFs in natural succession, in order to generate knowledge for restoration efforts focused on biodiversity recovery and conservation.

The tree populations that dominate in a community are those in which the species best adapt to the environmental conditions (Gastauer and Meira-Neto 2013). This adaptation is conferred by functional attributes that provide survival under suitable environmental conditions, that is, the species' niche (Tilman et al. 1997). However, after anthropogenic disturbances, species that have a smaller survival niche may not resist environmental variations, decreasing the size of their populations and increasing their extinction risk (Magnago et al. 2014; Barlow et al. 2016; Solar et al. 2016). Thus, anthropic disturbances can alter the climatic conditions of an area, the soil properties, and even cause the decrease and fragmentation of the natural habitat (Ewers and Didham 2006; Jakovac et al. 2015; Ribeiro et al. 2019), affecting the tree species niche (Tilman et al. 1997) . For example, after selective cutting of trees with high canopy cover, the so-called pioneer species are selected, that is, species with greater capacity to survive at high solar irradiation and higher temperatures (Rocha-Santos et al. 2016). Thus, disturbances usually select functional traits related to the growth and acquisition of resources, that is, the vegetative traits (e.g. wood density, maximum height, maximum diameter and leaf traits) (Díaz et al. 2004; Pérez-Harguindeguy et al. 2013; Boukili and Chazdon 2017). Furthermore, the reduction and fragmentation of natural habitat limits the size of populations and causes isolation between different populations, mainly affecting reproductive traits (e.g. seed and fruit traits) due to the limits imposed on pollination and dispersion of fruits and seeds (Tscharntke et al. 2012; Cote et al. 2017). Therefore, anthropogenic disturbances and human-modified landscapes have been considered currently as the main factors that drives communities assembly (Williams et al. 2015; Edwards et al. 2019).

In this sense, secondary growth forests are generally associated with a previous management intensity, which may have been of little duration or long duration and in highly human-modified areas (Arroyo-Rodríguez et al. 2017). The successive land use often expose degraded areas to high temperatures and solar radiation, affecting the soil properties and the soil seed bank and, consequently, the recovery of species in the secondary succession process (Guariguata and Ostertag 2001; Jakovac et al. 2015; Pyles et al. 2018; Villa et al. 2018). Similarly, patch configurations and landscape composition can also influence the recovery of diversity mainly due to the recolonization capacity of the species (Ewers and Didham 2006; Arroyo-Rodríguez et al. 2017). Thus, more isolated areas with little natural habitat coverage are less likely to be reached by plant propagules, mainly of larger sizes and dependent on zoochoric dispersion (Jakovac et al. 2015; Matos et al. 2020; Pérez-Cárdenas et al. 2021). Therefore, soil properties, management intensity, patch configurations, and landscape composition are drivers of community assembly and ecosystem functioning during forest regeneration process (Jakovac et al. 2016; Pinho et al. 2018; Villa et al. 2020; Piotto et al. 2021).

The Atlantic Forest is one of the biomes with the highest demand for forest restoration in Brazil and in the world, and has an intense history of devastation and land use, therefore it is highly fragmented (Nazareno et al. 2012; Scarano and Ceotto 2015; Rezende et al. 2018; Strassburg et al. 2020). Some studies have shown that neotropical forest regeneration areas naturally recover on average 80% of species richness and 50% of carbon richness in 20 years (Chazdon et al. 2016; Rozendaal et al. 2019; Oberleitner et al. 2021). However, specifically for the Atlantic forest, Safar *et al* (2020) found a lower recovery rate (52% of species richness and 16% of carbon stock in 20 years). This difference can be explained by soil properties (Teixeira et al. 2020), but also by the high degree of exploitation and fragmentation of the biome (Nazareno et al. 2012; Matos et al. 2020; Safar et al. 2020). Pyles *et al* (2018) found less diversity and carbon stock in SGFs that were regrowing after native forest clear cut (40 years of regeneration) than in forest with selective wood-cutting. Matos *et al* (2020) found lower diversity and carbon stock in more isolated and smaller-sized SGFs. Piotto *et al* (2021) also found a negative effect of isolation on the recovery of endemic species. However, studies are still needed to evaluate how multiples drivers affect community assembly in natural regeneration of the Atlantic Forest in order to propose possible interventions that increase the efficiency of biodiversity and carbon stock recovery of these areas.

In this way, here we evaluated how multiples drivers such as soil properties, management intensity, patch configuration and landscape composition affect the community assembly, assessed through functional composition of areas in natural regeneration in the Atlantic Forest. We hypothesized that soil properties and previously management intensity have more influence on vegetative traits, like wood density, maximum height, maximum diameter, leaf length, leaf width, and shade tolerance, while patch configuration and landscape composition have more influence on reproductive traits, like seed length, seed width, fruit length, fruit width, fleshy fruits, and zoochoric dispersion. To answer this question, we sampled 35 second-growth forests with different soil properties, management intensity, patch configuration and landscape composition and calculated the community weighted means (CWM) of these vegetative and reproductive traits.

Material and Methods

Study area

This study was carried out in a Semideciduous Tropical Forest of the Atlantic Forest domain, between the municipalities of São José do Goibal, Dionísio and Timóteo belong to ArcellorMittal BioForest areas. The region has an Aw climate, hot and humid, with well-defined periods of rain and drought, mean annual precipitation is 1450 mm, and mean temperature ranging between 20 and 23 ° C (Lopes et al. 2002; Alvares et al. 2013). The region is economically important and has an intense land use history for agriculture, livestock, and eucalyptus planting (Scarano and Ceotto 2015; Oliveira-Junior et al. 2020). There, were sampled 43 patches in fallow time after the last cut of eucalyptus. The sampling was carried out between January and March 2018. However, we excluded for this work seven areas that had different land use before eucalyptus planting, like pastures and coffee planting. Thus, all 36 patches used in this work were primary Atlantic Forests and were cutting for charcoal production and after used for eucalyptus planting.

Vegetation sampling

For each patch a transect of 20x50 meters (0.1 hectares) were randomly installed and all tree individuals with ≥4.8 cm in diameter at breast height (1.30 m above ground height) were sampled, following Matos *et al* (2020). We recorded the diameter at breast height, estimated height, and species of all individuals. The species were identified in the field or collected for later identification according to APGIV. The botanical material in reproductive stage were deposited in the Herbarium of the Federal University of Viçosa (VIC).

Functional attributes data collect

We divided the functional attributes into two groups: vegetative attributes and reproductive attributes. As vegetative traits we consider wood density, maximum diameter, maximum height, leaf length, leaf width, and shade tolerance. These traits were selected because they confer acquisitive capacity, mechanical resistance; and capacity of establishment after disturbances (Ribeiro et al. 2019; Rosenfield and Müller 2019; Coelho et al. 2020). As reproductive traits we consider seed length, seed width, fruit length, fruit width, fruit type and type of dispersion. These functional attributes mainly represent the ability to disperse and colonize different types of habitats, and thus to maintain the species life cycle (Pérez-Harguindeguy et al. 2013; Meira-Neto et al. 2019; Matos et al. 2020). Wood density was collected in the Global Wood Density database (GWD; Zanne et al. 2009). For species that were not available we used the average wood density among the species of the same genus present in the database (Magnago et al. 2014). For the diameter and maximum height of the species we consider the highest value found for the species in the plots in which they occur (Coelho et al. 2020). Leaf length and width were collected in virtual herbaria, by consulting in the data available in the SpeciesLink (for more details see: http://splink.cria.org.br/), where the values of the attributes were the mean measures of five exsiccates of the same species randomly found and of different herbaria (Meira-Neto et al. 2019). The attributes of shade tolerance and reproductive were collected from the database used by Magnago et al (2014) and Matos et al (2020), or SpeciesLink data bases, or taxonomic descriptive articles for the species. All traits are continuous measurements, except shade tolerance, fruit type and dispersal type that have been categorized into shade tolerant (value = 1) or non-shade tolerant species (value = 0), fleshy fruit (value = 1) or non-fleshy fruit species (value = 0), and zoochoric dispersed (1) or non-zoochoric dispersed species (0), respectively.

Community weighted means

The community weighted means (CWM) is a metric that measure functional composition weighed by the abundance of species and indicates dominance of a single functional attributes values (Ribeiro et al. 2019). This index was proposed by *Garnier et al* (2004) and is computed as:

$$CWM = \sum_{i=1}^{S} PiXi$$

where Pi is the relative abundance of species i ($i = 1, 2, \ldots, S$), and Xi is the trait value for species i (Ricotta and Moretti 2011). This analysis was performed in R software version 3.6.0 (R Development Core Team 2019) using *Tidyverse* functions from the *dplyr* package (Dplyr Package 2021).

Environmental variables collect

We divided our variables into four sets: soil properties, management intensity, local configuration, and landscape composition. For the soil characteristics, three random samples of 0-20 cm depth were taken in each patch. The three samples were later homogenized and analyzed for concentrations of phosphorus (P), magnesium (Mg^{2+}), calcium (Ca^{2+}), potassium (K), iron (Fe), aluminum (Al^{3+}) and pH. In addition, we analyzed the texture of theses homogenized samples through the percentage of clay, sand and silt. The soil analyses were performed in Soil Department of Federal University of Viçosa following protocol of Santos *et al* (2018).

For management intensity we considered the data of land-use history of the patches improved by the landowner company: planting cycle, numbers of times that each patch was used by eucalyptus planting; cutting cycle, number of times that the eucalyptus planting was cut in each patch; use time, time between de first cycle planting and last cycle cutting; and fallow age, time between the last cutting cycle and the sampling date of vegetation. Similar variables have been used by management intensity and land-use history in other studies (Jakovac et al. 2015; Villa et al. 2018; Pérez-Cárdenas et al. 2020).

We summarized the management intensity and soil properties variables performing two principal component analyses (PCA). The management intensity PCA was composed by planting cycle, cutting cycle, use time, and fallow age. While the soil properties PCA was composed by concentrations of phosphorus, magnesium, calcium, potassium, iron, aluminum, pH index, and percentages of clay, sand, and silt. These PCAs were separately performed using "FactorMiner" package (Husson et al. 2020). Second, we analyzed how many axes of PCA we needed to retain for both variables set applying the Horn's parallel analysis with 600 iterations and retaining the axes with an adjusted eigenvalue > 1. These parallel analyses were processed using *Paran* package (Dinno 2018) in R software version 3.6.0 (R Development Core Team 2019). Thus, were retained only one axis for management intensity and two axes for soil properties. We called the first axis of the soil properties PCA of soil fertility and the second axis of soil texture because strong correlations with chemical and physical properties, respectively (see more information in the results topic).

As local configurations were considered three variables: patch area in hectares (ha); patch isolation, the minor linear distance in meters between the patch sampled and other natural forest patch; and source distance, the minor linear distance between each patch sampled and some natural forest patch ≥ 500 ha (Matos et al. 2020). While for landscape composition we considered two metrics: forest cover, percentage of forest formations in the landscape; and silviculture cover, percentage of planted forests in the landscape. Both local configuration and landscape composition were obtained by classified images improved by Brazilian Annual Land Use and Land Cover Mapping Project (MapBiomas Collection 5) referent to 2018. The patch isolation and source distance were measured in ArcGis software (Environmental Systems Research Institute, Redlands, CA, USA). The patch area, forest cover and silviculture cover were calculated in "FRAGSTAT 4.2" software (McGarial et al. 2012) in a buffer of 2 km of radius since the center of each transect (Matos et al. 2016; Coelho et al. 2020) extracted from ArcGis software.

Statistical analyses

Variable correlations

We applied the Spearman's correlation test to evaluate the relationship between PCA axis of management intensity and soil properties, between the environmental variables collected, and also between the Community weighted means values obtained for each functional attributes considered. For this we used *psych* package in R software version 3.6.0 (R Development Core Team 2019).

Multiple drivers influence

To evaluate the influences of management intensity, soil properties, local configuration and landscape composition on diversity and carbon stock parameters we used global linear models (GLM) with the following variables in equation 1:

(1) Diversity and Carbon Stock ~ Management intensity + Soil fertility + Soil texture + Patch area + Patch isolation + Source distance + Forest cover + Silviculture cover

where management intensity was the first axis of management intensity of PCA, soil fertility the first axis of soil properties PCA, and soil texture the second axis of soil properties PCA. Using an information-theoretic approach and multi-model inference (Burnham et al. 2011) in the "MuMIn" package (Barton 2017) we calculated Akaike's information criterion (AICc indicated for small samples), by the combination of all candidate models. Were applied spearman correlation analyses to avoid variables with correlations > 0.6 in the same candidate models. We considered the models with $\Delta AICc \leq 5$ as the best models to explain the variation of variables effects and calculated the average models (Burnham and Anderson 2002; Matos et al. 2020). In addition, we obtained the importance of each environmental predictors from the sum of Akaike weights of average models (Burnham et al. 2011).

Results

Data collect and correlations analyses

The sampled soils were generally acidic pH, with very varied chemical and physical characteristics (Tab. 1). In the soil properties PCA were retained two axes: the first axis (adjusted eigenvalue = 5.293) was positively correlated with pH, Mg^{2+}, Ca^{2+}, K, P, and silt percentage, and negatively correlated with Fe, Al^{3+}, and clay percentage; and the second axis (adjusted eigenvalue = 1.144) was positively correlated with P, silt and clay percentages, and negatively correlated with sand percentage. Thus, we called the first axis of soil fertility, because strong correlation with nutrient contents, and the second axis of soil texture, because strong correlation with physical characteristics.

The fallow age of our second-growth forests varies between 3 and 32 years and the use time for eucalyptus plantation varied between 16 and 50 years. During the time of use these areas had 1 to 3 planting cycles, and 2 to 4 cutting cycles. Only the first axis of management intensity PCA was retained in the Horn's parallel analyses (adjusted eigenvalue = 2.170). This axis was positively correlated with cutting cycle and use time, and negatively correlated with fallow age.

The patch configuration and landscape composition were also quite varied among the secondary forests sampled. The area of forests ranged from 13.4 to 199 ha, and the isolation from 25 to 698 meters. The only forest fragment larger than 500 ha that was closer to all fragments was Rio do Doce state park, ranging from 25 to 21,632 meters. The landscape composition varied between 5 and 54% of forest cover and 9 to 62% of eucalyptus cover.

Only source distance and forest cover were higher significant negatively correlated (s = -0.61; p = 0.001) so they were not included in same models. Other variables were also significant correlated but with lower spearman values: source distance and silviculture cover (s = -0.11; p = 0.04) were negatively correlated, and patch isolation and patch area (s = 0.30; p = 0.032) were positively correlated.

The community weighted means of different evaluated traits confirm parameters expected in trait correlations: communities with higher wood density have higher maximum diameter (s = 0.42; p = 0.019), bigger seed length (s = 0.42; p = 0.004) and width (s = 0.42; p = 0.017). However, wood density was negatively correlated with fruit length (s = -0.43; p = 0.021) and leaf width (s = 0.42; p = 0.001). Fruit width was positively correlated with seed length (s = 0.89; p = 0.001), seed width (s = 0.88; p = 0.001), and shade tolerance (s = 0.50; p = 0.001), but negatively correlated with fleshy fruit attribute (s = -0.50; p = 0.001). In the same way shade tolerance was negatively correlated with fleshy fruit attribute (s = -0.78; p = 0.001).

Multiple drivers influence on functional composition

The vegetative attributes were little influenced by considered environmental drives and were not influenced by management intensity (Fig. 1). The wood density was negatively influenced by soil fertility (β = -0.01994 ± 0.007735 SE, z = 2.577, p = 0.00995). Maximum diameter was also negatively influenced by soil fertility (β=-0.8310 ± 0.2173 SE, z = 3.825, p = 0.000131). Maximum height was negatively influenced by source distance (β=-0.0002664 ± 0.0001189 SE, z= 2.239 p= 0.0251). Shade tolerance was positively influenced by forest cover. The leaf length and width were not influenced by considered drivers. However, reproductive traits were strongly influenced by patch configuration and landscape composition (Fig. 2). Fruit length was negatively influenced by patch isolation (β = -0.08589 ± 0.04260 SE, z = 2.016, p = 0.04378) and positively influenced by silviculture cover (β=2.049 ± 0.6585 SE, z = 3.112, p = 0.00186). Fruit width was negatively influenced by source distance (β = -0.0007864 ± 0.0003870 SE, z = 2.032, p = 0.0422) and positively influenced by forest cover (β = 0.5739608 ± 0.2348631 SE, z = 2.444, p = 0.0145). Seed length was negatively influenced by soil fertility (β = -0.8882434 ± 0.4264897 SE, z = 2.083, p = 0.0373). Seed width was also negatively influenced by soil fertility (β = -1.1757251 ± 0.5835641 SE, z = 2.015, p = 0.0439) and positively influenced by forest cover (β = 0.3067059 ± 0.1411305 SE, z = 2.173, p = 0.0298). Fleshy fruit was positively influenced by source distance (β = 0.00002528 ± 0.000009049, z = 2.794, p = 0.00521) and negatively influenced by forest cover (β

= -0.01351 ± 0.005702, z = 2.369, p = 0.01784). Finally, zoochoric dispersion was positively influenced by soil texture (β = 0.06971 ± 0.03338 SE, z = 2.088, p = 0.0368).

Table 2. Environmental variables used to evaluate influences in secondary succession in this study. The management intensity and soil properties were summarized into PCA axis. Parallel Horn's analyses retained only one axis for management intensity and two for soil properties. Because strong correlations between chemical characteristics and the first axis, and between the second axis and physical characteristics we called these axes of soil acidity and soil texture, respectively. Local configuration and landscape composition variables were directed inserted in the models.

Variable sets	*Unit*	*Minimum*	*Maximum*	*PCA axis 1*	*PCA axis 2*
Soil Properties					
pH	(H_2O)	3.48	6.41	0.968*	-0.0531
Mg^{2+}	cmol/dm³	0.05	1.23	0.9268*	0.1509
Ca^{2+}	cmol/dm³	0.32	6.36	0.9127*	0.1074
K	mg/dm³	11	195	0.8503*	0.1087
P	mg/dm³	1.3	9.9	0.5122*	0.4112*
Fe	mg/dm³	17.4	104.4	-0.8115*	0.2475
Al^{3+}	cmol/dm³	2.2	8.7	-0.8994*	0.0563
Silt	%	0.006	0.341	0.688*	0.6258*
Clay	%	0.295	0.757	-0.7823*	0.4947*
Sand	%	0.104	0.632	0.3066	-0.9184*
Explained variation by PCA	*%*	-	-	*62.6*	*17.6*
Management Intensity					
Planting cycle	Number	1	3	-0.0900	0.9921*
Cutting cycle	Number	2	4	0.9376*	-0.05
Use time	Years	16	50	0.8691*	0.15
Fallow age	Years	3	32	-0.9626*	-0.01
Explained variation by PCA	*%*	-	-	*64.2*	*25.2*
Local Configuration					
Patch area	ha	13.4	199	-	-
Patch isolation	m	25	698	-	-
Source distance	m	25	21632	-	-
Landscape composition					
Forest cover	%	5.011	54.610	-	-
Silviculture Cover	%	9.746	62.156	-	-

Significance correlation < 0.05.

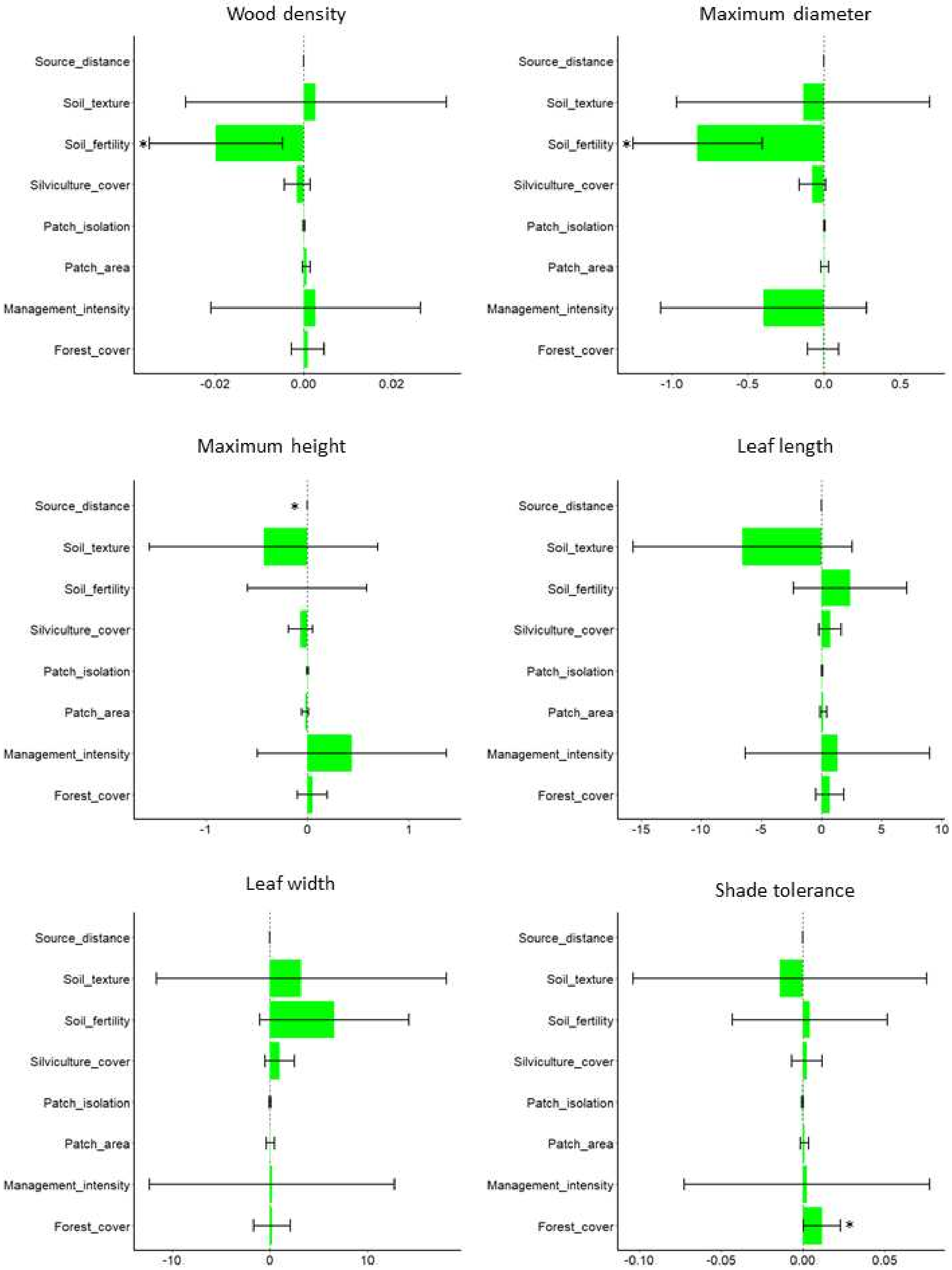
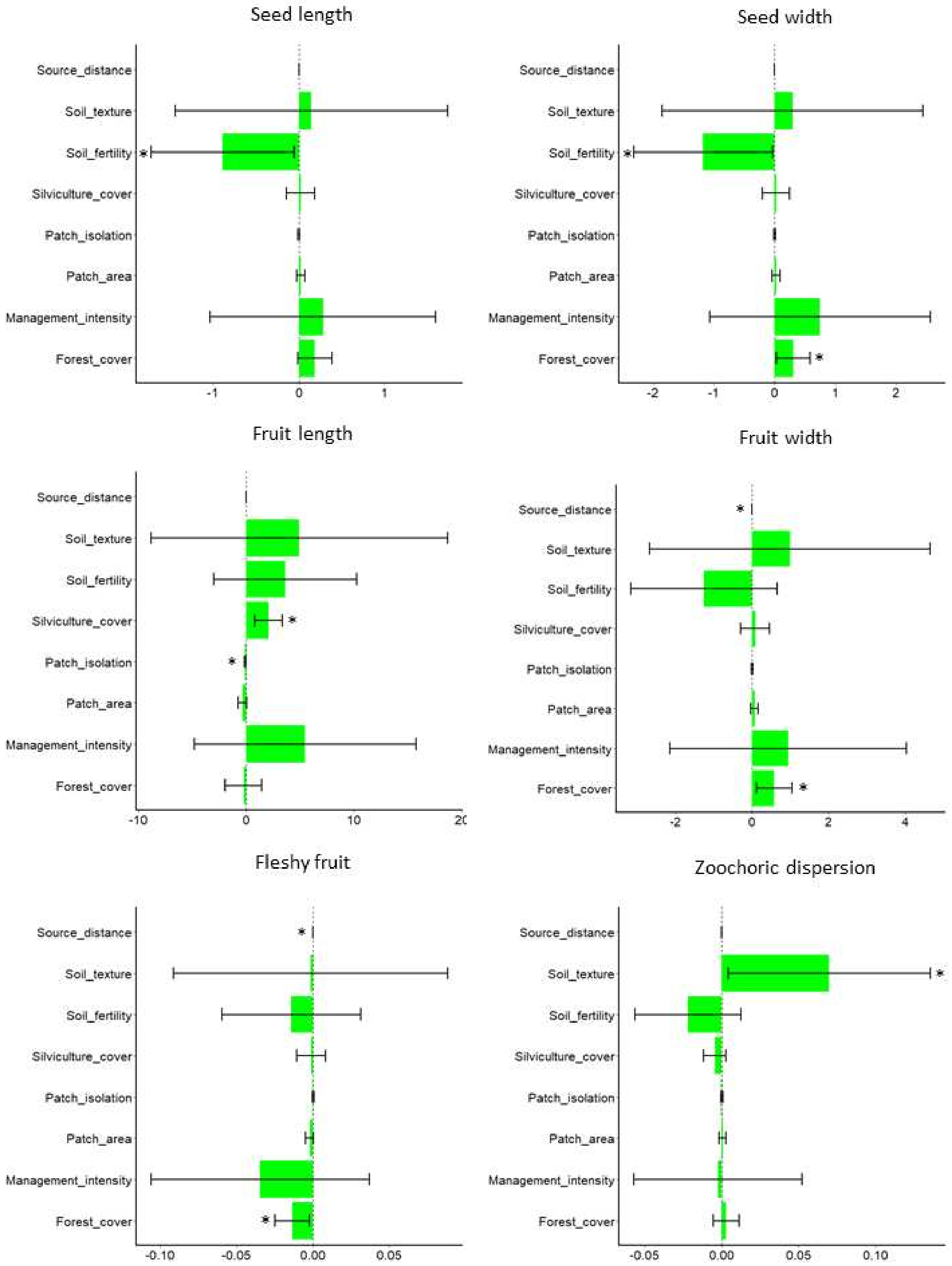


Figure 1. Multiple drivers influence vegetative attributes considering models with values of ΔAICc ≤ 5. The position of the bars represents positive or negative effect and error bars represent the (±) adjusted standard errors obtained after average model analysis. If the error bar is crossing the line of zero, the variable is not significant.


Seed length

Seed width

Fruit length

Fruit width

Fleshy fruit

Zoochoric dispersion

Figure 2. Multiple drivers influence reproductive attributes considering models with values of ΔAICc ≤ 5. The position of the bars represents positive or negative effect and error bars represent the (±) adjusted standard errors obtained after average model analysis. If the error bar is crossing the line of zero, the variable is not significant.

Discussion

Our results show how multiple factors influence the community assembly of SGFs in Atlantic Forest. We expected greater influences soil properties and management intensity on vegetative attributes, but only soil fertility increased the occurrence of plants with lower wood density and maximum diameter. However, as expected, we found strong influences of patch configuration and landscape composition in reproductive traits. The patch isolation and source distance decrease the occurrence of species with larger fruits and seeds, while the forest cover is important for maintaining species with larger seed widths and shade-tolerant species. Thus, we found that landscape changes are more important than soil properties and management intensity in the species composition of these SGFs. Our study strengthens theories of community assemblies through the selection of functional traits and serves as a basis for the implementation of methods in passive restoration in search of greater efficiency in the biodiversity and carbon stock recovery.

Effects of soil fertility on vegetative attributes

Elucidating the processes that influence plant-soil relationships is one of the most critical issues in forest ecology (Ali et al. 2017; Poorter et al. 2017). Soil fertility is an environmental filter for plant communities and influences vegetative traits as wood density, maximum diameter, maximum height, and leaf traits (Ali et al. 2017). Generally, in fertile soils are higher wood density, maximum diameter and maximum height, with leaves of smaller areas (Asefa et al. 2017; Pinho et al. 2018). However, communities may react in different ways to soil fertility (Gastauer and Meira-Neto 2014). Our results showed that soil fertility increased the occurrence of species with lower wood density. This can be explained by the positive relationship of soil fertility with potassium concentration, responsible for the increasing of exchanging cations concentrations and for selection of species with lower wood density (Quesada et al. 2012). This may also explain the negative influence of fertility on seed size, considering a positive correlation between wood density and seed length and width.

Another possible explanation for these results would be due to topographic effects in the studied areas. Topography is one of the most relevant factors that influence ecological process in tropical forests (Jucker et al. 2018; Rodrigues et al. 2019), playing an essential role in determining soil chemistry and fertility patterns (Moeslund et al. 2013; Jucker et al. 2018). Additionally, even short elevational gradients in a tropical forest may strongly affect soil properties (Daws et al. 2005). For example, soils in valleys tend to be wetter and more fertile than those near ridgetops (Balvanera et al. 2011). Furthermore, steeper sites have a higher nutrient output and, therefore, generally have fewer nutrients in the soil available than flatter sites (Balvanera et al. 2011). Thus, differences in plant traits can be found in a short topographical gradient (Rodrigues et al. 2019) because of the effects of soil properties variability on tree species distribution (Maestre and Reynolds 2006). Furthermore, availability and competition for resources must also be considered. For example, trees in valleys tend to have lower wood density and greater height in order to compete for light. On the other hand, on steeper sites where light is not a limiting resource, trees have high wood density and lower height, as a response to the low availability of nutrients (Moeslund et al. 2013). Thus, topography is an important dimension of plants' ecological niches, facilitating species coexistence in tropical forests (Jucker et al. 2018). However, it is necessary to continue research for specific measurements in this study.

Effect of patch configuration and landscape composition in reproductive attributes

The regenerating area isolation of the nearest forest patches and of the source of propagules decreases the chance of recolonization of species that were not present in the seed bank or that did not survive to the higher solar irradiation and temperature at the beginning of regeneration (Holp 1999; Villa et al. 2018). The sources of propagules are larger in forest patches, capable of housing larger populations of plants and animals, and are therefore improve dispersers and propagules for the recolonization of species in smaller fragments and in regenerating areas (Fahrig 2003; Ewers and Didham 2006; Magnago et al. 2015). Due to the inverse relationship of fruit and seed size with reach of dispersion, the chance of recolonization by larger fruit and seed species is lower in areas more distant from source fragments, and even lower in distant regeneration areas of any forest fragment (Collevatti et al. 2010; Pérez-Harguindeguy et al. 2013; Magnago et al. 2014; Cote et al. 2017; Zambrano et al. 2019).

The forest cover has an effect against the isolation and source distance being positively correlated with fruit and seed width. The effect of forest cover may be related to the habitat amount theory which says that the maintenance of diversity is more influenced by the natural habitat cover in the landscape than by the configuration of patches and landscape (Fahrig 2013). In this case, regions with higher forest cover maintains a higher number of populations, and thus greater chances of recolonization by species with larger sizes of fruits and seeds in the landscape. Thus, there is also a greater chance of recolonization by shade-tolerant species that, if present in the seed bank, may not germinate after disturbances because they do not tolerate high solar irradiation (Guariguata and Ostertag 2001; Chazdon 2014). Additionally, shade-tolerant species increases the occurrence of larger fruits and seeds, indicated by the positive relationship of community weighted means of these attributes, and decreases the occurrence of fleshy fruits, negatively correlated with shade-tolerant community weighted means.

The effect of silviculture cover on fruit length is probably related to the structural similarity between natural forests and eucalyptus forests (Ewers and Didham 2006; Tscharntke et al. 2012). Thus, eucalyptus forests can promote greater connectivity between forest patches and between regenerating areas than other types of soil occupation, allowing the circulation of animals and the dispersion of fruits of greater lengths by plots (Barlow et al. 2007; Carrilho et al. 2017; Brancalion et al. 2019). In addition, the structural similarity allows the establishment and recovery of species in the understory of eucalyptus plots, mainly favoring shade-tolerant species (Brancalion et al. 2020), increasing the size of their populations and facilitating the arrival of their propagules to the regeneration areas, which also increases the occurrence of higher fruits and seeds by the positive correlation between these attributes.

Implications for forest restoration

It is known that passive restoration in areas previously used for eucalyptus plantation is efficient and happens during use or after the eucalyptus cutting (Brancalion et al. 2019, 2020). However, our results show lower occurrence of species with larger fruits and seeds in more isolated fragments and landscapes with lower forest cover, and that these species are generally shade-tolerant species. These species are more sensitive to environmental variations, have slow growth, and longer life cycles, being more susceptible to extinctions (Guariguata and Ostertag 2001; Villa et al. 2018). Furthermore, they are responsible for the largest carbon stock in tropical forests (Tabarelli et al. 2010; Stephenson et al. 2014; Peres et al. 2016). Thus, areas in regeneration more isolated and with less forest cover are less efficient in the recovery and conservation of biodiversity and carbon stock. In this way, as these factors increase, interventions are more necessary in passive restoration of these areas, such as sowing or planting species of larger seed and fruit sizes, mainly shade-tolerant species in these SGFs.

References

Alvares CA, Stape JL, Sentelhas PC, et al (2013) K??ppen's climate classification map for Brazil. Meteorol Zeitschrift 22:711–728. https://doi.org/10.1127/0941-2948/2013/0507

Arroyo-Rodríguez V, Melo FPL, Martínez-Ramos M, et al (2017) Multiple successional pathways in human-modified tropical landscapes: new insights from forest succession, forest fragmentation and landscape ecology research. Biol Rev 92:326–340. https://doi.org/10.1111/brv.12231

Asefa M, Cao M, Zhang G, et al (2017) Environmental filtering structures tree functional traits combination and lineages across space in tropical tree assemblages. Sci Rep 7:1–11. https://doi.org/10.1038/s41598-017-00166-z

Balvanera P, Quijas S, Pérez-Jiménez A (2011) Distribution Patterns of Tropical Dry Forest Trees Along a Mesoscale Water Availability Gradient. Biotropica 43:414–422. https://doi.org/10.1111/j.1744-7429.2010.00712.x

Barlow J, Gardner TA, Araujo IS, et al (2007) Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. Proc Natl Acad Sci U S A 104:18555–18560. https://doi.org/10.1073/pnas.0703333104

Barlow J, Lennox GD, Ferreira J, et al (2016) Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. Nature 535:1–16. https://doi.org/10.1038/nature18326

Barton K (2017) 'MuMIn': Multi-Model Inference.

Boukili VK, Chazdon RL (2017) Environmental filtering, local site factors and landscape context drive changes in functional trait composition during tropical forest succession. Perspect Plant Ecol Evol Syst 24:37–47. https://doi.org/10.1016/j.ppees.2016.11.003

Brancalion PHS, Amazonas NT, Chazdon RL, et al (2020) Exotic eucalypts: From demonized trees to allies of tropical forest restoration? J Appl Ecol 57:55–66. https://doi.org/10.1111/1365-2664.13513

Brancalion PHS, Campoe O, Mendes JCT, et al (2019) Intensive silviculture enhances biomass accumulation and tree diversity recovery in tropical forest restoration. Ecol Appl 29:1–12. https://doi.org/10.1002/eap.1847

Burnham KP, Anderson DR (2002) Model Selection and Multimodel Inference: A Practical

Information-Theoretic Approach (2nd ed)

Burnham KP, Anderson DR, Huyvaert KP (2011) AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. Behav Ecol Sociobiol 65:23–35. https://doi.org/10.1007/s00265-010-1029-6

Carrilho M, Teixeira D, Santos-Reis M, Rosalino LM (2017) Small mammal abundance in Mediterranean Eucalyptus plantations: how shrub cover can really make a difference. For Ecol Manage 391:256–263. https://doi.org/10.1016/j.foreco.2017.01.032

Chazdon RL (2014) Second growth: the promise of tropical forest regeneration in an age of deforestation. University of Chicago Press

Chazdon RL, Broadbent EN, Rozendaal DMA, et al (2016) Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics

Coelho AJP, Magnago LFS, Matos FAR, et al (2020) Effects of anthropogenic disturbances on biodiversity and biomass stock of Cerrado, the Brazilian savanna. Biodivers Conserv 0123456789: https://doi.org/10.1007/s10531-020-02013-6

Collevatti RG, Lima JS, Soares TN, Telles MP de C (2010) Spatial genetic structure and life history traits in cerrado tree species: Inferences for conservation. Nat a Conserv 8:54–59. https://doi.org/10.4322/natcon.00801008

Cote J, Bestion E, Jacob S, et al (2017) Evolution of dispersal strategies and dispersal syndromes in fragmented landscapes. 56–73. https://doi.org/10.1111/ecog.02538

Daws MI, Pearson TRH, Burslem DFRP, et al (2005) Effects of topographic position, leaf litter and seed size on seedling demography in a semi-deciduous tropical forest in Panamá. Plant Ecol 179:93–105. https://doi.org/10.1007/s11258-004-5801-4

de Avila AL, van der Sande MT, Dormann CF, et al (2018) Disturbance intensity is a stronger driver of biomass recovery than remaining tree-community attributes in a managed Amazonian forest. J Appl Ecol 55:1647–1657. https://doi.org/10.1111/1365-2664.13134

Díaz S, Hodgson JG, Thompson K, et al (2004) The plant traits that drive ecosystems: Evidence from three continents. J Veg Sci 15:295. https://doi.org/10.1658/1100-

9233(2004)015[0295:tpttde]2.0.co;2

Dinno A (2018) Paran: Horn’s test of principal components/factors. 1–6

Edwards DP, Socolar JB, Mills SC, et al (2019) Conservation of Tropical Forests in the Anthropocene. Curr Biol 29:R1008–R1020. https://doi.org/10.1016/j.cub.2019.08.026

Ewers R, Didham R (2006) Confounding factors in the detection of species responses to habitat fragmentation. Biol Rev Camb Philos Soc 81:117–142. https://doi.org/10.1017/s1464793105006949

Fahrig L (2003) Effects of Habitat Fragmentation on Biodiversity. Annu Rev Ecol Environ Syst 34:487–515. https://doi.org/10.1146/132419

Fahrig L (2013) Rethinking patch size and isolation effects: The habitat amount hypothesis. J Biogeogr 40:1649–1663. https://doi.org/10.1111/jbi.12130

Garnier E, Cortez J, Billès G, et al (2004) Plant functional markers capture ecosystem properties during secondary succession. Ecology 85:2630–2637. https://doi.org/10.1890/03-0799

Gastauer M, Meira-Neto JAA (2013) Avoiding inaccuracies in tree calibration and phylogenetic community analysis using Phylocom 4.2. Ecol Inform 15:85–90. https://doi.org/10.1016/j.ecoinf.2013.03.005

Gastauer M, Meira-Neto JAA (2014) Interactions, Environmental Sorting and Chance: Phylostructure of a Tropical Forest Assembly. Folia Geobot 49:443–459. https://doi.org/10.1007/s12224-013-9181-1

Gellie NJC, Breed MF, Mortimer PE, et al (2018) Networked and embedded scientific experiments will improve restoration outcomes. Front Ecol Environ 16:288–294. https://doi.org/10.1002/fee.1810

Guariguata MR, Ostertag R (2001) Neotropical secondary forest succession : changes in structural and functional characteristics. For Ecol Manage 148:185–206. https://doi.org/10.1016/S0378-1127(00)00535-1

Hansen MC, Potapov P V, Moore R, et al (2013) High-Resolution Global Maps of. 134:850–854

Holp KD (1999) Factors Limiting Tropical Rain Forest Regeneration in Abandoned Pasture : Seed

Rain , Seed Germination , Microclimate , and Soil '. Biotropica 31:229–242

Husson AF, Josse J, Le S, et al (2020) Package ' FactoMineR '

Jakovac CC, Bongers F, Kuyper TW, et al (2016) Land use as a filter for species composition in Amazonian secondary forests. J Veg Sci 27:1104–1116. https://doi.org/10.1111/jvs.12457

Jakovac CC, Peña-Claros M, Kuyper TW, Bongers F (2015) Loss of secondary-forest resilience by land-use intensification in the Amazon. J Ecol 103:67–77. https://doi.org/10.1111/1365-2745.12298

Jucker T, Bongalov B, Burslem D, et al (2018) Topography shapes the structure , composition and function of tropical forest landscapes. 989–1000. https://doi.org/10.1111/ele.12964

Lopes W de P, Silva AF da, Souza AL de, Meira Neto JAA (2002) Estrutura fitossociólogа de um trecho de vegetação arbórea no Parque Estadual do Rio Doce - Minas Gerais , Brasil. Acta Bot Brasilica 16:443–456. https://doi.org/10.1590/s0102-33062002000400007

Maestre FT, Reynolds JF (2006) Spatial heterogeneity in soil nutrient supply modulates nutrient and biomass responses to multiple global change drivers in model grassland communities. Glob Chang Biol 12:2431–2441. https://doi.org/10.1111/j.1365-2486.2006.01262.x

Magnago LFS, Edwards DP, Edwards FA, et al (2014) Functional attributes change but functional richness is unchanged after fragmentation of Brazilian Atlantic forests. J Ecol 102:475–485. https://doi.org/10.1111/1365-2745.12206

Magnago LFS, Magrach A, Laurance WF, et al (2015) Would protecting tropical forest fragments provide carbon and biodiversity cobenefits under REDD+? Glob Chang Biol 21:3455–3468. https://doi.org/10.1111/gcb.12937

Matos FAR, Magnago LFS, Aquila Chan Miranda C, et al (2020) Secondary forest fragments offer important carbon and biodiversity cobenefits. Glob Chang Biol 26:509–522. https://doi.org/10.1111/gcb.14824

Matos FAR, Magnago LFS, Gastauer M, et al (2016) Effects of landscape configuration and composition on phylogenetic diversity of trees in a highly fragmented tropical forest. J Ecol. https://doi.org/10.1111/1365-2745.12661

McGarial K, Cushman SA, Ene E (2012) FRAGSTATS v4: spatial patern analysis program for categorical and continuous maps

Meira-Neto JAA, Nunes Cândido HM, Miazaki Â, et al (2019) Drivers of the growth–survival trade-off in a tropical forest. J Veg Sci 30:1184–1194. https://doi.org/10.1111/jvs.12810

Moeslund JE, Arge L, Bøcher PK, et al (2013) Topography as a driver of local terrestrial vascular plant diversity patterns. Nord J Bot 31:129–144. https://doi.org/10.1111/j.1756-1051.2013.00082.x

Nazareno AG, Feres JM, de Carvalho D, et al (2012) Serious New Threat to Brazilian Forests. Conserv Biol 26:5–6. https://doi.org/10.1111/j.1523-1739.2011.01798.x

Oberleitner F, Egger C, Oberdorfer S, et al (2021) Recovery of aboveground biomass, species richness and composition in tropical secondary forests in SW Costa Rica. For Ecol Manage 479:118580. https://doi.org/https://doi.org/10.1016/j.foreco.2020.118580

Oliveira-Junior ND de, Heringer G, Bueno ML, et al (2020) Prioritizing landscape connectivity of a tropical forest biodiversity hotspot in global change scenario. For Ecol Manage 472:. https://doi.org/10.1016/j.foreco.2020.118247

Package T (2021) Package ‘ dplyr ’

Peres CA, Emilio T, Schietti J, et al (2016) Dispersal limitation induces long-term biomass collapse in overhunted Amazonian forests. Proc Natl Acad Sci 113:892–897. https://doi.org/10.1073/pnas.1516525113

Pérez-Cárdenas N, Mora F, Arreola-Villa F, et al (2021) Effects of landscape composition and site land-use intensity on secondary succession in a tropical dry forest. For Ecol Manage 482:118818. https://doi.org/https://doi.org/10.1016/j.foreco.2020.118818

Pérez-Cárdenas N, Mora F, Arreola F, et al (2020) Effects of landscape composition and land use intensity on secondary succession in a Mexican tropical dry forest. For Ecol Manage

Pérez-Harguindeguy N, Díaz S, Lavorel S, et al (2013) New Handbook for standardized measurment of plant functional traits worldwide. Aust J Bot 23:167–234. https://doi.org/http://dx.doi.org/10.1071/BT12225

Pinho BX, de Melo FPL, Arroyo-Rodríguez V, et al (2018) Soil-mediated filtering organizes tree assemblages in regenerating tropical forests. J Ecol 106:137–147. https://doi.org/10.1111/1365-2745.12843

Piotto D, Magnago LFS, Montagnini F, et al (2021) Nearby mature forest distance and regenerating forest age influence tree species composition in the Atlantic forest of Southern Bahia, Brazil. Biodivers Conserv 30:2165–2180. https://doi.org/10.1007/s10531-021-02192-w

Pyles M V., Prado-Junior JA, Magnago LFS, et al (2018) Loss of biodiversity and shifts in aboveground biomass drivers in tropical rainforests with different disturbance histories. Biodivers Conserv 27:3215–3231. https://doi.org/10.1007/s10531-018-1598-7

Quesada CA, Phillips OL, Schwarz M, et al (2012) Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. Biogeosciences 9:2203–2246. https://doi.org/10.5194/bg-9-2203-2012

R Development Core Team (2019) R version 3.6.0.

Rezende CL, Scarano FR, Assad ED, et al (2018) From hotspot to hopespot: An opportunity for the Brazilian Atlantic Forest. Perspect Ecol Conserv 16:208–214. https://doi.org/10.1016/j.pecon.2018.10.002

Ribeiro EMS, Lohbeck M, Santos BA, et al (2019) Functional diversity and composition of Caatinga woody flora are negatively impacted by chronic anthropogenic disturbance. J Ecol 107:2291–2302. https://doi.org/10.1111/1365-2745.13177

Ricotta C, Moretti M (2011) CWM and Rao’s quadratic diversity: A unified framework for functional ecology. Oecologia 167:181–188. https://doi.org/10.1007/s00442-011-1965-5

Rocha-Santos L, Pessoa MS, Cassano CR, et al (2016) The shrinkage of a forest: Landscape-scale deforestation leading to overall changes in local forest structure. Biol Conserv 196:1–9. https://doi.org/10.1016/j.biocon.2016.01.028

Rodrigues AC, Villa PM, Neri AV (2019) Fine-scale topography shape richness, community composition, stem and biomass hyperdominant species in Brazilian Atlantic forest. Ecol Indic 102:208–217. https://doi.org/10.1016/j.ecolind.2019.02.033

Rosenfield MF, Müller SC (2019) Assessing ecosystem functioning in forests undergoing restoration. Restor Ecol 27:158–167. https://doi.org/10.1111/rec.12828

Rozendaal DMA, Bongers F, Aide TM, et al (2019) Biodiversity recovery of Neotropical secondary forests. Sci Adv 5:. https://doi.org/10.1126/sciadv.aau3114

Safar NVH, Magnago LFS, Schaefer CEGR (2020) Resilience of lowland Atlantic forests in a highly fragmented landscape: Insights on the temporal scale of landscape restoration. For Ecol Manage 470–471:118183. https://doi.org/10.1016/j.foreco.2020.118183

Santos HG dos, Jacomine PKT, Anjos LHC dos, et al (2018) Sistema brasileiro de classificação de solos, 5. ed. rev

Scarano FR, Ceotto P (2015) Brazilian Atlantic forest: impact, vulnerability, and adaptation to climate change. Biodivers Conserv 24:2319–2331. https://doi.org/10.1007/s10531-015-0972-y

Solar RR de C, Barlow J, Andersen AN, et al (2016) Biodiversity consequences of land-use change and forest disturbance in the Amazon: A multi-scale assessment using ant communities. Biol Conserv 197:98–107. https://doi.org/10.1016/j.biocon.2016.03.005

Stephenson NL, Das AJ, Condit R, et al (2014) Rate of tree carbon accumulation increases continuously with tree size. Nature 507:90–93. https://doi.org/10.1038/nature12914

Strassburg BBN, Iribarrem A, Beyer HL, et al (2020) Global priority areas for ecosystem restoration. Nature 586:724–729. https://doi.org/10.1038/s41586-020-2784-9

Tabarelli M, Aguiar A V., Girão LC, et al (2010) Effects of pioneer tree species hyperabundance on forest fragments in Northeastern Brazil. Conserv Biol 24:1654–1663. https://doi.org/10.1111/j.1523-1739.2010.01529.x

Teixeira HM, Cardoso IM, Bianchi FJJA, et al (2020) Linking vegetation and soil functions during secondary forest succession in the Atlantic forest. For Ecol Manage 457:117696. https://doi.org/10.1016/j.foreco.2019.117696

Tilman D, Knops J, Wedin D, et al (1997) The influence of functional diversity and composition on ecosystem processes. Science (80-) 277:1300–1302. https://doi.org/10.1126/science.277.5330.1300

Tscharntke T, Tylianakis JM, Rand TA, et al (2012) Landscape moderation of biodiversity patterns and processes - eight hypotheses. Biol Rev 87:661–685. https://doi.org/10.1111/j.1469-185X.2011.00216.x

Villa PM, Ali A, Martins SV, et al (2020) Stand structural attributes and functional trait composition overrule the effects of functional divergence on aboveground biomass during Amazon forest succession. For Ecol Manage 477:118481. https://doi.org/10.1016/j.foreco.2020.118481

Villa PM, Martins SV, Diniz ÉS, et al (2021) Taxonomic and functional beta diversity of woody communities along Amazon forest succession: The relative importance of stand age, soil properties and spatial factor. For Ecol Manage 482:118885. https://doi.org/https://doi.org/10.1016/j.foreco.2020.118885

Villa PM, Venâncio S, Nolasco S, et al (2018) Intensification of shifting cultivation reduces forest resilience in the northern Amazon. For Ecol Manage 430:312–320. https://doi.org/10.1016/j.foreco.2018.08.014

Williams M, Zalasiewicz J, Haff PK, et al (2015) The anthropocene biosphere. Anthr Rev 2:196–219. https://doi.org/10.1177/2053019615591020

Zambrano J, Garzon-Lopez CX, Yeager L, et al (2019) The effects of habitat loss and fragmentation on plant functional traits and functional diversity: what do we know so far? Oecologia 191:505–518

Zanne AE, Lopez-Gonzalez, G., Coomes DA, Ilic J, et al (2009) Data from: Towards a worldwide wood economics spectrum, Dryad

CONCLUSÕES GERAIS

Esta tese trouxe novas contribuições para a conservação do Cerrado e restauração da Mata Atlântica no âmbito de paisagens altamente modificadas por ações humanas. Mesmo sendo dois *hotspots* para a conservação da biodiversidade no mundo, existem poucos estudos que avaliam os impactos antrópicos na conservação e restauração destes biomas. Confirmamos que os distúrbios antrópicos locais podem alterar as condições ambientais dos remanescentes de vegetação natural, e assim causar mudanças na composição de espécies pela seleção de traços funcionais que conferem adaptabilidades as novas condições. Da mesma forma, os distúrbios em escala de paisagem (perda de habitat, fragmentação, e uso da terra) também alteram a composição de espécies em remanescentes naturais. Além disso, mostramos que estes distúrbios afetam também a regeneração de biomas naturais. A intensidade de manejo prévia em uma área afeta a capacidade de recuperação de biodiversidade e de estoque de carbono da vegetação original após o uso. O isolamento destas áreas de fragmentos fontes de propágulos também afeta essa capacidade, devido a seleção de traços funcionais dispersivos, favorecendo espécies com maior alcance de dispersão, geralmente de menores tamanhos de sementes e frutos. Mostramos aqui que a conservação do Cerrado e da Mata Atlântica em paisagens altamente modificadas apresentam grandes desafios e necessidade de estratégias que amenizem estes impactos. Inicialmente, é necessário inciativas que impeçam o desmatamento de novas áreas nestes biomas, e assim reduzir a perda de diversidade e de fontes de propágulos causada pela perda de habitat natural. Nossos resultados também auxiliam em orientações para manejo sustentável no uso do solo, sendo importante alternar as áreas em uso visando diminuir o efeito da matriz como filtro de dispersão de espécies, bem como o efeito da intensidade de manejo na recuperação de diversidade e estoque de carbono.