UNIVERSIDADE ESTADUAL DE SANTA CRUZ

PROGRAMA DE PÓSGRADUAÇÃO EM ECOLOGIA E CONSERVAÇÃO DA BIODIVERSIDADE

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DESVENDANDO FATORES QUE AFETAM A BIOMASSA ACIMA DO SOLO EM FLORESTAS TROPICAIS SECUNDÁRIAS

ILHÉUS – BAHIA

2023

PPG Ecologia & Conservação
Universidade Estadual de Santa Cruz

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Tese apresentada à Universidade Estadual de Santa Cruz, para obtenção do título de doutor em Ecologia e Conservação da Biodiversidade

Área de concentração: Ecologia e Conservação de Comunidades

Orientador: Prof. Dr. Daniel Piotto

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2023

R672 Rocha, Janaine Isabela da Silva.
Desvendando fatores que afetam a biomassa acima do solo em florestas tropicais secundárias / Janaine Isabela da Silva Rocha. – Ilhéus, BA: UESC, 2023.
105 f. : il.

Orientador: Daniel Piotto.
Co-orientador: Luiz Fernando Silva Magnago.
Tese (Doutorado) – Universidade Estadual de Santa Cruz. Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade.
Inclui referências.

1. Florestas tropicais. 2. Biomassa. 3. Biodiversidade – Conservação. 4. Solos. I.Título.

CDD 577.3

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AGRADECIMENTOS

Essa conquista da filha do agricultor rural e da dona de casa, que são meus orgulhos e minha vida, teve apoio de muitas pessoas, mas principalmente a minha família, agradeço aos meus pais, Isabel e Quintino e minhas irmãs Janine, Jamilly e Jaqueline, por acreditar em mim, me incentivar, me dar carinho e amor durante esse processo, principalmente a minha amiga/irmã Janine, por estar comigo em cada momento, cada lagrima e cada sorriso estava comigo. Ao meu companheiro Jonas, por me apoiar e estar comigo em todos os momentos, me incentivar e não me deixar desistir, por fazer parte da minha vida, principalmente por seu amor. A minha mãe de Ilhéus, Judith, que eu tenho muita gratidão, por me acolher sempre, e cuidar de mim como uma mãe, sou muito grata por tudo, esses 6 anos de muito amor e cuidado. Também quero expressar minha gratidão ao meu amigo querido Roberto, por andar comigo nessa jornada, pela paciência em me escutar e pela troca que a gente teve durante esses anos, foi grandão amigo! Aos amigos que a pós me deu, que também estiveram comigo, me ajudando direta e indiretamente, com ajudas diretas até conselhos de bar (que são os melhores), Aline, Priscila, Igor e Valentina.

Agradeço aos professores que me ajudaram nessa jornada, cada um colocando um tijolinho, ajudando a construir a profissional que sou hoje, meu querido Pavel Dodonov, que além de ser um profissional em quem me espelho, é um amigo, me salva na estatística e ainda me ajudou muito no campo, nem sei como te agradecer. Ao professor Jomar Jardim, que é um profissional que me inspira, pelas inúmeras conversas de corredores, de almoço, que foram valiosas em cada momento, e pela ajuda na identificação das plantas, te agradeço muito. Ao professor Arlicélio, por além de ceder o laboratório de solos para realizar minhas análises, também me ensinou muito e teve paciência para discutir os resultados da minha pesquisa. Ao meu querido orientador Daniel Piotto, por ter me acolhido, ter sido um parceiro e um profissional em quem me inspiro, dedicado, incentivador, e com quem aprendi muito durante essa jornada, tenho muita gratidão por tudo que você representa nessa caminhada.

Agradeço a Universidade Federal do Sul da Bahia e a CEPLAC pelo apoio estrutural, a equipe do Herbário André Mauricio de Carvalho, em especial aos técnicos Carlinhos e Débora, pela estrutura, contribuições, discussões no dia-a-dia. Ao Instituto Floresta

Viva, ao Rui Rocha e todos colaboradores, por me receber durante os dias cansativos de campo, além do estágio em gestão que foi enriquecedor, aos meus guias de campo Juscelino e Fabricio, pelo apoio no dia-a-dia de campo. Agradecer ao programa de pós-graduação em Ecologia e Conservação da Biodiversidade da UESC, aos professores que contribuíram na minha formação. Agradeço em especial a querida Amábille, pela paciência e carinho em tratar as vezes de assuntos tão chatos. Agradeço à Universidade Estadual de Santa Cruz a CAPES pela concessão da bolsa de doutorado. Ao FUNBIO pelo financiamento do projeto que foi essencial para a execução do mesmo.

SUMÁRIO

Desvendando fatores que afetam a biomassa acima do solo em florestas tropicais secundárias

RESUMO:

As florestas tropicais representam uma região de grande importância para a conservação da biodiversidade mundial, essas florestas desempenham diversos papeis ecológicos, como hábitat natural de muitas espécies, funcionamento do ecossistema, além de prestar diversos serviços ecossistêmicos como o armazenamento de carbono, que é essencial para a regulação do clima mundial. Porém essas florestas tropicais estão cada vez mais ameaçadas e sendo convertidas em outro tipo de uso do solo. Grande parte das florestas tropicais remanescentes são consideradas florestas secundárias, dessa forma essas florestas passaram a ter papel importante na prestação de serviços ecossistêmicos. No entanto, essas florestas são ambientes complexos e dinâmicos, e compreender quais fatores influenciam a regeneração desses ambientes se torna essencial. O presente trabalho está dividido/organizado em quatro capítulos, e em cada um destes utilizamos diferentes variáveis ambientais para entender os padrões de aumento da biomassa em florestas tropicais secundárias. Nossos resultados demonstraram que fatores como a densidade do solo afeta a biomassa nas regiões Neotropicais, mas não localmente, e que avaliar a diversidade de coberturas florestais são importantes no cenário de mudanças no uso do solo, porém as florestas maduras continuam sendo cruciais para o armazenamento de carbono. A serapilheira também pode ser um reservatório de biomassa, principalmente em florestas secundárias jovens. Por fim, demonstramos que a riqueza de espécies tem um poder preditivo para a biomassa, dentre os diversos fatores avaliados. A avaliação de diferentes fatores ambientais que podem afetar a biomassa acima do solo, podem auxiliar a prever futuras respostas nos ambientes modificados por ações humanas, contribuindo em estratégias mais eficientes para mitigação dos efeitos das mudanças climáticas globais e para conservação da biodiversidade em regiões tropicais.

ABSTRACT

Tropical forests represent a region of great importance for the conservation of world biodiversity, these forests play various ecological roles, such as natural habitat for many species, ecosystem functioning, in addition to providing various ecosystem services such as carbon storage, which is essential for regulating the world's climate. But these tropical forests are increasingly threatened and being converted into another type of land use, most tropical forests are considered secondary forests, so these secondary forests have come to play an important role in providing ecosystem services. However, these forests are complex and dynamic environments, and understanding which factors influence the regeneration of these environments becomes essential. We divide this work into four chapters, and in each of these we use different environmental variables to understand patterns of biomass increase in secondary tropical forests. Our results demonstrated that factors such as soil density affect biomass in neotropical regions, but not locally, and that evaluating forest cover diversity are important in the scenario of changes in land use, however mature forests remain crucial for storage. of carbon. Litter can also be a reservoir of biomass, mainly in young secondary forests. Finally, we demonstrate that species richness has a predictive power for biomass, among the various factors evaluated. Assessments of different environmental factors that may affect aboveground biomass can help predict future responses in environments modified by human actions, contributing to more efficient conservation strategies.

INTRODUÇÃO GERAL

As florestas tropicais armazenam em torno de 70 a 80% do carbono terrestre total (Houghton, 2008), 37% do carbono terrestre na forma de biomassa vegetal (Aguiar et al., 2016) e a maior parte da diversidade de árvores do mundo (Slik et al, 2015). Nos últimos anos esses estoques globais de carbono na biomassa florestal foram reduzidos principalmente pela degradação florestal, com a conversão de florestas para outros usos da terra (FAO, 2015; ter Steege et al, 2015). Poucas das florestas tropicais remanescentes podem ser consideradas florestas primárias, as florestas secundárias representam mais de 50% das florestas atuais (Willis et al. 2004; FAO, 2015; Lenox et al, 2018), florestas com algum grau de modificação, ou impactadas por práticas de manejo na agricultura, silvicultura e outras atividades humanas (Potapov et al., 2017) sejam elas florestas primárias degradadas florestas secundárias em regeneração (Chazdon et al., 2009).

As florestas secundárias se tornaram globalmente relevantes nas paisagens tropicais e a principal cobertura florestal remanescente em muitas regiões (Lenox et al., 2018). Estas podem se recuperar rapidamente, retornando a estrutura e biomassa da floresta madura em torno de 40 anos (Dent e Wright, 2009; Piotto et al, 2009). Essa recuperação da estrutura e diversidade de plantas possibilita a recuperação da fauna, representando um importante refúgio para muitas espécies silvestres (Chazdon et al, 2009; Dent e Wright, 2009), importante sumidouro global de carbono (Eva et al. 2012), podendo mitigar a extinção causada pelo declínio de áreas de hábitat naturais (Wright e Muller-Landau, 2006).

A Mata Atlântica representa um importante *hotspo*t de biodiversidade e endemismo mundial (Ribeiro et al. 2009), porém essa é considerada uma das regiões que ainda passam por processo de degradação e tem sido drasticamente transformadas suas florestas naturais em outros tipos de uso do solo, com sua vegetação original próximo de 12 a 28% (Rezende et al., 2018) e grande parte dessas florestas são consideradas florestas tropicais secundarias. O sul da Bahia possui um alto nível de riqueza e endemismo de espécies do que outras regiões da Mata Atlântica (Martini et al. 2007; Thomas et al. 1998), além de ser considerado um dos refúgios florestais do Pleistoceno (Whitmore e Prance 1987), porém essas florestas também foram historicamente convertidas em outros tipos de uso do solo.

Estudos tem mostrado que as mudanças na estrutura e na biomassa durante a regeneração das florestas são determinadas por interações complexas, principalmente em ambiente com alta diversidade de espécies como a mata atlântica. Essas interações podem ocorrer com fatores bióticos e abióticos, mudanças nas condições ambientais, como nutrientes, temperatura e luz (Brow e Lugo, 1990; Dent et al, 2012), por fatores como histórico no uso do solo, contexto da paisagem (Bowen et al, 2007; Chazdon et al, 2009, 2014) e riqueza e composição de espécies (Powers et al, 2009). Por exemplo, as características dos solos compõem fatores limitantes na recuperação florestal, e é afetada principalmente pela redução na oferta de nutrientes minerais no solo (Ceccon et al., 2002; Baker, 2003; Campo e Vazquez-Yanes, 2004), mas além disso a densidade do solo pode limitar a absorção de nutrientes pelas plantas, reduzindo a produtividade primária líquida (Wright et al, 2011; Alvarez-Clare et al, 2013), a capacidade fotossintética das plantas (Cordell et al., 2001), limitando as taxas de crescimento das árvores (Davidson et al, 2004) e por fim, altera a biomassa em florestas secundárias (Campo e Vazquez-Yanes, 2004).

Outro fator que já foi relatado pela literatura com importante efeito sobre a biomassa de florestas secundárias foi a riqueza de espécies (Rozendaal e Chazdon, 2015). A variação na produtividade do ecossistema pode ser determinada pela riqueza de espécies (Tilman et al., 2001; Finegan et al, 2015), pois ambientes com maior diversidade de espécies podem abrigar espécies com alta produtividade (Loreau e Hector, 2001; Cardinale et al. 2007; Finegan, 2015) e grandes árvores (Clark e Clark, 2000; Marshall et al., 2012; Slik et al., 2013). Nessas florestas secundárias, outro fator essencial a se avaliar é o histórico de uso do solo, que pode afetar as taxas de regeneração das florestas, principalmente o início da regeneração (Marín-Spiotta et al, 2007; Griscom e Ashton, 2011), aliado a intensidade e frequência dos eventos de perturbação (Barlow et al., 2012; Aragão et al., 2014).

Essas características são de extrema importância para entender quais fatores ambientais determinam a taxa de acumulação de biomassa na regeneração das florestas tropicais. Algumas pesquisas vêm sendo realizadas com intuído de entender o papel de variáveis ambientais que controlam a biomassa acima do solo em florestas tropicais (Clark e Clark, 2000; Zarin et al, 2001; Baker et al., 2004; Cleveland et al., 2011). No entanto, poucos estudos conseguiram compilar uma grande quantidade de variáveis ambientais e relacionar essas com a biomassa acima do solo.

Com intuito de abordar diferentes variáveis que podem afetar a biomassa de florestas secundárias, esta tese foi dividida em quatro capítulos. No capítulo 1, realizei uma revisão sistemática avaliando como a densidade do solo influenciava a biomassa acima do solo na região Neotropical. No capítulo 2, avaliei como a serrapilheira pode ser um importante reservatório de biomassa em florestas tropicais, em diferentes idades. No capítulo 3, utilizei diferentes coberturas florestais, os Sistemas Agroflorestais (SAF) cabrucas, SAF convencional, florestas maduras e florestas secundarias de 40, 25 e 10 anos, para avaliar como as diferentes coberturas florestais podem ser importantes para o armazenamento de carbono na paisagem. No capítulo 4, utilizei as variáveis riqueza de espécies, densidade de indivíduos, variáveis químicas do solo: Fósforo (P), pH, potássio trocável (K), potencial de acidez trocável (H + Al), sódio (Na), cálcio (Ca), magnésio (Mg), cálcio e magnésio (Ca+Mg), alumínio (Al), soma de bases (SB) matéria orgânica (OM), capacidade de troca catiônica (CTC), porcentagem de saturação de bases (V), capacidade efetiva de troca catiônica (CEC) e saturação por Al (m), características físicas do solo: densidade do solo e granulometria, histórico do uso do solo e declividade, para avaliar como essas variáveis afetavam a biomassa acima do solo.

REFERENCIAS:

Aguiar, A.P.D., Vieira, I.C.G., Assis, T.O., Dalla-Nora, E.L., Toledo, P.M., SantosJunior, R.A.O., (...) Ometto, J.P.H. (2016) Land use change emission scenarios: anticipating a forest transition process in the Brazilian Amazon. Global Change Biology, 22, 1821–1840

Aragão, L.E.O.C., Poulter, B., Barlow, J.B., Anderson, L.O., Malhi, Y., Saatchi, S. Phillips, O.L., Gloor, E. (2014) Environmental change and the carbon balance of Amazonian forests, Biol. Rev., 89(4), 913–931, doi:10.1111/brv.12088.

Baker, T.R., Swaine, M.D., Burslem, D.F.R.P. (2003) Variation in tropical forest growth rates: combined effects of functional group composition and resource availability. Perspectives Plant Ecology 6, 21–36

Barlow, J., Parry, L., Gardner, T. A., Ferreira, J., Aragão, L. E. O. C., Carmenta, R., (…) Cochrane, M. A. (2012) The critical importance of considering fire in REDD+ programs. Biological Conservation, 154, 1–8. https://doi.org/10.1016/j.biocon.2012.03.034.

Brown, S., e Lugo, A. E. (1990). Tropical secondary forests. Journal of Tropical Ecology 6:1-32.

Campo, J. e Vázquez-Yanes, C. (2004) Effects of Nutrient Limitation on Aboveground Carbon Dynamics during Tropical Dry Forest Regeneration in Yucatan, Mexico. Ecosystems. 7. 311-319. 10.1007/s10021-003-0249-2.

Cordell, S., Goldstein, G., Meinzer, F.C., Vitousek, P.M., (2001) Regulation of life-span and nutrient-use efficiency of Metrosideros polymorpha trees at two extremes of a long chronosequence. Oecologia 127:198–206.

Cardinale, B.J., Wright, J.P., Cadotte, M.W., Carroll, I.T., Hector, A., Srivastava, D.S., Loreau, M., Weis, J.J. (2007) Impacts of plant diversity on biomass production increase through time because of species complementarity. Proceedings of the National Academy of Sciences USA, 104, 18123–18128.

Clark, D.B., e Clark, D.A. (2000) Landscape-scale variation in forest structure and biomass in a tropical rain forest. For. Ecol. Manage. 137: 185–198.

Cleveland, C.C., Townsend, A.R., Taylor, P., .(..) Wieder, W.R. (2011). Relationships among net primary productivity, nutrients and climate in tropical rain forest: a pantropical analysis. Ecology Letters 14, 939–947.

Chazdon, R. L., Peres, C. A., Dent, D., Sheil, D., Lugo, A. E., Lamb, D., Stork, N. E., Miller, E. (2009) The potential for species conservation in tropical secondary forests. Conserv. Biol. 23: 1406–1417.

Davidson, E. A., de Carvalho, C. J. R., Vieira, I. C. G., de Figueiredo, R., Moutinho, P. F., Ishida, Y., dos Santos, M.T.P., Guerrero, J.B., Kalif, K., Sabá, R.T. (2004) Nitrogen and Phosphorus Limitation of Biomass Growth in a Tropical Secondary Forest. Ecol. Appl. 14: 150– 163.

Dent, D. H. DeWalt, S. J. Denslow, J. S. (2012) Secondary forests of central Panama increase in similarity to old-growth forest over time in shade tolerance but not species composition. J. Veg. Sci. 24, 530–542.

FAO. (2015) Global Forest Resources Assessment 2015: how are the world’s forests changing? Food and Agriculture Organization of the United Nations, Rome, Italy. Available at: http://www.fao.org/3/a-i4793e.pdf.

Finegan, B., Pena-Claros, M., de Oliveira, A., Ascarrunz, N., Bretharte, M. S., CarrenoRocabado, G., Casanoves, F., Diaz, S., Eguiguren Velepucha, P., Fernandez, F., Licona, J. C., Lorenzo, L., Salgadonegret, B., Vaz, M., Poorter, L. (2015) Does functional trait diversity predict above-ground biomass and productivity of tropical forests? Testing three alternative hypotheses. J. Ecol. 103: 191–201.

Griscom, H.P., Ashton, M.S. (2011) Restoration of dry tropical forests in Central America: a review of pattern and process. Forest Ecology and Management 261, 1564–1579.

Houghton, R. A., e S. J. Goetz (2008) New satellites help quantify carbon sources and sinks, Eos Trans. AGU, 89(43), 417–418, doi:10.1029/2008EO430001.

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. https://doi.org/10.1111/gcb. 14443.

Loreau, M. e Hector, A. (2001) Partitioning selection and complementarity in biodiversity experiments. Nature, 412, 72–76.

Piotto, D., Montagnini, F., Thomas, W., Ashton, M., Oliver, C. (2009) Forest recovery after swidden cultivation across a 40-year chronosequence in the Atlantic forest of southern Bahia, Brazil. Plant Ecol. 205: 261–272.

Rezende, C. L., Scarano, F. R., Assad, E. D., Joly, C. A., Metzger, J. P., Strassburg, B. B. N., . . . Mittermeier, R. A. (2018). From hotspot to hopespot: An opportunity for the Brazilian Atlantic Forest. Perspectives in Ecology and Conservation, 16(4), 208-214. doi:10.1016/j.pecon.2018.10.002

Rozendaal, D.M.A., e Chazdon R.L. (2015) Demographic drivers of tree biomass change during secondary succession in northeastern Costa Rica. Ecol. Appl. 25: 506–516.

Slik. J.W.F., Arroyo-Rodríguez, V., Aiba, S.I., (…) Venticinque, E.M. (2015) An estimate of the number of tropical tree species. Proc. Natl. Acad. Sci. U.S.A. 112, 7472–7477.

Ribeiro, M. C., Metzger, J. P., Martensen, A. C., Ponzoni, F. J., & Hirota, M. M. (2009). The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. Biological Conservation, 142(6), 1141-1153. doi:10.1016/j.biocon.2009.02.021

Tilman, D., Reich, P.B., Knops, J., Wedin, D., Mielke, T. Lechman,C. (2001) Diversity and product ivityina long-term grassland experiment. Science, 294, 843–845.

Willis, K., Gillison, L., Brncic, T. (2004) How “virgin” is virgin rainforest? Science 304:402–403.

Whight, S.J., Muller-Landau, H.C. (2006) The future of tropical forest species. Biotropica, 38,287–301.

Zarin, D.J., Ducey, M.J., Tucker, J.M., Salas, W.A. (2001) Potential biomass accumulation in Amazonian regrowth forests. Ecosystems 4: 658–668.

CAPITULO I

Effect of soil bulk density on aboveground biomass in Neotropical forests

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Abstract

Natural forests are of great importance for global carbon storage. Therefore, it is crucial to quantify and understand the spatial variation of forest biomass and to identify the main factors that control forest biomass across the globe. Many studies have been carried out to evaluate the influence of soil bulk density on commercial farming and annual crops, while few studies report the relationship with aboveground biomass in forests ecosystems. Here, we carried out a systematic review in order to compile information and evaluate how soil bulk density and aboveground biomass are related in neotropical natural forests. We conducted searches on three main research websites (SCOPUS, Web of Science and Scielo), in university libraries. We compiled data with 52 observations of aboveground biomass, containing the following information: average values of soil bulk density and aboveground biomass. Generalized linear mixed-effects models were used to evaluate significant relationships between soil bulk density and aboveground biomass. The results showed that aboveground biomass decrease significantly ($p < 0.01$) with increase in soil bulk density. Based on our results, we suggest that soil bulk density can be used as a predictor of aboveground biomass in neotropical natural forests, thus contributing to the assessment of impacts in forest ecosystems.

Keywords: biomass, carbon, soil bulk density, soil properties, soil compaction

Introduction

Forest ecosystems cover a large part of the earth's surface and play an important role in several aspects, be it in the functioning of the ecosystem, biodiversity protection (Reilly and Spies 2015) and regulation of the global carbon and climate cycle (Ahmad et al. 2014; Coulston et al. 2015; Lorenz and Lal 2010). Globally, forests account for more than 80% of the earth's plant biomass (Kindermann et al. 2008; Pan et al. 2013), of these, 80% is in above ground tissues and 20% below ground (Cairns et al. 1997). Tropical forests are responsible for storing 55% of forest carbon, while 32% are in boreal forests and 14% in temperate forests (Houghton 2005; Pan et al. 2011).

On a large scale, the main factors controlling forest biomass distribution are the climatic (Becknell et al. 2012; Myneni et al. 1997; Vilanova et al. 2018) and edaphic conditions (Baker et al. 2009; Becknell and Powers 2014; Lee et al. 2018). Soils have a fundamental role in forest ecosystems by providing water and nutrients that affect energy cycles responsible to ensure forest productivity (Dominati et al. 2010). Soil conditions have already been reported as one of the main variables that influence the structure and dynamics of forests (Quesada et al. 2012; Tokunaga 2006), with direct effects of soils on tree growth (Cleveland et al. 2011). Whilst chemical characteristics of soils (e.g. pH) affect nutrient availability, (Gourlet -Fleury et al. 2011; Ostertag 2010; Paoli and Curran 2007; Slik et al. 2010) physical properties affect plant anchorage and establishment, with soil bulk density being one of the main factors exerting a large effect on plant growth (Kozlowski 1999; Nawaz et al. 2013).

Soil bulk density can influence plant growth in several ways. The increase in density decreases the distribution and continuity of the soil pores (Benthaus and Matthies 1993), altering the roots growth, as well as their ability to expand in large volumes of the soil (Dunbabin 2007). Consequently, they reduce available spaces for air and water, and the water filled pores influence the amount of stored water available for plants and soil aeration (Hallett and Bengough 2012). The water available in the soil pores also alters the ability of nutrients to move in the soil solution (Martinez and Zinck 2004).

The lack of aeration in the pore spaces of a soil is determinant for the ability to carry oxygen through the soil to the roots (Lipiec and Hatano 2003). When oxygen diffusion is reduced in the soil, it may cause roots damage that leads to their inability to function (Engelaar and Yoneyama 2000). This partial O_2 deficiency due to pore spaces reduction, can cause plants to send a hormonal signal by the roots, such as ethylene production and abscisic acid, which inhibit roots and stems growth and causes leaf abscission (Grichko and Glick 2001; Passioura 2002; Silva et al. 2004). Thus, these stresses caused by soil bulk density increment can limit plant growth and aboveground biomass storage (Ferry et al. 2010; Hirai et al. 2003; Schoenholtz et al. 2000).

In forest ecosystems, soils can be naturally compacted by the weight of growing trees (Kozlowski 1999), especially in soils with a fine texture, with higher clay content (Arshad et al. 1996). In contrast, the anthropic soil compaction is mainly caused by mechanization, farming and grazing (Silva et al. 2008). According to a global assessment, more than 60% of forests are recovering from anthropogenic past disturbances (FAO 2006), with many areas having already undergone some process of soil alteration. This represents a major problem to the maintenance of the productivity and functioning of these forests, as their recovery can take many years.

The increase in soil bulk density is a global concern, as it indicates harsh physical conditions for plant establishment with possible effects on their productivity (FAO 2005). However, this relationship has been reported in the literature in many studies on the influence of soil bulk density as effect of soil compaction in crops and commercial planting trees systems (Carter 1990; Cambi et al. 2015; Horn et al. 2007), but few studies reported its influence on plant growth in natural forests (Zhao et al. 2010), and study of relationships in natural forests can improve the management of degraded areas. Here, we use a systematic review approach to gather information and evaluate if the soil bulk density affects aboveground biomass storage in neotropical forests.

Material and methods

Data sources

Articles published up to 2020 were collected from the following databases: Web of Science (www.webofknowkedge.co), SCOPUS (https://www.scopus.com), SCIELO (www.scielo.com.br) and in some university libraries. The combinations of search terms: “Soil bulk density," AND, "biomass" OR "tropical forest", were used. Searches were filtered to remove articles from unrelated areas, such as veterinary, engineering, biochemistry and others. A second filter by document type was applied to remove notes and editorial material. With the search results, we selected articles by title and abstract. Afterwards, the articles were analyzed to check if they contained the necessary information, previously highlighted, and finally, the inclusion criteria were established to perform data extraction. To minimize potential uncertainties in data collection and analysis, the following criteria were applied to select appropriate studies. Five inclusion criteria were established to avoid possible bias in relation to soil bulk density and natural vegetation: 1) natural forests were considered primary forests (see Smith et al. 2002) that have not undergone any recent disturbance, and secondary forests that were free of disturbance for at least 50 years and that were naturally regenerated, 2) if studies utilized a chronosequence design for secondary forest, the data obtained from the oldest forest were used, 3) areas of planted forests, agriculture or experimental areas were excluded, 4) samples of soil bulk density were used for superficial soil layers (0-20 cm depth), and 5) the articles should necessarily present data on biomass and soil bulk density, but these articles did not necessarily test a relationship between the variables.

The selected articles that had vegetation structure variable: aboveground biomass (Mg/ha), and soil variable, soil bulk density (g/cm^3). These data were extracted from tables, texts, graphs and supplementary material. The following information was also extracted: country, latitude and longitude, type of vegetation and type of soil. For each study, a set of climatic data using the studies geographic location was extracted. First, we extract the geographic coordinates (latitude and longitude), then we used a set of global climate data (http://www.worldclim.org/) to obtain data on average annual temperature and precipitation for each location, which are main variables affecting aboveground biomass (Ali et al. 2019).

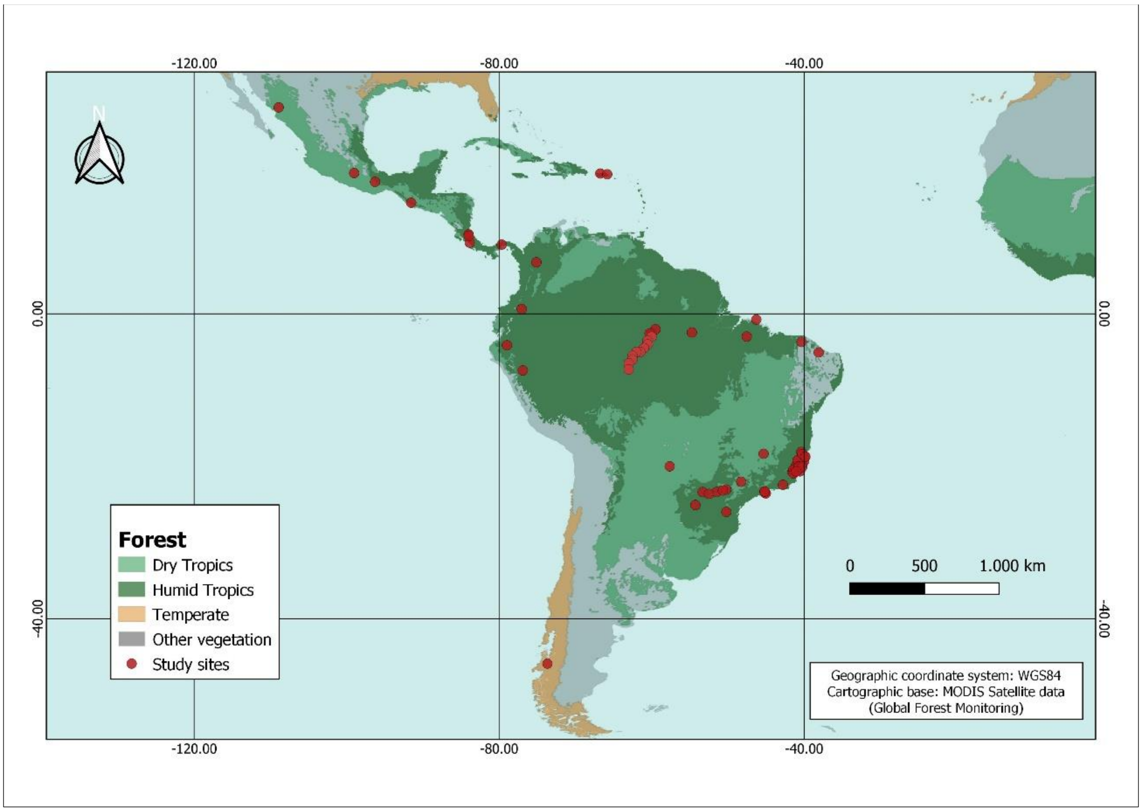

Fig 1. Global forest cover map, with geographic distribution of the 52 observations included in this study, which assess the aboveground biomass and the soil bulk density. Forest cover data based on MODIS satellite data, the Global Forest Monitoring (Hansen et al. 2010) (https://glad.geog.umd.edu).

Data analysis

To evaluate the relationship between soil bulk density and aboveground biomass, different generalized linear mixed-effects model (GLMM) was adjusted, with soil density as fixed predictor variable, and aboveground biomass as response variable, and considering the studies with as a random factor in all models to prevent data alignment in studies containing more than one observation (studies with sampling sites in different locations) (Zuur et al. 2009). We included climatic variables in the models to assess whether the relationship between aboveground biomass could be better explained by these variables. We used five models to explore the relationship of soil bulk density with aboveground biomass: 1) a complete linear model, with soil bulk density, average annual temperature and total precipitation, as explanatory variables; 2) a model with the soil bulk density and total precipitation, as explanatory variables; 3) a simple model with only the soil bulk density as an explanatory variable; 4) a simple model with only total precipitation as an explanatory variable; 5) a null model (only the intercept) (Table 1). Then, we calculated the Akaike information criterion corrected for the small sample size (AICc; Burnham and Anderson 2002) for each model and, for each response variable, we selected the simplest model among those with an ΔAICc ≤ 2.0. We performed all analyzes in R 3.4.4 (R Core Team 2017), with the bbmle (Bolker and R Development Core Team 2017), lme4 (Bates et al. 2015) and lavaan (Rosseel 2012) packages.

Results

A total of 56 observations were selected in the present study. The studies were carried out in Brazil, México, Costa Rica, Panama, Guatemala, Colombia and Porto Rico (Fig. 1). Soil bulk density ranged from 0.5 to 2.28 g cm^{-3}, aboveground biomass ranged widely among studies locations from 80 to 294 Mg ha^{-1}, and these values varied according to geographic location.

The results of generalized linear mixed-effects models showed that soil bulk density is correlated the aboveground biomass, since the best model with presents only density presented ΔAICc<2, in relation to the complete model and the null model (Table 1). We found that the increase in soil bulk density has a significant negative effect on aboveground biomass (Model 3; b= -0.2689; p<0.001) in Neotropical forests (Fig. 2; Table 1).

Table 1. Model selection results, showing the difference in the values of the corrected Akaike information criterion (ΔAICc) for each model of each response variable. (Δi: Difference in Akaike Information Criterion corrected value; k: number of parameters estimates in the model; Wi: Akaike weights).

		Parameters					
Metric	Model	Δ*i*	k	W*i*	Intercept	Slope	p
Aboveground Biomass	1. Soil Bulk Density + Temperature + Total precipitation	3.2	6	0.1386	4.8428	-0.2500 -0.1084 0.1607	0.0006*** 0.2426 0.1911
	2. Soil Bulk density + precipitation	2.7	5	0.1721	4.8826	-0.2563 0.1040	0.0005* 0.3844
	3. Soil Bulk density	**0**	4	0.6799	4.8969	-0.2689	0.0002*
	4. Total precipitation	10.1	4	0.0044	5.0360	0.2026	0.118

	5. Null	9.8	3	0.0050	5.0816	-	

*Model selected for each response variable and corresponded to the model with the lowest AICc are in bold.

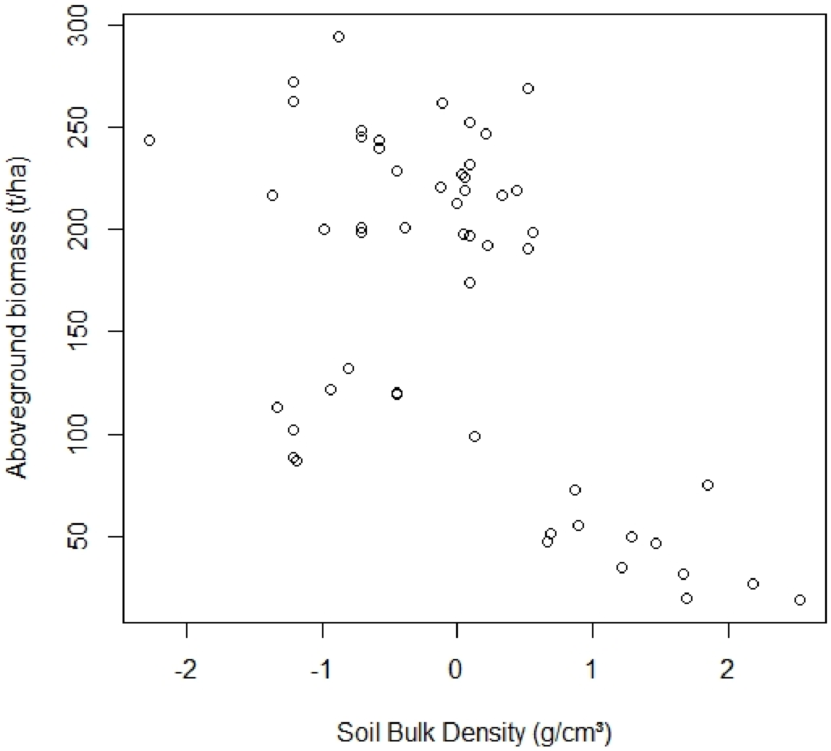

Fig. 2 Effect of soil bulk density and aboveground biomass, in Neotropical forests.

Discussion

Based on the collected data from field studies, our analyses demonstrated that soil bulk density influences aboveground biomass. And this being the first work to evaluate this relationship in Neotropical scale, it reinforces what has been reported locally (Cheatle 1991; Gebauer and Martinková 2005; Martins et al. 2014). Some mechanisms can explain these results, for example, the increase in soil bulk density reduces the pore spaces of the soil (Benthaus and Matthies 1993). These pore diameters in the soil are the places of water and nutrients passaging, which implies in limited spaces available for the growth of roots, root penetration and rooting depth

(Kristoffersen and Riley 2005). The increase in soil bulk density implies more restrictive soil conditions to growth and root elongation to obtain water and nutrients (Quesada et al. 2009; Nawaz et al. 2013). Another important factor is that lack of aeration in porous soil spaces, caused by the increase in density, directly affects the redox transformations of some soil elements, as well as the diffusive transport of nutrients from soil to plants roots, especially under severe anoxia conditions (Lipiec and Stpniewski 1995).

Climatic variables can be considered one of the main factors that influence aboveground biomass globally (Myneni et al. 1997), mainly the ones that affect water availability for plants. However, our results did not demonstrate a significant relationship between biomass and climate variables. Soil bulk density can indirectly affect the availability of water in the soil, with hydrological restrictions, can reduce infiltration rates and water flow in the soil (Kozlowski 1999, Gregory et al. 2015), increase water outflow, which may cause soil erosion, and accelerate leaching and nutrient loss (Kang and La1 1981; Nawaz et al. 2013). These factors can then lead to water deficits in the soil (Kramer and Boyer, 1995), strongly influencing the growth and productivity of plants (Schoenholtz et al. 2000; Dedecek et al. 2001).

Even with the knowledge that soil characteristics vary widely, as these depend mainly on characteristics of geomorphological formation processes, origin of the geological material, age and type of soil (Hartshorn 1983), we can notice that the main plants response in the present study is about characteristics that influence the growth capacity of roots, like the soil bulk density, which can cause roots stunted growth, height and diameter reductions (Zhao et al. 2010). In the present work we found that soils physical properties, such as soil bulk density, have negative relationship on forest biomass. For example, trees grow where there are suitable soil bulk density conditions for root growth and plant development, as observed in low density soil locations, where we found the highest values of biomass.

Understanding the distribution of forest aboveground biomass is important for calculating carbon sources and how it responds to different environmental factors. We understand that other variables affect aboveground biomass, but we focus on soil characteristics, as a factor that affects plant growth. The results of this review indicated a negative relationship of soil bulk density on aboveground biomass, and that some factors may explain this relationship, such as the restriction of root growth. Although soil bulk density has been widely used to assess growth in cropping systems, it has been little used to assess the resilience of forest ecosystems. We know that assessing soil bulk density, requires a large field effort for collections, but their incorporation into biomass assessments can contribute to the results of the assessments and here we show is an important factor that affects aboveground biomass. Finally, we suggest that more attention should be paid to reporting soil bulk density in ecological studies since it is an important factor affecting aboveground biomass worldwide.

Acknowledgements

This work was supported by the Fundo Brasileiro para a Biodiversidade (Funbio) and Humanize Institute, for the author ROCHA JIS (grant number: 111/2019). JISR received a doctoral scholarship from the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001. I thank Alesandro Souza for the help in the statistical analysis.

References

Ahmad A, Mirza SN, Nizami SM (2014) Assessment of biomass and carbon stocks in Coniferous Forest of Dir Kohistan, KPK. – Pakistan Journal of Agriculture Sciences 51: 335-340.

Ali A, Lin SL, He JK, Kong FM, Yu JH, Jiang HS (2019) Climatic water availability is the main limiting factor of biotic attributes across large-scale elevational gradients in tropical forests. Science of the Total Environment 647: 1211–1221

Arshad MA, Lowery B, Grossman B (1996) Physical tests for monitoring soil quality, in: Doran JW and Jones AJ. Methods for Assessing Soil Quality. Soil Sci. Soc. Am., SSSA Special Publication 49:123–141

Baker TR, Phillips OL, Laurance WF, Pitman NCA, Almeida S, Arroyo L, DiFiore A, Erwin T, Higuchi N, Killeen TJ, Laurance SG, Nascimento H, Monteagudo A, Neill DA, Silva JNM, Malhi Y, Lopez-Gonzalez G, Peacock J, Quesada CA, Lewis SL, Lloyd, J (2009) Do species traits determine patterns of wood production in Amazonian forests? Biogeosciences, 6:297–307

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1-48. https://doi.org/10.18637/jss.v067.i01

Balvanera P, Aguirre E (2006) Tree diversity, environmental heterogeneity, and productivity in a Mexican tropical dry forest. Biotropica 38:479–491

Becknell JM, Kucek LK, Powers JS (2012) Aboveground biomass in mature and secondary seasonally dry tropical forests: A literature review and global synthesis. Forest Ecology and Management 276:88–95

Becknell JM, Powers JS (2014) Stand age and soils as drivers of plant functional traits and aboveground biomass in secondary tropical dry forest. Can. J. For. Res. 44: 604–613

Benthaus M, Matthies D (1993) Regeneration befahrener Waldböden. Allgemeine Forstzeitschrift. *48*:448–451

Bolker B and R Development Core Team (2017) bbmle: Tools for General Maximum Likelihood Estimation. R package version 1.0.20

Borchert R, Rivera G, Hagnauer W (2002) Modification of vegetative phenology in a tropical semi-deciduous forest by abnormal drought and rain. Biotropica, 34, 27–39.

Bueckling et al., 2017 A. Bueckling, P.H. Martin, C.D. Canham (2017) Climate and competition effects on tree growth in Rocky Mountain forests J. Ecol., 105: 1636-1647, 10.1111/1365-2745.12782

Burnham KP, Anderson DR (2004) Multimodel Inference: Understanding AIC and BIC in Model Selection. Sociol Methods Res. https://doi.org/10.1177/0049124104268644

Cai H, Li F, Jin G (2019) Fine root biomass, production and turnover rates in plantations versus natural forests: effects of stand characteristics and soil properties. Plant Soil 436:463–474

Cairns MA, Brown S, Helmer EH, Baumgardner GA (1997) Root biomass allocation in the world’s upland forests, Oecologia, 111: 1– 11

Carter MR (1990) Relative measures of soil bulk density to characterize compaction in tillage studies on fine sandy loams. Can. J. Soil Sci. 70(3): 425–433

Cheatle RJ (1991). Tree growth on a compacted oxisol. Soil & Tillage Research, 19:331–344

Coulston JW, Wear DN, Vose JM (2015) Complex Forest dynamics indicate potential for slowing carbon accumulation in the southeastern United States. Scientific Reports 5: 8002

Cleveland CC, Townsend AR, Taylor P, Alvarez-Clare S, Bustamante MMC, Chuyong G, Dobrowski SZ, Grierson P, Harms KE, Houlton BZ, Marklein A, Parton W, Porder S, Reed SC, Sierra CA, Silver WL, Tanner EVJ, Wieder WR (2011) Relationships among net primary productivity, nutrients and climate in tropical rain forest: a pan-tropical analysis. Ecology Letters 14:939–947

Dedecek RA, Bellote AFJ, Gava JL, Menegol O (2001) Site characterisation and the 30 effects of harvesting on soil tillage on the productivity of Eucalyptus grandis plantations in Brazil, in: Kobayashi S, Turnbull JW, Toma T, Mori T, Majid NMNA (1999) Rehabilitation of Degraded Tropical Forest Ecosystems: Workshop Proceedings Bogor, Indonesia 157–164

Dominati E, Patterson M, Mackay A (2010) A framework for classifying and quantifying the natural capital and ecosystem services of soils. Ecol. Econ. 69, 1858–1868

Dunbabin V (2007) Simulating the role of rooting traits in crop-weed competition. Field Criop Res. 104: 44-51

Engelaar WMHG, Yoneyama T (2000) Combined effects of soil waterlogging and compaction on rice (*Oryza sativa* L.) growth, soil aeration, soil N transformations and N discrimination. Biology and Fertility of Soils 32: 484-493

Eisenhauer N, Bowker MA, Grace JB, Powell JR (2015) From patterns to causal understanding: structural equation modeling (SEM) in soil ecology. Pedobiologia 58, 65–72. https://doi.org/10.1016/j.pedobi.2015.03.002.

FAO (2005) Global forest resources assessment. FAO Forestry Paper 147. FAO, Rome

FAO (2006) Global forest resources assessment 2005. For. pap. 147, FAO, Rome

Ferry B, Morneau F, Bontemps J, Blanc L, Freycon V (2010) Higher treefall rates on slopes and waterlogged soils result in lower stand biomass and productivity in a tropical rain forest, Journal of Ecology 98:106–116

Gebauer R, Martinková M (2005). Effects of pressure on the root systems of Norway spruce plants (Picea abies [L.] Karst.). Journal of Forest Science 51:268–275

Gourlet-Fleury S, Rossi V, Rejou-Mechain M, Freycon V, Fayolle A, Saint-André L, Cornu G, Gérard J, Sarrailh JM, Flores O, Baya F, Billand A, Fauvet N, Gally M, Henry M, Hubert D, Pasquier A, Picard N (2011) Environmental filtering of dense-wooded species controls above-ground biomass stored in African moist forests. Journal of Ecology 99(4): 981–990

Gregory AS, Ritz K, McGrath SP, Quinton JN, Goulding KWT, Jones RJA, Harris JA, Bol R, Wallace P, Pilgrim ES, Whitmore AP (2015) A review of the impacts of degradation threats on soil properties in the UK, Soil Use Manage., 31, 1–15, https://doi.org/10.1111/sum.12212

Grichko VP, Glick BR (2001) Ethylene and flooding stress in plants. Plant Physiology 39: 1-9

Hallett PD, Bengough AG (2012) Managing the soil physical environment for plants. In: Gregory, P and Nortcliff, S. (ed) Soil conditions and plant growth. Wiley-Blackwell p.238

Hansen M, Stehman S, Potapov P (2010) Quantification of global gross forest cover loss. Proceedings of the National Academy of Sciences of the U.S.A. (https://glad.geog.umd.edu/projects/gfm/global/gindex.html)

Hartshorn GS (1983) Plants. In: Janzen DH (Ed.) Costa Rican Natural History. University of Chicago Press, Chicago pp. 118–157

Heninger R, Scott W, Dobkowski A, Miller R, Anderson H, Duke S (2002) Soil disturbance and 10-year growth response of coast Douglas-fir on non-tilled and tilled skid trails in the Oregon Cascades. Can. J. For. Res. 32:233–246

Hirai K, Ferraz JBS, Kobayashi M, Ferreira SJF, Sales PC, Lopes MC, Hotta I (2003) Physical properties of the soils under degraded areas in the Central Amazon, In: Projecto Jacaranda Fase II: Pesquisas Florestais na Amazonia Central, CPST-INPA, Manaus, Brazil,153–167

Houghton RA (2005) Aboveground forest biomass and the global carbon balance, Global Change Biol., 11: 945 – 958, doi:10.1111/j.1365- 2486.2005.00955.x.

Horn R, Vossbrink J, Peth S, Becker S (2007) Impact of modern forest vehicles on soil physical properties. For. Ecol. Manage. 248: 56–63

Jackson PC, Cavelier J, Goldstein G, Meinzer FC, Holbrook NM (1995) Partitioning of water resources among plants of a lowland tropical forest. Oecologia, 1995, 101, 197–203.

Kang BT, Lal R (1981) Nutrient losses in water runoff from agricultural catchments. In: Lal R, Russel EW (ed) Tropical Agricultural Hydrology, 153 - 161

Kindermann G, et al. (2008) Global cost estimates of reducing carbon emissions through avoided deforestation. Proc Natl Acad Sci USA 105:10302–10307

Kozlowski TT (1999). Soil compaction and growth of woody plants. Scandinavian Journal of Forest Research, 14:596– 619

Kramer PJ, Boyer JS (1995) Water Relations of Plants and Soils. Academic Press, San Diego, CA

Kristoffersen A, Riley H (2005) Effects of soil compaction and moisture regime on the root and shoot growth and phosphorus uptake of barley plants growing on soils with varying phosphorus status. NutrCycl Agroecosys 72:135–146

Lee E, Kumar P, Barron-Gafford GA, Hendryx SM, Sanchez-Canete EP, Minor RL, Colella T, Scott RL (2018) Impact of Hydraulic Redistribution on Multispecies

Vegetation Water Use in a Semiarid Savanna Ecosystem: An Experimental and Modeling Synthesis. Water Resources Research. DOI: 10.1029/2017WR021006

Lipiec J, Stcpniewsk W (1995) Effects of soil compaction and tillage systems on uptake and losses of nutrients. Soil & Tillage Research 35: 37-52

Lipiec J, Hatano R (2003) Quantification of compaction effects on soil physical properties and crop growth. Geoderma,116:107-136

Lorenz K, Lal R (2010) Carbon Sequestration in Forest Ecosystems Springer, Dordrecht, The Netherlands

Martins DL, Schietti J, Feldpausch TR, Luizão FJ, Phillips OL, Andrade A, Castilho CV, Laurance SG, Oliveira A, Amaral IL, Toledo JJ, Lugli LF, Purri JL, Pinto V, Mendoza EM, Quesada CA (2015) Soil-induced impacts on forest structure drive coarse woody debris stocks across central Amazonia, Plant Ecology & Diversity, 8:2, 229-241, DOI: 10.1080/17550874.2013.879942

Markesteijin L, Iraipif J, Bongers F, Poorter L (2010) Seasonal variation in soil and plant water potentials in a Bolivian tropical moist and dry forest. Journal of Tropical Ecology (2010) 26:497-508

Martınez LJ, Zinck JA (2004) Temporal variation of soil compaction and deterioration of soil. Soil & Tillage Research 75: 3–17

Myneni RB, Keeling CD, Tucker CJ, Asrar G, Nemani RR. 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. Nature 386:698–702

Nawaz MF, Bourrié G, Trolard F (2013) Soil compaction impact and modelling. A review. Agron. Sustain. Dev. 33, 291–309 doi.org/10.1007/s13593-011-0071-8

Ostertag R (2010) Foliar nitrogen and phosphorus accumulation responses after fertilization: an example from nutrient-limited Hawaiian forests. Plant and Soil 334(1-2): 85–98. doi: 10.1007/s11104-010-0281-x.

Pan Y, Birdsey RA, Fang J et al (2011) A large and persistent carbon sink in the world’s forests. Science 333:988–93

Pan Y, Birdsey RA, Phillips OL, Jackson RB (2013) The Structure, Distribution and Biomass of the World's Forests. Annu. Rev. Ecol. Evol. Syst. 44:593-62

Paoli GD, Curran LM (2007) Soil nutrients limit fine litter production and tree growth in mature lowland forest of southwestern Borneo, Ecosystems, 10, 503–518

Passioura JB (2002) Soils conditions and plant growth. Plant, Cell, and Environment 25: 311-318

Poorter L, van der Sande MT, Arets EJMM et al (2017) Biodiversity and climate determine the functioning of neotropical forests. Glob. Ecol. Biogeogr. 26, 1423–1434

Peña-Claros M, Poorter L, Alarcón A et al (2012) Soil Effects on Forest Structure and Diversity in a Moist and a Dry Tropical Forest. Biotropica, 44, 276–283

Quesada CA, Lloyd J, Schwarz M, Baker TR, Phillips O, Ramırez H (2009) Regional and large-scale patterns in Amazon forest structure and function are mediated by variations in soil physical and chemical properties, Biogeosciences Discuss. 6:3993–4057

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

R Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Reilly MJ, Spies TA (2015) Regional variation in stand structure and development in forests of Oregon, Washington, and inland Northern California. Ecosphere 6:192

Rosseel Y (2012) Lavaan: Na r package for structural equation modeling. J. Stat. Softw. 48, 1–36. http://www.jstatsoft.org/v48/i02/.

Sanchez-Azofeifa GA, Quesada M, Rodriguez JP, Nassar JM, Stoner KE, Castillo A, Garvin T, Zent EL, Calvo-Alvarado JC, Kalacska MER, Fajardo L, Gamon JA, Cuevas-Reyes P (2005) Research priorities for neotropical dry forests. Biotropica 37:477–485

Schenk HJ, Jackson RB (2002) The global biogeography of roots. Ecol Monogr 72:311–328

Schoenholtz SH, Van Miegroet H, Burger JA (2000) A review of chemical and physical properties as indicators of forest soil quality: challenges and opportunities, Forest Ecol. Manag., 138:335–356

Silva AP, Imhoff S, Kay B (2004) Plant response to mechanical resistance and air-filled porosity of soils under conventional and no-tillage system. Sci. agric. (Piracicaba, Braz.) Piracicaba 61: 451-456

Silva S, Barros N, Costa L, Leite F (2008) Soil compaction and eucalyptus growth in response to forwarder traffic intensity and load. Rev Bras Cienc Solo 32:921–932

Slik JWF, Aiba S, Brearley FQ, Forshed CHCO, Kitayama K, Nagamasu H, Nilu R, Payne J, Paoli G, Poulsen AD, Raes N, Sheil D, Sidiyasa K, Suzuki E, van Valkenburg JLCH (2010) Environmental correlates of tree biomass, basal area, wood specific gravity and stem density gradients in Borneo’s tropical forestsgeb. Global Ecol. Biogeogr. 19: 50–60

Smith CK, Oliveira FDA, Gholz HL, Baima A (2002) Soil carbono stocks after forest conversion to tree plantations in lowland Amazonia, Brazil. For Ecol Manag 164:257–263

Stan K, Sanchez-Azofeifa A (2019) Tropical Dry Forest Diversity, Climatic Response, and Resilience in a Changing Climate. *Forests*, 10(5):443. https://doi.org/10.3390/f10050443

Tokunaga AA (2006) Effects of bulk density and soil strength on the growth of blue wildrye (Elymus glaucus Buckl.). MA Thesis, Humboldt State University, California, USA

Vilanova E, Ramírez-Angulo H, Torres-Lezama A et al (2018) Environmental drivers of forest structure and stem turnover across Venezuelan tropical forests. PLoS One.13(6):e0198489. Published 2018 Jun 21. doi:10.1371/journal.pone.0198489

Zhao Y, Krzic M, Bulmer CE, Schmidt GM, Simard S (2010) Relative bulk density as a measure of compaction and its influence on tree height. Canadian J. Forest Res., 40: 1724-1735

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed Effects Models and Extensions in Ecology with R. Statistics for Biology and Health, New York

CAPÍTULO II

Litter production in successional forests of southern Bahia, Brazil

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Manuscrito publicado na revista Journal of Tropical Ecology. (Anexo I)

Abstract

Litter production plays an important role in the functioning of the ecosystem, providing several ecosystem services, such as nutrients cycling and carbon storage. We studied litter production patterns and its relationship with forest structure over a chronosequence of secondary forests in southern Bahia, Brazil. In the study area, 15 pairs of mature and secondary forest were used, in a chronological sequence, being 10, 25 and 40-year-old secondary forests and mature forests. Plots were created for the collection of aboveground biomass data, and within these plots, litter collectors were installed and monitored for one year. The results showed that litter production was lower in 10-year-old secondary forests when compared to older forests. On the other hand, in the 10-year-old forests, annual litter production represents 47,8% of the stored biomass, while in mature forests annual litter production represents only 4%. We found that structural variables (basal area, number of stems and canopy opening) influence significantly litter production, as well as litter as percentage of forest biomass. The study emphasizes the importance of biomass production through litterfall in regenerating tropical forests, and its importance for carbon storage and for the maintenance of ecosystem services.

Keywords: ecosystem functioning, regeneration, carbon, secondary succession, successional, tropical forests

Introduction

Tropical forests are responsible for storing around 37% of the terrestrial carbon of the planet in the form of plant biomass (Aguiar et al.2016, USDOE 2010). Forest biomass is stored in about 80% of the aboveground biomass (Cairns et al.1997) which is related to vegetation structure (Houghton et al.2009). In tropical forests, more than 50% of primary annual production is returned to the soil in the form of organic debris in litter (Wardle et al.2004). The IPCC identified litter as one of the five carbon reservoirs in forest ecosystem (Nizami 2012), with 5% of the aboveground biomass being stored in litter (Pan et al.2011).

The return of organic matter to the soil is one of the main processes of ecosystem functioning (Alves et al.2010); it represents the transfer route of organic matter and mineral elements from the vegetation to the soil (Camargo et al.2015, Silver et al.2014, Vitousek & Sanford 1986). This process is essential in tropical forests as those are environments with highly weathered soils (Poggiani 2012) and with low fertility (Vitousek & Sanford 1986). Because of that, the vegetation depends on the cycling of nutrients contained in plant debris for the absorption of nutrients (Kuruvilla et al.2016, Rawat et al. 2010). In addition, litter production becomes essential for the functioning of the ecosystem, transferring nutrients to the soil (Pandey et al.2007), maintaining soil fertility in forest ecosystems (Guendehou et al.2014, Montagnini & Jordan 2002, Tripathi et al.2006) and for the global carbon cycle (Berg & Mcclaugherty 2014).

Litter production occurs by the elimination of vegetative parts of plants, which can be caused by senescence, abiotic factors, stress and these factors combined, as well as by the death of a plant (Chakravarty et al.2019, Krishna & Mohan 2017). The pattern of litter production depends on some factors such as climate (Sayer 2006) and vegetation structure and composition (Nickmans et al.2019, Vital et al.2007). There is a significant number of studies designed to understand the effect of climate in litter production patterns. For example, the relationship of seasonality with increased litter production (An et al. 2019), as in the warmer seasons of the year, on increasing light time, plants can prepare for more favorable growth, and thus replace the old leaves with new ones (Devi & Garkoti 2013), higher production in the dry season (Barlow et al.

2007), and decrease the production of litter with increase elevation (Majila et al.2005, Zhou et al.2007).

In addition to climate, vegetation characteristics can modify litter production, such as vegetation structure and composition (Nickmans et al.2019, Schumacher et al.2011) and the changes in development strategies of the plants with forest succession (Poorter & Bongers 2006). As the forest develops, there is an increase in the size of large trees, increase in the basal area, and the well-developed forest structure reflects a well-developed canopy, which can favor the production of litter (Kunhamu et al.2009, Vidal et al.2007). Changes in plant functional traits can affect litter production with the change of plants dominance from acquisitive to conservative traits, during secondary succession (Craven et al.2015, Facelli & Pickett 1991; Werneck et al.2001).

In theory, litter production pattern is related to the canopy development that occurs differently, depending on the individual characteristics of the species (Carrera et al. 2008). For example, in young secondary forests, the dominant species have resource acquisition characteristics, with high growth and mortality potential (Rozendaal & Chazdon 2015), fragile tissues (Reich 2014), low-density wood and short-lived leaves (Adler et al.2013), contributing more to litter production because they have leaves and branches with less lignified materials, in addition to being rich in N and low C/N ratio that can accelerate litter turnover (Zhou et al. 2019). With forest development, dominance gradually changes towards species with conservative resource characteristics, which present production of denser tissues (as a higher density of wood), high C/N ratio, long-lived leaves, low renewal leaves rates (Adler et al.2013, Craven et al.2015, Reich 2014). Thus, areas in advanced stage of forest development, with higher species diversity and abundance of late-successional species, show the poorest litter in terms of N concentrations, and with a high C/N ratio, which leads to lower litter turnover rates (Parton et al.2007, Zhou et al.2019). In this way, changes in species dominance will modify the quantity and quality of the litter and, consequently, the flows of biomass and nutrients with forest development.

Here, we used a chronosequence of secondary and mature forests of the Atlantic Forest, in Brazil, biome to assess changes of litter production with forest development. In addition, we studied the relationship of litter production and standing aboveground biomass to detect changes in plant characteristics with forest development. We hypothesized that (a) there would be an increase of litter production because of the increase in standing aboveground biomass with forest development; (b) there would be a significant shift in the relationship of litter production and standing aboveground biomass with forest development because of changes in dominance from plants with acquisitive to conservative strategies, (c) and the increase of litter production is associated with successional changes in forest structure.

Study site

The study was carried out in the Serra do Conduru State Park - PESC, located in southern Bahia, Brazil, at 14º 30'16" S, and 39º 6'36" W (Figure 1). The Park has an area of approximately 10,000 ha, composed of a forest mosaic in different stages of regeneration, from secondary forests at different ages to well-preserved areas (Piotto et al. 2009). The vegetation is classified as tropical rain forest, in the Atlantic Forest biome, with emergent, canopy, sub-canopy and herbaceous layers and extremely high species diversity (Thomas 2003). The average monthly temperature is 24°C, with an average annual rainfall of 2,000 mm evenly distributed throughout the year (Santos et al. 2018). The selected secondary forest areas were established after deforestation and burnings, followed by 1 to 2 years of cassava cultivation (Piotto et al. 2009).

Methods

Classification of chronosequence

Based on aerial photographs, it was possible to estimate changes in forest cover and land use. Subsequently, using GIS, maps of the age groups of the forests were built with aerial photo sets, using remote sensing data from 1965 to 2009. Interviews with local farmers were conducted to validate information on the type and intensity of use of the land. In this way, 75 secondary forests measuring more than 3ha and adjacent to mature forests were selected. Fifteen pairs of secondary forests adjacent to mature forests were randomly selected to represent three age groups of secondary forests: 10 years (10 to 12 years), 25 years (22 to 25 years), 40 years (37 to 43 years) (Figure 1).

Aboveground biomass data

A total of 75 plots were installed in secondary forests and 15 plots in mature forests (in total we used 90 plots). In each pair of mature and secondary forests five plots of 20x10m (200 m²) were established in each age class (10, 25 and 40 years) in secondary forests and one plot of 20x30m (600m²) in mature forest. All trees with a diameter at breast height (dbh) equal to or greater than 5cm were considered in this study, and we measure the height for all the trees We calculated for each plot its basal area (m²/ha) and tree density (number of trees with dbh>5cm/ha). In addition, we estimated aboveground biomass using the following allometric equation for tropical forests (Chave et al.2014):

$AGB= 0.0673\ (\rho D^2H)^{0.976}$

based on diameter *D* (cm), height H (m), and wood specific gravity ρ ($g.cm^{-3}$). Aboveground AGB is in Kg. Plot biomass represents the estimated biomass of all trees within a plot, which was then extrapolated to estimate the aboveground biomass (AGB) in Mg per ha. specific wood density data were collected for each species in the world database (Zane et al 2009), when species data were not available, we used genus data, and when this was not available, we used family data.

Litter and canopy data

Litter production was sampled using 90 collectors established in mature and secondary forests. In each pair of mature and secondary forests, six collectors were installed with a distance of 20m between each collector, located at the central point of the forest inventory plots. The collectors consisted of a cone of a fine mesh fabric (2mm) attached to a circular wire of $1m^2$, installed at 50 cm aboveground. The collections of material deposited in the collectors were carried out monthly from February 2008 to January 2009. The collected litter was dried in a lab oven at 50º for 48 hours. After drying, each monthly sample was weighted, to obtain the monthly dry mass per collector. For the calculations, results from each collector for all months were added and then transformed into hectares, thus obtaining the values of litter in total weight in tons per hectare per year. At every collector, canopy opening was estimated using hemispherical photographs.

Besides aboveground biomass and structural variables, we also used as a response variable the ratio between litter biomass and aboveground biomass (here considered as a proportion of litter related to aboveground biomass), where we consider the percentage of biomass that is stored in litter in relation to aboveground biomass. For the calculation of the ratio, litter production values were divided by the aboveground biomass values, both in Mg/ha, and were multiplied by 100, to be represented in %.

Statistical analysis

To assess the relation between litter production with age and the relation of aboveground biomass and litter biomass with age, we adjusted a linear mixed model (LMM), including the site as a random factor. We used LMM approach to control temporal pseudoreplication (Zuur et al.2009). Thus, for each response variable (litter production and relation of aboveground and litter biomass), we use one model with age as an explanatory variable. For the validation of the model, we tested the normality of the residues, using the Shapiro-wilk test, and plot of the residues.

Then, we investigated how the stems density (number/ha), canopy openness (%), and basal area (m^2/ha), can influence litter production and how these variables influence the aboveground and litter biomass ratio. As the forest structure data was considered non-normal, we used Generalized Linear Models (GLM). For each response variable (annual litter production and aboveground and litter biomass ratio) we fit four models for each explanatory variable (stems density (number/ha), canopy openness (%), and basal area (m^2/ha)): 1) a model with annual litter production as the response variable in relation to an explanatory variable (stems density or canopy openness or basal area), 2) a model with annual litter production in relation to the log of the explanatory variable (stems density or canopy openness or basal area), 3) model with a log of annual litter production and log of the explanatory variable (stems density or canopy openness or basal area), and finally 4) a model with log annual litter production in relation to an explanatory variable (stems density or canopy openness or basal area). The same was done with the other response variable (aboveground and litter biomass ratio). We considered the best model when its AICc was at least two units lower than the subsequent best model. The relationships were considered significant with $p<0.05$. The models were validated using the relationship between standardized residuals and standardized normal quantiles and, the residuals were tested for deviation from the normal distribution using the Shapiro-Wilk test. All analyzes were performed using the free software R 4.0 (R Development Core Team 2020), using the packages “lme4" and “lmerTest” (Bates et al. 2015, Kuznetsova et al. 2017).

Results

In total, the annual average production of litter was 7.89 Mg/ha^1/y-1. The annual average production of 10-year-old secondary forests differed significantly from the other age classes (6.58± 2.28 Mg/ha^1/y-1; $p <0.05$, Figure 2), showing the lowest values of annual litter production. Whereas 25-year-old secondary forests (7.96 ± 1.93 Mg/

ha^1/y-1), 40-year-old (8.86 ± 2.38 Mg/ha^1/y-1, Figure 2), and mature forest (8.31 ± 1.02 Mg/ha^1/y-1) presented similar annual litter production. The results showed that annual litter production had a strong positive relation with forest age, with a rapid increase in annual litter production early in succession.

Annual litter production represented 20.36% (from 6,63 to 47,8%) of the total standing aboveground biomass in 10-year-old plots. These values decreased significantly with forest development ($p<0.05$), with average of 13.16% (3.92 to 37.28%) in 25-year-old plots, 7.14% (2.77 to 34,17%) in 40-year-old plots and 2,33% in mature forests (1.02 to 4.22%) (Figure 3). The results showed a negative and significant effect of age in the relation of annual litter production and total standing biomass ($p <0.05$) (Figure 3).

In general, our Generalized Linear Models showed a significant influence of vegetation structure on annual litter production (Figure 4). The basal area and stem density significantly and positively influenced annual litter production ($p <0.01$), whereas canopy opening had a negative influence on annual litter production ($p <0.01$; Figure 4). The ratio of annual litter production in relation to total standing aboveground biomass showed a significant association with all forest structure variables. Basal area and stem density significantly and negatively influenced the ratio of annual litter production and total standing aboveground biomass ($p <0.001$) while canopy opening had a positive influence ($p <0.001$; Figure 5).

Discussion

Our results reflect the gradual recovery in aboveground primary productivity during tropical forest succession, which tends to stabilise at around 20 years (Ewel, 1976; Brown & Lugo, 1990). The recovery and stability in litter production between secondary and mature forests were also reported in other studies carried out in tropical forests (Barlow et al. 2007; Ostertag et al 2008). This stability of litter production early in succession (20 and 40 years old) can be effective in restoring ecosystem processes such as litter production and decomposition, which can represent one of the major pathways of nutrient cycling (Camargo et al.2015), essential for maintaining soil fertility in forest ecosystems (Li & Ye 2014, Montagnini & Jordan 2002, Tripathi et al.2006).

In young secondary forests, there is a dominance of pioneer species (Rozendaal & Chazdon 2015; van Breugel et al. 2006). These early successional species generally have the characteristics of being resource acquisitive, presenting less lignified materials with rich N constitution and low C/N ratio (Reich 2014; Hantschet al., 2014). N concentration can have a positive effect on litter mass loss (Cornwell et al.2008; Patoine et al, 2017), because the consumption of N-rich plant material is necessary for detritivores (Eisenhauer et al, 2009; Schwarz et al, 2015). The content of nitrogen and carbon are also commonly used as predictors of decomposition rate (Cornwell et al. 2008; Eichenberg et al. 2014). Pioneer species also have low content of secondary compounds (phenolics and tannins), which can accelerate decomposition process (Parton et al, 2007). What happens in the opposite way to late successional species, with high leaf carbon content, high leaf toughness (Garnier et al.2004, Cortez et al. 2007). Thus, litter quality is expected to change over the course of succession, with high decomposition rates in early successional forests (Garnier et al. 2004).

In our study, we found litter production as an important biomass reservoir. In recently modified forests, annual litter production represents more than 47% of the total standing biomass, demonstrating its importance as a biomass reservoir early in succession. Our data showed that in these forests (10 years old) the vegetation has a more simplified structure, such as areas with lower average DBH, lower basal area and lower density of individuals. In addition, litter has greater representation when compared to total standing aboveground biomass, as well as areas with the largest canopy opening (Figure 5). These areas have a dominance of pioneer species, which have high growth rates, but short longevity (Reich et al. 2008, Rees 2001), making their litter biomass more representative at this stage of succession. Thus, when compared to forests in more advanced stages, younger areas depend much more on litter biomass to maintain various ecosystem services, such as those related to soils, a favorable soil environment, such as maintaining the microclimate, regulating temperature and humidity of soil (Amatangelo et al.2008, Bond-Lamberty & Thomson 2010, Sayer 2006) and ecosystem services related to climate regulation, as an important carbon reservoir (Sayer et al.2007), since the vegetation structure is less developed.

In the final stages of the succession, we found a greater basal area and greater density of individuals, as well as greater canopy closure. Forests in the final stages of succession are more complex ecosystems, with a better developed canopy structure (Werneck et al.2001), in addition to having greater surface area of branches and foliage (Lowman & Schowalter 2012). This more complex vegetation structure is generally associated with the majority of species that have a longer life span (Rees et al.2001), high density of wood, slow growth and thus greater survival (Chave et al.2009, Rees et al. 2001). In this way, even having a more developed structure, with a greater amount of trees, branches and leaves, which could contribute to a greater production of litter, these mature forests contribute in a similar way to secondary forests (20 and 40 years old) for the production of litter, as its species tend to retain plant parts longer than species present in younger areas (Rees et al. 2001). So, the litter contribute less to the storage of biomass, which represents less than 4% of the total biomass, as shown by our results, most of the aboveground biomass is stored in tree trunks, in resource conservative species (Reich 2014, Adler et al.2013). This relation explains that vascular plants change from rapid acquisition of resources to the conservation of resources during the succession (Jackson et al.2013, Poorter & Bongers 2006).

Conclusion

Implications for forest management and climate mitigation

High rates of litter production in secondary forests can represent major contributions to organic matter and nutrients for biogeochemical cycles. In addition to representing an improvement of chemical, physical and biological properties of the soil (León & Osorio 2014, Sánchez-Silva et al.2018). Our results highlight the fundamental role of another ecosystem service provided by litter production, as a carbon reservoir in tropical forests, especially in young secondary forests, just as it has been reported for woody debris by Yang et al (2021), who demonstrated that these woody debris store carbon and delay the release of CO_2 to the atmosphere after tree mortality in Amazon and African forests. In general, our results showed that litter production increases with the development of the forest structure, stabilizing at age 40 and that annual litter production represents an important biomass reservoir in the early stages of succession, reaching 47% of the aboveground biomass.

Our results demonstrated the importance of conserving secondary forests, mainly by the storage of carbon in litter maintaining some ecosystem services. These services can contribute to the regeneration of modified environments, such as the maintenance of soil microclimate and nutrient cycling that are essential for areas in the initial stage of succession (Guendehou et al.2014). This highlights the importance of understanding how litter affects the carbon balance of tropical ecosystems. The flows of these carbon storage components should be considered in future work, further improving our forecasts of regional carbon dynamics in future climate scenarios. The results should also be used in conservation strategies with the quantification of litter as a place for carbon storage, contributing as an ecosystem service and mitigating climate change and REDD +.

Acknowledgements

JISR received a doctoral scholarship from the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001.

Financial support

This work was supported by the Fundo Brasileiro para a Biodiversidade (Funbio) and Humanize Institute (grant number: 111/2019)

Competing interests

The authors declare none.

Ethical statement

None

References

Adler PB, Salguero-Gómez R, Compagnoni A, Hsu JS, Ray-Mukherjee J, Mbeau-Ache C and Franco M (2013) Functional traits explain variation in plant life history strategies. *PNAS* **111***,* 740–745.

Amatangelo KL, Dukes JS, and Field CB (2008) Responses of a California annual grassland to litter manipulation, *Journal of Vegetation Science* **19**, 605–612.

An JY, Han SH, Youn WB, Lee SI, Rahman A, Dao HTT, Seo JM, Aung A, Choi H, Hyun HJ and Park BB (2019) Comparison of litterfall production in three forest types in Jeju Island, South Korea. *Journal of Forestry Research,* pp.1993-0607.

Alves LF, Vieira SA, Scaranello MA, Camargo PB, Santos FAMC, Joly A and Martinelli LA (2010) Forest structure and live aboveground biomass variation along an elevational gradient of tropical Atlantic moist forest (Brazil). *Forest Ecological Management* **260**, 679–691.

Aguiar APD, Vieira ICG, Assis TO, Dalla-Nora EL, Toledo PM, Santos-Junior RAO, Batistella M, Coelho AS, Savaget EK, Aragão REOC, Nobre CA and Ometto JPH (2016) Land use change emission scenarios: anticipating a forest transition process in the Brazilian Amazon. *Global Change Biology* **22,** 1821–1840.

Barlow J, Gardner TA, Ferreira LV and Peres CA (2007) Litter fall and decomposition in primary, secondary and plantation forests in the Brazilian Amazon. *Forest Ecological Management* **247**, 91–97.

Bates D, Maechler M, Bolker B and Walker S (2015) Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* **67**, 1-48.

Berg B and Mcclaugherty C (2014) Plant Litter: Decomposition, Humus Formation, Carbon Sequestration. Berlin Heidelberg: Springer Verlag.

Bond-Lamberty B and Thomson A (2010) Temperature-Associated Increases in the Global Soil Respiration Record. *Nature* **464**(7288):579-82. DOI:10.1038/nature08930

Brown S and Lugo AE (1990) Tropical secondary forests. *Journal of Tropical Ecology*. **6**,1–32.

Cairns MA, Brown S, Helmer EH and Baumgardner GA (1997) Root biomass allocation in the world's upland forests, *Oecologia,* **111**, 1– 11.

Camargo M, Giarrizzo T and Jesus AJS (2015) Effect of seasonal flooding cycle on litterfall production in alluvial rainforest on the middle Xingu River (Amazon basin, Brazil). *Brazilian Journal Biology* **75**, 250–256.

Carrera AL, Bertilier MB and Larreguy C (2008) Leaf litter fall, fine root production, and decomposition in shrub lands with different canopy structure induced by grazing in the Pantagonian Monte, Argentina. *Plant and Soil* **311,**39–50. doi:10.100711104-008-9655-8

Chakravarty S, Rai P, Vineeta V, Pala NA, Shukla G (2019) Litter Production and Decomposition in Tropical Forest

Chave J, David C, Steven J, Simon LL, Nathan GS and Amy EZ (2009) Towards a worldwide wood economics spectrum. *Ecology Letters* **12**, 351–366.

Chave J, Réjou-Méchain M, Búrquez A, Chidumayo E, Colgan MS, Delitti WBC, Duque A, Eid T, Fearnside PM, Goodman MHRC, Martínez-Yrízar A, Mugasha WA, Muller-Landau HC, Mencuccini M, Nelson BW, Ngomanda A, Nogueira EM, Ortiz-Malavassi E, Pélissier R, Ploton P, Ryan CM, Saldarriaga JG, Vieilledent G (2014) Improved pantropical allometric models to estimate the aboveground biomass of tropical forests. *Glob Change Biol.* **72,**763–768 doi:10.1111/gcb.12629

Cornwell WK, Cornelissen JHC, Amatangelo K, Dorrepaal E, Eviner VT, Godoy O, Hobbie SE, Hoorens B, Kurokawa H, Pérez-Harguindeguy N, Quested HM, Santiago LS, Wardle DA, Wright IJ, Aerts R, Allison SD, Van Bodegom P, Brovkin V, Chatain A, Callaghan TV, Díaz S, Garnier E, Gurvich DE, Kazakou E, Klein JA, Read J, Reich PB, Soudzilovskaia NA, Vaieretti MV and Westoby M (2008) Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters* **11**:1065–1071. http://dxdoi.org/10.1111/j.1461-0248.2008.01219.x.

Cortez J, Garnier, E, Pérez-Harguindeguy N, Debussche M and Gillon D (2007) Plant traits, litter quality and decomposition in a Mediterranean old-fi eld succession. – *Plant Soil* **296**:19 – 34.

Craven D, Hall JS, Berlyn GP, Ashton MS and van Breugel M (2015) Changing gears during succession: shifting functional strategies in young tropical secondary forests. *Oecologia* **179**,293-305

Devi AF and Garkoti SC (2013) Variation in evergreen and deciduous species leaf phenology in Assam, India. *Trees* **27,**985–997. https://doi.org/10.1007/s00468-013-0850-8

Eichenberg, D. et al. 2014. Shifts in community leaf functional traits are related to litter decomposition along a secondary forest succession series in subtropical China. *Journal Plant Ecology* **8**: 401 – 410

Eisenhauer N, Milcu A, Sabais ACW, Bessler H, Weigelt A, Engels C and Scheu S (2009) Plant community impacts on the structure of earthworm communities depend on season and change with time. *Soil Biol. Biochem*. **41**: 2430–2443. http://dx.doi. org/10.1016/j.soilbio.2009.09.001.

Ewel JJ (1976) Litter fall and leaf decomposition in a tropical forest succession in eastern Guatemala. *Journal of Ecology* **64** (1): 293−308.

Facelli JM and Pickett STA (1991) Plant Litter: Its Dynamics and Effects on Plant Community Structure. *The Botanical Review* **57,** 1-32.

Garnier E, Cortez J, Billes G, Navas M, Roumet C, Debussche M, Laurent G, Blanchard A, Aubry D, Bellmann A, Neill C and Toussaint J (2004) Plant functional markers capture ecosystem properties during secondary succession. *Ecology* **85**: 2630 – 2637.

Guendehou GHS, Liski J, Tuomi M, Moudachirou M, Sinsin B, and Makipaa, R (2014) Decomposition and changes in chemical composition of leaf litter of five dominant tree species in a West African tropical forest. *Tropical Ecology* **55**,207–220

Houghton RA, Hall F and Goetz, SJ (2009) Importance of biomass in the global carbon cycle. *Journal of Geophysical Research* 114.

Jackson BG, Peltzer D A & Wardle DA (2013) Are functional traits and litter decomposability coordinated across leaves, twigs and wood? A test using temperate rainforest tree species. *Oikos* **122**,1131–1142.

Kuruvilla T, Jijeesh CM and Seethalakshm KK (2016) Litter production and decomposition dynamics of a rare and endemic bamboo species Munrochloa ritcheyi of Western Ghats, India. *Tropical Ecology* **57**, 601-606.

Kuznetsova A, Brockhoff PB, Christensen RHB (2017). “lmerTest Package:Tests in Linear Mixed Effects Models. *Journal of Statistical Software* **82**, 1-26.

Kunhamu TK, Kumar BM and Viswanath S (2009) Does thinning affect litterfall, litterdecomposition, and associated nutrient release in *Acacia mangiumstands* of Kerala inpeninsular India? *Canadian Journal Forest Research* **39**(4):792-801

Krishna MP and Mohan H (2017) Litter decomposition in forest ecosystems: A review. Energy. *Ecology & Environment* **2**,236–249.

León JD and Osorio NW (2014) Role of Litter Turnover in Soil Quality in Tropical Degraded Lands of Colombia. *The Scientific World Journal,* **2014**:11 pages. https://doi.org/10.1155/2014/693981

Li Y and Ye Y (2014) Dynamics of decomposition and nutrient release of leaf litter in *Kandelia obovata* mangrove forests with different ages in Jiulongjiang Estuary, China. *Ecological Engineering* **73**,454–460. doi:10.1016/j.ecoleng.2014.09.102

Lowman MD and Schowalter TD (2012) Plant science in forest canopies – the first 30 years of advances and challenges (1980–2010). New Phytologist. 194: 12–27 doi: 10.1111/j.1469-8137.2012.04076.x

Majila BS, Joshi GC and Kala CP (2005) Patterns in litter fall and litter decomposition along an altitudinal gradient in the Binsar Wildlife Sanctuary, Central Himalaya. *The International Journal of Sustainable Development & World Ecology* **12**, 205-212.

Montagnini F and Jordan CF (2002) Reciclagem de nutrientes. In Guariguata MR and Kattan GH (ed.), *Ecología y conservación de bosques neotropicales*. Cartago: Libro Universitario Regional, pp.167-191.

Nickmans H, Jonarda M, Verheyen J and Ponette Q (2019) Modelling leaf dispersal and nutrient return in tree species mixtures. *Forest Ecology and Management* **436**, 68–78.

Ostertag R, Marın-Spiotta E, Silver WL, and Schulten J (2008) Litterfall and Decomposition in Relation to Soil Carbon Pools Along a Secondary Forest Chronosequence in Puerto Rico. *Ecosystems* 11: 701–714

Pan Y, Birdsey RA, Fang J, Houghton R, Kauppi PE, et al. 2011. A large and persistent carbon sink in the world's forests. *Science* 333:988–93

Pandey RR, Sharma G, Tripathi SK and Singh AK (2007) Litterfall, litter decomposition and nutrient dynamics in a subtropical natural oak forest and managed plantation in northeastern India. *Forest Ecology Management* **240**,96–104.

Patoine G, Thakur MP, Friese J, Nock C, Hönig L, Haase J, Scherer-Lorenzen M, Eisenhauer N (2017) Plant litter functional diversity effects on litter mass loss depend on the macro-detritivore Community. *Pedobiologia - Journal of Soil Ecology* **65**:29–42

Parton W, Silver WL, Burke IC et al. (2007) Global-scale similarities in nitrogen release patterns during long-term decomposition. *Science* **315**,361–4

Piotto D, Montagnini F, Thomas W, Ashton M and Oliver C (2009) Forest recovery after swidden cultivation across a 40-year chronosequence in the Atlantic forest of southern Bahia, Brazil. *Plant Ecology* **205**,261-272.

Poggiani F (2012) Ciclagem de nutrientes em florestas do Brasil. In Martins SV (ed.), *Ecologia de Florestas Tropicais do Brasil*. Viçosa: Editora UFV, pp. 175-251.

Poorter L and Bongers F (2006) Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology* **87**, 1733– 1743.

Rawat N, Nautiyal BP and Nautiyal MC (2010) Litter decomposition rate and nutrient release from different litter forms in a Himalayan alpine ecosystem. *The Environmentalist* **30**, 279–288. doi:10.100710669-010-9275-8

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rees M, Condit R, Crawley M, Pacala S and Tilman D (2001) Long-Term Studies of Vegetation Dynamics. *Science* 293- 600.

Reich PB, Tjoelker MG, Pregitzer KS, Wright IJ, Oleksyn J and Machado JL (2008) Scaling of respiration to nitrogen in leaves, stems, and roots of higher land plants. *Ecology Letters* **11**, 793–801.

Reich PB (2014) The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. *Journal of Ecology* **102**, 275–301.

Rozendaal DMA and Chazdon RL (2015) Demographic drivers of tree biomass change during secondary succession in northeastern Costa Rica. *Ecological Society of America* **25**, 506-516.

Sánchez-Silva S, De Jong BHJ, Aryal DR, Huerta-Lwanga E and Mendoza-Vega J (2018) Trends in leaf traits, litter dynamics and associated nutrient cycling along a secondary successional chronosequence of semi-evergreen tropical forest in South-Eastern Mexico. *Journal of Tropical Ecology* **34**,364–377. doi:10.1017/S0266467418000366

Santos FM, Terra G, Chaer GM, Monte MA (2018) **Modeling the height–diameter relationship and volume of young African mahoganies established in successional agroforestry systems in northeastern Brazil.** New For, 10.1007/s11056-018-9665-1

Sayer EJ (2006) Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems, *Biology Review* **81**, 1–31.

Sayer EJ, Powers JS, and Tanner EVJ (2007) Increased litterfall in tropical forests boosts the transfer of soil CO2 to the atmosphere, *PLoS ONE* 2,10.

Schwarz B, Dietrich C, Cesarz S, Scherer-Lorenzen M, Auge H, Schulz E and Eisenhauer N (2015) Non-significant tree diversity but significant identity effects on earthworm communities in three tree diversity experiments. *Eur. J. Soil Biol.* **67:**17–26. http://dx.doi.org/10.1016/j.ejsobi.2015.01.001.

Schumacher MV, Truby P, Marafiga JM, Viera M and Szymczak DA (2011) Espécies predominantes na deposição de serapilheira em fragmento de floresta estacional decidual no Rio Grande do Sul. *Ciência Florestal* **21**, 479–486.

Silver WL, Hall SJ and González G (2014) Differential effects of canopy trimming and litter deposition on litterfall and nutrient dynamics in a wet subtropical forest. Forest *Ecology Management* **332**, 47–55.

Thomas WW (2003) Natural vegetation types in southern Bahia. In: Prado P.I., Landau E.C., Moura R.T., Pinto L.P.S., Fonseca G.A.B., Alger K. (orgs.) *Corredor de Biodiversidade da Mata Atlântica do Sul da Bahia*. Publicação em CD-ROM, Ilhéus, IESB / CI / CABS / UFMG / UNICAMP.

Tripathi SK, Sumida A, Shibata H, Ono K, Uemura S, Kodama Y and Hara T (2006) Leaf litterfall and decomposition of different above- and belowground parts of birch (Betula ermanii) trees and dwarf bamboo (Sasa kurilensis) shrubs in a young secondary forest in Northern Japan. *Biology and Fertility of Soils* **43,**237–246

U.S.D.O.E. (2010) Climate Research Roadmap Workshop: Summary Report. U.S. Department of Energy Office of Science.

van Breugel M, Martınez-Ramos M, and Bongers F (2006) Community dynamics during early secondary succession in Mexican tropical rain forests. *Journal of Tropical Ecology* **22**:663–674

Vidal MM, Pivello VR, Meirelles ST and Metzger JP (2007) Produção de serapilheira em floresta Atlântica secundária numa paisagem fragmentada (Ibiúna, SP): importância da borda e tamanho dos fragmentos. *Revista Brasileira de Botânica* **30**,521-532.

Vitousek PM (1984) Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology* **65**, 285–298.

Vitousek P and Sanford RL (1986) Nutrient cycling in moist tropical forest. *Annual Review of Ecology and Systematics* **17**, 137–167.

Zanne AE, Lopez-Gonzalez G, Coomes DA, Ilic J, Jansen S, Lewis SL, Miller RB, Swenson NG, Wiemann MC and Chave J (2009. Global wood density database. Dryad. Identifier: http://hdl.handle.net/10255/dryad.235.

Zhou G, Guan L, Wei X, Zhang D, Zhang Q, Yan J, Wen D, Liu D, Liu S, Huang Z, Kong G, Mo J and Yu Q (2007) Litterfall production along successional and altitudinal gradients of subtropical monsoon evergreen broadleaved forests in Guangdong, China. *Plant Ecology* **188**,77–89.

Zhou G, Shan Xu, Ciais P, Manzoni S, Fang J, Yu G, Tang X, Zhou P, Wang W, Yan J, Wang G, Ma K, Li S, Du S, Han S, Ma Y, Zhang D, Liu J, Liu S, Chu G, Zhang Q, Li Y, Huang W, Ren H, Lu X and Chen X (2019) Climate and litter C/N ratio constrain soil organic carbon accumulation. *National Science Review* **6**: 746–757.

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed Effects Models and Extensions in Ecology with R. Statistics for Biology and Health, New York

Yang H, Ciais P, Chave J, Huang Y, Ballantyne AP, Yu K, Berzaghi F and Wigneron JP (2021) Coarse woody debris are buffering mortality-induced carbon losses to the atmosphere in tropical forests. *Environ. Res. Lett.* **16**.

Wardle DA, Bardgett RD, Klironomos JN, Setalã H, van der Putten WH, Wall DH (2004) Ecological Linkages Between Aboveground and Belowground Biota. Science 304.

Werneck MS, Pedralli G, Gieseke LF (2001) Produção de serapilheira em três trechos de uma floresta semidecidual com diferentes graus de perturbação na Estação Ecológica de Tripuí, Ouro Preto, MG. *Revista Brasileira de Botânica.* **24**: 195-198.

Table 1. Structural features of vegetation present at sites of different ages along the succession, at the ages of 10, 25 and 40 years and mature forests, in the Serra do Conduru State Park, Bahia, Brazil. Mean ± SD.

Figure 1. Location map of the Serra do Conduru State Park, with location of the study plots, Bahia, Brazil.

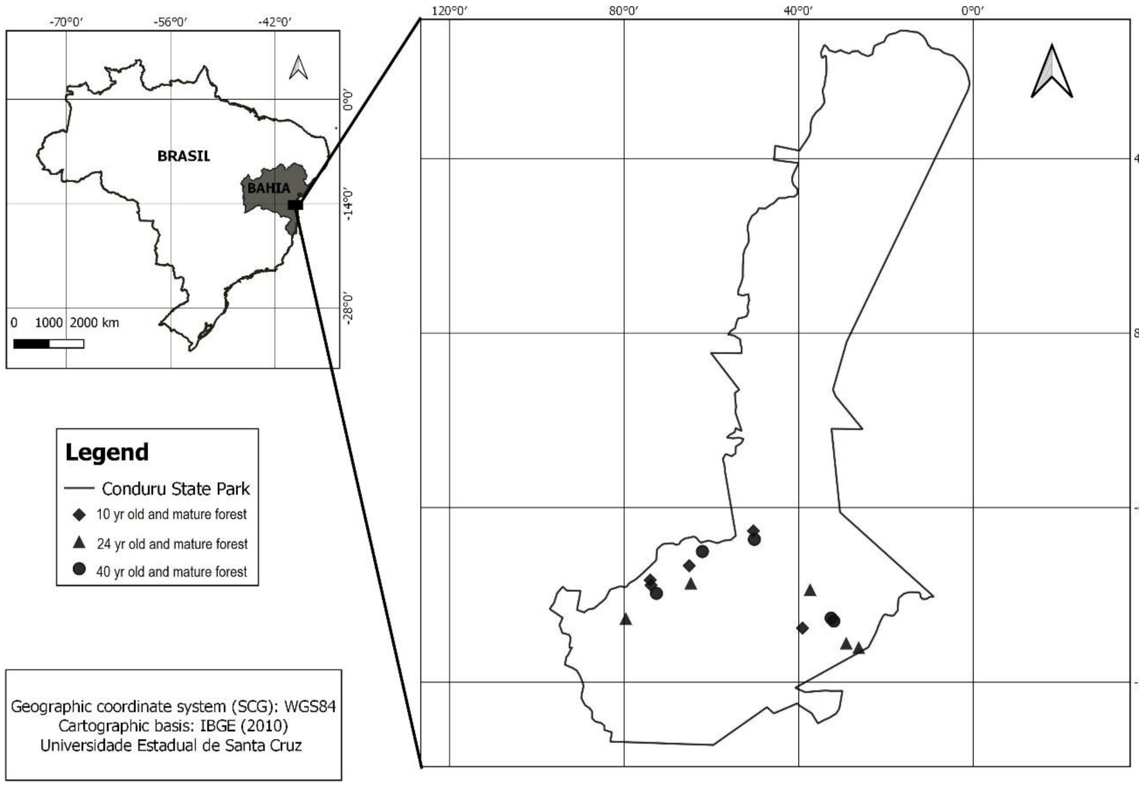
Figure 2. Annual litter biomass production in Mg/ha^1/y-1along succession, at the ages of 10, 25 and 40 years and mature forests, in the Serra do Conduru State Park, Bahia, Brazil.

Figure 3. Relation between annual litter production and the total aboveground biomass at the ages of 10, 25, 40 years and mature forest, in the Serra do Conduru State Park, Bahia, Brazil.

Figure 4. Relations between annual litter production and structural variables: (a) stems (number/ha), (b) basal area (m^2/ha) and (c) percentage of canopy opening.

Figure 5. Relations between the ratio of annual litter production and total standing aboveground biomass and structural variables: (a) stems (number/ha), (b) basal area (m^2/ha) and (c) percentage of canopy open.

Parameters	Ages along succession			
	10 -years-old	25 -years-old	40 -years-old	Mature Forest
Aboveground biomass (Mg/ha)	41.13 ±22.55	80.77 ± 48.75	159.67± 70.93	391.65 ± 138.7
Basal area (m^2/ha)	10.91 ± 4.52	18.15 ± 8.14	28.32 ± 8.76	42.1 ± 11.96
Density (number/ha)	1810 ± 728.16	2096 ± 681.29	2990 ± 755.53	3040 ± 394.36
Canopy openness (%)	20.28 ± 8.6	16.57 ± 3.25	13.61 ± 3.21	13 ± 1.86


-70°0′
-56°0′
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BRASIL
BAHIA
0 1000 2000 km
Legend
Conduru State Park
◆ 10 yr old and mature forest
▲ 24 yr old and mature forest
● 40 yr old and mature forest
Geographic coordinate system (SCG): WGS84
Cartographic basis: IBGE (2010)
Universidade Estadual de Santa Cruz
120°0′
80°0′
40°0′
0°0′
40°0′
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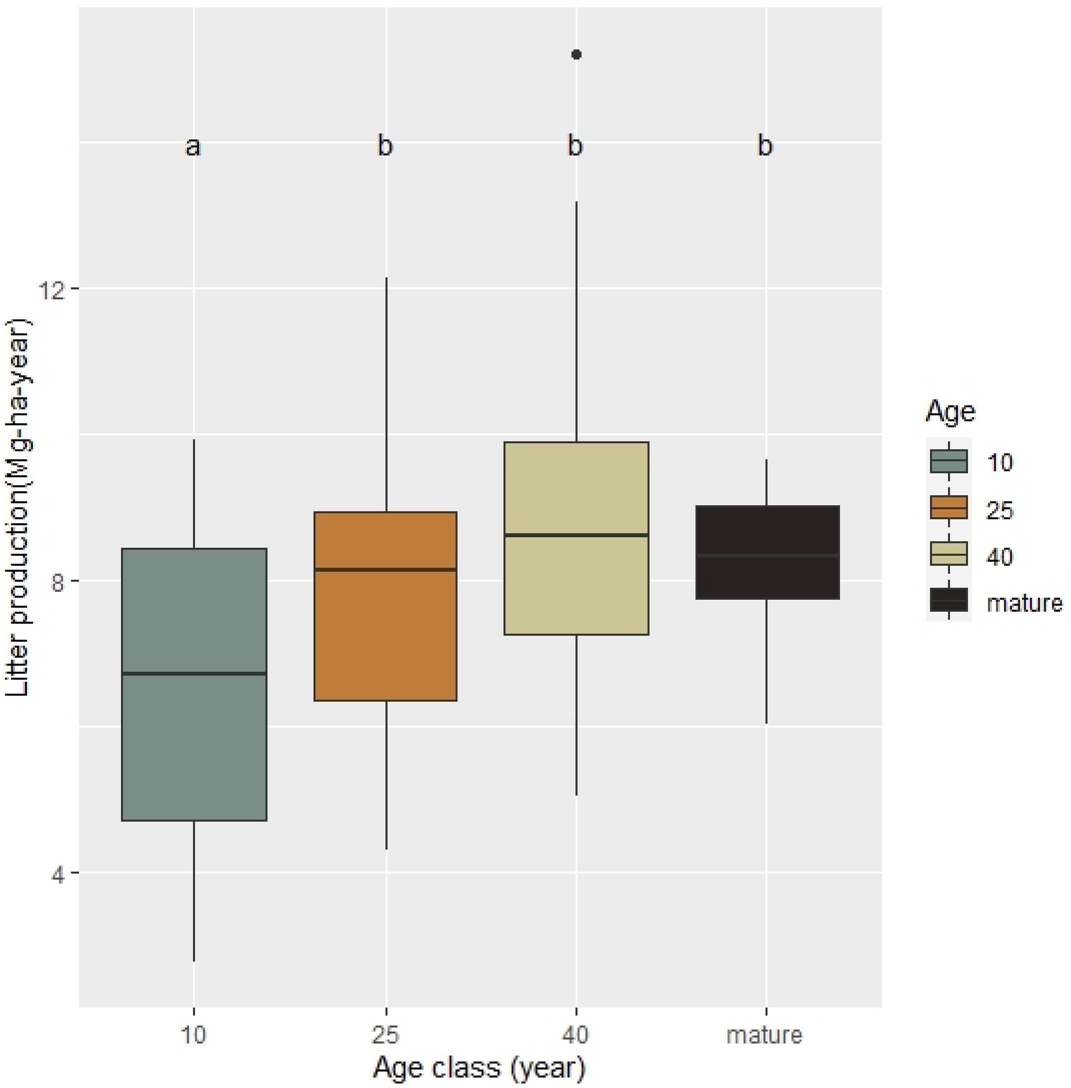
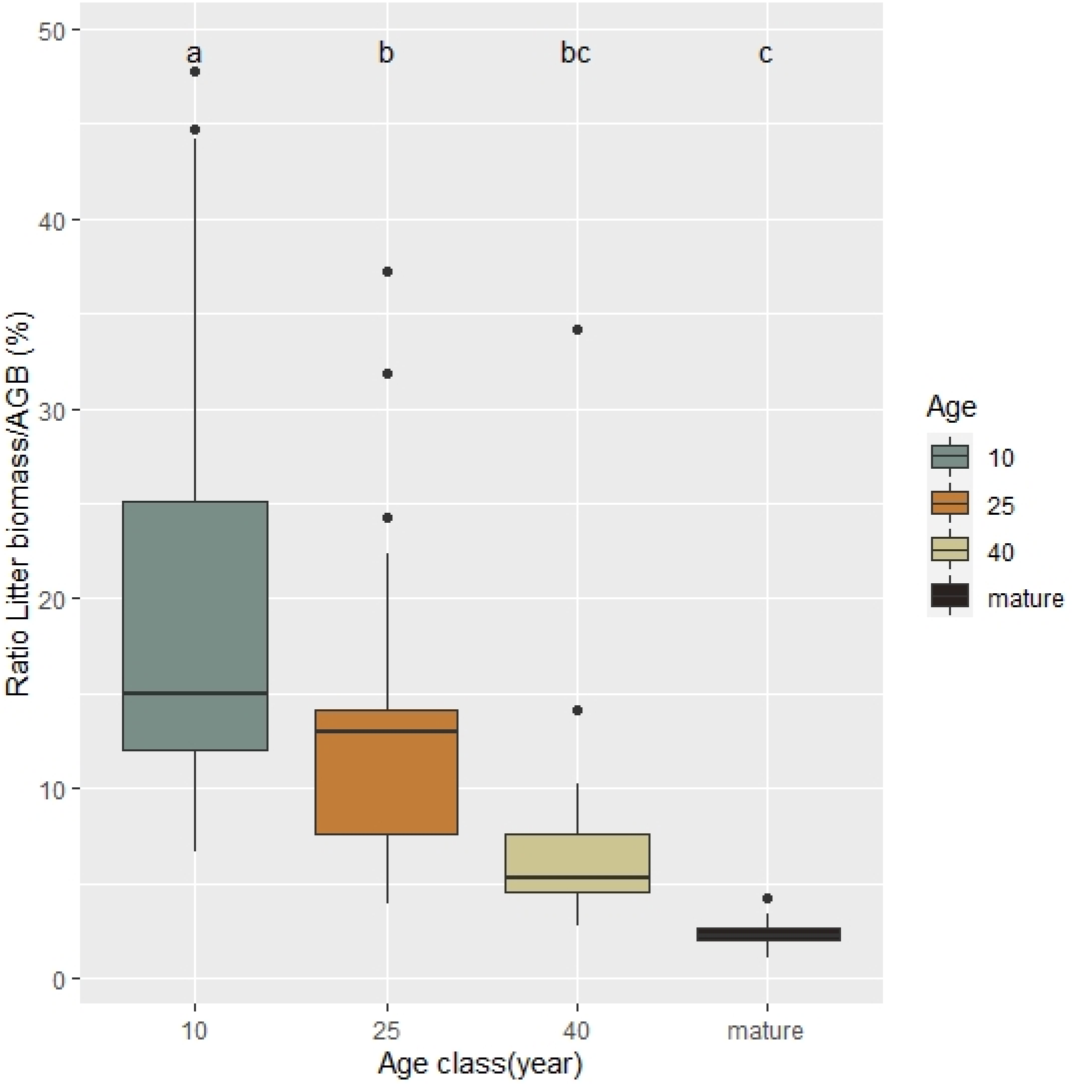
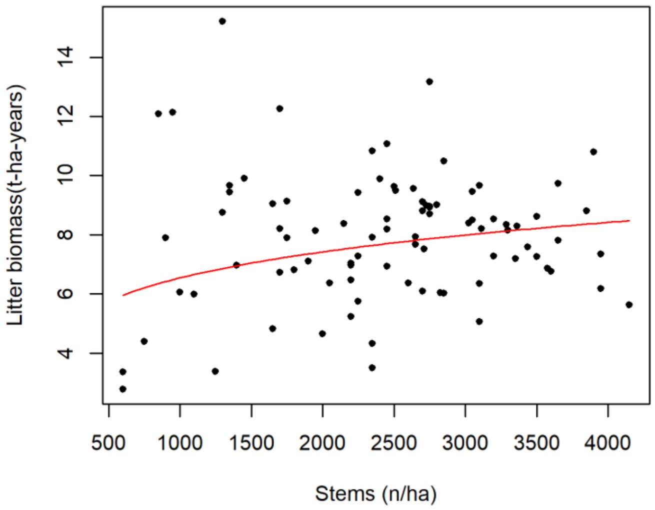
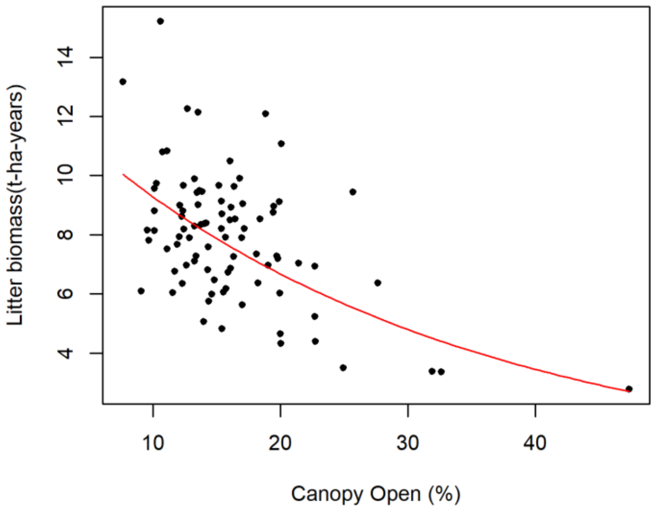
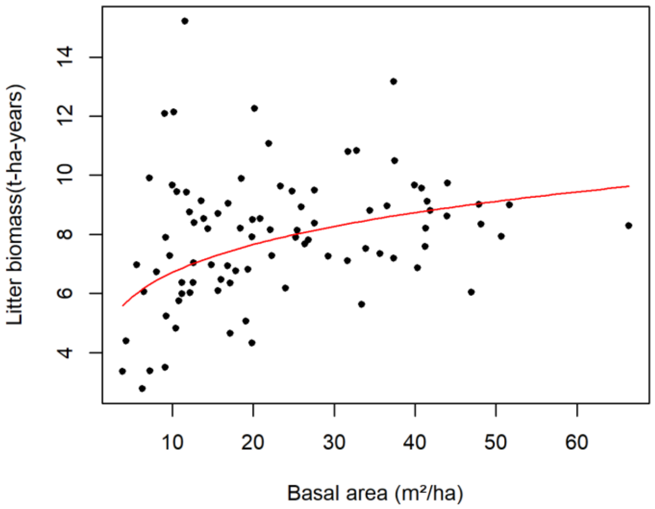
-60°0′
-20°0′

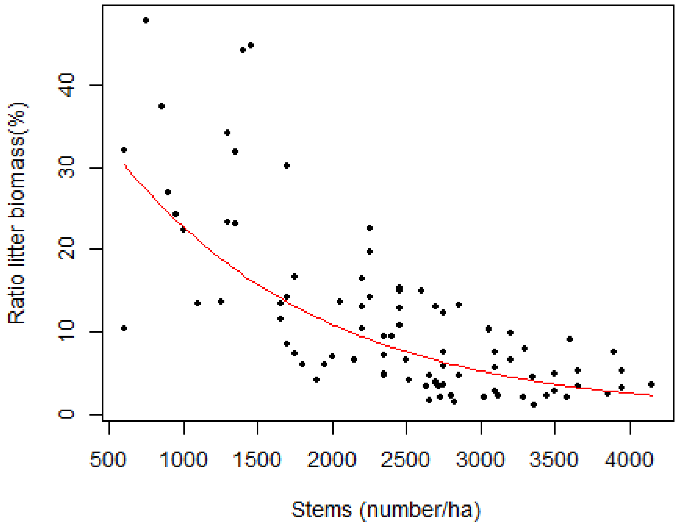

a
b
b
b
12
8
4
Litter production(Mg-ha-year)
10
25
40
mature
Age class (year)
Age
10
25
40
mature

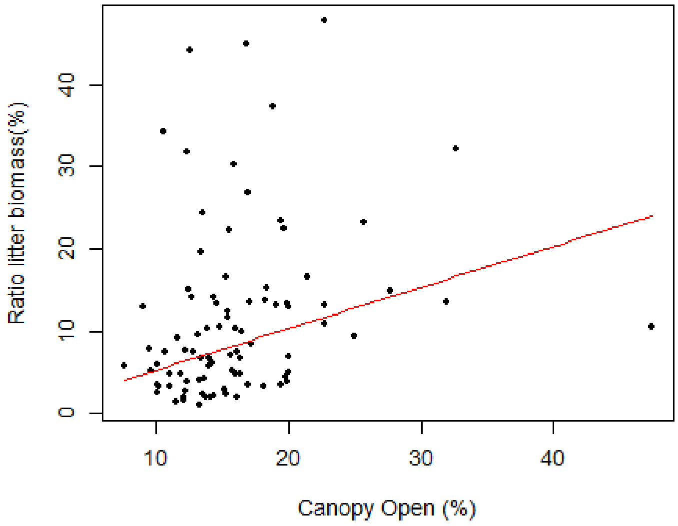

a
b
bc
c
50
40
30
20
10
0
Ratio Litter biomass/AGB (%)
10
25
40
mature
Age class(year)
Age
10
25
40
mature

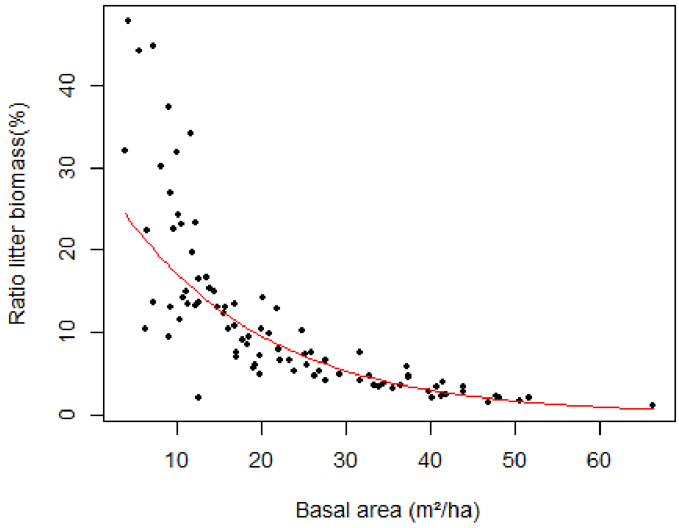

Litter biomass(t-ha-years)
4
6
8
10
12
14
500
1000
1500
2000
2500
3000
3500
4000
Stems (n/ha)


Litter biomass(t-ha-years)
4
6
8
10
12
14
10
20
30
40
Canopy Open (%)


Litter biomass(t-ha-years)
4
6
8
10
12
14
10
20
30
40
50
60
Basal area (m²/ha)


Ratio litter biomass(%)
0
10
20
30
40
500
1000
1500
2000
2500
3000
3500
4000
Stems (number/ha)


Ratio litter biomass(%)
0
10
20
30
40
10
20
30
40
Canopy Open (%)


Ratio litter biomass(%)
0
10
20
30
40
10
20
30
40
50
60
Basal area (m²/ha)

CAPITULO III

Aboveground biomass variation in working landscapes of southern Bahia, Brazil

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Manuscrito submetido a revista Environmental Conservation.

Abstract

Native tropical forests have been increasingly modified in different land uses. Many of these lands have regrown into secondary forests and agroforestry systems. In this study, we investigate how different forest covers in a working landscape contribute to aboveground biomass in the southern region of Bahia, Brazil. We used Generalized Linear Models (GLM) to compare aboveground biomass in different forest covers, as follows: secondary forests of 10, 25 and 40 years old, mature forests and two different agroforestry systems (AFS): ‘cabruca’ and ‘conventional’. Our results showed that mature forests store the highest amount of biomass compared to other forest cover, followed by advanced stage secondary forests (40 years-old), AFS cabruca and AFS conventional. The lowest biomass was found in early-stage secondary forests (10 and 25 years-old). We emphasize here the importance of mature forests for carbon storage, in addition to maintaining various ecosystem services. Furthermore, we stress the importance of working landscapes that include agroforestry systems and secondary forests, as they provide timber and non-timber products, reduce the pressure on native forest resources, and contribute to the provision of ecosystem services such as carbon storage.

Keywords: carbon, tropical forest, secondary forests, agroforestry system, cabruca

Statements and Declarations

Acknowledgements

JISR received a doctoral scholarship from the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001. We thank the Fundo Brasileiro para a Biodiversidade (Funbio) and Humanize Institute (grant number: 111/2019), for funding this work.

Introduction

Tropical forests are of high importance to biodiversity (Reilly and Spies 2015; Barlow et al. 2018) and for carbon storage (Pan et al. 2011). In these forests, about 80% of the carbon is stored above ground (Pan et al. 2013). However, the conversion of tropical forests into agricultural land and other types of land uses is one of the main causes of biodiversity loss and reduction of ecosystem services provided by forests (Geist and Lambin 2002). Today, about 80% of tropical forests are considered to have some degree of modification, or impacted by management practices in agriculture, forestry and other human activities (Potapov et al. 2017), including degraded primary forests and regenerating secondary forests (Chazdon et al. 2009a).

These modified, secondary tropical forests are expanding in many deforested areas of the Neotropics (Chazdon 2014) and currently account for about half of the world's tropical forests (FAO 2020). The natural regeneration in these secondary forests is considered an effective mechanism for carbon sequestration (Houghton et al. 2015; Canadell and Raupach 2008). For this reason, these forests represent an important component of biodiversity, and the accumulation of biomass in them represents a sink for anthropogenic carbon emissions (Silver et al. 2000; Feldpausch et al. 2005; Chazdon, 2014; 2016; Matos et al. 2020). Despite the differences between secondary and mature forests in terms of structure and floristic composition (Chazdon et al 2009b), it has been shown that they can provide important ecosystem services, such as refuges for biodiversity in a fragmented landscape. (Chazdon 2003), sources of timber and non-timber forest products (Britto et al. 2019; Fantini et al. 2019) and carbon sequestration (Grace 2004; Feldpausch et al. 2005).

Among the different types of forest cover, agroforestry systems (AFS) are becoming more relevant, especially with the recognition of their multiple uses for rural development and ecosystem services (Montagnini 2017). AFS can favor associated crops, providing shade, thermal comfort, nutrient cycling and other services aimed at the productivity of agricultural crops (Ashton and Montagnini 2000). In addition, to traditional AFSs, cocoa agroforests represent a more complex type of AFS, which combine cocoa planting (*Theobroma cacao* L.) shading of forests after understory removal, along with a great diversity of native and planted trees (Rice and Greenberg 2000). In this way, AFS can contribute, for example, to the connectivity of fragmented landscapes (Jose and Gordon 2008; Nair and Garrity 2012), for the conservation of biodiversity, and adaptation to climate change through the fixation of atmospheric carbon (FAO 2012; Montagnini 2015), and a viable alternative for Programs REDD + (Reduction of Emissions from Deforestation and Degradation) (Van Noordwijk et al. 2015).

Working on landscape conservation becomes essential in the mosaic of existing landscapes around the world, which takes into account the importance of managing agricultural lands to complement the conservation of species, maintaining biodiversity, providing ecosystem services in addition to contributing to the increase of production of food, fuel and forest products (Kremer and Merenlender 2018). A study of working landscapes carried out in Costa Rica, in the San-Juan-La Selva Biological Corridor, found that deforestation was contained and increased incentives for forest regeneration (Morse et al. 2009). In another study carried out in southern Brazil with silvopastoral grazing, the results showed that small producers doubled food production and income without increasing the planted area and without affecting protected areas (Alves et al. 2012). The southern region of Bahia has an extensive mosaic of primary and secondary forests (Project MapBiomas 2021), and extensive areas of shaded cocoa (cabrucas), with approximately 430,051 ha of cocoa planted (IBGE/SIDRA 2019). This landscape represents an important working landscape in Brazil, as these areas of AFS are important carbon reservoirs and provide products, ecosystem services, and better livelihoods, especially for poor people (Schroth et al. 2015).

In the light of a rapidly increase in deforestation and land use change in tropical regions in the past decades and their effect on global climate change (Geist and Lambin 2002), several initiatives have been launched to promote forest restoration and the integration of production and conservation within the same landscapes (working landscapes) (UN Restoration Decade/2021; ITTO 2020). In southern Bahia, conversion of natural forests and high-diverse AFS to other land uses such as pastures and agriculture has increased in the past decade (Project MapBiomas 2021). In this regard, understand the potential of different forest production systems and areas of natural forests to sequester and store carbon is pivotal to the management these landscapes for conservation purposes (Vandermeer and Perfecto 2007), as well as to develop mechanisms of payment for environmental services to reduce deforestation trends in the region. Here we aimed to quantify the contribution of different forest cover, including secondary forests in different stages of succession (10, 25 e 40 years old), AFS conventional, AFS cabruca and mature forests, for aboveground biomass stocks in the southern region of Bahia, Brazil. We also compared the number of individuals between the different types of forest cover, and how the aboveground biomass and the number of individuals differ within DBH size classes in order to highlight the role of this working landscape in mitigating climate change.

Material and methods

Study location

The present study was carried out in different forest covers located in southern Bahia, Brazil. This region has one of the highest values of plant species richness per unit of land area and a high degree of endemism of plants globally (Thomas et al. 1998; Amorim et al. 2005; Martini et al. 2007) and animals (Tabarelli et al. 2010). The vegetation is of the dense ombrophilous type, in the Atlantic Forest biome (Thomas 2003), with monthly average temperature of 24°C and average annual rainfall of 2,000 mm, evenly distributed throughout the year (Alvares et al. 2013).

Data collection was carried out in the following types of forest cover: a) secondary forests of 10, 25 and 40 years, located within a protected area (14º 30’16” S e 39º 6’36” W; Figure 1) in the Parque Estadual da Serra do Conduru – PESC, in the city of Uruçuca. The protected area has an area of 10,000 ha and is composed of a forest mosaic in different stages of regeneration, with secondary forests at different ages, some areas in the beginning of regeneration to well preserved areas. (Piotto et al. 2009); b) agroforestry systems were inventoried, being one AFS of the type “cabruca” and the other AFS, with planted tree species, in the city of Ilhéus. The evaluated AFS is located in an experimental area of the Centro de Pesquisas do Cacau (CEPEC) (14º 45’ S e 39° 13’ W; Figure 1). The AFS was planted in 2005, where three timber forest species used were *Cordia alliodora* (claraíba), *Tectona grandis* (teca), and *Swietenia macrophylla* (mogno-brasileiro). The three species are known for their high timber value and great silvicultural potential (Ugalde 2013, Piotto et al. 2020). The AFS cabruca is an area where the cacao tree was planted under the shade of native tree species present in the original natural forest.

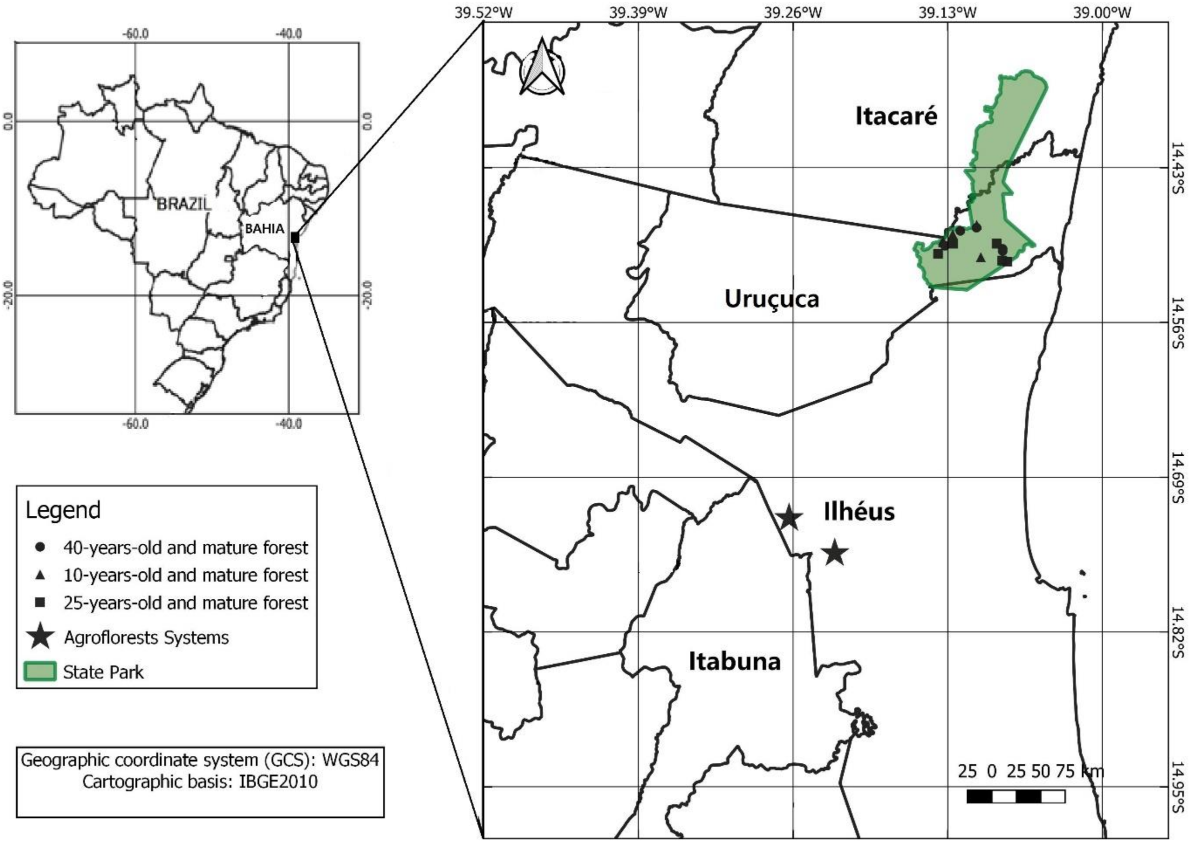

Fig. 1 Location map with location of the study plots, Bahia, Brazil

Data collect

For this study, we used data from inventories carried out in naturally regenerated secondary forests with 10, 25 and 40 years old mature forests and two types of agroforestry systems. In order to obtain data on forest structure in secondary forests, 15 plots of 10×100 (1,000m²) in five plots for each of the three age classes (10, 25- and 40-year-old) respectively. For mature forests, 15 plots of 20×30 (600m²). In the AFS conventional areas, three areas with 0.5ha each were evaluated and the AFS cabruca were evaluated four areas with different sizes 4,7, 4,2, 2,8 e 2,6 ha.

Within the plots, all trees with diameter at breast height were measured (DBH) equal to or above 5 cm, the total height (m), and identified at the species level, and a collection of botanical material was collected for later identification in the Herbarium André Maurício Vieira de Carvalho, Centro de Pesquisas do Cacau (CEPEC). We estimated aboveground biomass using an allometric equation for tropical forests (Chave et al. 2014):

$AGB= 0.0673\ (\rho D^2H)^{0.976}$

based on diameter D (cm), height H (m) and wood density ρ (g/cm³). The AGB was estimated in kilograms. Plot biomass represents the estimated biomass of all trees in a plot, which was then extrapolated to estimate aboveground biomass (AGB) in Mg per ha. Additionally, we calculated for the forest structure, the tree density (individuals/ha) and basal area (m²/ha). And we evaluated the differences in forest cover by grouping individuals into three classes DBH: 5 <15 cm, 15 <30 cm e ≥ 30 cm.

Statistical analysis

We fit different models to assess the effect of forest cover type on aboveground biomass and basal area. As the forest structure data was considered non-normal, we used Generalized Linear Models (GLM). For each response variable (aboveground biomass and basal area) we fit four models for the explanatory variable, type forest cover (secondary forests 10, 25 and 40 years old, mature forest, two types of agroforestry systems): 1) a model with aboveground biomass as the response variable in relation to an explanatory variable, 2) a model with aboveground biomass in relation to the log of the explanatory variable, 3) model with a log of aboveground biomass and log of the explanatory variable, and finally 4) a model with log aboveground biomass in relation to an explanatory variable. The same was done with the other response variable (basal area). We considered the best model when its AICc was at least two units lower than the subsequent best model. The relationships were considered significant with $p<0.05$. The models were validated using the relationship between standardized residuals and standardized normal quantiles and, the residuals were tested for deviation from the normal distribution using the Shapiro-Wilk test. To evaluate the relationship between the different DBH size classes, in relation to individual density and aboveground biomass within the classes, we fitted a linear mixed model (LMM), including the location as a random factor. We use the LMM approach to control temporal pseudo-replication (Zuur et al.2009). All analyzes were performed using the free software R 4.0 (R Development Core Team 2020), using the packages “lme4" and “lmerTest” (Bates et al. 2015, Kuznetsova et al. 2017).

Results

Aboveground biomass ranged from 38.8 a 391.75 Mg/ha among forest covers. Aboveground biomass increased in this order: 10-year secondary forests (38.80 Mg/ha), 25-year secondary forests (80.76 Mg/ha), AFS conventional (86.34 Mg/ha), AFS cabruca (106.07 Mg/ha), 40-year secondary forests (159.67 Mg/ha), and mature forests, with the highest accumulated biomass (391.65 Mg/ha), significantly differing from other forest covers ($p<0.001$).

Table 1. Means and standard deviation of density of individuals, aboveground biomass, and basal area of secondary forests (10, 25 and 40 years-old), agroforestry systems (AFS) and mature forest in southern Bahia, Brazil. Means that share the same letter are not different at the $P<0.001$ level.

Forest Cover	Density of individuals (number/ha)	Aboveground biomass (Mg/ha)	Basal area (m²/ha)
Secondary forest 10-years-old (n=5)	2092 ± 550 **a**	38.80 ± 7.95 **a**	11.71 ± 1.91 **a**
Secondary 25-years-old (n=5)	2402 ± 692 **ab**	80.76 ± 28.36 **b**	20.26 ± 4.78 **ab**
Secondary 40-years-old (n=5)	3180± 503 **bd**	159.67 ± 35.57 **b**	30.05 ± 4.12 **bc**
AFS Cabruca (n=4)	129 ± 118 **c**	106.07 ± 44.91 **b**	12.52 ± 2.16 **c**
AFS conventional (n=3)	74 ± 13 **c**	86.34 ± 22.2 **b**	8.74 ± 1.85 **a**
Mature Forest (n=15)	3372 ± 553 **d**	391.65 ± 138.7 **c**	53.92 ± 12.43 **a**

The density of trees varied among forest covers from 74 to 3,372 ind./ha, with an average of 2,424 ind/ha (±1323 ind/ha). The density of trees was statistically higher in mature forests compared to other forest covers, and lower in AFS and AFS cabruca, statistically smaller than that of other forest covers. The basal area ranged from 11.71 to 53.92 m²/ha, with higher values in mature forests, followed by 40-year secondary forests, which presented higher basal area values when compared to 25-year secondary forests, but not differing significantly from each other. The AFS conventional had the smallest basal area, which was statistically similar to 10-year secondary forests and AFS cabruca.

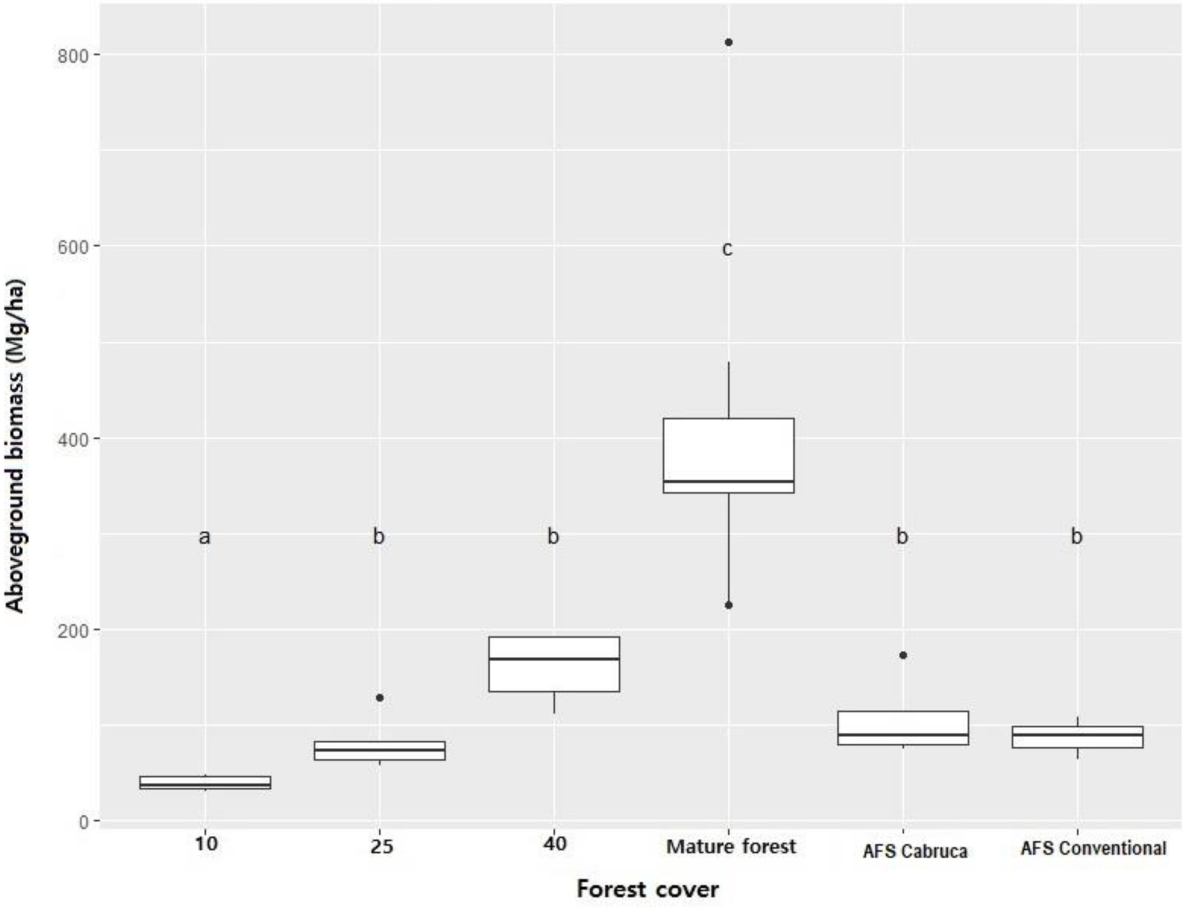

Fig. 2 Aboveground biomass in Mg/ha of secondary forests (10, 25 and 40 years-old), agroforestry systems (AFS) and mature forest in southern Bahia, Brazil.

Tree density differed between the types of forest cover for the DBH classes. In the 10-year-old secondary forests, there was a predominance of small trees (DBH 5 <15 cm). These small DBH trees were more abundant in secondary forests (Fig. 3a, b e c), while they were less common in mature forests and in AFS cabruca and not present in AFS areas. Medium-sized (DBH 15 <30 cm) and large trees (DBH≥ 30 cm) appear more densely in the 40-year-old secondary forests, and in the AFS areas (Figure 3d, e, f), which was statistically higher from the others.

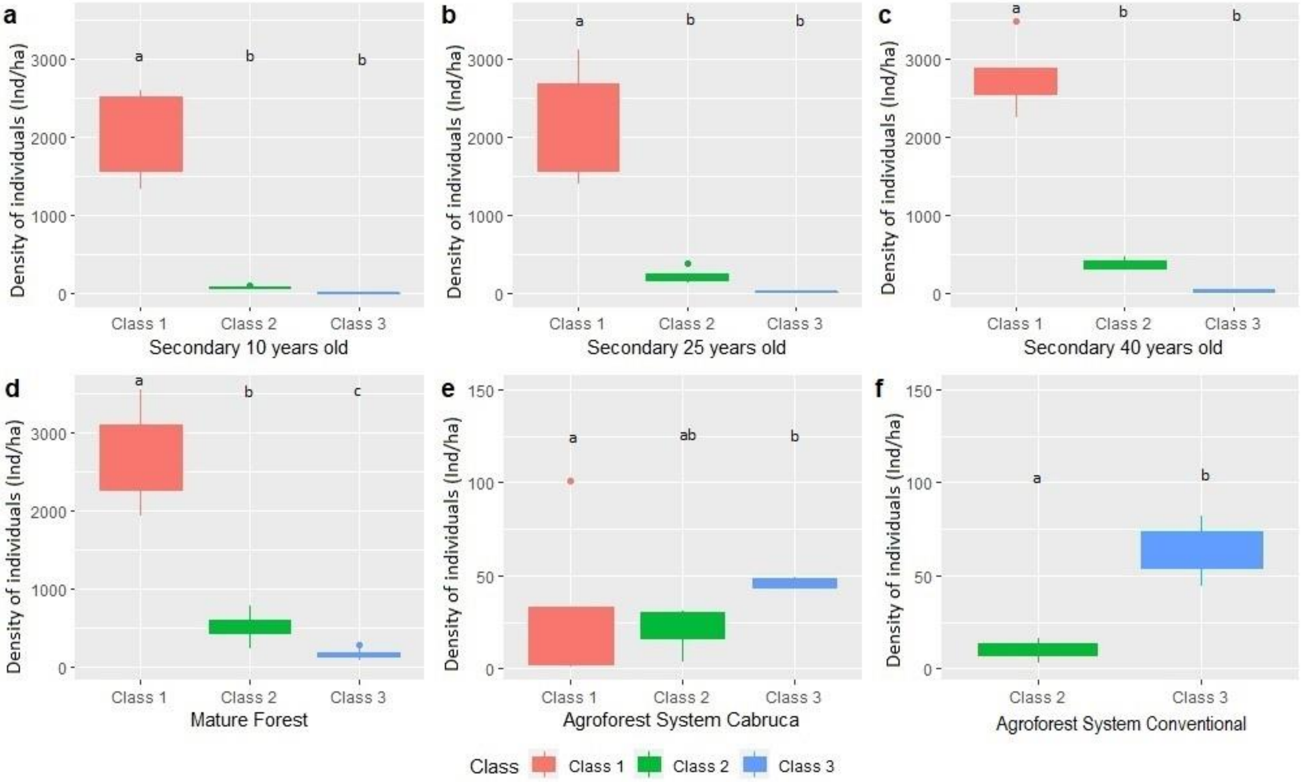

Fig. 3 Density of individuals (individuals per hectare) in the following classes of DBH: Class 1: 5<15 cm; Class 2: 15<30 cm and Class 3: >=30 cm, in different forest covers located in southern Bahia, Brazil.

Aboveground biomass differed statistically within DBH size classes and forest cover types. In secondary forests (10 and 25 years old), there was a greater amount of biomass in the class of small trees (5<15 cm) (Figure 4 a and b). In the 40-year-old forests, the biomass was concentrated in the intermediate DBH classes (15<30 cm) (Figure 4c). The small trees (5<15 cm) became less significant with the advancement of the forest succession and not present in the AFS areas (Figure 4e). The trees with the largest DBH (≥ 30 cm) represented the highest amount of biomass in mature forests, AFS cabrucas and AFS conventional (Figure 4d, e and f).

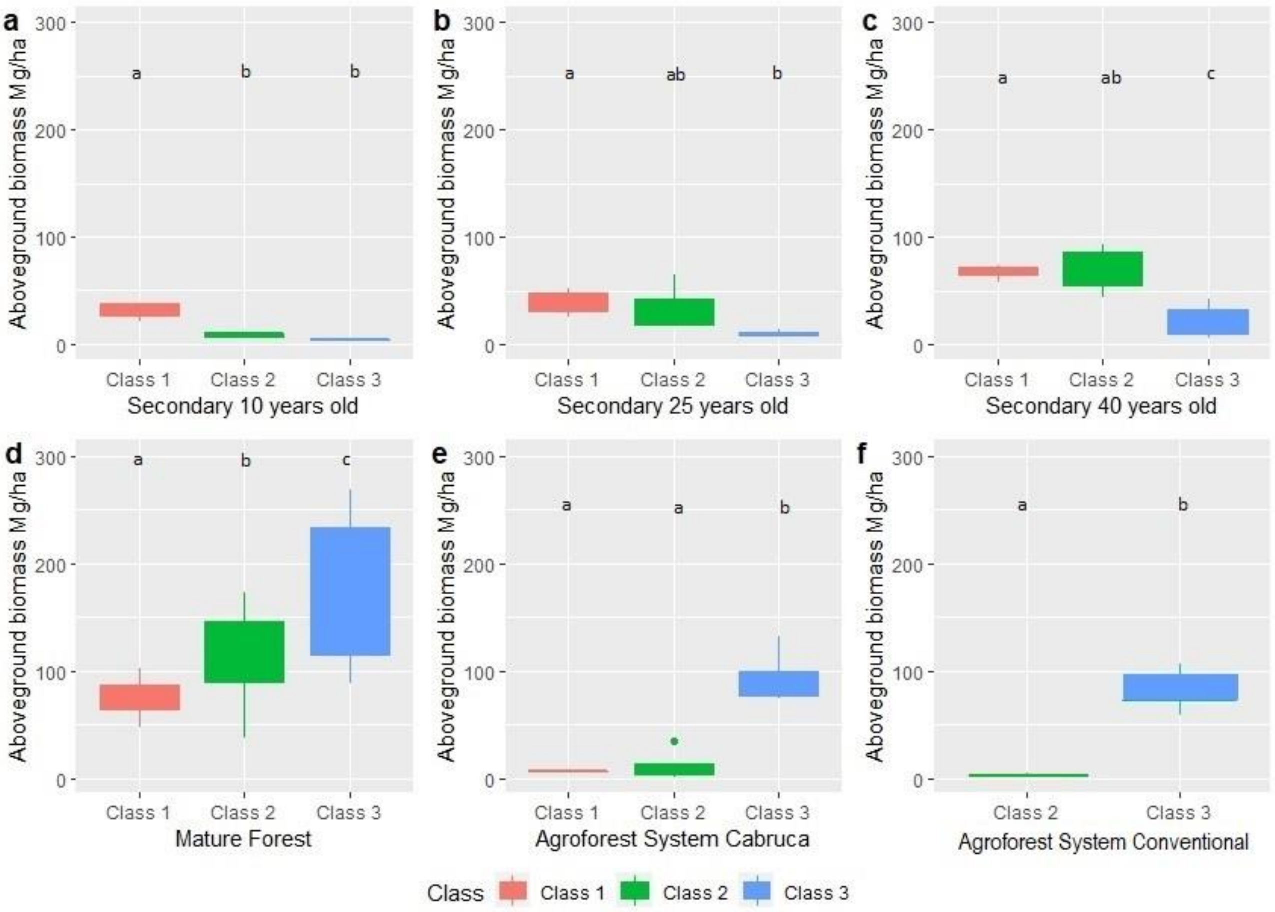

Fig. 4 Aboveground biomass in the following classes of DBH: Class 1: 5<15 cm; Class 2: 15<30 cm and Class 3: >=30 cm, in different forest covers located in southern Bahia, Brazil.

Discussion

In our study, we found the highest aboveground biomass accumulation in mature forests compared to the other studied forest covers, as reported in other studies comparing aboveground biomass between natural forests and agroforestry systems (Soazafy et al. 2021). In a study carried out in Malaysia, aboveground biomass of agroforestry systems was compared with mature forests, and they found similar results, with greater biomass stored in mature forests in relation to forest fragments, vanilla agroforests, forest-derived agroforests and woody fallows, respectively (Soazafy et al. 2021). In Ghana, a study evaluating carbon stored in forests in relation to cocoa-dominated agroforest and mixed food crops agroforest, demonstrated the highest carbon storage in natural forests, followed by agroforests and with lower carbon storage in mixed food crops agroforest (Asase and Tetteh 2016). Thus, these results reinforce the importance of conserving mature forests as an important reservoir of biomass (Pan et al. 2011), and that these services cannot be provided in the same way by other forms of forest cover. In addition, our results emphasize the importance of conserving mature forests in the region, mainly for sheltering great species richness and endemism (Thomas et al. 1998; Martini et al. 2007). However, the last remnants of mature forests may not be enough to sustain viable populations of several species, and so other forest covers become important for the maintenance of several services in working landscapes (Garibaldi et al. 2020).

Studies of secondary forests have become increasingly essential, given that these forests represent a high percentage of forests worldwide (FAO 2020). Here, we found that these forests presented high values of accumulated biomass, mainly forests in an advanced stage of succession (>40 years). Biomass recovers quite rapidly at mature forest levels in a short period of time, which has been reported in other studies (Feldpausch et al 2005; Letcher and Chazdon 2009; Poorter et al. 2016) and stagnates with higher biomass in mature forests (Peña-Claros 2003; Gehring et al. 2005). Secondary forests play a very important role in working landscapes, as they sequester carbon dioxide and are home for several native tree species. In addition, secondary forests with proper forest management can be very productive in both ecological and economic terms (Schwartz et al. 2015), providing timber and non-timber forest products (Zambiazi et al. 2021; Finegan 1992, Chazdon and Coe 1999), as well as several ecosystem services, such as carbon storage (Silver et al. 2000; Zarin et al. 2001).

Our results showed that AFS cabruca have high values of stored biomass, with values similar to secondary forests in an advanced stage of succession. These ecosystems conserve some of the native tree vegetation, mainly by keeping large-sized native tree species to shade cocoa plantations. These large-sized trees concentrate most of the biomass (Schroth et al. 2015; 2016; Osen et al. 2021). AFS cabruca also sustain and maintain the longevity of several endemic tree species in these working landscapes, as they are seed sources for in situ natural regeneration and for restoration projects in the region (Martin et al. 2021). As AFS cabruca exhibit a great diversity of native tree species, these ecosystems help to connect natural forest fragments in the region, as they somehow resemble natural forests in southern Bahia (Schroth et al. 2004). Finally, AFS cabruca, in addition of having a good performance in carbon storage, produce a great diversity of food, which contributes to meeting the needs of farmers and the cocoa plantation itself, with the management of soil nutrients (Tondoh et al. 2015; Asigbaase et al. 2019) and increased benefits of co-products such as wood and fruits (Tscharntke et al. 2011; Asigbaase et al. 2019).

In this study, the AFS conventional areas showed lower values of aboveground biomass accumulation when compared to natural, late secondary and AFS cabruca. However, other types of AFS have showed great potential to store carbon. For example, in a work carried out in the Himalayas, comparing different areas of AFSs, the silvopastural system stored a greater amount of biomass than the others, with woody perennial trees contributed with 95.92 and 94.85% in aboveground and total biomass, respectively. Thus, the use of a mix of tree species with timber potential in AFS plays an important role in maintaining higher productivity and more sustainable landscapes (Piotto 2008; Liang et al. 2016). Therefore, use of AFS can greatly contribute to regional and global timber markets, increasingly needed to reduce the pressure for timber from native forests (Paquette and Messier 2010).

In the current context of great pressure on native forests and the growing need for food and wood products, working landscapes with different types of forest cover performing different functions is fundamental and, therefore, should be considered as potential carbon sinks (Chazdon et al. 2009a; Pagiola et al. 2007). Brazil has high potential to implement working landscapes through the use of AFS in several regions, as AFS have been recognized an important tool towards large-scale forest restoration in tropical regions, in addition to bring several other economic and social benefits (Shennan-Farpón et al. 2021). Even though Brazil, among Latin American countries, has several landscape initiatives of multi-objective management such as in the southern region of Bahia, there is still a lack of policies to enhance effectiveness and scalability of these working landscapes (Estrada-Carmona et al. 2014).

Assessing the capacity of working landscapes becomes increasingly essential, because of the rapid conversion from natural to anthropogenic areas around the world. From this study we showed the potential of different forest covers to store carbon, in addition to highlighting how these covers are important for the conservation of biodiversity, provide ecosystem services and increase production of food and forest products (Kremer and Merenlender 2018). In addition, forest restoration through AFS and secondary forests has the potential for rural subsistence and to meet the demands of timber products (Lin et al. 2008, Zambiazi et al 2021). As shown in the present study, native forests have the greatest capacity to store carbon and biodiversity, while AFS can supply food and wood products, in addition to providing ecosystem services. The region of southern Bahia, where this study was conducted, represents a great example of a working landscape with a wide variety of types of forest cover, with productive AFS and native forests with high diversity, both types of cover with high potential to provide ecosystem services. The maintenance of these working landscapes through conservation policies can ensure great reservoirs of carbon and biodiversity while providing wealth for local communities.

References

Alvares CA, Stape JL, Sentelhas PC, Gonçalves JLM, Sparovek G (2013) Koppen climate classification map for Brazil. Meteorologische Zeitschrift 22:711–728. http://dx.doi.org/10.1127/0941-2948/2013/0507

Alvez J, Schmitt Filho AL, Farley J, Alarcon G, Fantini AC (2012) The potential for agroecosystems to restore ecological corridors and sustain farmer livelihoods: Evidence from Brazil. Ecol Restor 30:288–290. https://doi: 10.3368/ er.30.4.288

Amorim AM, Thomas WW, Carvalho AMV, Jardim JG (2009) Floristics of the Una Biological Reserve, Bahia, Brazil. Mem New York Bot Gard 100:67–146. https://doi.org/10.1590/S0100-84042009000100007

Asase A, Tetteh DA (2016) Tree diversity, carbon stocks, and soil nutrients in cocoadominated and mixed food crops agroforestry systems compared to natural forest in southeast Ghana. Agroecol. Sustain Food Syst 40:96–113. https://doi.org/ 10.1080/21683565.2015.1110223

Ashton MS, Montagnini F (200) The Silvicultural Basis for Agroforestry Systems. Agrof Syst 50:195–197. https://doi.org/10.1023/A:1006435021290

Asigbaase M, Dawoe E, Lomax BH, Sjogersten S (2021) Biomass and carbon stocks of organic and conventional cocoa agroforests, Ghana. Agricul, Ecosyst and Envir 306: 107192. https://doi.org/10.1016/j.agee.2020.107192

Bates D, Maechler M, Bolker B and Walker S (2015) Fitting Linear Mixed-Effects Models Using lme4. J of Stat Software 67:1-48

Barlow J, França F, Gardner TA et al (2018). The future of hyperdiverse tropical ecosystems. Nature 559:517–526. https://doi.org/10.1038/ s41586-018-0301-1

Britto PC, Jaeger D, Hoffmann S, Robert RCG, Fantini AC, Vibrans AC (2017) Productivity assessment of timber harvesting techniques for supporting sustainable forest management of secondary Atlantic Forest in southern Brazil. Ann For Res 60:203–215. https://doi.org/10.15287/afr.2017.898

Canadell JG, Raupach MR (2008) Managing forests for climate change mitigation. Science 320:1456–1457

Chave J, Réjou-Méchain M, Búrquez A, Chidumayo E et al (2014) Improved pantropical allometric models to estimate the aboveground biomass of tropical forests. Glob Change Biol 72:763–768. https://doi:10.1111/gcb.12629

Chazdon RL, Coe FG (1999) Ethnobotany of woody species in second-growth, old-growth, and selectively logged forests of northeastern Costa Rica. Conserv Biol 13: 1312–1322

Chazdon RL (2003) Tropical forest recovery: Legacies of human impact and natural disturbances. Perspect Plant Ecol 6:51–71

Chazdon RL, Peres CA, Dent D, Sheil D, Lugo AE, Lamb D, Miller SE (2009a) The potential for species conservation in tropical secondary forests. Conserv Biol 23:1406–1417. https ://doi.org/10.1111/j.1523-1739.2009.01338.x

Chazdon RL, Harvey CA, Komar, O et al (2009b) Beyond reserves: A research agenda for conserving biodiversity in human-modified tropical landscapes. Biotropica 41:142–153

Chazdon RL (2014) Second Growth: The Promise of Tropical Forest Regeneration in an Age of Deforestation. University of Chicago Press, Chicago

Chazdon RL, Broadbent EN, Rozendaal DMA et al (2016) Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics. Sci Adv 2: e1501639. https ://doi.org/10.1126/sciadv.1501639

Estrada-Carmona N, Hart AKH, DeClerck FAJ, Harvey CA, Milder JC (2014) Integrated landscape management for agriculture, rural livelihoods, and ecosystem conservation: An assessment of experience from Latin America and the Caribbean. Landsc Urban Plan 129:1–11

Fantini AC, Schuch C, Siminski A, Siddique I (2019) Small-scale Management of Secondary Forests in the Brazilian Atlantic Forest. Flor e Amb 26:1–11

FAO (2012) Moving forward with climate-smart agriculture. Available in www.fao.org/climatechange/climate-smart

FAO, UNEP (2020) The State of the World's Forests 2020: Forest, biodiversity and People. https://doi.org/10.4060/ca8642en

Feldpausch TR, Riha S, Fernandes ECM, Wandelli EV (2005) Development of forest structure and leaf area in secondary forests regenerating on abandoned pastures in Central Amazonia. Earth Interact 9:1–22

Finegan B (1992) The management potential of Neotropical secondary lowland rain forests. For Ecol Manag 47:295–321

Garibaldi LA, Carvalheiro LG, Vaissière BE, Gemmill-Herren B, Hipólito J, Freitas BM,Ngo HT, Azzu N, Sáez A, Astrom J, Na J, Blochtein B, Buchori D, García FJC, Silva FO, Devkota K, Ribeiro MF, Freitas L, Gaglianone MC, Goss M, Irshad M, Kasina M, Pacheco Filho SJS, Kiill LHP, Kwapong P, Parra GN, Pires C, Pires V, Rawal RS, Rizali A, Saraiva AM, Veldtman R, Viana BF, Witter S, Zhang H (2016) Mutually beneficial pollinator diversity and crop yield outcomes in small and large farms. Science 351: 6271

Grace J (2004) Understanding and managing the global carbon cycle. J Ecol 92:189–202

Geist HJ, Lambin EF (2002) Proximate causes and underlying driving forces of tropical deforestation. Biosc 52:143–150. https://doi:10.1641/0006-3568

Gehring C, Denich M, Vlek PLG (2005) Resilience of secondary forest regrowth after slash-and-burn agriculture in central Amazonia. J Trop Ecol 21: 519–527

Houghton RA, Byers B, Nassikas AA (2015) A role for tropical forests in stabilizing atmospheric CO2. Nat Clim Chang 5:1022–1023

IBGE/SIDRA (2019) Sistema IBGE de Recuperação Automática https://sidra.ibge.gov.br/acervo (2019). (access in february 2022)

ITTO (2020) Guidelines for forest landscape restoration in the tropics. ITTO Policy Development Series No. 24. International Tropical Timber Organization (ITTO), Yokohama, Japan.

Jose S, Gorson A (2008) Ecological Knowledge and Agroforestry Design: An Introduction. In: Jose S, Gorson A. Toward Agroforestry Design: An Ecological Approach pp 3 -13

Kremer C, Merenlender A (2015) Landscapes that work for biodiversity and people. Science 362:6020. https://doi:10.1126/science.aau602

Kuznetsova A, Brockhoff PB, Christensen RHB (2017) “lmerTest Package:Tests in Linear Mixed Effects Models. J of Stat Soft 82:1-26

Letcher S, Chazdon RB (2009) Rapid Recovery of Biomass, Species Richness, and Species Composition in a Forest Chronosequence in Northeastern Costa Rica. Biotropica 41: 608–617

Liang J, Crowther TW, Picard N, Wiser S, Zhou M, Alberti G, Schulze ED, McGuire AD, Bozzato F, Pretzsch H (2016) Positive biodiversity-productivity relationship predominant in global forests. Science 354: aaf8957

Matos FAR, Magnago LFS, Miranda CAC, Menezes LFT, Gastauer M, Safar NVH, Schaefer CEGR, Silva MP, Simonelli M, Edwards FA, Martins SV, Meira-Neto JAA, Edwards DP (2020) Secondary forest fragments offer important carbon and biodiversity cobenefits. Glob Change Biol 26:509–522

Martini AMZ, Fiaschi P, Amorim AM, Paixão JL (2007) A hot-point within a hot-spot: a diverse site in Brazil’s Atlantic forest. Biodivers Conserv 16:3111–3128. https:// doi:10.1007/s10531-007-9166-6

Martin DA, Wurz A, Osen K, Grass I, Holscher D, Rabemanantsoa T, Tscharntke T, Kreft H (2021) Shade-tree rehabilitation in vanilla agroforests is yield neutral and may translate into landscape-scale canopy cover gains. Ecosystems 24:1253–1267. https://doi.org/10.1007/s10021-020-00586-5

Montagnini F (2000) Strategies for the recovery of biodiversity indeforested landscapes. In: Krishnapullay B, Soepadmo E, Arshad M, Wong A, Appanah S, Wan Chik S, Manokaran N, Tong H, Choon K (Eds.) Forests and Society: The Roleof Research. IUFRO World Congress, August 6–12. Sub-plenary Sessions, vol. 1. International Union of ForestryResearch Organizations, Kuala Lumpur, Malaysia pp 310–319

Montagnini F (2015) Función de los sistemas agroforestales en la adaptación y mitigación del cambio climático. In: Montagnini F, Somarriba E, Murgueitio E, Fassola H, Eibl B (eds) Sistemas agroforestales: funciones productivas, socioeconómicas y ambientales, Serie técnica informe técnico No. 402. CATIE/Editorial CIPAV, Turrialba/Cali, pp 269–297

Montagnini F (2017) Introduction: Challenges for Agroforestry in the New Millennium. In: Montagnini F. Integrating Landscapes: Agroforestry for Biodiversity Conservation and Food Sovereignty. Adv in AgroforSpringer 501p

Morse WC, Schedlbauer JL, Sesnie SE et al (2009) Consequences of environmental service payments for forest retention and recruitment in a Costa Rica biological corridor. Ecol Soc 14:23. https://doi: 10.5751/ ES-02688-140123

Nair PKR, Garrity DP (2012) Agroforestry: the future of global land use, Advances in Agroforestry. In: Jose S, Gordon AM (eds) Advances in agroforestry volume 4: toward agroforestry design: an ecological approach. Springer, Dordrecht. 314 pp

Osen K, Soazafy MR, Martin DA, Wurz A, Marz A, Ranarijaona HLT, Hölscher D (2021) Land- use history determines stand structure and tree diversity in vanilla agroforests of northeastern Madagascar. Appl Veget Scie 24:e12563

Pan Y, Birdsey RA, Fang J et al (2011) A large and persistent carbon sink in the world's forests. Science 333: 988–993 https://doi.org/10.1126/scien ce.1201609

Pan Y, Birdsey RA, Phillips OL, Jackson RB (2013) The Structure, Distribution, and Biomass of the World's Forests. Annu Rev of Ecol, Evol, and Syst 44:593-62

Pagiola S, Ramirez E, Gobbi J, deHaan C, Ibrahim M, Murgueittio E, Ruiz JP (2007) Pa ying for the environmental services of silvopastoral practices in Nicaragua. Ecol Econ 64:374–385

Paquette A, Messier C (2010) The role of plantations in managing the world's forests in the Anthropocene. Frontiers in Ecol and the Envir 8:27–34

Penâ-Claros M (2003) Changes in forest structure and species composition during secondary forest succession in the Bolivian Amazon. Biotropica 35:450–461

Potapov P, Hansen MC, Laestadius L et al (2017) The last frontiers of wilderness: Tracking loss of intact forest landscapes from 2000 to 2013. Sci Adv 3(1): e1600821. https ://doi.org/10.1126/sciadv.1600821

Poorter L, Bongers F, Aide T et al (2016) Biomass resilience of Neotropical secondary forests. Nature 530:211–214. https://doi.org/10.1038/nature16512

Piotto D (2008) A meta-analysis comparing tree growth in monocultures and mixed plantations. For Ecol Manag 255:781–786

Piotto D, Montagnini F, Thomas W, Ashton M, Oliver C (2009) Forest recovery after swidden cultivation across a 40-year chronosequence in the Atlantic Forest of southern Bahia, Brazil. Plant Ecol 205:261-272

Piotto D, Marques JRB, Nunes ACP (2020) Desempenho de espécies madeireiras em sistema agroflorestal de cacaueiro e seringueira no sul da Bahia, Brasil. Agrotrópica 32: 97 - 104

Project Map Biomas – Collection 2021 of Brazilian Land Cover & Use Map Series, accessed on June 09 2022, through the link: https://mapbiomas.org/estatisticas

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Reilly MJ, Spies TA (2015) Regional variation in stand structure and development in forests of Oregon, Washington, and inland Northern California. Ecosphere 6:192

Rice R, Greenberg R (2000) Cacao Cultivation and the Conservation of Biological Diversity. J oh the Hum Envir 29(3):167-173

Soazafy MR, Osen K, Wurz A, Raveloaritiana E, Martin DA, Ranarijaona HLT, Holscher D (2021) Aboveground carbon stocks in Madagascar's vanilla production landscape – exploring rehabilitation through agroforestry in the light of land-use history. Glob Ecol and Conserv 31: 01853

Silver WL, Ostertag R, Lugo AE (2000) The potential for carbono sequestration through reforestation of abandoned tropical agricultural and pasture lands. Restor Ecol 8:394–407

Schwartz G, Ferreira MS, Lopes JC (2015) Silvicultural intensification and agroforestry systems in secondary tropical forests: a review. Revista de Ciências Agrarias 58:319-326

Schroth G, Fonseca GAB, Harvey CA, Gascon C, Vasconcelos HL, Izac A-MN (2004) Agroforestry and biodiversity conservation in tropical landscapes. Island Press, Washington

Schroth G, Bede LC, Paiva AO, Cassano CR, Amorim AM, Faria D, Mariano-Neto A, Martini AMZ, Sambuichi RHR, Lôbo RN (2015) Contribution of agroforests to landscape carbon storage. Mitig Adapt Strateg Glob Chang 20:1175-1190. https://doi10.1007/s11027-013-9530-7

Schroth G, Laderach P, Martinez-Valle AI, Bunn C, Jassogne L (2016) Vulnerability to climate change of cocoa in West Africa: Patterns,opportunities and limits to adaptation. Scie of the Tot Envir 556:231–241

Shennan-Farpón Y, Mills M, Souza A, Homewood K (2022) The role of agroforestry in restoring Brazil's Atlantic Forest: Opportunities and challenges for smallholder farmers. People and Nature, 4:462–480.

Tabarelli M, Aguiar AV, Ribeiro MC, Metzger JP, Peres CA (2010) Prospects for biodiversity conservation in the Atlantic Forest: lessons from aging human-modified landscapes. Biol Conserv 143:2328–2340

Thomas WW, Carvalho AMV, Amorim AM, Garrison J, Arbelaez AL (1998) Plant endemism in two forests in southern Bahia, Brazil. Biodivers Conserv 7:311–322. https://doi:10.1023/A:1008825627656

Thomas WW (2003) Natural vegetation types in southern Bahia. In: Prado P.I., Landau E.C., Moura R.T., Pinto L.P.S., Fonseca G.A.B., Alger K. (orgs.) Corredor de

Biodiversidade da Mata Atlântica do Sul da Bahia. Publicação em CD-ROM, Ilhéus, IESB / CI / CABS / UFMG / UNICAMP.

Tondoh JE, Kouamé FN, Guéi AM, Sey B, Koné AW, Gnessougou N (2015) Ecological changes induced by full-sun cocoa farming in Côte d’Ivoire. Glob Ecol and Conserv 3: 575–595

Tscharntke T, Clough Y, Bhagwat SA, Buchori D, Faust H, Hertel D, Holscher D, Juhrbandt J, Kessler M, Perfecto I, Scherber C, Schroth G, Veldkamp E and Wanger TC (2011) Multifunctional shade-tree management in tropical agroforestry landscapes – a review. J of Appl Ecol 48:619–629. https://doi: 10.1111/j.1365-2664.2010.01939.xÓ2011

UN Restoration Decade (2021) Publications. Disponivel em: https://www.decadeonrestoration.org/es. access in April 2022.

Ugalde L (2013) Teak: New Trends in Silviculture, Commercialization and Wood Utilization. Intern For and Agrofor, Cartago, 552 p

Vandermeer J, Perfecto I (2007) The agricultural matrix and a future paradigm for conservation. Conserv Biol 21:274–277. https://doi:10.1111/j.1523-1739.2006.00582.x

van Noordwijk M, Bizard V, Wangpakapattanawong P, Tata HL, Villamor GB, Leimona B (2014) Tree cover transitions and food security in Southeast Asia. Glob Food Sec 3(3):200–208

Zambiazi DC, Fantini AC, Piotto D, Siminski A, Vibrans AC, Oller DC, Piazza GE, Pena-Claros M (2021) Timber stock recovery in a chronosequence of secondary forests in Southern Brazil: Adding value to restored landscapes. For Ecol and Manag 495:119352

Zarin DJ, Ducey MJ, Tucker JM, Salas WA (2001) Potential biomass accumulation in Amazonian regrowth forests. Ecosystems 4:658–668

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed Effects Models and Extensions in Ecology with R. Statistics for Biology and Health, New York

CAPITULO IV

Fatores que afetam a biomassa acima do solo em florestas tropicais secundárias

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Resumo

As florestas tropicais secundarias são cada vez mais importantes de serem estudadas, visto que cada vez mais florestas maduras são convertidas em outros tipos de paisagens. Aqui nos testamos como diferentes variáveis ambientais influenciam a biomassa acima do solo (BAS) em florestas tropicais secundarias. Realizamos coletas de dados em campo localizadas no Parque Estadual da Serra do Conduru, Bahia, Brasil, utilizando 30 parcelas de 50x50 m (0.25ha), dentro destas parcelas medimos todas as árvores com DAP>5, coletamos material botânico para identificação das espécies, coletamos amostras compostas de solo para avaliação química e granulométrica, e amostras para avaliação de densidade do solo, realizamos caracterizações do ambiente, e perguntas para moradores locais para avaliar o histórico do uso do solo. Utilizamos modelos lineares generalizados, para avaliar como as variáveis riqueza de espécies, densidade de indivíduos, variáveis químicas e físicas do solo, histórico do uso do solo e declividade afetariam a biomassa. Encontramos 9.562 indivíduos pertencentes a 410 espécies em 56 famílias. A biomassa variou de 6,62 a 481,95 t/ha, e foi influenciada principalmente pela riqueza de espécies, histórico do uso de solos, pH e Potássio (K). Aqui ressaltamos a importância de compreender como quais fatores ambientais mais influenciam a biomassa acima do solo em florestas tropicais secundarias.

Palavras-chave: biomassa, biodiversidade, florestas tropicais, solos.

Introdução

As florestas tropicais são ecossistemas terrestres que desempenham importantes funções para a manutenção e prestação de serviços ecossistêmicos (Myers 1990; Reilly e Spies 2015). As regiões tropicais abrigam a maior biodiversidade da terra (Barlow et al. 2018), particularmente ricas em espécies de árvores (Sullivan et al. 2017). Dessa forma, funcionam na regulação do ciclo global do carbono e do clima (Pan et al., 2011; Ahmad et al. 2014; Coulston et al. 2015). Porém, as florestas tropicais maduras estão sendo reduzidas drasticamente por diversos distúrbios antrópicos, e estão sendo convertidas em outros tipos de uso do solo. As florestas em regeneração apresentam altas taxas de acúmulo de biomassa, principalmente nas fases iniciais de sucessão, e por isso essas florestas estão recebendo mais atenção (Chazdon 2014), possuindo grande importância para mitigação das mudanças climáticas (Bastin et al., 2019, Lewis et al., 2019).

As florestas tropicais secundarias são altamente produtivas, podendo recuperar grande parte da biomassa acima do solo (BAS) nos primeiros anos de regeneração. Um estudo realizado na região Neotrópical demonstrou que até 90% da biomassa foi recuperado aos 66 anos após a degradação (Poorter et al. 2016), e outro estudo realizado na Costa Rica demonstrou que a biomassa se recupera aos níveis da floresta primaria aos 40 anos após o abandono (Letcher and Chazdon 2007). Porém muitos estudos já demonstraram que há uma enorme variação na recuperação da BAS (Becknell & Powers 2014, Rozendaal & Chazdon 2015, Poorter et al. 2016), e que pode ser devido a natureza estocástica da sucessão florestal (Norden et al. 2015).

A variação da biomassa pode responder a diferentes fatores ambientais, podendo variar como resultados de perturbações naturais (Houghton, 2005). A variação nas condições do solo já foi relatada como uma das principais variáveis que afetam a produtividade florestal (*eg.,* Davidson et al. 2004 Becknell & Powers 2014, Quesada et al. 2012), estudos demonstraram que cerca de 30% da variação da biomassa é explicada por fatores do solo (Laurance et al.,1999). As características químicas do solo, como por exemplo pH, podem alterar a capacidade das plantas de absorver nutrientes, e essa redução na oferta de nutrientes minerais no solo, afetam o desenvolvimento das plantas (Gourlet -Fleury et al. 2011; Ostertag 2010; Paoli e Curran 2007; Slik et al. 2010; Baker, 2003). Juntamente com as propriedades físicas, como as alterações na densidade e no teor de argila do solo (Kozlowski 1999; Nawaz et al. 2013). Estes fatores podem limitar as taxas de crescimento das plantas, alterando a produtividade primária líquida (Wright et al, 2011; Alvarez-Clare et al, 2013), com efeitos diretos dos solos no crescimento das árvores (Cleveland et al. 2011).

Muitos estudos demonstram que a diversidade e a composição de espécies podem desempenhar importante papel na distribuição da biomassa (Finegan et al. 2015). Como por exemplo a presença de espécies com alta produtividade (Loreau e Hector, 2001; Cardinale et al. 2007; Finegan, 2015), grandes árvores (Clark e Clark, 2000; Marshall et al., 2012; Slik et al., 2013), espécies com alta densidade da madeira, e a riqueza de espécies, principalmente na região que o estudo foi desenvolvido, altamente diverso floristicamente (Thomas et al. 1998, Martini et al. 2007). Esses fatores podem determinar a produtividade do ecossistema (Tilman et al., 2001; Finegan et al, 2015).

Entender a variabilidade das taxas de recuperação da biomassa em florestas tropicais secundarias se torna essencial visto que a biomassa pode ser afetada por diferentes fatores ambientais (Norden et al. 2015). Mas, a limitação de informações sobre fatores potenciais como histórico do uso do solo, características físicas e químicas do solo, inclinação e riqueza de espécies, podem fornecer informações importantes para identificar padrões de recuperação da biomassa nessas florestas secundárias. Aqui nós analisamos como essas variáveis ambientais afetam o acúmulo de biomassa em florestas tropicais secundarias.

Material e Métodos

Local de estudo

O estudo foi realizado na região sul da Bahia, Brasil, em uma área de proteção ambiental, o Parque Estadual da Serra do Conduru - PESC, localizado nas coordenadas 14º 30'16” S e 39º 6'36” W (Figura 1). O Parque possui uma área de 10.000 ha, composta por florestas em diferentes estágios de regeneração, com matas secundárias em diferentes idades a áreas bem preservadas (Piotto et al. 2009). A temperatura média mensal é de 24°C, com precipitação média anual de 2.000 mm distribuída uniformemente ao longo do ano (Santos et al. 2018). A vegetação é classificada como floresta tropical úmida, no bioma Mata Atlântica, com estratos emergentes, dossel, subdossel e herbáceo e altíssima diversidade de espécies (Thomas 2003), que já foi classificada como uma região com um dos maiores números de espécies de árvores no

Brasil e do mundo (Martini et al. 2007), além de ser uma região com diversas espécies endêmicas e ameaçadas de extinção.

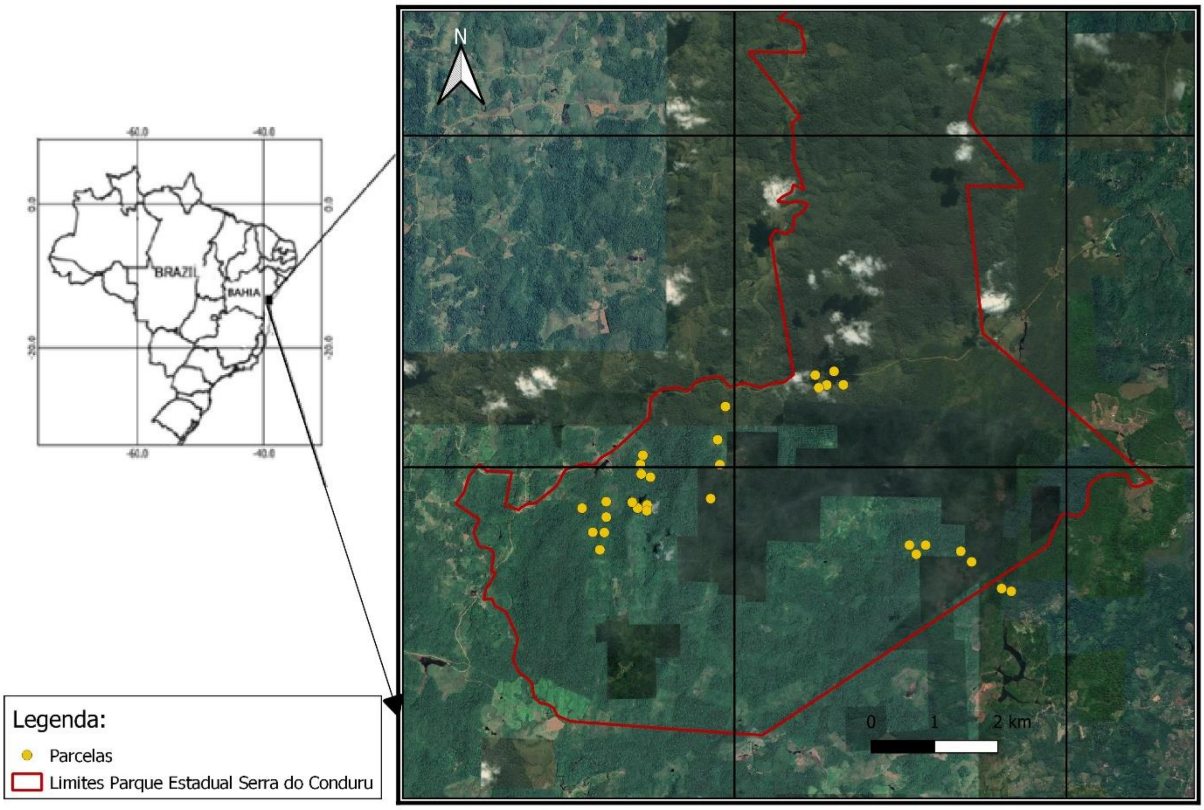

Figura 1. Mapa de localização da área de estudo, no Parque Estadual da Serra do Conduru, Bahia, Brasil.

Os dados utilizados para selecionar as parcelas de acordo com a quantidade de biomassa foram pré-determinados em uma coleta realizada no ano de 2016, utilizando um sensor Lidar, que utilizou um sensor Optech Orion M300 de múltiplos retornos, acoplado a um avião voando a uma altitude média de 850 m acima do nível do solo, em uma área de 4.529ha, sobre a região sul do Parque Estadual Serra do Conduru. Os dados de biomassa produzidos a partir da coleta de dados do Lidar foram disponibilizados em arquivo raster com uma resolução espacial com escala de 50m de pixel, porque as parcelas de inventário de campo usadas para desenvolver a relação lidar-AGB foram de 50x50 m.

Idade das parcelas

Para a determinação da idade das parcelas utilizamos uma série temporal de imagens de satélite Landsat de 1984 a 2016, para construir mapas de idade das florestas, utilizando dados de sensoriamento remoto. Nós utilizamos áreas que foram classificadas como florestas secundarias, com menos de 32 anos, durante a classificação das idades 23% das áreas foram classificadas como floresta secundária com menos de 32 anos (em 2016). 9% como áreas não florestadas e os outros 69% restantes abrigavam florestas secundárias com mais de 33 anos ou florestas intactas.

Medidas de Biomassa acima do solo

Utilizamos 30 parcelas de 0,25ha (50 x 50m) divididas em classes de idade e quantidade de biomassa acima do solo. Nós utilizamos as seguintes classes de idade: Classe 1: 0 a 10 anos; Classe 2: 11 a 20 anos; Classe 3: 21 a 32 anos, dentro de cada classe de idade. Com base no banco de dados coletados com o sensor Lidar, foram escolhidas cinco (5) parcelas com alto e cinco (5) com baixa biomassa, totalizando assim, na classe de idade 1: 5 parcelas com alta AGB e cinco parcelas com baixa AGB; Classe de idade 2: 5 parcelas com alta AGB e 5 parcelas com baixa AGB; Classe de idade 3: 5 parcelas com alta AGB e 5 parcelas com baixa AGB. Para localizar as parcelas dentro das classes pré-estabelecidas, nós usamos o *software* QGIS (QGIS Development Team, 2020), plotando os arquivos *shapefile* com dados das idades e arquivo *raster* da biomassa para selecionar as parcelas.

Determinação da biomassa acima do solo

Para determinar a biomassa nas parcelas, medimos todas as árvores com DAP >5cm a 1,3m de altura do solo. Realizamos coleta do material botânico para todas as espécies, as coletas foram identificadas com a ajuda da literatura, de especialistas e por comparações com espécimes constantes no herbário André Mauricio Vieira de Carvalho, do Centro de Pesquisas do Cacau (CEPEC/ CEPLAC), mun. de Ilhéus, Bahia. Os nomes das famílias das plantas estão de acordo com a classificação do APG IV (2016). Todos os espécimes coletados foram depositados no herbário CEPEC.

Para estimar BAS nós usamos uma equação alométrica geral proposta por Chave et al. (2014), como descrita a seguir:

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

que utiliza as seguintes variáveis: D: diâmetro da árvore à altura do peito (DAP, cm), ρ: densidade da madeira para espécie (g/cm^3), E: um índice climático, que combina sazonalidade da precipitação, sazonalidade da temperatura e um índice de déficit hídrico climático (Chave et al. 2014).

A densidade da madeira foi atribuída a cada espécie coletada, para isso usamos dados do Global Wood Density Database (Chave et al. 2009; Zanne et al. 2009) para obter a densidade da madeira de cada espécie, quando os dados para a espécie não estavam disponíveis usamos dados do gênero, quando esses não estavam disponíveis usamos dados atribuídos à família. A biomassa total acima do solo por parcela foi a soma da BAS das árvores individuais.

Propriedades do solo

Avaliação Química do solo

Para avaliar as propriedades químicas do solo, as coletas foram realizadas em campo, utilizando um trado (0-20 cm de profundidade), coletadas 5 amostras simples, para formar uma composta para cada parcela. Todas as amostras de solo foram enviadas para o Laboratório de Solos e Nutrição de Plantas na Embrapa Mandioca e Fruticultura na cidade de Cruz das Almas, Bahia. Os seguintes parâmetros foram avaliados: Fósforo (mg/dm^3), pH (H2O), potássio trocável (K, cmol$_c$ /dm^3), potencial de acidez trocável (H + Al, cmol$_c$ /dm^3), sódio (Na, cmol$_c$ /dm^3), cálcio (Ca2+, cmol$_c$ /dm^3), magnésio (Mg2+, cmol$_c$ /dm^3), cálcio e magnésio (Ca+Mg, cmol$_c$ /dm^3), alumínio (Al, cmol$_c$ /dm^3), soma de bases (SB, cmol$_c$ /dm^3) matéria orgânica (OM, g/Kg), capacidade de troca catiônica (CTC, cmol$_c$ /dm^3), porcentagem de saturação de bases (V, %). Os parâmetros capacidade efetiva de troca catiônica (CEC, cmol$_c$ /dm^3) e saturação por Al (m%), foram calculados posteriormente.

Avaliação Física do solo

Densidade do solo

Os dados de densidade do solo realizados usando o método de amostra indeformada, utilizando anéis volumétricos de Kopecky, anel de aço inoxidável, com 5 cm de diâmetro e 2,5 cm de profundidade e volume de aproximadamente 50 cm^3. Uma amostra composta de cinco subamostras retiradas de cada parcela a 5 cm de profundidade cravado no solo com um martelo com ponta de borracha. As amostras foram protegidas com plástico, para evitar sua deformação e rotuladas imediatamente após a remoção, e armazenadas para posteriormente ser levadas a laboratório. No Laboratório de Física do Solo, na Universidade Estadual de Santa Cruz (UESC), foram extraídas dos cilindros pesados (extraindo o peso úmido), secos a 105 °C por 48 h e pesados novamente (peso seco) a diferença entre peso úmido e seco em estufa, foi usado para determinar o teor de umidade do solo. A densidade do solo foi determinada pela razão entre o peso do solo seco em estufa e o volume do anel.

Análise de Granulometria

A textura do solo foi medida usando o método de micropipeta modificado (Miller & Miller 1987), usando 10g de amostras de terra fina seca ao ar (solo seco e passado na peneira com malha de 2mm de abertura) foram suspensas com 40mL de hidróxido de sódio (NaOH) 0,1 mol L-1, agitadas no agitador rotatório de Wagner a 30 rpm, durante 16 horas, posteriormente essa amostra foi passada em peneira com malha de 0,053mm para separar a porção de areia, e o que restante da amostra foi diluída em 500ml de agua destilada para a separação da amostra de argila. Posteriormente foram calculados os teores de areia, argila e silte de cada amostra.

Histórico do uso do solo

Para o levantamento das informações sobre o histórico do uso da terra (aquele que ocorria antes da área ser abandonada) foram realizados levantamento de informações com moradores locais, e coletadas informações nas áreas de estudo, como presença de espécies plantadas como cacau, seringa, coqueiro, entre outras e presença de construções abandonadas e cercas nas parcelas de estudo. Usamos as seguintes classes de histórico do uso do solo: área queimada, corte raso, exploração Seletiva, área alagada, Sistemas Agroflorestais (SAF) e não identificado (onde não possuía nenhum tipo de informação).

Análise de dados

Para evitar sobredispersão dos modelos com parâmetros do solo, que geralmente estão correlacionados e reduzir o número de variáveis redundantes, realizamos uma análise de componentes principais (PCA) com os parâmetros de química do solo: Fósforo, pH, potássio trocável, potencial de acidez trocável, sódio, cálcio, magnésio, cálcio e magnésio, alumínio, soma de bases, matéria orgânica, CTC, saturação de bases

(V), CEC e saturação por Al (m). Para a realização do PCA, padronizamos as variáveis para equalizar suas combinações na mesma escala nos eixos de ordenação do PCA (Schmitz et al. 2020). Como resultados os dois primeiros componentes do PCA explicaram 75% dos dados, assim utilizamos as variáveis que estavam presentes nos dois primeiros componentes nos modelos. PC1 está correlacionado com SB, K, CTC e MO, e PC2 está relacionado principalmente com pH, Al, V, m.

Usamos análises modelos lineares generalizados para avaliar as variáveis que influenciam o aumento de BAS em florestas tropicais secundárias. Para a seleção de modelos usamos os parâmetros químicas do solo selecionados pela análise de PCA: SB, K CTC, MO, pH, Al, V e m, utilizamos a textura (areia e argila), densidade do solo (Ds), histórico de uso da terra antes do abandono (SAF, corte raso, cabruca e pastagem), ocorrência de queimadas, riqueza de espécies, densidade de indivíduos e declividade. Os modelos completos iniciais com todas as variáveis foram reduzidos gradualmente até que apenas os fatores significativos permanecessem. Todas as análises estatísticas foram calculadas com R 3.5.1 (www.r-project.org).

Resultados

Encontramos no total 9.562 indivíduos pertencentes a 410 espécies diferentes em 56 famílias, nas 30 parcelas de floresta secundária amostradas. A densidade de indivíduos variou entre 164 a 2.424 indivíduos ≥5cm DAP/ha e a área basal variou entre 3,66 e 41,34m^2/ha. A densidade média da madeira variou de 0,53 a 0,68 (Tabela 1) e foi relacionado com a AGB (p=0.0205) e a média de p em florestas secundarias com maior biomassa foi significativamente maior do que em florestas de baixa biomassa.

Tabela 1. Características da área em parcelas de floresta secundária no Parque Estadual Serra do Conduru, Bahia, Brasil. BAS: Biomassa acima do solo, Área basal, número de indivíduos, Riqueza de espécies, pH, CTC: capacidade de troca catiônica, v: saturação por bases, m: saturação por Al, Ds: densidade do solo, Areia e Argila.

	BAS	**Area basal**	**Dens. Ind.**	**Riqueza**	**ph**	**CTC**	**v**	**m**	**Ds**	**Areia**	**Argila**
	(Mg/ ha)	m^2/ha	Ind/ha		em água	cmol /dm	%	%	cm^3	g/kg^{-1}	g/kg^{-1}
Mínimo	6.62	3.66	164	15	4.70	1.30	13.00	3.57	0.82	159.20	102.56
Máximo	481.95	41.3	2424	142	5.40	10.01	39.00	49.72	1.35	843.30	623.36
Média	153.88	17.95	1258	73	5.03	6.84	23.70	22.65	1.07	621.50	257.92
Desvio Padrão	104.25	9.9	499	36	0.20	1.89	6.65	10.71	0.13	144.06	117.08

AGB variou entre 6,62 t/ha e 481,95 t/ha entre as diferentes parcelas avaliadas (Tabela 1). Embora a AGB não tenha variado com a idade, o melhor modelo selecionado foi com a riqueza de espécies que foi positivamente relacionada a AGB (Figura 2), com as variáveis: densidade de indivíduos, densidade da madeira (p), pH, potássio (K) e ocorrência de fogo como histórico de uso do solo, apresentou AIC<2 (Tabela 2).

Tabela 2. Resultados da seleção de Modelos lineares generalizados, das variáveis ambientais sobre a biomassa acima do solo.

		Parâmetros		
Métricas	Modelos	Δ_i	k	W_i
Biomassa acima do solo	1. Número de Indivíduos + Riqueza + pH +SB +K +Al +CTC +V +m + MO + CWD + Ds + Areia + Argila + Ocorrência de Fogo + Histórico de uso do solo + Inclinação	73.7	18	<0.001
	2. Riqueza + Indivíduos + pH + V + p + idade + Ocorrência de fogo	2.6	7	0.102
	3. Riqueza + Indivíduos + pH + K + Ocorrência de	**0**	3	0.873

	fogo			
	4. Null	16.7	2	<0.001

SB: soma de bases; CTC: capacidade de troca catiônica; V: saturação por bases; m: saturação por Al; MO: matéria orgânica; CWD: Ds: densidade do solo.

Diversidade de espécies

A biomassa acima do solo aumentou significativamente com o aumento na riqueza de espécies (Tabela 3; p=0.000; Figura 2). As parcelas que obtiveram o maior número de espécies foram as que apresentaram maior biomassa, enquanto as áreas com menor biomassa apresentou menor número de espécies e muitas parcelas dominadas por espécies consideradas pioneiras como *Henriettea succosa*, *Miconia mirabilis* e *Tapirira guianensis*.

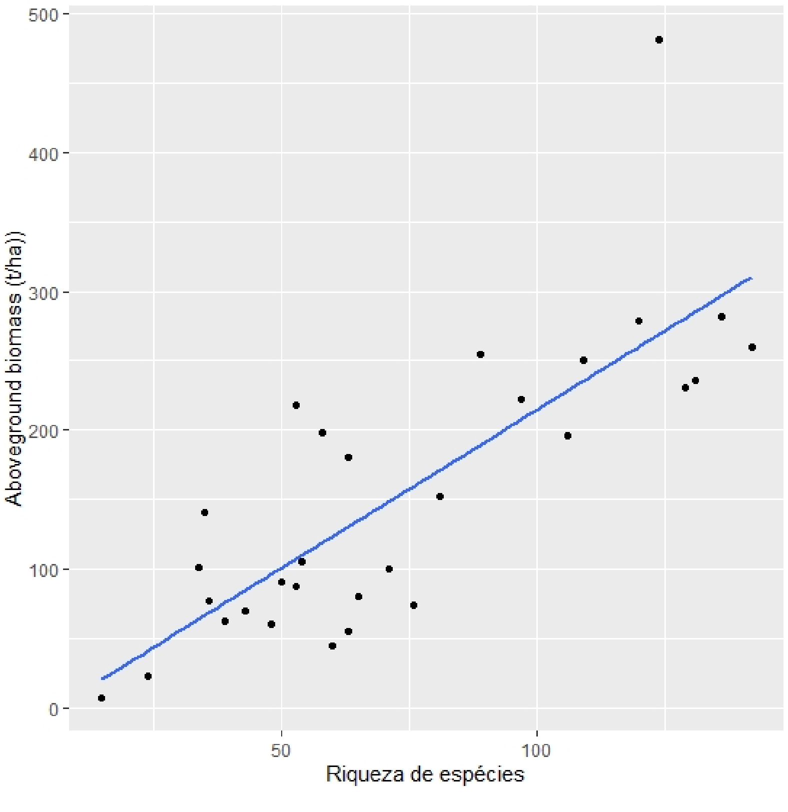

Figura 2. Influência da riqueza de espécies sobre a biomassa acima do solo em florestas tropicais secundarias.

Tabela 3. Variáveis com efeitos significativos na biomassa acima do... em florestas secundárias.

Biomassa acima do solo			
	Estimate	t-value	p
Riqueza	0.0084	-5.40	0.0000***
Dens. ind	0.1417	4.901	0.0003***
K	4.84	2.65	0.0016**
pH	0.017	2.76	0.0109*
Ocorrência de queimadas	-0.0247	1.97	0.0490*

O histórico do uso do solo não foi significativamente relacionado com a biomassa, porém a ocorrência de fogo previamente à regeneração das áreas foi fortemente significativo com a biomassa (Figura 3; p=0.049). em relação as variáveis de solo, a granulometria, densidade do solo e variáveis químicas do solo como, ctc, alumínio, soma de bases e matéria orgânica não foram significativamente relacionadas com a biomassa. Porém o pH e saturação por bases (v) foram relacionados com a biomassa (p=0.010 e p=0.002 respectivamente, Figura 4).

Parâmetros do solo e uso prévio da terra não tiveram efeito significativo sobre AGB.

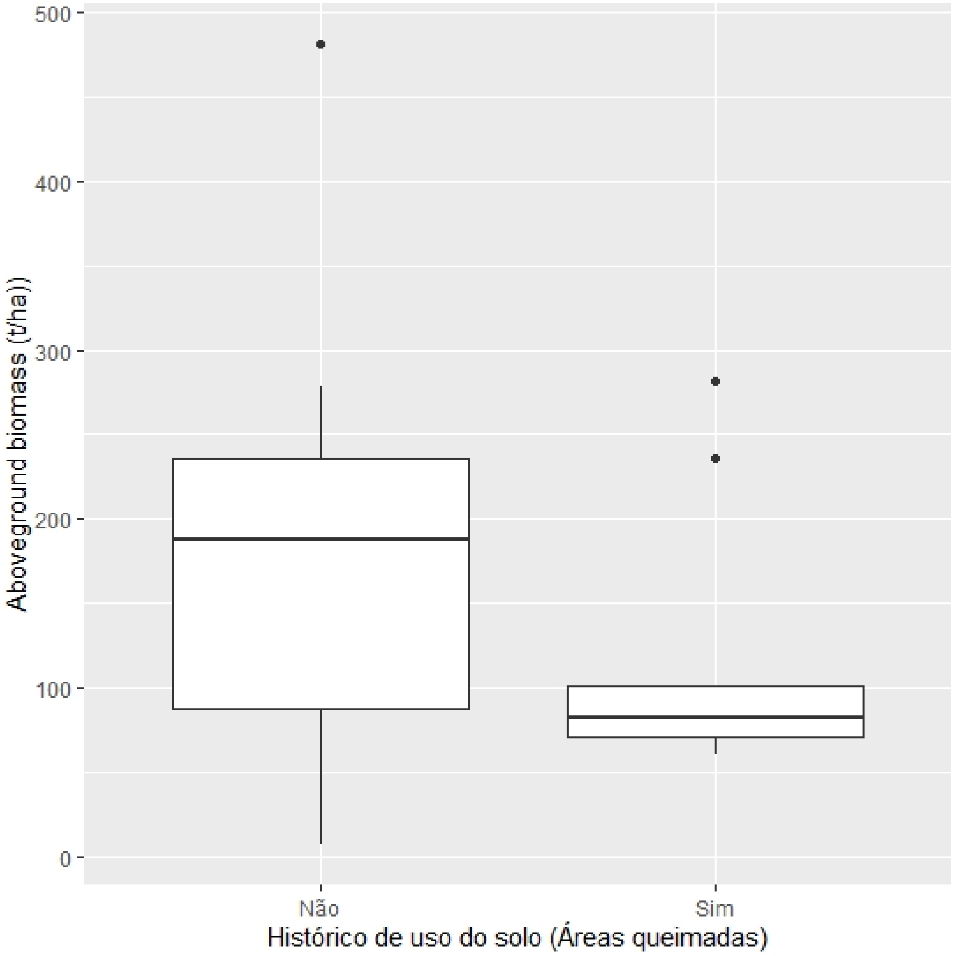

Figura 3. Influência do histórico de uso do solo, com as áreas queimadas anteriormente à regeneração das florestas, sobre a biomassa acima do solo em florestas tropicais secundarias.

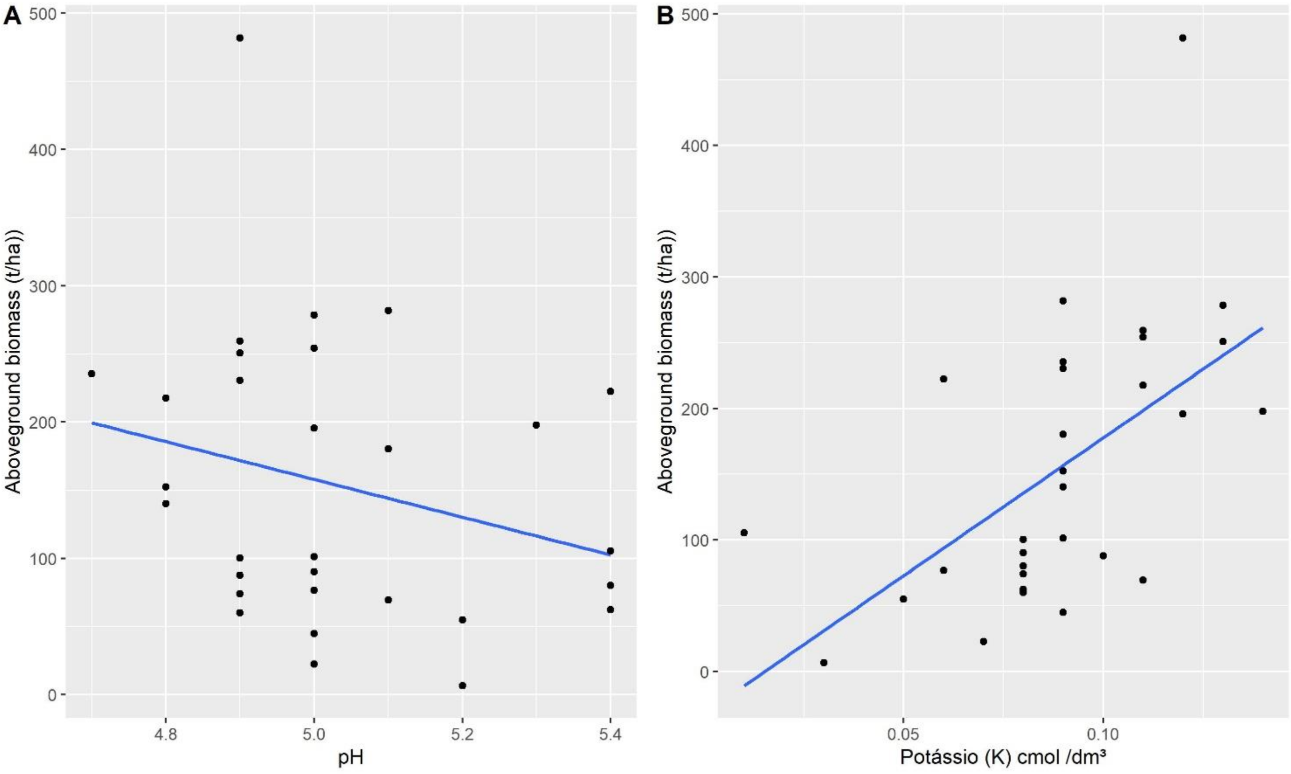

Figura 4. Influência das variáveis de solo: pH e Potássio (K) sobre a biomassa acima do solo em florestas tropicais secundarias.

Discussão

Estudos realizados em florestas tropicais contribuem para a aumento de informações sobre a recuperação da biomassa, essa que pode ser considerada muito variável (Becknell & Powers 2014, Rozendaal & Chazdon 2015). Essa grande variação na biomassa acima do solo, é influenciado por diferentes variáveis ambientais, que podem alterar os estoques de biomassa nas florestas tropicais. Aqui nós utilizamos uma grande quantidade de variáveis ambientais para tentar explicar como essas relações ocorrem em florestas tropicais secundárias, um ambiente altamente complexo. Nossos modelos explicaram a variação da biomassa em apenas poucas variáveis, essas foram, riqueza de espécies, número de indivíduos, ocorrência de queimadas, pH e Potássio do solo.

Encontramos aqui a riqueza de espécies como a variável que melhor explica a maior quantidade de biomassa. Podemos acreditar que essa tendência foi impulsionada pelo fato de que a maior diversidade nessas florestas secundarias pode ser devido a uso diversificado dos nichos, pela ocorrência de espécies pioneiras que ainda persistem no ambiente, juntamente com espécies de sucessão tardia, tolerantes à sombra que se estabelecem na sombra das pioneiras (Norden et al. 2009; Breugel et al. 2013) que possuem necessidades diferentes e muitas vezes complementares. Essa alta diversidade de espécies em florestas jovens pode ocorrer também devido pela presença de árvores remanescentes, muitas delas de grande porte (Clark e Clark, 2000; Marshall et al., 2012; Slik et al., 2013), que podem atrair agentes dispersores de sementes (Chazdon 2014), pela proximidade com florestas naturais, além de ser importantes reservatórios de biomassa. Por exemplo, um trabalho realizado na Costa Rica demonstrou que 31% da diversidade de árvores com DAP >10 cm foi recuperada próximo aos 20 anos de regeneração (Oberleitner et al. 2021). Considerando que nosso trabalho foi realizado em uma região com alta diversidade de espécies (Martini et al. 2017), esses resultados demonstram a importância da conservação dessas florestas hiperdiversas para a regulação do clima.

Após a riqueza de espécies, a ocorrência de queimadas apresentou efeito sobre distribuição de biomassa, porém não foi impactada pelas outras tipos de uso anterior do solo, resultados similares foram relatados em outros estudos (Poorter et al. 2016; Oberleitner et al. 2021). Acreditamos que a ocorrência de fogo como histórico do uso da terra, demonstra alta capacidade explicativa, pois os incêndios são distúrbios antropogênicos com alto impacto, modificando diretamente a estrutura florestal, a dinâmica e composição de espécies em florestas tropicais (Bond e Keeley 2005; Cochrane et al., 2004). Além disso, como os incêndios podem remover grande parte da vegetação (Menezes et al.2019), reduções no banco de sementes e na serrapilheira do solo (Dodonov et al. 2013) e da chuva de sementes (Rocha et al. 2022), isso pode afetar a velocidade de regeneração do ambiente, alterando o crescimento das plantas, e a regeneração das florestas (Dupuy & Chazdon 2008).

As condições do solo demonstram ser importantes variáveis preditivas da biomassa em florestas tropicais em regeneração (Wang et al. 2015; Hofhansl et al. 2020) por afetar o crescimento das plantas (Soong et al. 2020). Dessa forma espera-se que essas variáveis tenham efeito sobre a recuperação da biomassa em florestas secundárias, porém em nossos estudos não encontramos essa relação, o que foi relatado em outros estudos similares ao nosso (Poorter et al. 2017; Rozendaal et al. 2019; Oberleitner et al. 2021), embora todas as variáveis de solo tenham sido medidas diretamente em campo. Somente as variáveis pH e K apresentaram relação significativa com a biomassa. O pH do solo representa uma das mais importantes variáveis do solo, pois pode afetar como os nutrientes do solo poderão ser ou não absorvidos pelas plantas, e nossos resultados demonstraram que os nossos solos podem ser considerados com acidez elevada, por apresentar valores menores que 5.

Conclusões

O aumento dos estudos realizados nesses ambientes complexos, são essenciais para detectar padrões durante a sucessão das florestas. E compreender quais fatores ambientais melhor respondem a biomassa, podem contribuir para uma melhor previsão dos caminhos sucessionais desses novos ambientes. Porém para entendermos melhor os fatores ambientais, necessitamos de levantamentos mais completos de fatores ambientais e das condições locais.

De fato, a riqueza de espécies influencia na biomassa em florestas tropicais secundárias, e assim podem promover o fornecimento de outros serviços ecossistêmicos como o sequestro e armazenamento de carbono (Poorter et al. 2015; Chazdon et al. 2016), e nós reforçamos essa relação com os resultados dos nossos estudos. Nós usamos aqui amostragem com tamanhos de parcelas maiores (0,25ha) que o comumente utilizado, e isso contribui para melhor amostragem, e utilizamos uma grande quantidade de variáveis ambientais que foram exaustivamente amostradas em campo, demonstrando que a biomassa é controlada por fatores ambientais como riqueza de espécies, densidade de indivíduos, pH, K e histórico do uso do solo. Esses resultados são importantes pois documentam efeitos que muitas vezes não estão disponíveis e podem limitar a compreensão da recuperação, dinâmica e sequestro de carbono em florestas tropicais secundárias. Assim os esforços de conservação devem dar mais atenção para as florestas tropicais secundarias e seu potencial de conservação da biodiversidade e manutenção de diversos serviços ecossistêmicos.

Referências

Ahmad A, Mirza SN, Nizami SM (2014) Assessment of biomass and carbon stocks in Coniferous Forest of Dir Kohistan, KPK. – Pakistan Journal of Agriculture Sciences 51: 335-340.

Alvarez-Clare, S., Mack, M.C., Brooks M. (2013) A direct test of nitrogen and phosphorus limitation to net primary productivity in a lowland tropical wet forest. Ecology, 4:1540–51

Baker TR, Phillips OL, Laurance WF, Pitman NCA, Almeida S, Arroyo L, DiFiore A, Erwin T, Higuchi N, Killeen TJ, Laurance SG, Nascimento H, Monteagudo A, Neill DA, Silva JNM, Malhi Y, Lopez-Gonzalez G, Peacock J, Quesada CA, Lewis SL, Lloyd, J (2009) Do species traits determine patterns of wood production in Amazonian forests? Biogeosciences, 6:297–307

Barlow, J., França, F., Gardner, T.A., Hicks, C.C., Lennox, G.D., Berenguer, E., et al., 2018.The future of hyperdiverse tropical ecosystems. Nature 559, 517–526

Bastin, J.-F., Finegold, Y., Garcia, C., Mollicone, D., Rezende, M., Routh, D., et al., 2019. The global tree restoration potential. Science 365, 76–79.

Bond WJ, and Keeley JE (2005) Fire as a global ‘herbivore’: the ecology and evolution of flammable ecosystems. Trends in Ecology & Evolution20 7: 387–394.https://doi.org/10.1016/j.tree.2005.04.025

Breugel M. van, Hall JS, Craven D, Bailon M, Hernandez A, Abbene M, Breugel P (2013) Succession of ephemeral secondary forests and their limited role for the conservation of floristic diversity in a human-modified tropical landscape. PLOS ONE 8, e82433

Chazdon RL, Second Growth: The Promise of Tropical Forest Regeneration in an Age of Deforestation (University of Chicago Press, 2014)

Chazdon RL, E. N. Broadbent, D. M. A. Rozendaal, F. Bongers, A. M. A. Zambrano, T. M. Aide, P. Balvanera, J. M. Becknell, (2016) Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics. Sci. Adv. 2, e1501639 (2016)

Cochrane M, Skole DL, Matricardi EAT, Barber C, Chomentowski WH (2004) Selective logging, forest fragmentation, and fire disturbance. In: Working Forests in the Neotropics: Conservation through Sustainable Management? (eds DJ Zarin, JRR Alavalapati, FE Putz, M Schmink), pp. 310– 324. Columbia University Press, New York.

Chave, J.; Coomes, D.; Jansen, S.; Lewis, S.L.; Swenson, N.G.; Zanne, A.E. Towards a worldwide wood economics spectrum. Ecol. Lett. 2009, 12, 351–366.

Chave J, Réjou-Méchain M, Búrquez A, Chidumayo E, Colgan MS, Delitti WBC, Duque A, Eid T, Fearnside PM, Goodman MHRC, Martínez-Yrízar A, Mugasha WA, Muller-Landau HC, Mencuccini M, Nelson BW, Ngomanda A, Nogueira EM, Ortiz-Malavassi E, Pélissier R, Ploton P, Ryan CM, Saldarriaga JG, Vieilledent G (2014) Improved pantropical allometric models to estimate the aboveground biomass of tropical forests. Glob Change Biol. 72,763–768 doi:10.1111/gcb.12629

Clark, D.B., e Clark, D.A. (2000) Landscape-scale variation in forest structure and biomass in a tropical rain forest. For. Ecol. Manage. 137: 185–198.

Cleveland CC, Townsend AR, Taylor P, Alvarez-Clare S, Bustamante MMC, Chuyong G, Dobrowski SZ, Grierson P, Harms KE, Houlton BZ, Marklein A, Parton W, Porder S, Reed SC, Sierra CA, Silver WL, Tanner EVJ, Wieder WR (2011) Relationships among net primary productivity, nutrients and climate in tropical rain forest: a pan-tropical analysis. Ecology Letters 14:939–947

Coulston JW, Wear DN, Vose JM (2015) Complex Forest dynamics indicate potential for slowing carbon accumulation in the southeastern United States. Scientific Reports 5: 8002

Dodonov P, Harper KA and Silva-Matos DM (2013) The role of edge contrast and forest structure in edge influence: vegetation and microclimate in the Brazilian cerrado. Plant Ecology 214:1345-1359

Dupuy JM and Chazdon RL (2008) Interacting effects of canopy gap, understory vegetation and leaf litter on tree seedling recruitment and composition in tropical secondary forests. Forest Ecology and Management, 255: 3716-3725

Fick, S.E. and R.J. Hijmans, 2017. WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37 (12): 4302-4315.

Finegan, B., Pena-Claros, M., de Oliveira, A., Ascarrunz, N., Bretharte, M. S., CarrenoRocabado, G., Casanoves, F., Diaz, S., Eguiguren Velepucha, P., Fernandez, F., Licona, J. C., Lorenzo, L., Salgadonegret, B., Vaz, M., Poorter, L. (2015) Does functional trait diversity predict above-ground biomass and productivity of tropical forests? Testing three alternative hypotheses. J. Ecol. 103: 191–201.

Hofhansl, F., Chacón-Madrigal, E., Fuchslueger, L., Jenking, D., Morera-Beita, A., Plutzar, C., et al., 2020. Climatic and edaphic controls over tropical forest diversity and vegetation carbon storage. Sci. Rep. 10, 5066.

Kammesheidt, L. 2002. Perspectives on secondary forest management in tropical humid lowland America. Ambio 31: 243–250.

Kozlowski TT (1999). Soil compaction and growth of woody plants. Scandinavian Journal of Forest Research, 14:596– 619

Laurance, S.G.W., Laurance, W.F., Andrade, A., Fearnside, P.M., Harms, K.E., Vicentini, A., et al., 2010. Influence of soils and topography on Amazonian tree diversity: a landscape-scale study. J. Veg. Sci. 21, 96–106.

Lewis, S.L., Wheeler, C., Mitchard, E.T.A., Koch, A., 2019. Regenerate natural forests to store carbon. Nature 568, 25–28.

Marshall, A.R., Willcock, S., Platts, P.J., (…) Lewis, S.L. (2012) Measuring and modelling aboveground carbon and tree allometry along a tropical elevation gradient. Biological Conservation, 154, 20-33.

Menezes GSC, Cazetta E and Dodonov P (2019) Vegetation structure across fire edges in a Neotropical rain forest. Forest Ecological Management 453, 17587.

Myers, N., 1990. The biodiversity challenge: expanded hot-spot analysis. Environmentalist 10, 243–256.

Norden N, Chazdon RL, Chao A, Jiang AH, Vilchez-Alvarado B (2009) Resilience of tropical rain forests: Tree community reassembly in secondary forests. Ecol. Lett. 12, 385–394

Norden, N., Angarita, H.A., Bongers, F., Martínez-Ramos, M., Granzow-de la Cerda, I., van Breugel, M., et al., 2015. Successional dynamics in Neotropical forests are as uncertain as they are predictable. PNAS 112, 8013–8018.

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. Forest Ecology and Management 479:118580.

Ostertag R (2010) Foliar nitrogen and phosphorus accumulation responses after fertilization: an example from nutrient-limited Hawaiian forests. Plant and Soil 334(1-2): 85–98. doi: 10.1007/s11104-010-0281-x.

Paoli GD, Curran LM (2007) Soil nutrients limit fine litter production and tree growth in mature lowland forest of southwestern Borneo, Ecosystems, 10, 503–518

Pan Y, Birdsey RA, Fang J et al (2011) A large and persistent carbon sink in the world’s forests. Science 333:988–93

Piotto, D., Montagnini, F., Thomas, W., Ashton, M., Oliver, C. (2009) Forest recovery after swidden cultivation across a 40-year chronosequence in the Atlantic forest of southern Bahia, Brazil. Plant Ecol. 205: 261–272

Poorter, L., van der Sande, M.T., Arets, E.J.M.M., Ascarrunz, N., Enquist, B.J., Finegan, B., et al., 2017. Biodiversity and climate determine the functioning of Neotropical forests. Global Ecol. Biogeogr. 26, 1423–1434.

Poorter L, M. T. van der Sande, J. Thompson, E. J. M. M. Arets, A. Alarcón, J. Álvarez-Sánchez, et al. (2015) Diversity enhances carbon storage in tropical forests. Glob. Ecol. Biogeogr. 24, 1314–1328

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

Rocha JIS, Menezes GSC, Cazetta E, Dodonov P and Talora DC (2022a) Seed rain across fire-created edges in a neotropical rainforest. Plant Ecology 223: 247-261.

Rozendaal, D.M.A., Bongers, F., Aide, T.M., Alvarez-Dávila, E., Ascarrunz, N., Balvanera, P., et al., 2019. Biodiversity recovery of Neotropical secondary forests. Sci. Adv. 5, eaau3114.

R Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Santos FM, Terra G, Chaer GM, Monte MA (2018) Modeling the height–diameter relationship and volume of young African mahoganies established in successional agroforestry systems in northeastern Brazil. New For, 10.1007/s11056-018-9665-1

Soong, J.L., Janssens, I.A., Grau, O., Margalef, O., Stahl, C., Van Langenhove, L., et al., 2020. Soil properties explain tree growth and mortality, but not biomass, across phosphorus-depleted tropical forests. Sci. Rep. 10, 2302.

Slik JWF, Aiba S, Brearley FQ, Forshed CHCO, Kitayama K, Nagamasu H, Nilu R, Payne J, Paoli G, Poulsen AD, Raes N, Sheil D, Sidiyasa K, Suzuki E, van Valkenburg JLCH (2010) Environmental correlates of tree biomass, basal area, wood specific gravity and stem density gradients in Borneo's tropical forestsgeb. Global Ecol. Biogeogr. 19: 50–60

Sullivan, M.J.P., Talbot, J., Lewis, S.L., Phillips, O.L., Qie, L., Begne, S.K., et al., 2017.

Diversity and carbon storage across the tropical forest biome. Sci. Rep. 7, 39102.

Tilman, D., Reich, P.B., Knops, J., Wedin, D., Mielke, T. Lechman,C. (2001) Diversity and product ivityina long-term grassland experiment. Science, 294, 843–845.

Wang, Y.-P., Zhang, Q., Pitman, A.J., Dai, Y., 2015. Nitrogen and phosphorous limitation reduces the effects of land use change on land carbon uptake or emission. Environ. Res. Lett. 10, 014001.

Wright, S.J., Yavitt, J.B., Wurzburger, N., Turner, B.L., Tanner, E.V.J., Sayer, E.J., Santiago, L.S., Kaspari, M., Hedin, L.O., Harms, K.E. (2011) Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest. Ecology 92:1616–25

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. Data from: Towards a Worldwide Wood Economics Spectrum. Dryad Digital Repository. Available online: https://doi.org/10.5061/dryad.234.