Francisco d'Albertas Gomes de Carvalho

Modulação do estoque de carbono em
paisagens fragmentadas da Mata Atlântica
em função dos efeitos de borda

Edge effects modulation of carbon stocks in
fragmented Atlantic forest landscapes

São Paulo
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À minha mãe

Epígrafe

“Our posturings, our imagined self-importance, the delusion that we have some privileged position in the Universe, are challenged by this point of pale light. Our planet is a lonely speck in the great enveloping cosmic dark. In our obscurity, in all this vastness, there is no hint that help will come from elsewhere to save us from ourselves. It is up to us. It's been said that astronomy is a humbling, and, I might add, a character-building experience. To my mind, there is perhaps no better demonstration of the folly of human conceits than this distant image of our tiny world. To me, it underscores our responsibility to deal more kindly and compassionately with one another and to preserve and cherish that pale blue dot, the only home we've ever known.”

Carl Sagan. Pale Blue Dot

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GRATIDÃO

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Introdução Geral

Serviços ecossistêmicos

Após a revolução industrial, o processo de transformação de paisagens naturais em paisagens antrópicas se intensificou de tal maneira que o período em que vivemos é definido por alguns autores como uma nova era, o Antropoceno (Steffen *et al.*, 2011). Verdadeira força geológica, nossa espécie converteu ou modificou mais da metade das áreas naturais do planeta e um quarto de toda a superfície terrestre hoje é ocupada por produção agrícola para atender a crescente demanda por comida, transporte e moradia (MEA, 2005).

É cada vez mais evidente que o esgotamento dos recursos naturais em favor do crescimento econômico não pode ser estendido indefinidamente e não beneficia a todos (Arrow *et al.*, 1995; Rockstrom *et al.*, 2009). Ao mesmo tempo em que continuamos a modificar intensamente os ecossistemas naturais, a demanda por benefícios providos pelos ecossistemas cresce de modo insustentável (Carpenter *et al.*, 2009). Neste sentido, ainda que reconheçamos que os benefícios providos pela natureza são cruciais para a manutenção da vida no planeta, paradoxalmente, estes benefícios não são adequadamente considerados no atual sistema econômico ou quantificados em termos comparáveis aos serviços econômicos e de capital manufaturado. Isto faz com que os benefícios providos dos recursos naturais tenham um peso desproporcionalmente pequeno nas decisões políticas globais. Esta negligência pode comprometer a permanência dos seres humanos na biosfera (Costanza *et al.*, 1997).

Logo, é fundamental compreender os limites em que é possível garantir a qualidade de vida de nossa espécie e continuar a alimentar uma população mundial crescente, que deverá chegar ainda em 2050 a 9,6 bilhões de pessoas (United Nations, 2013), sem comprometer os recursos da Terra. É necessário, portanto, encontrar maneiras de atribuir a devida importância aos recursos naturais vitais à nossa sobrevivência no processo de tomada de decisões e de criação de políticas de médio e longo prazo. Esta é a ideia central por trás do conceito de serviços ecossistêmicos. Dentro desta abordagem, podemos entender

os processos e funções ecológicas que beneficiam o Homem ou “as contribuições diretas e indiretas dos ecossistemas ao bem-estar humano” (TEEB, 2010) como serviços prestados pelos ecossistemas. A degradação dos recursos naturais, considerando os SE, deixa de ser considerada apenas um mal necessário ao desenvolvimento, mas como uma perda de serviços importantes para os seres humanos, para os quais muitas vezes não dispomos de substitutos, e quando dispomos, eles são bastante custosos. Isto completa o desenvolvimento de um marco, em que a natureza é definida em uma linguagem compatível com a economia.

Nas ultimas décadas, houve um grande aumento na preocupação em se incorporar serviços ecossistêmicos à economia (de Groot *et al.*, 2002). Este movimento culminou na publicação da “Avaliação Ecossistêmica do Milênio” (MEA, 2005), cujo objetivo foi avaliar as consequências das mudanças nos ecossistemas sobre o bem-estar humano e estabelecer uma base científica para fundamentar as ações necessárias para assegurar a conservação e uso sustentável dos ecossistemas. Este documento faz uma síntese dos serviços ecossistêmicos e consolida uma classificação que é amplamente adotada, inclusive no presente trabalho. Os serviços ecossistêmicos são agrupados em quatro categorias: (i) serviços de suporte, tais como formação do solo, fotossíntese e ciclo de nutrientes; (ii) serviços de provisão, incluindo alimentos, água, madeira e fibras; (iii) serviços de regulação, relacionados ao clima, à ocorrência de inundações, propagação doenças, regulação da qualidade da água, entre outros; (iv) serviços culturais, que fornecem benefícios recreacionais, estéticos e espirituais.

Paisagem e carbono

Na fase atual do Antropoceno, há um intenso processo de fragmentação e conversão de florestas tropicais em florestas secundárias (Achard *et al.*, 2002; Wright, 2010; Hansen *et al.*, 2013). Grande parte do conhecimento acerca das consequências ecológicas da fragmentação de florestas tropicais provém do projeto BDFFP (*Biological Dynamics of Forest Fragments Project*), que estuda este tema desde 1979 em experimentos na Amazônia. O processo de fragmentação -

ou subdivisão - das florestas tropicais, ao alterar o arranjo espacial da paisagem, reduz a possibilidade das plantas e animais de se moverem através da paisagem, afetando assim diversos processos ecológicos, entre eles os movimentos de forrageamento, dispersão e migração (Haddad *et al.*, 2015; Mitchell *et al.*, 2015). Além disso, manchas de habitat menores abrigam menos espécies, contêm populações menores, com maior risco de extinção e sofrem mais efeitos de borda, o que afeta negativamente a persistência de espécies nativas (Mitchell *et al.*, 2015).

A fragmentação degrada os recursos naturais, causa perda de biodiversidade e altera diversos serviços ecossistêmicos (Mitchell *et al.*, 2015), como a produção primária e a capacidade da vegetação em absorver o gás carbônico e assim armazenar carbono na biomassa. O desmatamento, já disseminado em regiões temperadas, cresceu intensamente nos trópicos nos últimos 50 anos, o que resultou na perda de um terço da cobertura florestal do planeta (Hansen *et al.*, 2013). Apenas entre os anos 2000 e 2010, mais de 90 mil quilômetros quadrados de florestas tropicais foram suprimidos a cada ano, o que representou cerca de 70% das perdas globais neste período (FAO & JRC, 2012). Esta “quebra” de habitats naturais em fragmentos menores e isolados, imersos em matrizes adversas dominadas por pastos, agricultura e áreas urbanas, é a principal causa do declínio da biodiversidade global, juntamente com as mudanças climáticas (Sala *et al.*, 2000; Pereira *et al.*, 2010; Rands *et al.*, 2010; IPCC, 2014).

As florestas têm um papel fundamental no ciclo global do carbono e na mitigação do aquecimento global. Elas armazenam grande quantidade de carbono, quase a mesma quantidade que a atmosfera (Grace, 2004; Bonan, 2008). A maior parte deste carbono está em florestas tropicais (Houghton *et al.*, 2009). Portanto, ao suprimir e queimar a vegetação nos trópicos, estamos emitindo grandes quantidades de carbono. De fato, estimativas apontam que aproximadamente 12% do carbono emitido anualmente para a atmosfera, (1,2 Pg) é proveniente de desmatamento e degradação florestal (van der Werf *et al.*, 2009). Além da emissão via supressão, o aquecimento global pode elevar a emissão de carbono ao aumentar a taxa de mortalidade e decomposição de árvores (Apps and Price, 1996).

Apesar de sua importância, ainda existe grande incerteza na quantificação do balanço de carbono de florestas tropicais (Houghton, 2005; Houghton *et al.*, 2009; van der Werf *et al.*, 2009; Malhi, 2010; Pan *et al.*, 2011; Baccini *et al.*, 2012). Uma fonte importante de incertezas está associada a processos que não destroem a floresta, mas alteram sua estrutura, como é justamente o caso da fragmentação. Um dos principais processos ecológicos desencadeados pela fragmentação é o efeito de borda, ou seja, as alterações associadas à criação de fronteiras artificiais e abruptas na floresta (Laurance *et al.*, 2011). A abertura de fronteiras expõe partes do ambiente florestal às influências da matriz adjacente, em particular às condições climáticas externas, que são bastante distintas das encontradas no interior das florestas (Ewers and Banks-Leite, 2013). Isto provoca um aumento na mortalidade de árvores nas bordas (Laurance *et al.*, 1998), principalmente árvores de grande porte, mais suscetíveis à turbulência dos ventos e ao estresse fisiológico (Laurance *et al.*, 2000; Laurance *et al.*, 2001; D'angelo *et al.*, 2004). Logo, estas árvores grandes declinam em abundância (Oliveira *et al.*, 2004) e são substituídas por espécies pioneiras de crescimento rápido e lianas, que possuem madeira menos densa e menor biomassa (Laurance *et al.*, 2001; Laurance, 2002; Laurance *et al.*, 2006; Laurance *et al.*, 2011).

Na Amazônia, o aumento na mortalidade de árvores se dá principalmente nos primeiros 100 m de borda em direção ao interior do fragmento (Laurance *et al.*, 1997). Este fenômeno provoca uma queda na biomassa florestal acima do solo e uma perda significativa de carbono, além do que é emitido diretamente pelo desmatamento. Calcula-se que o montante de carbono emitido devido aos efeitos de borda pelas florestas tropicais corresponde a 9-24% da perda anual de carbono devido ao desmatamento (van der Werf *et al.*, 2009; Pan *et al.*, 2011; Baccini *et al.*, 2012; Ciais *et al.*, 2013). Ainda assim, a ação de efeitos de borda é em geral desconsiderada no balanço de carbono na vegetação (Putz *et al.*, 2014).

A perda de carbono devido aos efeitos de borda está relacionada à área e ao formato dos fragmentos. Ademais, como a estrutura da maior parte das manchas de florestas em paisagens humanas é complexa, boa parte da vegetação está sujeita a influência de duas ou mais bordas, com diferentes idades, histórias e usos da terra adjacente. Esta influência combinada é capaz de gerar respostas

mais intensas do que o esperado pela ação dos efeitos de borda considerados individualmente (Ries *et al.*, 2004). Supreendentemente, poucos estudos focaram na interação de múltiplas bordas em paisagens fragmentadas, ou seja, nos **efeitos aditivos de borda** (Malcolm, 1994; Harper *et al.*, 2005).

Além destes efeitos aditivos, o tempo de criação das bordas também é um parâmetro importante a se levar em consideração em estimativas de estoque de carbono. Resultados de simulação sugerem que as mudanças estruturais na floresta entram em equilíbrio após 100 anos de criação das bordas e que a maior parte das mudanças acontece nos primeiros 30 anos, com 50% de perda de carbono (Putz *et al.*, 2014). Para fragmentos localizados na Amazônia, estima-se que a redução na biomassa pode chegar à metade após quatro anos de ruptura da floresta e 80% após apenas 10 anos (Numata *et al.*, 2009).

Muitos trabalhos se propõem a investigar a regulação e a provisão de serviços ecossistêmicos em diferentes escalas, algumas mais locais outras mais globais (e.g. Costanza *et al.*, 1997; Costanza, 2008; RS *et al.*, 2013). Porém, estudos em escala local são insuficientes para incorporar todos os padrões e processos ambientais, econômicos e sociais relevantes aos seres-humanos. Por outro lado, em escalas muito globais, é difícil integrar detalhadamente os mecanismos que ocorrem em escala local, pois não há resolução suficiente (Wu, 2013). Logo, existe uma lacuna de conhecimento em escalas intermediárias de paisagem, que possibilitem aliar o entendimento dos mecanismos reguladores com uma maior precisão no poder de extrapolação espacial. Deste modo, estudos de serviços ecossistêmicos em uma escala regional, que englobe os elementos que constituem a paisagem, parecem ser promissores (Wu, 2006; Forman, 2008). Afinal, é nesta escala que as pessoas enxergam o espaço que as circunda, de modo que a configuração e a composição da paisagem as afetam e são afetadas por elas (Wu, 2013). Isto aumenta a importância em compreender e manejar as paisagens para manter tanto os serviços ecossistêmicos como a biodiversidade (Bennett *et al.*, 2005; Mitchell *et al.*, 2015).

Objetivos e premissas

Tendo isto em conta, partimos da seguinte premissa: se os padrões da paisagem afetam a biodiversidade e os processos ecológicos, eles também devem ser fundamentais no controle da geração e provisão de SE. Portanto, deve haver configurações mais adequadas (ou ótimas) para a manutenção das funções e serviços ecossistêmicos. Uma pergunta central que deriva desta premissa, e que norteia a busca por paisagens sustentáveis, é compreender como a estrutura da paisagem afeta a manutenção duradoura dos serviços ecossistêmicos e do bem-estar humano, diante das incertezas existentes quanto as consequências das complexas interações entre pessoas e suas paisagens.

Como já discutimos, a biodiversidade de plantas na floresta e o fornecimento de armazenamento e sequestro de carbono são reduzidos com a fragmentação (Numata *et al.*, 2011; Putz *et al.*, 2014). Além disso, maior biodiversidade de plantas esta relacionada à maior oferta de outros serviços ecossistêmicos (Mitchell *et al.*, 2015). A produção primária e o armazenamento de carbono pela vegetação são, portanto, serviços importantes para o bem-estar humano. Desse modo, relacionando medidas de estoque de carbono com parâmetros da estrutura da paisagem, como a proximidade e quantidade de bordas entre fragmentos de vegetação nativa e áreas agrícolas, buscamos contribuir com o entendimento dos efeitos da perda de habitat sobre este serviço. Para isso, investigamos a quantidade de carbono estocada em manchas de floresta nativa em paisagens fragmentadas, levando em consideração a idade das bordas e o seu formato. Propomos as seguintes hipóteses: (i) bordas têm menos carbono armazenado do que o interior de fragmentos, maior densidade de árvores pequenas e menor densidade de árvores grandes, menor área basal e menor altura mediana das árvores; (ii) bordas antigas estão a mais tempo sofrendo ação dos efeitos de borda e devem apresentar menor quantidade de carbono estocado do que bordas mais recentes, menor área basal, menor altura mediana das árvores e menor densidade de árvores; (iii) borda em quinas estão sobre a ação de mais bordas, considerando efeitos aditivos, por isso, devem ter menos carbono estocado do que bordas retas, menor área basal, menor altura mediana das árvores e menor densidade de árvores.

O sistema de estudo

Para testar estas hipóteses, utilizamos como modelo de estudo a Mata Atlântica brasileira. A Mata Atlântica abriga uma biota tropical diversa e altos níveis de endemismo (Mittermeier *et al.*, 2005), entretanto, como muitas outras florestas tropicais, tem um longo e intenso histórico de desmatamento (Dean, 1996), sendo por isso considerada um dos cinco principais *hotspots* globais de biodiversidade (Myers *et al.*, 2000). Sua distribuição atual corresponde a 11,4 a 16% da cobertura original (150 milhões de hectares), essencialmente em fragmentos pequenos, menores que 50 hectares e em que 46% da área de floresta está a menos de 100 metros das bordas (Ribeiro *et al.*, 2009a). Existe ainda uma forte pressão exercida pela expansão de cultivos agrícola, como a cana-de-açúcar e o eucalipto, além das áreas urbanas e da extensa ocupação por áreas de pastagem (Ribeiro *et al.*, 2011).

Além da importância em termos de biodiversidade, a Mata Atlântica é também fonte de serviços ecossistêmicos de valor inestimável como, por exemplo, a provisão de água para mais de 125 milhões de brasileiros, regulação climática (Joly *et al.*, 2014) e armazenamento de carbono (Putz *et al.*, 2014). Putz *et al.* (2014) estimam que a Mata Atlântica perde em média 0.43 Mg C ha⁻¹ ano⁻¹ devido aos efeitos negativos da fragmentação. No entanto, apenas uma proporção muito reduzida da Mata Atlântica (1,05%) está em Unidades de Conservação de Proteção Integral (Ribeiro *et al.*, 2009a). Dessa maneira, é muito importante garantir a conservação das áreas de Mata Atlântica inseridas em propriedades privadas (Melo *et al.*, 2013) e neste sentido, o estudo, quantificação e valoração de serviços ecossistêmicos, como o estoque de carbono, podem sustentar ações dos proprietários de terra em prol da manutenção destas florestas.

O trabalho de campo foi realizado na região da Cantareira-Mantiqueira, no Planalto Atlântico ao norte do Estado de São Paulo (Ponçano, 1981; Fig. 1), onde predomina a Floresta Ombrófila Densa Submontana (IBGE, 2012). O relevo é caracterizado por colinas suaves e morros mais inclinados, com elevação entre 700 a 1700 metros (N-S 22°50' - 23°26' e L-O 45°53'-46°46'; Fig. 1). Esta região abriga um importante corredor ecológico e tem um alto valor para a conservação

da biodiversidade (MMA, 2007). Além do mais, ela contém o Sistema Cantareira, que é responsável pelo abastecimento de água de quase 50% da população da cidade de São Paulo, o que o torna um dos maiores sistemas de abastecimento do mundo (Whately and Cunha, 2007).

Até os anos 60, a principal atividade econômica na região era a pecuária, entretanto, a inundação das áreas férteis para construção dos reservatórios de abastecimento de água provocou mudanças econômicas profundas (Whately and Cunha, 2007). As áreas de pasto vêm sendo substituídas por projetos imobiliários para casas de férias e condomínios residenciais, bem como reflorestamentos de *Eucalyptus spp* (Whately and Cunha, 2007). Este processo de ocupação da paisagem levou ao cenário atual, em que mais de 70% da área é caracterizada por uso antrópico, enquanto apenas 26,3 % é composto de vegetação nativa (IF, 2010), essencialmente em locais declivosos, onde a ocupação humana não é viável (Whately and Cunha, 2007). Esta vegetação remanescente é composta principalmente de florestas secundárias, em diferentes estágios sucessionais (Ditt *et al.*, 2008).

Implicações

Esperamos que os dados gerados por este estudo possam auxiliar na elaboração de políticas públicas de ordenamento territorial e manutenção de serviços ecossistêmicos em paisagens agrícolas. Acreditamos que uma melhor compreensão de como a configuração da paisagem modula o estoque de carbono poderá auxiliar a mensurar o efeito das alterações no uso da terra sobre esses serviços. Além disso, a estrutura florestal que mantém o estoque de carbono afeta também diversos outros SE, como a proteção do solo, ciclagem de água e provisão de produtos florestais (Putz and Redford, 2010). Desse modo, estimativas confiáveis de estoque de carbono podem também contribuir para determinar como ocorre a perda de outros serviços ecossistêmicos.

Figura 1. Mapa de Conectividade do Estado de São Paulo (SMA, 2007) com um ranking de prioridade para estabelecimento de corredores ecológicos, que varia de 1 (menor prioridade) a 8 (maior prioridade) (A); Localização da região de estudo, o corredor Cantareira-Mantiqueira(B), área com alta prioridade de conexão ; Cobertura florestal (verde) de Mata Atlântica na região (IF, 2010) (C).

Capítulo único

Carbon stocks in tropical forests with a long history of fragmentation are extensively modulated by edge effects

Abstract

Despite the importance of fragmentation for tropical forest carbon (C) balance, most of our knowledge comes from few sites in the Amazon and disregard underlying processes that relates landscape configuration with C stocks. Particularly, accurate estimation of CO₂ emission from fragmentation must account for *additive edge effects* and *edge age*. Here we investigated those effects on carbon stock and forest structure (density, height, basal area) in eight old-growth forest (≥ 70 years) fragments (13 to 362 ha), surrounded by pasture, in the Brazilian Atlantic forest region. We sampled 5,297 stems in four distinct treatments, distributed in each fragment: fragment interiors; old (> 50 years) corner edge; old straight edge; and new (< 50 years) straight edge. Aboveground biomass (AGB) was estimated from tree height and diameter at breast height (DBH), and converted to carbon. C stock was highly variable between treatments, scoring from 6.61 Mg ha⁻¹ up to 87.96 Mg ha⁻¹ (average of 29.55 ± 14.97 Mg ha⁻¹). Interior treatments had higher C stock, basal area, tree stem density and taller trees than edges. We found no significant effects of edge age or additive edge effects on C stocks. These results suggest that edge effects in the heavily-disturbed Atlantic rainforest may differ than those observed in more recently fragmented tropical forests, such as the Amazonian forest. In heavily human-modified landscapes, edge effects on tree mortality and reduction on AGB may contribute to overall higher levels of degradation across entire forest fragments, reducing the observed difference between edge and interior habitats, and suggesting that existing Amazonian forest models may underestimate the true impacts of tropical forest fragmentation for C storage.

Keywords: Ecosystem services, Climate regulation, REDD+, Tropical forest restoration, Human disturbance.

1. Introduction

Tropical forests contain one-third of terrestrial global carbon (C) stocks (Dixon *et al.*, 1994). The conversion of natural landscapes into cultivated systems and concomitant degradation of remaining forest fragments are responsible for the emission of an estimated 1.2 Pg C yr⁻¹ to the atmosphere (van der Werf *et al.*, 2009). This input to greenhouse gas concentration accumulation in the atmosphere contributes significantly to global climate change, which is considered a major driver of global biodiversity and ecosystem service loss (MEA, 2005; IPCC, 2014). Deforestation and forest degradation continue to increase in tropical regions (Achard *et al.*, 2002; Hansen *et al.*, 2013), where over 90 thousand km² yr⁻¹ were deforested between 2000 and 2010 (FAO & JRC, 2012). Damages from global climate change currently cost the global economy an estimated \$1.2 trillion dollars annually (DARA and the Climate Vulnerable Forum, 2012), making the primary-production-mediated regulation of climate through carbon storage an essential ecosystem service (ES).

Besides directly causing CO₂ emissions, deforestation frequently results in increased fragmentation of remaining forest, resulting in smaller and more isolated forest patches (Fahrig, 2003), as well as an increase in edge density and subsequent edge-effects (Lovejoy *et al.*, 1986). Edges expose parts of the forest environment to the microclimatic and biotic conditions of the matrix surrounding forest fragments (e.g. pasture and agriculture areas) (Laurance *et al.*, 2011), and reduce the forests capacity to buffer external climatic conditions (Ewers and Banks-Leite, 2013), particularly within the first 100 m (Laurance *et al.*, 1997; Santos *et al.*, 2008; Tabarelli *et al.*, 2008). Tree mortality is one of the most important biological consequences of edge-effects (Laurance *et al.*, 1998), particularly for large trees, which are disproportionately susceptible to wind turbulence and physiologic stress (Laurance *et al.*, 2000; Metzger, 2000; D'angelo *et al.*, 2004; Lindenmayer *et al.*, 2012). As large tree abundance declines, vegetation with lower wood density is favored, including early succession pioneer species and lianas (Laurance *et al.*, 2001; Laurance, 2002; Laurance *et al.*, 2006; Santos *et al.*, 2008; Tabarelli *et al.*, 2008). One consequence of edge-effects is thus a decrease in aboveground biomass (AGB). However, most current

models of CO₂ emission due to deforestation disregard this process (e.g. van der Werf *et al.*, 2009), suggesting that CO₂ emission in fragmented landscapes may be underestimated. Recently, Putz *et al.* (2014) estimated that the additional carbon loss due to forest edge creation can be responsible for 9-24% of the total annual C loss associated with tropical forest deforestation.

More accurate estimation of carbon emission from forest edges must take into account the spatial configuration of forest edges and the edge age. In fragmented landscapes with high edge density, many locations are close to two or more edges (Ries *et al.*, 2004), greatly increasing the impact of edge-effects in an *additive edge effects* (termed additive edge-effects; Malcolm, 1994). In a recent quantitative meta-analysis (see Porensky and Young, 2013), ten from eleven studies that reported empirical data on edge interactions demonstrated that additive edge-effects can boost the magnitude of ecological processes occurring at edges (Zheng and Chen, 2000; Ries *et al.*, 2004; Fletcher, 2005; Laurance *et al.*, 2007). Despite the clear need to understand how single and interactive edge effects influence key ecosystem services, including carbon storage, there is a lack of knowledge on the mechanisms that govern those relationships, especially in the complex patch and landscape geometry of fragmented landscapes (Ries *et al.*, 2004; Fletcher, 2005; Porensky and Young, 2013).

The impact of edges on biomass can be modulated not just by distance from edges (a common proxy for edge effects), but also by the period of time since edge creation, or the *edge age*. Data from Amazonian landscapes shows that most biomass loss occurs in the first years after edge creation, and tapers off in subsequent years (Ferreira and Laurance, 1997; Laurance *et al.*, 1997; Numata *et al.*, 2009). This may be driven by tree mortality, which is especially intense in the first years after edge creation (Lovejoy *et al.*, 1986; Sizer and Tanner, 1999; D'angelo *et al.*, 2004) with the rapid onset of microclimatic changes in newly opened edges that are more susceptible to heat, light and wind penetration from the matrix (Kapos, 1989; Didham and Lawton, 1999). Simulated data show a tendency for edge-induced structural change in forests structure to slow only 100 years after edge creation, despite most change are expected to happen in the first 30 years.

Carbon emission from fragmented forest has most commonly been estimated through simulations or remote sensing techniques, based mostly on observed patterns from a single Amazonian research project, the Biological Dynamics of Forest Fragments Project (BDFFP) (Laurance *et al.*, 2011; Berenguer *et al.*, 2014). There is a surprising lack of empirical studies for most tropical forests linking edge effects to carbon. Indeed, a recent systematic review of the literature that investigated how edge-effects influence AGB found only nine publications, with apparently context-dependent positive, negative and neutral relationships between edge effects and aboveground biomass (Melito *et al.*, submitted) .

Beyond the relative paucity of studies documenting edge effects on C stocks in tropical forests, there is also a knowledge gap in understanding how different landscape configurations may regulate C stocks and balance. Therefore, the true potential of tropical anthropogenic landscapes to provide carbon services is unknown (Houghton, 2005; van der Werf *et al.*, 2009; Malhi, 2010; Pan *et al.*, 2011). The discovery of mechanistic links between C outcomes and landscape structure parameters would enable a more precise estimation of the potential C storage capacity of different human modified landscapes. Moreover, those links can help to generalize results across spatial scales (Bennett *et al.*, 2005; Wu, 2006; Forman, 2008; Mitchell *et al.*, 2015) and improve estimations conducted at global scales (FAO, 2006; Putz *et al.*, 2014).

To contribute to fill this data gap, we investigated how *additive edge effects* and *edge age* affect forest structure and carbon stock in fragmented landscapes from the Brazilian Atlantic Rain forest. Specifically, we compared forest structure (plot density, height, basal area and C stock) between fragment edges and interiors across different edge ages, and accounting for additive edge effects, within secondary forest fragments. We predicted that C stock, density of larger trees, basal area, median tree height will be lower and density of small trees will be higher: **(i)** in edges when compared to fragment interiors; **(ii)** in older edges in relation to more recently created edges; and **(iii)** in corner edges when compared with straight edges.

2. Materials and methods

2.1. Study site

The Brazilian Atlantic forest hosts a very diverse tropical biota with high levels of endemism (Mittermeier *et al.*, 2005). As many tropical forests around the globe, the Atlantic forest's long history of deforestation and fragmentation (Dean, 1996) has resulted in present-day archipelagos of small forest fragments, surrounded by relatively inhospitable matrices, dominated by pastures, agriculture and urban areas. The Atlantic forest is consequently considered one of the top five global biodiversity hotspots (Myers *et al.*, 2000). The current Atlantic forest distribution covers only 11.4 - 16.0% of its original extent (150 million ha), mostly in small fragments (< 50 ha). Nearly half of this remaining forest (46%) is located within less than 100 m of a forest edge (Ribeiro *et al.*, 2009a). Besides its importance for the maintenance of biodiversity, the Atlantic forest is also a source of essential ecosystem services, including water provisioning for over 125 million people (three-quarters of Brazil's population), climate regulation (Joly *et al.*, 2014) and carbon stocks (Putz *et al.*, 2014).

The study was conducted in the Cantareira-Mantiqueira region of the Atlantic Plateau of São Paulo state (Ponçano, 1981). The biodiversity conservation value of the Cantareira region has been formally recognized by the Environmental Ministry of Brazil (MMA, 2007). In addition the Cantareira-Mantiqueira region is responsible for almost 50% of the water supply of the city of São Paulo, constituting one of the world's largest urban water supply systems (Whately and Cunha, 2007). This region is covered with low montane evergreen forest and is characterized by rolling and steep convex hill with elevation ranging between 700 to 1700 m of altitude (N-S 22°50' - 23°26' and E-W 45°53'-46°46'; Fig. 2). This humid subtropical climate has dry winters and hot and humid summers, with annual rainfall that varies between 1350 and 2000 mm, and a mean annual temperature range of 15-22°C (www.cpa.unicamp.br). The approximately 26.3% of remaining forest in the region (IF, 2010) is classified as ombrophilous dense forest (IBGE, 2012) in different successional stages (Ditt *et al.*, 2008; Ribeiro *et al.*, 2009a; Teixeira *et al.*, 2009), and is relegated to steep slopes of lower agropastoral value (Whately and Cunha, 2007). The region continues to undergo

land-use change, with much of the extensive cattle pasture area being further converted either into large-scale real estate development or incorporated into 'reforestation' projects, planted with *Eucalyptus spp.* (Fadini, 2005; Whately and Cunha, 2007).

2.2. Site selection and sampling design

Sample sites were selected in order to contrast edge ages (> 50 years vs < 50 years), and edge configurations (straight edges vs corner edges), but controlling forest fragment age (> 70 years). In order to select the studied fragments and sites, we first identified areas with land use and land cover changes that would potentially create edges with different ages. We considered available low resolution (pixel = 30 m) land use maps (1989, 1999, 2000, 2003 and 2010; Whately and Cunha, 2007; IF, 2010), and produced a temporal series of detailed land cover maps (1:5,000), using high resolution satellite images (SPOT and Digital Globe) and aerial photography (1:20,000-1:35,000) for the reference years 1962, 1978, 2003, 2007 and 2010. Considering the oldest forest fragments (the ones existing in the oldest available photograph of 1962 with a forest structure), we looked for changes in border limits to determine different edge age classes. We were able to identify eight old-growth fragments (replicates) with two categories of border age (edges created before 1962, hereafter 'old' edges; and edges created after 1962, hereafter 'new' edges) and with the two categories of edge location (corner, and straight). Fragments ranged from 13 to 362 ha.

In each fragment, we placed five ($n = 5$) samples grouped into four treatments: fragment interior ($n = 2$); old corner edge ($n = 1$); old straight edge ($n = 1$); and new straight edge ($n = 1$) (Fig. 3). To be considered a straight edge, a site's sampling plot had to be at least 50 m far from corners. We avoided placing plots in slopes higher than 20 degrees, and attempted to standardize soil type to latosols - the predominant soil type in the region. Once matrix type can strongly modulate the impact of edge effects (Bender and Fahrig, 2005), we only considered edges with agricultural fields, a relatively inhospitable matrix that can magnify edge effects (Laurance *et al.*, 2006). Each sample treatment

consisted of five circular plots with 10 m radius and center distant at least 20 m from one another. Edge plots were placed 5-40 m from the closest edge; interior plots were placed at least 110 m distant from every edge. All GIS analyses were conducted in ArcGIS 10 (ESRI, 2015).

2.3. Estimation of above ground biomass (AGB)

Measurements of aboveground carbon were conducted in April-September, 2014. In each circular plot, we measured the height and diameter at breast height (DBH) at 1.3 m from the ground of all trees, palms and ferns with DBH higher than 10 cm, including standing dead trees and palms.

We calculated aboveground biomass of individual trees using the allometric equation developed for secondary Atlantic forest by Burger and Delitti (2008):

$$B = \exp(-3.676 + 0.951 \times (\ln d^2 \times h)), \quad (1)$$

where B = tree above ground biomass (kg), d = diameter at breast height (cm), and h = tree height (m).

Allometric equations for palms and ferns were provided by Hughes *et al.* (2013) and Tiepolo *et al.* (2002), respectively:

$$PB = \exp((0.9285 \times \ln d^2 + 5.7236) \times 1.050001)/10^3 \quad (2)$$

$$FB = -4266348/(1 - 2792284 \times \exp -0.313677 \times h), \quad (3)$$

where PB = palms above ground biomass (kg), FB = tree ferns above ground biomass (kg).

Then, we calculated biomass per plot by the sum of individual biomass within each sampled plot, expressed as Mg ha^{-1} . The conversion of AGB to carbon stock follows Martinelli *et al.* (2000):

$$C = AGB \times 0.474 \quad (4)$$

2.4. Response variables

Data on carbon stock density (Mg ha^{-1}) were averaged across all plots to obtain plot-level estimates. We separated this C stock into two tree size classes, grouped by tree DBH (i.e. small, 10-30 cm and larger ≥ 30 cm) to explore possible differences in the proportion of DBH classes across different edge types. However, the small number of trees over 30 cm DBH prevented us from using this class as a response variable in the following analyses. Complementary to carbon stock, we utilized tree density, median tree height and basal area as response variables.

2.5. Explanatory variables

To evaluate the additive effects of edges, we used a model that considers the influence of all edges, as the integral of all edge effects within a predetermined distance from a focal point (D_{max}) (Malcolm, 1994). We called this index the total edge effect index (**EEI**). In the present study, we assume that the most intense effect on AGB loss due to edge effects occurs within 100 m from edges to the interior of the fragment (i.e. $D_{\text{max}} = 100$ m). The model was implemented using the R package 'edgex' (Goldberg and Ries, 2010) in the R statistical environment (R Core Team, 2014). We used our forest /non-forest classification map (year 2012) with 5 m pixel resolution, to generate raster images of edge density for each fragment (Fig. S1).

Besides edge age (> 50 years vs < 50 years) and position (straight edges vs corner edges), for each plot we considered an additional explanatory variable, the degree of human disturbance. To capture human disturbance across the study region, we adopted the disturbance or anthropogenic index (**ADI**) proposed by Magalhães *et al.* (2015). This index considers 14 indicators divided into three groups, with different weights in the final index score. Group 1 indicators (weight=1) are those with implications for ecosystem simplification and local biodiversity loss, such as hunting or non-timber forest product extraction. Group 2 indicators (weight=1.5) are associated with ecosystem destruction or substitution, including livestock grazing, conversion to agriculture or logging.

Group 3 indicators (weight=2) have the potential to impact ecosystems in both manners, promoting biodiversity loss and ecosystem substitution (e.g. fire). The index ranges from 0 in areas without visible current human impact to 1 for fully impacted areas.

$$I_i = (g_0/g_m) \times p \quad (5)$$

$$AI = \sum_i^n I_i / P \quad (6)$$

Where g_0 is the observed level of the indicator i , g_m is the maximum value of each indicator, p is the correspondent weight for each group and P is the sum of the weights of all indicators.

2.6. Statistical analysis

To test the hypothesis that edges will have lower C stock and smaller values of forest structure parameters (tree density, median tree height, basal area) than fragment interiors (hypothesis i), we built a linear mixed model of C stock as a function of plot position (edge or interior). Response variables for edge type comparisons were transformed in a ratio of edge plot type divided by the mean value of interior plots from the same fragment, in a paired approach. To test the effect of edge age (hypothesis ii) and edge position (hypothesis iii) on C stock and forest structure, we first fit C stock ratio as a function of *edge age*, **EI** and **AI** in a series of additive and interactive models. Additionally, we fitted other models using the ratio of basal area per plot, median height per plot and tree density per plot as response variables. For all models, we included fragment identity as a random effect, assuming that plots from the same fragment are expected to be more similar in comparison with plots from other fragments. We also included in model selection a null model with the response variable in function of a constant value. We selected the most plausible model using Akaike criterion Information (AIC), comparing the likelihoods of all candidate models. We considered models with $AIC \leq 2$ as having substantial support evidence and being equally plausible (Burnham, 2004). We fitted the models using lme4 package (Bates *et al.*, 2014) for R software version 3.1.0 (R Core Team, 2014).

3. Results

General pattern

Across the eight fragments, we sampled a total of 5,297 stems (≥ 10 cm DBH), comprising 3,006 stems in edge plots and 2,291 in interior plots. The total edge and interior plot areas sampled were 3.77 ha and 2.48 ha, respectively. The majority of sampled stems were trees (89%), followed by tree ferns (2.41%), palms (1.58%), and dead woody biomass (7.28%). For all plots, thin (DBH ≤ 30 cm) and short (height < 11 m) trees composed the majority of stems sampled, followed by medium trees (DBH 30 – 50 cm; height 11–16 m), while large (DBH > 50 cm) and tall trees (≥ 21 m height) were almost absent (Fig. 4A and 4B). C stock was highly variable between plots, ranging from 6.61 – 87.96 Mg, with a total average of 29.55 ± 14.97 Mg ha⁻¹. Despite this variability, mean C stocks per edge treatment were quite similar (Fig. 5), and only interior plots seems to be substantially different from edge treatments. Tree density per treatment shows a tendency to be in accordance with our predictions, with old corner edge having lower density, followed by old straight edges, new straight edges and interior treatment. Such trend does not seem to occur for basal area and median tree height, in which edge treatments have similar scores and interior treatments are slightly higher (Fig. S2A, S2B and S2C, respectively). We excluded tree ferns, palms, dead stems and one unusually large tree from all further analyses, as live trees were responsible for 99 % C pool.

Edge effects

The AIC top model for the contrast between interior and edge plots demonstrated that interior plots (mean = 33.52 ± 16.81 Mg ha⁻¹) have higher C stock than edge plots (mean = 27.51 ± 13.29 Mg ha⁻¹) (Fig. 6), in accordance with the first hypothesis. In fact, interior plots had higher tree density, basal area and median tree height (Table 1; Fig. S3, S4 and S5, respectively) in comparison with edge plots.

We failed to detect any significant age and additive edge effects intensity on C stocks between edge types (Table 2). Nevertheless, using only C stock from trees

of 10-30 cm DBH, we did find that this class diameter composes a bigger fraction of C pool in new edges, in comparison with old edges (Fig. 7). In addition, new edges have higher tree density than old edges (Fig. S6). Besides, for both new and old edges, tree density increases with the decrease of additive edge effects index (*EI*). For basal area and median height, we did not find any relation with edge effects (Table 2).

4. Discussion

We assessed the implications of edge effects for carbon stocks in a tropical forest disturbed and fragmented for a long time with a well-sampled dataset, comprised of over 5,000 sampled stems within eight forest fragments considering additive edge effects and edge age. We corroborate our initial hypothesis that interior forests have different tree structure than edge forests in Atlantic rainforest patches, with higher carbon stock, basal area, tree density and taller trees. However, contrary to our expectations, we found few differences in C stocks in edges with different ages and configurations, suggesting a distinct pattern of edge effect in those disturbed tropical landscapes.

Interior vs edges C stocks in disturbed tropical forests

The structural differences observed between edge (0-50 m) and interior (>100 m) were less pronounced than the clear patterns observed in the *Biological Dynamics of Forest Fragments Project* (BDFFP), in the Amazon forest. This long-running project has provided the vast majority of theoretical and empirical work on tropical forest above-ground carbon response to fragmentation and edge effects (Laurance *et al.*, 2011). A key difference between Atlantic forest and Amazonian forest study sites is the intensity of recent and modern-historical human disturbance. Anthropogenic disturbance is a major driver of heterogeneity in forest environments, and influences community structure and dynamics (Pickett and White, 1985; Caswell and Cohen, 1991) by favoring species with 'fast' spectrum demographic traits (Carreño-Rocabado *et al.*, 2012), including pioneer tree species (Oliveira *et al.*, 2004; Tabarelli *et al.*, 2008). In the Amazon, most fragments are old growth, rather than secondary

forest such as most fragments across the Atlantic forest fragments (Dean, 1996). In those old growth forests, edge effects are essentially related with the higher mortality of old trees, which concentrate most of above-ground carbon stocks (Stephenson *et al.*, 2014). However, those old trees are largely absent from most secondary Atlantic forest fragments, even within fragment interiors, considerably reducing the differences between interior and edges. Moreover, many human disturbances in the Amazon are relatively recent (e.g. from the early 1980s) and additional human disturbances such as major fires and logging were prevented in the BDFFP sites (Laurance *et al.*, 2011). We suggest thus that the long history of human disturbance in the Atlantic forest creates a heterogeneous mosaic of forest with different degrees and ages of disturbance, which may mask clearer differences between edges and interior areas.

Our results suggest thus that C stock in the Atlantic forest is widely affected by human disturbance and edge effects, creating a situation of low C stocks across the entire extent of remaining fragments, independent of edge distance, age or location. Indeed, previous studies in the Atlantic forest present evidence for strong reductions in AGB even into central areas of fragments up to 500 m from forest edges (de Paula *et al.*, 2011). The same authors were only able to find a clear distinction between interior (defined as 200-1000 m) and edge plots for a very large (3,500 ha) reserve – where anthropogenic disturbances were intentionally minimized over time. Interior plots retained a large amount of carbon ($202.8 \pm 23.7 \text{ Mg ha}^{-1}$), essentially concentrated in the emergent layer that was preserved. This stock is approximately three times larger than the one found in edges and other fragments from the same region, and six times more than interior plots sampled across our study region, showing the high potential of well-conserved Atlantic forests to stock carbon. Unfortunately, this situation is atypical for Atlantic forests, where most remnant patches are smaller than 50 ha and 46 % of all forest areas are under 100 m from edges (Ribeiro *et al.*, 2009a) and are highly disturbed. The vast majority of old fragments in our study region do not even have interior areas farther than 200 m from edges, reason why we did not sample more distant areas. This scenario may as well be the future of

other tropical forests, such as the Amazonian forest, if present rates of deforestation persist for a long time.

While the overall small size and complex shapes of our forest fragments suggests that even our interior plots may be submitted to edge effects, we still found differences in tree size between interior and edge plots. Probably, two inter-related processes are acting to influence tree size. First, frequent and long-term disturbance may be retarding the regeneration process, resulting in a prevalence of small tree species and pioneers throughout fragments. Second, increased mortality due to edge effects tends to influence entire small forest fragments, though with higher intensity in the edges. Wind and abiotic factors such as aridity and higher temperatures (Murcia, 1995; Chen *et al.*, 1999) cause structural changes in the forest, altering tree proportions and making stems shorter for a given basal DBH (Oliveira *et al.*, 2008; de Paula *et al.*, 2011). Oliveira *et al.* (2008) reported that trees were 30% shorter in edges when compared with edge-effect free areas in the Atlantic forest. In addition, the relaxing of competition for light in edges might further reduce tree height for the same DBH (Osuri *et al.*, 2014), as trees do not need to trespass the canopy to receive light. Consequently, trees in edge plots with the same DBH as interior plots tend to be a little smaller. In fact, observational (Feldpausch *et al.*, 2011) and experimental (Holbrook and Putz, 1989) data shows that both plot density and shade can modulate tree H:DBH and, as a consequence, carbon stock.

It is important to highlight that although we expected to find contrasting differences in forest structure and above-ground carbon between fragment interiors and edges, there is remarkably little evidence to support this in the literature (Melito *et al.*, submitted). One of the reasons raised to explain the lack of difference is related to tree density. Schedlbauer *et al.* (2007), for example, observed elevated tree density at forest edges, as well as higher AGB, and did not detect significant differences in forest structure or AGB along 350 m edge-interior transects in forest-pasture edges with more than 20 years in Costa Rica. High tree density in forest edges is a function of increased light availability and subsequent seedling and sapling growth (Williamslinera, 1990; Sizer and Tanner, 1999). This dense edge vegetation can contribute to AGB similarity between

forest edge and interior environments (Schedlbauer *et al.*, 2007). It is very probable that the same phenomenon has happened in forest patches from our study region and the elevated density at some forest edges created situations in which edge plots had higher AGB than interior plots, reducing general contrast between edges and interiors.

Edge age and additive effects

Initially we supposed that old edges would have accumulated more negative microclimate effects than new edges, and for this reason, they would have lower AGB than new edges. Likewise, we supposed that corner edges submitted to the effects of more than one edge would be more negatively affected by edges. However, results did not support these predictions suggesting that climatic-driven edge effects could be masked by anthropogenic disturbances, time since edges were submitted to those disturbances in sampled edges and retarded successional process.

Edges are subject to relatively higher intensity of microclimate changes, especially in terms of light regime and water balance (Kapos, 1989; Williams-Linera, 1990; Laurance and Yensen, 1991), which often results in high tree mortality (Lovejoy *et al.*, 1986; Sizer and Tanner, 1999; Laurance *et al.*, 2002; Numata *et al.*, 2009). However, this overall biomass decay can occur rapidly, in the immediate few years after edge creation (Numata *et al.*, 2009). Given that even our 'new' edges (< 50 years) would have already passed through this acute biomass decay stage, older edges may actually have relatively higher or similar AGB than new edges (an opposite effect than we predicted). Compounding this loss of biomass in fragment edges, the increased exposure and improved access to forest edges by humans may drive the selective logging and removal of larger trees in both new and older edges.

The high density of bamboo and lianas in the field sites sampled may further contribute to the degradation of the forest fragments. Griscom and Ashton (2006) detected a reduction in tree height about 50–55% relative to trees in the same size classes in bamboo-free plots in the Peruvian Amazon. Also in the

Amazon, Alvira and Putz (2004) found that largest trees were the most affected by lianas and had more crown damage than trees without lianas. As the fragments visited here were extensively disturbed by lianas and bamboos (37 % of all plots), at interior and edges areas, it is reasonable to suppose that physical damage imposed on trees might have contributed to the low density of larger trees, with subsequent impacts on C storage, independently of forest edge location or age.

Our results do not support as well the pattern of additive edge effects observed in the Amazonian forest (e.g. Malcolm, 1994; Laurance *et al.*, 2007). The edge effect index (*EEI*) was selected in an additive model with edge age, interacting with the anthropic index (*AI*), when we considered only small trees (Table 2). Areas under high rate of anthropic disturbance and closer to edges have a high proportion of small trees, particularly for new edges. It seems that beyond the occurrence of edge effects in the remnant forests, the study region is under very strong confounding effect of direct anthropogenic disturbance.

Additionally, previous studies variously suggest that secondary Atlantic forest may recover the structure of old growth forests after approximately 25–45 years (do Nascimento *et al.*, 2014; Zanini *et al.*, 2014), or much longer (Piotto *et al.*, 2009). Even though all fragments visited have at least 70 years, the range of C stock values exhibited by edge and interior plots correspond to early (< 25 y old) or mid-successional secondary forest (25-45 yr old) (Figure 8.). Indeed, we have clear evidence of a retarded successional process. For example, it is expected that large (DBH > 50 cm) and very large trees (DBH > 100 cm) play an important role in AGB pool for the Atlantic forest, similar to other Neotropical forests (DeWalt and Chave, 2004; Alves *et al.*, 2010; Lindner, 2010). However, those size classes were almost absent from both interior and edge plots in this study (4A). Santos *et al.* (2008) suggested that these successional pathways may be crucially distinct for smaller forest patches, and that small fragments may instead become less structurally similar to old growth forests, through the gradual replacement of shade-tolerant trees species by fast-growing, low biomass pioneer species (Chave *et al.*, 2006)(Fig. 9). Such a process would correspond with an increasing

homogeneity of forest structure and resultant carbon stocks between interior and edge areas, as we report previously.

Conservation implications

Tropical forests contain approximately one-third of terrestrial carbon pool (Dixon *et al.*, 1994). Consequently, changes in C balance fluxes in tropical forest AGB have potentially important consequences on global C cycle, warming and biodiversity (Fearnside, 2004; Chave *et al.*, 2005; Malhi, 2010), and accurate landscape measurements of C stocks are critical to generating a global view of the capacity of tropical forests to contribute to climate regulation. To date, published works are overly based on observations from the Amazon forest (Melito *et al.*, submitted). Unfortunately, the Amazonian scenario may not be representative of most tropical forests in the near future, as human-modified forests are becoming the rule in the humid tropics (Achard *et al.*, 2002; Melo *et al.*, 2013; Haddad *et al.*, 2015).

Differently from the Amazon forests, where edge effects have a clear and measurable influence in AGB and C stock, considering edge age and additive effects, such patterns are much less pronounced in human dominated landscapes, where long-history of disturbance greatly increases local heterogeneity in forest structure. In those landscapes, remnant forest patches are in an early-to-middle-successional state and forest regeneration is not expected to result in late-successional or mature old-growth forests (Melo *et al.*, 2013), at least without restoration. Our results of the carbon stock on early-stage and disturbed tropical forests have implications for improving our understanding of the carbon storage potential of restored tropical forests.

The UN Framework Convention on Climate Change (UNFCCC) has already recognized forest degradation as a major contributor to CO₂ emissions and incorporated it into the Reducing Emissions from Deforestation and Forest Degradation (REDD+) mechanism (Gibbs *et al.*, 2007). Therefore, REDD+ and other mechanisms of payment for ecosystem services (PES) are possible finance options for reforestation projects in those human-dominated landscapes. The

Cantareira region, particularly, is very suitable for investment, as reforestation and degradation mitigation can greatly enhance carbon storage, water supply and biodiversity (Ditt *et al.*, 2010; Shimamoto *et al.*, 2014). With proper management, restoration projects have the potential to triple C stocks and enhance other ecosystem services.

Conclusions

We found no significant age or additive edge effects on carbon stocks in the studied Atlantic forest fragments. Structural differences between different edge types and even with interior areas were much less pronounced than the clear patterns observed for the Amazon forest. Besides, the carbon stock values we found are particularly low suggesting a significant effect of C loss by human disturbances in the fragmented Atlantic forest landscapes. Despite the difficulty to link historical disturbance with present forest structure, the legacy of past and present human impacts, with complex interactions, must play a fundamental role on determining spatial heterogeneity of tree community structure and dynamics in tropical forests. Our results suggest that much of unexplained variability in vegetation surveys in tropical forests could be related to the unique history of human use of each forest site.

We can thus conclude that studied fragments are essentially composed by early successional stage of forest, submitted to frequent or intense disturbance regimes, resulting in a distribution of AGB that is almost independent of forest distance or age pattern. Our results suggest that incorporating edge effects in models to extrapolate C stocks at larger scales can be a challenging and complex task, and that local heterogeneity will generate high levels of error in large-scale estimation based on local data. We interpret our data as additional evidence of complex, and still poorly-understood effects of anthropogenic disturbance in human dominated landscapes.

5. Figures

Figure 2. Location of study fragments, near the municipality of Nazaré Paulista, in the northeast of São Paulo State. Light gray shade is the Atlantic forest domain; dark gray shades are remnant forest patches; black shades are the studied fragments (1-8). Plots locations are indicated in Fig. S1.

Figure 3. Schematic representation of the sampling design. In all fragments we inventoried 5 treatments (black dots) **I** - one in a new straight edge; **II** - two in the fragment interior; **III** - one in an old corner edge; and **IV** - one in an old straight edge.

Figure 4. Log trees ha⁻¹ per size classes of DBH (A) and height (B). white – old corner edge plots; lightgray – old straight edge plots ; gray – new straight edge plots; dark gray – interior plots.

Figure 5. Mean C stocks and standard error of plot treatments: old corner edge, old straight edge; new straight edge; interior. Bars are divided by DBH classes, in cm: white – 10-30 cm DBH; light gray – 30-50 cm DBH; gray – 50-60 cm DBH; dark gray – larger than 70 cm DBH.

Figure 6. Carbon stock distribution of interior treatment plots versus edge treatment plots. Interior plots have higher carbon stocks ($t=2.24$; $p=0.025$). Middle black bars represent median value, boxes are first and third quartiles, and whiskers are 95% confidence intervals.

Figure 7. Contribution of C stock in trees of 10-30 cm in relation to the total C stock. Ratio values represent this contribution from all edge plots in relation to interior plots (paired by fragment). New edges have a higher contribution of trees of 10-30 cm DBH ($t=-3.09$; $p=0.002$). Middle black bars represent median value, boxes are first and third quartiles, and whiskers are 95% confidence intervals.

Figure 8. C stocks from Atlantic forest in initial, medium and advanced stage of regeneration, compared with our values. Middle black bars represent median value, boxes are first and third quartiles, and whiskers are 95% confidence intervals.*Romitelli (2014), de Souza *et al.* (2011), de Paula *et al.* (2011), Tiepolo *et al.* (2002), Groeneveld *et al.* (2009), Torres *et al.* (2013), Ditt *et al.* (2010);** de Souza *et al.* (2011), Tiepolo *et al.* (2002), Burger (2005);*** de Paula *et al.* (2011), Groeneveld *et al.* (2009), Alves *et al.* (2010), Cunha *et al.* (2009), Ribeiro *et al.* (2009b), Amaro *et al.* (2013), Vilela *et al.* (2000), Ditt *et al.* (2010), Lindner and Sattler (2011).

Figure 9. Hypothetical increases in carbon stock during successional time in two different scenarios: connected and large patches (solid line); isolated small patches (dotted line). We predict that while connected and large patches can recover levels of carbon stock similar to primary forests after enough time, isolated forest patches will remain with lower levels and will take longer to recover this partial carbon stock.

6. Tables

Table 1. Candidate model sets following AIC model selection for the comparison between edge and interior treatments. We used as response variables carbon stock values per plot, basal area per plot, median tree height per plot and density per plot. The predictor variable **Position** indicates whether the plot is located in the interior (>110 m) or at the edge of the fragments sampled (5-40 m).

Model	ΔAIC	weight
Carbon stock ~ position + (1 fragment)	0.000	0.797
Null	2.731	0.203
Basal area ~ position + (1 fragment)	0.000	1.000
Null	16.781	0.000
Median height ~ position + (1 fragment)	0.000	0.998
Null	12.487	0.002
Density ~ position + (1 fragment)	0.000	0.778
Null	2.505	0.222

Table 2. Candidate model sets following AIC model selection for the comparison between edge treatments. We used as response variables the ratio of overall data on carbon stock values per plot (C); the ratio of the contribution of C stock in trees of 10-30 cm in relation to the total C stock (C₁₀₋₃₀), the ratio of basal area per plot, the ratio of median tree height per plot and the ratio of density per plot. Ratio values represent the contribution of each edge treatment plots in relation to interior plots (paired by fragment). We considered all models with $\Delta AIC \leq 2$ as equally plausible. Models coefficients are presented in Table S1.

Model	ΔAIC	Weight
Null	0	0.253
Ratio C ~ edge age + (1/fragment)	0.23	0.225
Ratio C ~ AI + edge age + (1/fragment)	1.431	0.124
Ratio C ~ edge age + EI + (1/fragment)	1.868	0.1
Ratio C ~ EI + (1/fragment)	1.994	0.093
Ratio C ~ AI+ edge age + EI + (1/fragment)	3.025	0.056
Ratio C ~ edge age + AI*EI + (1/fragment)	3.066	0.056
Ratio C ~ AI + edge age *EI + (1/fragment)	3.27	0.049
Ratio C ~ AI + EI + (1/fragment)	3.43	0.045
Ratio C ₁₀₋₃₀ + edge age + (1/fragment)	0	0.391
Ratio C ₁₀₋₃₀ ~ edge age + AI*EI + (1/fragment)	0.352	0.328
Ratio C ₁₀₋₃₀ ~ AI + edge age + (1/fragment)	0.914	0.211
Null	3.338	0.062
Ratio C ₁₀₋₃₀ ~ AI+ edge age + EI + (1/fragment)	3.587	0.055
Ratio C ₁₀₋₃₀ ~ AI + EI + (1/fragment)	5.397	0.022
Ratio C ₁₀₋₃₀ ~ edge age + EI + (1/fragment)	5.663	0.02
Ratio C ₁₀₋₃₀ ~ AI + edge age *EI + (1/fragment)	7.079	0.01
Ratio C ₁₀₋₃₀ ~ EI + (1/fragment)	7.753	0.007
Ratio density ~ edge age + EI + (1/fragment)	0	0.534
Ratio density ~ AI+ edge age + EI + (1/fragment)	1.923	0.204
Ratio density ~ edge age + AI*EI + (1/fragment)	3.461	0.095
Ratio density ~ AI + edge age *EI + (1/fragment)	3.575	0.089
Ratio density ~ edge age + (1/fragment)	4.323	0.061
Ratio density ~ EI + (1/fragment)	7.801	0.01
Ratio density ~ AI + EI + (1/fragment)	9.399	0.005
Null	18.17	0
Ratio density ~ AI + edge age + (1/fragment)	19.7	0
Null	0	0.285
Ratio basal area ~ EI + (1/fragment)	0.731	0.198
Ratio basal area ~ AI + edge age + (1/fragment)	1.332	0.146
Ratio basal area ~ edge age + (1/fragment)	1.825	0.114
Ratio basal area ~ AI + EI + (1/fragment)	2.183	0.096
Ratio basal area ~ edge age + EI + (1/fragment)	2.73	0.073
Ratio basal area ~ AI+ edge age + EI + (1/fragment)	4.18	0.035

Model	ΔAIC	Weight
Ratio basal area ~ edge age + $AI*EI + (1/\text{fragment})$	4.67	0.028
Ratio basal area ~ $AI + \text{edge age} *EI + (1/\text{fragment})$	4.825	0.025
Null	0	0.657
Ratio median height ~ $AI + \text{edge age} + (1/\text{fragment})$	1.514	0.308
Ratio median height ~ edge age + $(1/\text{fragment})$	7.611	0.015
Ratio median height ~ $EI + (1/\text{fragment})$	7.795	0.013
Ratio median height ~ $AI + EI + (1/\text{fragment})$	9.296	0.006
Ratio median height ~ edge age + $EI + (1/\text{fragment})$	15.28	0
Ratio median height ~ edge age + $AI*EI + (1/\text{fragment})$	16.26	0
Ratio median height ~ $AI + \text{edge age} + EI + (1/\text{fragment})$	16.76	0
Ratio median height ~ $AI + \text{edge age} *EI + (1/\text{fragment})$	20.03	0

Supporting Information

Figure S1. Location of studied plots in the eight selected fragments. All fragments are represented in the same spatial scale. Each black dot represents a 10 m radius plot. We have inventoried 25 plots in each fragment. Gray shades represent the total edge effect index (EI) value of all edges within 100 from the matrix in each pixel of the image. The darker the color, the more edges density are being considered in the pixel.

Figure S2. Mean tree density (A), basal area (B) and median tree height (C) per treatments, with standard error.

Figure S3. Tree density of interior plots versus edge plots. Interior plots have higher values ($t=2.09$; $p=0.044$). Middle black bars represent median value, boxes are first and third quartiles, and whiskers are 95% confidence intervals.

Figure S4. Basal area of interior plots versus edge plots. Interior plots have higher values ($t=2.09$; $p=0.044$). Middle black bars represent median value, boxes are first and third quartiles, and whiskers are 95% confidence intervals.

Figure S5. Median tree height of interior plots versus edge plots. Interior plots have higher values ($t=2.34$; $p=0.025$). Middle black bars represent median value, boxes are first and third quartiles, and whiskers are 95% confidence intervals.

Figure S6. Ratio of tree density in function of additive edge effects (*EI*). *EI* values were rescaled by centering values and dividing by 2 standard deviations. Tree density is higher in plots under less edge density. Besides, new edges have higher tree density than old edges ($t=-3.22$; $p= 0.001$). Ratio values represent the contribution from all edge plots in relation to interior plots (paired by fragment). Black dots and black trend line represent old edges plot tree density in function of *EI*. Gray dots and gray trend line represent new edges plot tree density in function of *EI*. Gray shades are 95% confidence intervals.

Table S1. Candidate model sets following AIC model selection for the comparison between edge treatments. Response variables for edge type comparison were transformed in a ratio of edge plot type divided by the mean value of interior plots from the same fragment, in a paired approach. (*EI*) - additive edge effect index; edge age - old or new; (*AI*) - index of anthropic disturbance. We have included fragment as a random variable.

Explanatory variables	AI	edge age	<i>EI</i>	edge age: <i>EI</i>	<i>AI</i> : <i>EI</i>	Δ AIC	Weight
Ratio C							
						0	0.253
		+				0.23	0.225
	1.031					1.431	0.124
		+	0.044			1.868	0.1
			0.005			1.994	0.093
	1.285	+	0.042			3.025	0.056
	1.522	+	0.096		-3.769	3.066	0.056
	1.27	+	0.28	+		3.27	0.049
	1.03		0			3.43	0.045
Ratio C₁₀₋₃₀							
		+				0	0.391
	1.952	+	0.035		-3.236	0.352	0.328
	1.815					0.914	0.211
						3.338	0.062
	1.638	+				3.587	0.055
	1.783		0.001			5.397	0.022
		+	0.069			5.663	0.02
	1.659	+	0.002			7.079	0.01
			0.08	+		7.753	0.007
Ratio density							
		+	0.169			0	0.534
	0.299	+	0.169			1.923	0.204
	-0.146	+	0.149		2.218	3.461	0.095
	0.291	+	0.229	+		3.575	0.089
		+				4.323	0.061
			0.228			7.801	0.01
	0.736		0.227			9.399	0.005
						18.171	0
	0.88					19.699	0
Ratio basal area							
						0	0.285
			0.067			0.731	0.198
	0.927	+				1.332	0.146
						1.825	0.114

Explanatory variables	AI	edge age	EI	edge age:EI	AI:EI	Δ AIC	Weight
	0.83	+	0.063			2.183	0.096
		+	0.066			2.73	0.073
	0.837	+	0.065		-3.038	4.18	0.035
	1.183	+	0.103			4.67	0.028
	0.836	+	0.213	+		4.825	0.025
Ratio median height							
						0	0.657
	0.245					1.514	0.308
		+				7.611	0.015
			-0.005			7.795	0.013
	0.248		-0.005			9.296	0.006
		+	-0.001			15.283	0
	0.333	+	0.006		-0.802	16.256	0
	0.256	+	-0.001			16.756	0
	0.274	+	0.067	+		20.034	0

Table S2. Published carbon (C) stock values from tropical forest inventories. We divided data into Atlantic Forest publications and other tropical forest publications. Sampling method, stage of forest succession, forest type and country where the inventory were done are presented when available. Inventory methodologies to sample stems and calculate C stocks are not standardized.

Sampling	Stage of forest sucessions		Forest type	Country	Carbon stock	Source
Atlantic forest						
Edge plots	Initial		Montane moist forest	Brazil	27.28±13.18	This study
Edge transect	Initial		Montane moist forest	Brazil	30.91±11	Romitteli (2014)
Edge plots	Mature (protetected area)		Lowland semi-deciduous forest	Brazil	42.1	Paula <i>et al.</i> (2011)
Fragment plots	Initial		Submontane moist forest	Brazil	42.89	Tiepolo <i>et al.</i> (2002)
Fragment plots	Initial	(protected area)	Lower montaine moist forest	Brazil	45.12	Groeneveld <i>et al.</i> (2009)
Fragment plots	Initial		Seasonal semideciduous forest	Brazil	56.31	Torres <i>et al.</i> (2013)
Fragment plots	Initial		Montane moist forest	Brazil	71.6	Ditt <i>et al.</i> (2010)
Fragment plots	Medium		Seasonal semideciduous forest	Brazil	36.54	Souza (2011)
Fragment plots	Medium		Submontane moist forest	Brazil	101.96	Tiepolo <i>et al.</i> (2002)
Fragment plots	Medium		Atlantic moist forest	Brazil	116.13	Burger (2005)
Fragment plots	Medium/advanced		Seasonal semideciduous forest	Brazil	79.38	Souza (2011)
Fragment plots	Medium/advanced		Submontane moist forest	Brazil	106.19	Tiepolo <i>et al.</i> (2002)

Sampling	Stage of forest sucessions	Forest type	Country	Carbon stock	Source
Fragment plots	Advanced (protetected area)	Lower montane moist forest	Brazil	65.8	Groeneveld <i>et al.</i> (2009)
Fragment plots	Advanced (protected area)	Seasonally flooded forest	Brazil	72.996	Alves <i>et al.</i> (2010)
Fragment plots	Advanced	Atlantic moist forest	Brazil	79.06	Cunha <i>et al.</i> (2009)
Fragment plots	Advanced (protected area)	Lowland moist forest	Brazil	94.04	Alves <i>et al.</i> (2010)
Fragment plots	Advanced	Montane moist forest	Brazil	94	Vilela <i>et al.</i> (2012)
Fragment plots	Advanced	Montane moist forest	Brazil	113	Vilela <i>et al.</i> (2000)
-	Advanced	Montane moist forest	Brazil	113.43	Ditt <i>et al.</i> (2010)
Fragment plots	Advanced	Montane moist forest	Brazil	127	Vilela <i>et al.</i> (2000)
Fragment plots	Mature	Seasonal semideciduous forest	Brazil	83.34	Ribeiro <i>et al.</i> (2009)
Fragment plots	Mature (protetected area)	Semideciduos seazonal forest	Brazil	108.98 ± 35.33	Amaro <i>et al.</i> (2013)
Fragment plots	Mature (protected area)	Submontane moist forest	Brazil	113.43	Alves <i>et al.</i> (2010)
Fragment plots	Mature	Submontane ombrophilous forest	Brazil	118.5±37.87	Lindner and Sattler (2012)
Fragment plots	Mature (protected area)	Montane moist forest	Brazil	124.52	Alves <i>et al.</i> (2010)

Sampling	Stage of forest sucsessions	Forest type	Country	Carbon stock	Source
Fragment plots	Mature (protetected area)	Montane ombrophilous forest	Brazil	148.36 ±22.75	Lindner and Sattler (2012)
Fragment plots	Mature	Lowland semideciduous forest	Brazil	158.553	Rolim et al. (2005)
Fragment plots	Mature (protetected area)	Dense ombrophilous forest	Brazil	206.95	Lindner(2010)
Interior plots	Initial	Montane moist forest	Brazil	33.24±16.7	This study
Interior plots	Advanced (protetected area)	Lower mountane moist forest	Brazil	117.5	Groeneveld <i>et al.</i> (2009)
Interior plots	Mature (protetected area)	Montane moist forest	Brazil	124.52	Alves <i>et al.</i> (2010)
Other tropical forest					
Edge transect	Mature (protetected area)	Tropical wet forest	Costa Rica	170.3 ± 4.5	Schedlbauer <i>et al.</i> (2007)
-	Initial	Lower montaine moist forest	Puerto Rico	53.1	Marin-Spiotta <i>et al.</i> (2007)
-	Old growth	Lower montane moist forest	Puerto Rico	103.9	Marin-Spiotta et al(2007)
-	Old growth (protetected area)	Lowland moist forest	Singapure	104.12	Ngo <i>et al.</i> (2013)
	Mature (protetected area)	Lowland moist forest	Panama	84.89	DeWalt and Chave (2004)
-	Mature (protetected area)	Lowland moist forest	Singapure	111.21	Ngo <i>et al.</i> (2013)
-	Mature (protetected area)	Lowland moist forest	Panama	133.19	Chave <i>et al.</i> (2003)

Sampling	Stage of forest sucessions	Forest type	Country	Carbon stock	Source
Plots	Mature (protetected area)	Lowland moist forest	Brazil	133.29	Vieira <i>et al.</i> (2004)
Plots	Mature	Lowland semideciduous forest	Brazil	138.45	Nascimento <i>et al.</i> (2007)
-	Mature (protetected area)	Central Amazonian	Brazil	154.29	Nascimento and Laurance (2002)
-	Mature (protetected area)	Lowland wet forest	Brazil	170.74	Vieira <i>et al.</i> (2004)

Conclusões gerais

Corroboramos nossa primeira hipótese ao constatar que o interior dos fragmentos possui uma estrutura florestal distinta das bordas, com maior estoque de carbono acima do solo, maior área basal, maior densidade de árvores e árvores mais altas. Além disso, pudemos constatar que as bordas novas possuem uma proporção maior de troncos finos (10 a 30 cm de diâmetro a altura do peito) compondo o estoque de carbono. Esta classe de diâmetro também apresentou maior densidade de indivíduos nas bordas novas. Entretanto, não encontramos diferenças em termos de estoque de carbono comparando os diferentes tipos de borda, tanto em relação à idade como a efeitos aditivos de borda analisando a totalidade dos dados. Deste modo, refutamos as hipóteses iniciais nas quais esperávamos encontrar maior estoque de carbono em bordas velhas e em bordas em quinas, respectivamente. Além disso, os valores de estoque de carbono que encontramos foram surpreendentemente baixos, dentre os menores publicados para a Mata Atlântica.

Apesar de termos detectado diferenças na estrutura florestal entre o interior e as bordas dos fragmentos, mesmo considerando distâncias relativamente curtas, estas diferenças são menos pronunciadas do que os padrões claros já descritos para a floresta Amazônica. Esses dados sugerem que o padrão observado na Amazônia (Laurance *et al.*, 2011) não deve ser utilizado como modelo de estudos para outras paisagens tropicais, em particular aquelas que têm um longo histórico de fragmentação e perturbação, como as da Mata Atlântica. Nossos resultados demonstram que incorporar efeitos de borda nos modelos para extrapolação de estoques de carbono é algo complexo e que a alta heterogeneidade local deve gerar imprecisões em estimativas de larga escala.

Uma diferença essencial entre a região Amazônica e a Mata Atlântica está ligada ao histórico de distúrbios antrópicos. A Mata Atlântica, desde o início da colonização portuguesa, sofreu um intenso processo de destruição e degradação florestal (Dean, 1996), o que ainda não ocorreu nas áreas investigadas na Amazônia como, por exemplo, nos fragmentos do BDFFP (*Biological Dynamics of Forest Fragments Project*). As alterações provocadas pela ação humana direta no

caso da mata Atlântica geram uma grande heterogeneidade local nos ambientes florestais, alterando a estrutura da comunidade de árvores (Pickett and White, 1985; Caswell and Cohen, 1991) e afetando negativamente o balanço de carbono (MEA, 2005). Portanto, em situações de distúrbios constantes e intensos, como no caso da maior parte dos fragmentos de Mata Atlântica, os efeitos de borda sobre a comunidade de árvores e, conseqüentemente, sobre o estoque de carbono, podem ser mascarados, dificultando a detecção de padrões.

Considerando que as florestas tropicais armazenam cerca de um terço de todo o estoque global terrestre de carbono (Dixon *et al.*, 1994), fatores que levam a alterações nos fluxos de carbono nestas florestas são de suma importância em termos de regulação climática e biodiversidade (Fearnside, 2004; Chave *et al.*, 2005; Malhi, 2010). Deste modo, estes fatores devem ser levados em consideração se desejamos realizar estimativas precisas e realistas da capacidade regional das paisagens tropicais em armazenar carbono, que possam ser usadas posteriormente em extrapolações globais. No entanto, atualmente, os trabalhos publicados que estimam o estoque de carbono em larga escala são baseados nos padrões observados na Amazônia (Melito *et al.*, submitted), que, conforme demonstrado com este estudo, não podem ser usados como modelo para outras florestas tropicais, principalmente aquelas mais longamente perturbadas (Achard *et al.*, 2002; Melo *et al.*, 2013; Haddad *et al.*, 2015). Nestas paisagens mais modificadas, as manchas remanescentes de floresta tendem a se manter em estágios sucessionais iniciais ou intermediários e é pouco provável que elas se tornem florestas com a estrutura de uma floresta madura (Melo *et al.*, 2013). Portanto, é provável que estimativas globais de estoques de carbono em paisagens antrópicas baseadas no modelo amazônico incorram em um elevado grau de imprecisão.

Em uma perspectiva da ecologia de paisagens, áreas degradadas, como nossa região de estudo, oferecem ótimas oportunidades para restauração e conservação de florestas, pois com o manejo correto, é possível elevar consideravelmente a provisão de diversos serviços ecossistêmicos importantes, como o controle de erosão e provisão de água e armazenamento de carbono (Ditt *et al.*, 2010), e contribuir com os esforços de mitigação das mudanças climáticas

(Chisholm, 2010; Hall *et al.*, 2012; Gilroy *et al.*, 2014). O sistema Cantareira, em particular, é um local bastante promissor para este tipo de iniciativa devido a sua grande importância para o suprimento de água para a cidade de São Paulo, além de ter um alto potencial de aumento na capacidade de armazenamento de carbono. Comparando os valores de carbono com outros trabalhos publicados na Mata Atlântica, é possível constatar um potencial de triplicar o estoque de carbono na região.

A Organização das Nações Unidas já reconhece a degradação de florestas tropicais como um vetor importante de emissão de CO₂ para a atmosfera, e incorporou a degradação nos mecanismos de REDD+ (redução de emissão por desmatamento e degradação (Gibbs *et al.*, 2007). Logo, REDD+ e outros mecanismos de mercado, como pagamento por serviços ambientais, podem se basear em nossos resultados e serem usados para financiar projetos de restauração em paisagens altamente fragmentadas.

Deste modo, nosso estudo tem importantes implicações ao aumentar a compreensão sobre o potencial de armazenamento de carbono em fragmentos inseridos em paisagens humanas. Nossos dados podem ser interpretados como uma evidência adicional da predominância de efeitos de borda em paisagens antrópicas (*sensu* Santos *et al.*, 2008), somados a uma complexa e ainda pouco compreendida interação com distúrbios antrópicos. Assim, para mitigar os efeitos da elevação da concentração de CO₂ na atmosfera e as alterações climáticas decorrentes, precisamos reduzir a degradação florestal nas florestas tropicais e investir em amplos programas de restauração florestal.

Resumo

Apesar da reconhecida importância da fragmentação no balanço de carbono (C) das florestas tropicais, a maior parte do conhecimento a cerca deste assunto provém de estudos conduzidos na floresta Amazônica e desconsidera processos relacionados à influência da configuração da paisagem. Em particular, estimativas precisas da emissão de CO₂ devido à fragmentação devem levar em consideração efeitos aditivos de borda e a idade das bordas. Nós investigamos estes efeitos sobre parâmetros estruturais de florestas (densidade, altura e área basal das árvores) e no estoque de C em oito fragmentos florestais (13 a 362 ha) antigos (≥ 70 anos), cercados de pastagens, em uma região de Mata Atlântica. Amostramos 5297 troncos, divididos em quatro tratamentos em cada um dos fragmentos: interior dos fragmentos; bordas antigas (> 50 anos) em quina; bordas antigas retas; bordas novas (< 50 anos) retas. Calculamos a biomassa acima do solo (BAS) através de equações alométricas que consideram a altura do tronco e seu diâmetro à altura do peito (DAP) e convertimos esse valor em carbono estocado na vegetação. O estoque de C foi altamente variável entre tratamentos, abrangendo valores entre 6.61 Mg ha⁻¹ até 87.96 Mg ha⁻¹ (média = 29.55 ± 14.97 Mg ha⁻¹). As áreas de interior continham um estoque de C maior, bem como maior área basal, densidade de árvores e árvores mais altas do que as de borda. No entanto, a seleção de modelos não detectou influência da idade ou de efeitos aditivos no estoque de C. Nossos resultados sugerem que os padrões de efeitos de borda para a Mata Atlântica são diferentes dos observados em florestas tropicais fragmentadas mais recentemente, como é o caso da Amazônia. A Mata Atlântica tem um longo histórico de perturbação humana e uma dinâmica complexa de desmatamento e regeneração, que pode levar a uma condição de degradação generalizada, posto que até áreas mais distantes das bordas em manchas remanescentes de Mata Atlântica já perderam quantidades significativas de carbono. Nestas paisagens antrópicas, os efeitos de borda que atuam sobre a mortalidade de árvores e na redução da BAS podem ser mais abrangentes do que inicialmente estimado pelos modelos construídos para a floresta Amazônica.

Palavras-chave: Serviços ecossistêmicos, Regulação climática, REDD+, Restauração de florestas tropicais, Distúrbios humanos.

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