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**Efeitos da Fragmentação Florestal na Biomassa
em Florestas Tropicais**

*Effects of Forest Fragmentation on Biomass in
Tropical Forests*

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*Effects of Forest Fragmentation on Biomass in
Tropical Forests*

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Resumo

Apesar das florestas tropicais serem a mais importante fonte mundial de carbono da porção terrestre do globo devido ao armazenamento de carbono na biomassa acima do solo, elas são também o alvo primário do desmatamento. A conversão das florestas Tropicais em áreas antropogênicas pode interromper o fluxo biológico e também levar a severas mudanças microclimáticas na borda dos fragmentos. A combinação desses efeitos pode engatilhar profundas mudanças na composição da vegetação através tanto da mortalidade de espécies sensíveis à fragmentação como também pela proliferação de espécies adaptadas a distúrbios, com impactos finais nos estoques de carbono. Assim, o maior objetivo desse estudo foi compreender o papel dos distúrbios induzidos pelo homem na modulação da dimensão da perda de biomassa em florestas Tropicais. Nós aplicamos uma revisão sistemática da literatura procurando por evidências empíricas de que o efeito de borda pode levar a perda de biomassa em florestas tropicais (Capítulo 2). Nossos resultados destacam a lacuna de conhecimento entre padrões e processos relacionados à perda de biomassa em florestas Tropicais. Para fortalecer esse conhecimento, nós formulamos um modelo conceitual conectando estrutura da paisagem e atributos na escala do fragmento à severidade do efeito de borda, e assim afetando a biomassa acima do solo. Nosso modelo hipotetiza que a quantidade de hábitat, o isolamento, o tempo desde a formação da borda e o sinergismo entre tamanho do fragmento, distância da borda e tipo de matriz são os principais condutores de perda de biomassa em florestas Tropicais antropogênicas. Utilizando um grande banco de dados (18 503 árvores ≥ 10 cm dap) provenientes de 146 locais distribuídos em quatro regiões de floresta úmida no México e quatro no Brasil, nós então testamos as previsões do nosso modelo conceitual. Especificamente, a influência da cobertura florestal, isolamento, distância da borda, tamanho do fragmento e tipo de matriz sobre a biomassa (Capítulo 3). Nós observamos que áreas com muito carbono apresentaram espécies típicas de florestas maduras (tolerantes ao sombreamento, zoocóricas, com sementes grandes) contrastando com áreas com pouco carbono compostas por espécies adaptadas a distúrbio (pioneiras ocupando o sub-bosque). Árvores grandes tolerantes ao sombreamento (≥ 40 cm dap) foram impactadas severamente pela combinação de perda de cobertura florestal e efeitos de borda. Distância da borda, tamanho do fragmento e a extensão da área de matriz

aberta influenciaram fortemente as árvores pequenas tolerantes a sombreamento (≤ 20 cm dap). Apesar dos nossos resultados não corroborarem completamente as previsões iniciais do nosso modelo conceitual, eles dão suporte à ideia de que a composição da paisagem interage com a estrutura do fragmento com impactos finais nos estoques de biomassa em florestas Neotropicais. Por fim, nós investigamos se o nível de distúrbio da região pode influenciar nas respostas da estrutura da vegetação à perda de cobertura florestal. Biomassa, mas não a densidade de indivíduos, foi afetada pela perda de cobertura florestal em regiões com nível intermediário de distúrbio, *i.e.* regiões apresentando uma combinação de níveis moderados de desmatamento (20-40% de cobertura florestal remanescente) em que a perturbação ocorreu ao longo dos últimos 30-60 anos, com alto grau de defaunação mas ainda abrigando populações relictuais de grandes mamíferos e, em sua maioria, compostos por uma matriz heterogênea. Em geral, nossos resultados destacaram que tanto a composição da paisagem como a estrutura do fragmento são os principais condutores de perda de biomassa em florestas Neotropicais e que o contexto da paisagem deve ser considerado para se obter estimativas mais confiáveis de emissão de carbono devido à degradação florestal. O planejamento da paisagem (*e.g.* restauração da cobertura florestal) deve ser incluído em estratégias de conservação em ordem de sustentar o armazenamento de carbono. Além disso, nós defendemos que iniciativas de conservação serão menos custosas e mais efetivas se implementadas em áreas sob níveis intermediários de distúrbio.

Palavras-chave: estoques de carbono, árvores de grande porte, degradação florestal, estrutura da paisagem, paisagens modificadas pelo homem, mudança no uso do solo, florestas tropicais.

Abstract

In spite tropical forests are the most important terrestrial global carbon sinks due to carbon storage in aboveground biomass, it is also the primary target of deforestation. The conversion of Tropical forests into anthropogenic areas might disrupt biological flux and also lead to severe microclimatic changes at forest edges. These combined effects can trigger profound changes in plant composition through both high mortality of fragmentation-sensitive species and proliferation of disturbed-adapted species which will ultimately impacts carbon storage. Thus, our main objective in this study was understand the role of human-induced disturbances in modulate the dimension of biomass loss at tropical forests. We applied a systematic literature review searching for empirical evidences that edge effects can drive biomass loss in tropical forests (Chapter 2). Our findings highlighted the gap of knowledge about the pattern and process related to biomass loss in tropical forests. To strengthen this understanding, we formulated a conceptual model linking landscape structure and patch-level attributes to severity of edge effects affecting aboveground biomass. Our model hypothesizes that habitat amount, isolation, time since edge creation, and the synergism between edge distance, patch size, and matrix type are the main drivers of biomass loss in anthropogenic tropical forests. We thus used a large plant dataset (18 503 trees ≥ 10 cm dbh) from 146 sites distributed across four Mexican and four Brazilian rainforest regions to test our conceptual model predictions, specifically the influence of forest cover, site isolation, edge distance, patch size and type of matrix on biomass (Chapter 3). We observed that carbon-rich sites presented species that are typical of old-growth forests (shade-tolerant, large-seeded, zoocoric) contrasting to carbon-poor sites composed by disturbed-adapted species (pioneer occupying the understory). Large shade-tolerant trees (≥ 40 cm dbh) were impacted severely by the combination of forest loss and edge effects. Edge distance, patch size, and the amount of open-matrix strongly influence small shade-tolerant trees (≤ 20 cm dbh). Although our results do not fully corroborate the initial predictions of the conceptual model, they support the idea that landscape composition interact with patch structure and ultimately impacts biomass stocks in fragmented tropical forests. Finally, we further investigated if the disturbance level of the region influences plant-structure responses to forest loss (Chapter 4). Biomass, but not plant density, was

affected by forest loss in regions with intermediate disturbance levels, *i.e.* regions showing a combination of moderate deforestation (20-40% of remaining forest cover) disturbed during the past 30-60 years, high defaunation but harboring relictual populations of large-mammals, and areas mostly composed by heterogeneous matrices. In general, our findings highlight that both landscape composition and patch structure are the main drivers of biomass loss in Neotropical forests, and that the landscape context must be considered to obtain more reliable estimations of carbon emissions due to forest degradation. Landscape planning (*e.g.* restoration of forest cover) should be included in conservation strategies in order to sustain carbon storage. Moreover, we advocate that conservation initiatives will be less costly and more effective if implemented in areas under intermediate disturbance levels.

Keywords: carbon stocks, large trees, forest degradation, landscape structure, human-modified landscapes, land-use change, tropical forests

CHAPTER 1

General Introduction

Introduction

There is a crescent global interest of the scientific community, nations, and the society in general on greenhouse gas emissions and climatic changes. The recognition that climate change is a reality was marked by the creation in 1994 of the United Nations Framework Convention on Climate Change (UNFCCC). Since then, several conferences with the participation of the United Nations member states, such as the Conference of the Parties (COP), were organized by the UNFCCC with the main goal of achieve “stabilization of greenhouse gas concentrations in the atmosphere at the level that would prevent dangerous anthropogenic interference with the climate system” (UNFCCC¹). COP and Kyoto protocol recognized that human activities involving land use, land use change and forestry impact global carbon stocks, therefore there is an urgent necessity to reduce emissions from deforestation and forest degradation in developing countries (REDD+)². Thus, in the next sections we explore how human activities can impact carbon stocks through forest degradation.

The role of tropical forests in the global carbon cycle

Terrestrial ecosystems are an essential piece in the global carbon cycle due to their role as carbon storages (Houghton *et al.*, 2009) (Fig. 1.1). One of the main contributions of terrestrial ecosystems to carbon cycle is by the absorption of roughly 60 PgC yr⁻¹ of atmospheric carbon through plant photosynthesis at forests (Malhi *et al.*, 2002) (Fig. 1.1). About 50% of carbon absorbed by forests is assimilated in plant biomass (Malhi *et al.*, 2002; Chave *et al.*, 2005), especially as aboveground biomass which accounts for 70-90% of total forest biomass (Cairns, 1997). Tropical forests contribute disproportionally to forest carbon cycle since compound 13% of global forest area but stores up to 680 PgC (Malhi *et al.*, 2002; Houghton *et al.*, 2009), which is about 55% of global forest carbon (Pan *et al.*, 2011), thus

¹ documents available at: <http://unfccc.int>

² for more information access: http://unfccc.int/land_use_and_climate_change/items/8792.php

configuring the great importance of tropical forests as carbon sinks³. However, not all trees in tropical forests contribute equally to carbon stocks. Recent studies found patterns of hyperdominance on carbon stocks, *i.e.* few individuals and species concentrate most of the carbon. At Amazon and African tropical forests, for example, roughly 1% of species are responsible for 50% of carbon storage (Bastin *et al.*, 2015; Fauset *et al.*, 2015). At the Atlantic forest large trees (≥ 30 cm diameter of breast height - dbh) were represented by few individuals (6%) but contributed to 72% of aboveground biomass (Lindner, 2010). Furthermore, only the annual growth of big trees (≥ 100 cm dbh) was equivalent to the addition of a tree between 10 to 20 cm dbh *per year*, or 103 kg yr^{-1} , at woody forests (Stephenson *et al.*, 2014). In summary, tropical forests play an important role at the global carbon cycle, especially by the maintenance of few, large trees that store most part of carbon.

Fig. 1.1. Diagram of carbon cycle showing the terrestrial carbon store and pathways of carbon exchange. Carbon stored is represented by white numbers, natural fluxes (sources and sinks) by yellow and emissions from human activities by red. Numbers are in gigaton of carbon *per year*. Adapted from: NASA - Earth Observatory (2011). Diagram available at: <http://earthobservatory.nasa.gov/Features/CarbonCycle/>

³ “any process, activity or mechanism which removes a greenhouse gas, an aerosol or a precursor of a greenhouse gas from the atmosphere” (UNFCCC, 1992)

Linking tropical forests with carbon emissions

Terrestrial carbon sinks are strongly affected by anthropogenic disturbances due to human activities related to land use, land use change and forest management. The AFOLU sector (Agriculture, Forestry and other Land Use) is considered the third largest source of carbon emissions from 1750 to 2011 and accounted for 25% of emissions in 2010 (IPCC, 2014; Smith *et al.*, 2014). These activities result in emissions of greenhouse gases (methane, nitrous oxide, ozone-precursors and mainly carbon dioxide) mostly due to land clearing, logging, decomposition of organic material, and burning vegetation (Malhi *et al.*, 2002; Smith *et al.*, 2014).

Tropical forests are the main targets of land use changes due to human activities and have lost 7 million ha *per year* only between 2000 and 2007 (FAO, 2016). The high rates of conversion of natural tropical areas into human-modified areas can result in 7 to 14% of the global anthropogenic CO₂ emissions (Harris *et al.*, 2012; Achard *et al.*, 2014). Moreover, carbon debts from tropical deforestation are expected to release 8.6 PgC of committed emissions, the equivalent of 5 to 10 years of deforestation emissions (Rosa *et al.*, 2016). These high rates of carbon emissions from anthropic activities can disrupt the global carbon cycle because they unbalance the natural pathways and exchanges of carbon (Malhi *et al.*, 2002) (Fig. 1.1).

Forest degradation, *i.e.* the decrease in forest quality (*e.g.* by logging, regrowth and ground fires), also triggers significant carbon losses, though forest degradation is still poorly accounted in carbon emissions (Smith *et al.*, 2014). At humid tropics carbon emissions by forest degradation represent approximately 5% of the total released by deforestation (Achard *et al.*, 2004). However, in tropical Africa these degradation-related carbon emissions exceeded those from deforestation by 132% (Gaston *et al.*, 1998). At the Amazon forest, degradation induced by selective logging resulted in an additional 15-19% emission of CO₂ in relation to emissions from deforestation (Huang & Asner, 2010). Although Laurance *et al.* (1997) already hypothesized that the process of forest fragmentation could be a significant indirect source of carbon emissions, only recently studies incorporated fragmentation-induced forest degradation in their estimates. At Amazon forests, for example, was estimated losses of 126–221 Tg C at forest edges, representing up to 6% of emissions by

deforestation (Numata *et al.*, 2011). Estimates of edge-related carbon losses based on deforestation patterns at Amazon and Atlantic forest showed that tropical forest degradation could release between 9 to 24% of deforestation-derived global emissions (Pütz *et al.*, 2014). Although there is great uncertainty in the deforestation and degradation estimates, they might account for 6-17% of global emissions (van der Werf *et al.*, 2009).

Forest degradation in human-modified landscapes

The process of anthropogenic expansion, mainly because of agriculture expansion (Smith *et al.*, 2014), result in fragmented landscapes composed by a mosaic of scattered forest patches surrounded by non-natural areas (Fahrig, 2003), an arrangement that is most times unfavorable for the maintenance of biodiversity (Melo *et al.*, 2013). Due to anthropogenic expansion, edge-affected areas are created at the intersection between forested and non-forested areas (Harper *et al.*, 2005). Those areas are characterized by profound microclimatic changes in relation to the interior of forest fragment. For example, declines in vapor deficit pressure, soil moisture, and increases in photosynthetically active radiation were observed at edges (Kapos, 1989; Williams-Linera, 1990) triggering the acceleration of decomposition and nutrient cycling (Harper *et al.*, 2005), therefore, leading to more fertile and less acid soils (Magnago *et al.*, 2016) in these edge-affected areas. The increase in wind turbulence, air humidity, and temperature are also important abiotic modifications promoted by edge creation, and recent studies showed that the severity of these changes rely on landscape and patch structure (Magnago *et al.*, 2016; Arroyo-Rodríguez *et al.*, 2017).

One of the consequences of abiotic modification at forest edges is the changes of plant community composition, which can result in biomass loss. Some species can be favored (the “winners”) while others will be negatively affected (the “losers”, *sensu* Tabarelli *et al.*, 2012) due to edge creation. The higher wind turbulence at edges increase plant damage and large trees mortality (Laurance *et al.*, 2000; Harper *et al.*, 2005) leading to a collapse of the emergent layer (Oliveira *et al.*, 2008). Indeed, large-seeded, emergent and shade tolerant species can have their abundance reduced by one third at tropical forests edges, being the most affected species in these areas (Santos *et al.*, 2008). The combination of several factors, such as high mortality of large trees, increased light incidence, and arrival

of small-seeded species from the matrix (Tabarelli *et al.*, 2008), favors the proliferation of pioneer species at edges (Laurance *et al.*, 2006). In general, pioneer trees increase their density, basal area, growth rates and recruitment at edges profiting their long term persistence (Tabarelli *et al.*, 2008). However, edge environments do not benefit all pioneer trees. Adult's recruitment rate of long-lived pioneer trees decrease under edge influence resulting in changes on the demographic structure of these species (Santos *et al.*, 2012). Additionally, proximity to edge and small fragment size favors small-seed softwood species, but not the large-seeded softwood ones (Michalski *et al.*, 2007). Thus, edge-creation can drive shifts in the demographic parameters of plant-communities leading to a species turnover with trees typical from late-successional stages (*e.g.*, large trees, shade-tolerant, large-seeded) being replaced by pioneer (Nascimento & Laurance, 2004; Laurance *et al.*, 2006), especially the short-lived (Santos *et al.*, 2012).

Floristic and functional simplification of plant communities due to edge-related forest degradation drive tropical forests to a retrogressive succession, *i.e.* the degeneration of forest moving it into early-successional stages (Santos *et al.*, 2008; Lôbo *et al.*, 2011; Tabarelli *et al.*, 2012), which impacts carbon stocks because large trees are the most sensitive fragmentation-affected species (Laurance *et al.*, 2000; Lindenmayer & Laurance, 2016) and also the principal components of above-ground biomass (Bastin *et al.*, 2015; Fauset *et al.*, 2015). Apparently, even though pioneer and lianas proliferate at edges, they do not compensate the biomass loss caused by the mortality of large trees (Laurance *et al.*, 1997; Magnago *et al.*, 2016) because of their small size and low wood density (Nascimento & Laurance, 2004; Michalski *et al.*, 2007). In fact, recent estimates show that edge effects can drive biomass losses of 25% (relative to patch interior) within the first 500 m from forest edge, and up to 10% over distances of 1.5 km from the edge (Chaplin-Kramer *et al.*, 2015). Moreover, the extension and intensity of edge-related carbon losses are related with patch size (Magnago *et al.*, 2015, 2016) and matrix type (Chaplin-Kramer *et al.*, 2015), indicating that landscape and patch structure influence carbon stocks. Matrix type, for example, can increase the magnitude and extension of edge effects because of the high structural contrast in relation to forest patch (Mesquita *et al.*, 1999; Ewers & Didham, 2006). Reductions in forest cover driven a structural simplification of the vegetation at anthropogenic tropical forests by decreasing the density of large trees and plant height, besides drastically decaying trees dbh and basal area (Rocha-Santos *et al.*, 2016), suggesting a biomass reduction

triggered by forest loss. However, plant responses to forest loss may rely on the degree of deforestation at the regional level (*e.g.* Arroyo-Rodríguez *et al.*, 2009). In synthesis, deforestation and land use changes can promote modifications in landscape composition and patch structure inducing a process of forest degradation that reduce biomass in human-modified landscapes. As the mechanisms driving fragmentation-induced forest degradation still poorly understood it may result in misleading degradation-related carbon emissions estimates and overshadow anthropogenic impacts in greenhouse emission.

Objectives

In face of the great importance of tropical forest biomass to estimate global carbon emissions and the present scenario of increasingly rates of deforestation and edge-affected landscapes, it is urgent to determine the anthropogenic drivers of biomass loss in fragmented landscapes. This study was structured in three chapters with the main objective of understand the role of human-induced disturbances modulating the dimension of biomass loss at tropical forests.

In the second chapter we searched for empirical evidences of edge-related carbon loss at tropical forests. Through a systematic review of the literature we searched for (i) evidences of edge effects on biomass in tropical forests and (ii) the role of matrix type in mediating this biomass loss. We did not found patterns of a pervasive biomass loss due to edge effects in human-modified tropical landscapes. The little empirical evidence suggests that the extension and magnitude of edge effects may be mediated by landscape structure. To fulfill this gap of knowledge, we proposed a conceptual model linking landscape configuration and composition to biomass stocks in tropical forests. Additionally, we proposed a sampling protocol to test our conceptual model.

In the third chapter we used a large database to test our conceptual model and verify the role of landscape and patch structure mediating aboveground biomass. Specifically, we investigated (i) non-linear relations among forest cover and biomass, (ii) the influence of isolation on biomass loss at intermediate values of forest cover, (iii) the effect of the interaction of edge distance, patch size and matrix type in biomass loss.

In the fourth chapter we tested if responses of plant-community structure (density and aboveground biomass) due to changes in forest cover, one of the main drivers of biomass loss, relied on regional disturbance level. We expected (i) variability on plant structure responses to be higher at regions with intermediate disturbance levels, (ii) forest loss to impact negatively biomass at regions with intermediate disturbance levels, and (iii) plant density will be negatively affected by increases in forest cover at intermediate disturbance levels but positively influenced at regions with high disturbance levels.

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CHAPTER 2

Fragmentation Effects on Above-Ground Biomass of Tropical Forests: a Conceptual Framework

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Article submitted as commentary to Biotropica

Schematic diagram:

Abstract

Despite the general recognition that fragmentation can reduce plant biomass through edge effects, a systematic review of the literature does not reveal a clear role of edges in modulating biomass loss. Additionally, edge effects appear to be constrained by matrix type, suggesting that landscape composition has an influence on biomass stocks. The lack of empirical evidence of pervasive edge-related biomass losses across tropical forests highlighted the necessity for a general conceptual model linking fragmentation with above-ground biomass. Here, we propose a model in which landscape composition and configuration mediate the magnitude of edge effects and seed-flux among habitat patches, which ultimately has an influence on biomass. Our model hypothesizes that habitat amount and isolation, the synergism between fragment size and matrix type, and the time since edge creation are the main drivers of biomass loss in fragmented tropical forests. To test our conceptual framework, a sampling protocol is presented, whereby the effects of edges, habitat amount, habitat isolation, fragment size, and matrix type on biomass stocks can be assessed both collectively and individually.

Key-words: biotic homogenization; carbon stock; edge effect; habitat amount, shade-tolerant; large tree; forest degradation, landscape structure

Introduction

Deforestation is recognized as the main factor leading to biomass loss in tropical regions (Achard *et al.*, 2014); however, the indirect biomass loss caused by deforestation due to forest fragmentation is still poorly understood (Pütz *et al.*, 2014). Fragmentation can affect biomass through the creation of edge-affected areas, which are widespread in tropical landscapes (Haddad *et al.*, 2015). Edge creation can induce floristic and functional simplification of plant communities (*e.g.*, Lôbo *et al.*, 2011; Michalski *et al.*, 2007), leading to a winner–loser system (Tabarelli *et al.*, 2012). Large trees are the main losers (Benchimol & Peres, 2015). These are mostly shade-tolerant species, and since they are the principal components of above-ground biomass (AGB), their loss can negatively affect carbon stocks (Bastin *et al.*, 2015; Fauset *et al.*, 2015). Despite this general understanding, there has been limited research on the specific mechanisms that modulate edge effects on AGB in tropical forests. For example, recent models demonstrate that matrix size influences the magnitude and extension of edge-related carbon loss (Chaplin-Kramer *et al.*, 2015).

Edge Effects on Biomass: Empirical Evidence

Considering the lack of strong evidence of edge effects on biomass and the current focus on carbon emissions from tropical forests, we conducted a systematic review (a full description is presented in the supplementary material) of the literature, searching for (1) evidence of edge effects on AGB in tropical forests and (2) the role of matrix type in mediating this biomass loss.

Surprisingly, only nine studies from amongst almost 9,000 titles investigated, analyzed how edge affects AGB (Table S2.1) in 82 sites. Despite the general recognition that edge effects drive biomass loss in tropical forests (*e.g.*, Laurance *et al.*, 1997; Pütz *et al.*, 2014), our review highlights the insufficient empirical evidence supporting this relationship. Few studies reported edge effects on AGB, and these tended to be inconclusive due to contrasting results: AGB at edges decreased in six sites, was unaffected in four, and increased in two. The results are even more inconclusive with regards to tropical dry forest,

with only one negative effect of edge on biomass reported (Table S2.1). We also highlight the lack of replicates among different types of tropical forest and along a broader climate gradient (Table S2.1), as we predict distinct susceptibility to edge effects depending on the forest type: dry forests are more resilient to edge-related desiccation and wind turbulence than moist forests (Chaplin-Kramer *et al.*, 2015). These results shows that although the first article indicating a negative effect of edges on biomass was from the late nineties (Laurance *et al.*, 1997), very little empirical data on this topic have been obtained in subsequent years, making it difficult to corroborate this pattern among tropical forests.

The findings of the systematic review also reveal that matrix may mediate biomass loss, suggesting that landscape composition might modulate edge effects (Table S2.2): the more similar the habitat structure of the surrounding matrix, the lower is the biomass loss. For example, matrix type has modulated plant community change in the Amazon (Laurance *et al.*, 2006) and amplified edge-related carbon loss throughout the tropics (Chaplin-Kramer *et al.*, 2015).

Although this systematic review does not provide evidence of landscape configuration effects on edges, the scale and magnitude of edge effects appear to be affected by the spatial arrangement of patches, with direct effects on plant communities. For example, patch isolation was shown to affect biomass in tropical dry (Hernández-Stefanoni *et al.*, 2011) and wet (Magnago *et al.*, 2015) forests. Thus, even though spatial information on carbon stock conservation remains limited (*e.g.*, Ziter *et al.*, 2013), landscape configuration and composition almost certainly affect edge-related biomass loss.

Implications for Carbon Emission Estimates

The gap in knowledge regarding the effect of forest fragmentation on biomass implies that estimates of carbon emissions can be misleading. For example, it has been estimated that carbon loss through forest degradation due to edge creation in the Amazon and Atlantic forests represents between 9% and 24% of the world annual loss of carbon caused by deforestation (Pütz *et al.*, 2014), although these estimates of edge-related carbon losses were based on only a few sites in the Amazon (Laurance *et al.*, 1997) and Atlantic forests

(Pütz *et al.*, 2011). However, Chaplin-Kramer *et al.* (2015) recently demonstrated that these studies possibly underestimated the extension of edge effects, through observation of carbon losses up to 1.5 km into forest interior (reductions of >10% relative to forest interior). In fact, we noticed that most estimates of carbon emissions caused by forest fragmentation - generally by simulation (*e.g.*, Groeneveld *et al.* 2009, Pütz *et al.* 2011) or interpolating biomass loss using satellite imagery (*e.g.*, Numata *et al.* 2010, 2011) - are mainly based on observed edge effect data obtained by a unique Amazonian fragmentation project (BDFFP; but see Chaplin-Kramer *et al.* 2015). The lack of information regarding the mechanisms promoting biomass loss also affects programs of ecosystem services payments, such as REDD+, which financially reward developing countries that reduce emissions from deforestation and forest degradation. Therefore, the potential of fragmented tropical landscapes to provide carbon services is uncertain.

The Landscape Effect on Biomass Loss Model

Herein, we propose a conceptual model to predict the response of biomass to changes in landscape structure. Our conceptual model considers that the presence of biomass in remaining forest is mediated by (i) the influx of shade-tolerant species from local patches and surrounding fragments, guaranteeing the long-term persistence of large trees, and (ii) the extension and magnitude of edge-affected habitats. Seed-flux relies on the amount and isolation of habitat and the surrounding matrix. Matrix type also influences edge effects, as does time since fragmentation, as described below. Further, we predict that landscape change has a stronger influence on biomass loss in moist compared to dry tropical forests.

Habitat amount effect

Below a threshold of habitat amount, the fragmentation or the spatial arrangement of patches in the landscape can affect biological flow among patches, thereby affecting species abundance and persistence - the so-called fragmentation threshold (Andrén, 1994). We

predict that the abundance of shade-tolerant species would be affected below this fragmentation threshold (~50% of habitat amount) due to a reduction in the richness and abundance of forest-specialist seed dispersers, as observed for tropical birds (Morante-Filho *et al.*, 2015), leading to a long-term biomass decline. Additionally, a decrease in habitat amount below this fragmentation threshold may also decrease the number and size of patches (Fahrig, 2003), which could cause declines in shade-tolerant biomass when edge effects have an influence on patch core areas (Fig. 2.1A). When habitat loss and fragmentation intensify, biological flow among patches may be markedly reduced, enhancing the risk of species extinction (Pardini *et al.* 2010). Accordingly, population persistence depends upon a minimum amount of habitat - the extinction threshold *sensu* Fahrig (2003, 2002). In the Brazilian Atlantic forest, the extinction threshold for more sensitive (*e.g.*, endemic or forest-dependent) species of vertebrate (birds, small mammals, and amphibians; Banks-Leite *et al.* 2014), Sapotaceae (Lima & Mariano-Neto, 2014), and Myrtaceae (Rigueira *et al.*, 2013) is a habitat cover of approximately 30%. For biomass-related traits of forest structure (*e.g.*, basal area and diameter), Rocha-Santos *et al.* (2016) observed an extinction threshold of between 35% and 40% forest cover. Furthermore, populations inhabiting small patches in severely deforested landscapes may be more susceptible to sample-area effects (Fahrig, 2003, 2013), which can decrease plant richness (*e.g.*, Benchimol & Peres 2015), and possibly reduce biomass (Fig. 2.1A). Thus, we predict severe biomass declines below the fragmentation threshold of habitat amount due to a synergistic effect among habitat loss, proliferation of edges, and higher extinction risk in small populations.

We highlight the necessity to evaluate the proper scale of the habitat amount effect (Fig. 2.1F) (Jackson & Fahrig, 2015), in order to direct conservation efforts to the best scale for assessing carbon response. Habitat amount can influence biomass on small or broad scales depending on the movement patterns of seed dispersers and seed predators. We suggest that habitat amount should be estimated by considering the movement pattern of shade-tolerant seed dispersers, as shade-tolerant species are the main contributors to biomass stocks.

Figure 2.1. Conceptual model of the influence of landscape configuration and composition on above-ground biomass (AGB) of tropical forests. (A) Expected non-linear relationship between AGB in a gradient of habitat amount. AGB per area is mainly driven by shade-tolerant species (continuous line). Pioneers (dotted line) increase their biomass with low habitat amount but insufficiently to compensate for loss of the biomass of large trees. The small graphic represents the predicted slopes in distinct moments (I, II, and III) of the relationship between habitat amount and biomass. We predicted a stronger effect of habitat amount on biomass between the fragmentation and extinction thresholds (line II). (B) Above

the habitat fragmentation threshold (FT), shade-tolerant species should not be affected by habitat configuration, being affected essentially by habitat loss. Below the FT, habitat configuration is highly variable (Villard & Metzger 2014), and thus we anticipate that seed dispersal of shade-tolerant species will become more dependent of patch isolation, resulting in an additive effect of isolation in the reduction of AGB per area with habitat loss. The gray shadow between the FT and the extinction threshold (ET) represents the possible trajectories of AGB depending on the degree of habitat isolation, where highly clustered habitat patches (trajectories closer to the solid line) are less affected by habitat configuration. When habitat cover reaches an amount that is just sufficient to sustain viable populations (the ET) of shade-tolerant species, which are markedly affected in degraded landscapes, the declines in AGB will be affected only by habitat loss. We thus predict that configuration will affect the pattern of AGB loss mostly between FT and ET. (C) and (D) represent the expected relationships between AGB and increasing fragment size for plots near and distant from the edges in a landscape dominated by a high- and low-contrast matrix, respectively. Biomass in edges and small fragments in a high-contrast matrix is mostly composed of pioneer species; otherwise, the biomass comprises shade-tolerant species. (E) Temporal trajectory of biomass amount considering shade-tolerant and pioneer species (large and small dashed lines) and total biomass from the plant community. (F) Illustration of the study design to evaluate the proper scale of habitat amount and isolation effect.

Isolation effect

Isolated populations have a higher extinction probability because of reduced immigration rates from source-patches (McArthur & Wilson, 1967). In anthropogenic landscapes, isolation is predicted to influence species' persistence only at intermediate values of habitat amount, specifically between the fragmentation and extinction thresholds (Fahrig, 2002, 2003; Villard & Metzger, 2014). Moreover, the strength of this dependency will be higher for fragmentation-sensitive species, for which minor changes in patch isolation can substantially limit biological flux among source–sink patches (Villard & Metzger, 2014) and prevent “rescue effects” (Brown & Kodric-Brown, 1977). Carbon stocks can undergo abrupt changes when isolated from source-patches in Neotropical forests (Hernández-Stefanoni *et al.* 2011, Magnago *et al.* 2015). Thus, for landscapes below the fragmentation threshold of forest cover, we predict additive decreases in biomass through the elevated mortality of shade-

tolerant species with increasing isolation (Fig. 2.1B). Below the extinction threshold, populations of shade-tolerant species depend on minimal habitat requirements for persistence, with isolation only influencing the point at which the extinction threshold occurs (Villard & Metzger, 2014) (Fig. 2.1B). Isolation should also be evaluated across different scales.

Synergistic effect between matrix and fragment size

Harshness of the surrounding matrix can restrict the pool of pollinators and seed dispersers reaching patches, decreasing pollination and seed-rain in degraded landscapes (Laurance *et al.*, 2011). Structural contrast between matrix and patch also influences the magnitude and extent of edge effects by increasing microclimatic differences (Didham & Lawton, 1999; Tabarelli & Gascon, 2005). Therefore, we anticipate that areas near edges in contact with a high-contrasting matrix will have a low biomass stock due to severe edge effects, independent of fragment size (Fig. 2.1C). In turn, within a landscape with a high-contrast matrix, fragment size will influence the extension of edge effects into the fragment, resulting in a non-linear decrease in biomass with decrease in fragment size in the central patch area (Fig. 2.1C). We predict a similar pattern in landscapes dominated by a low-contrast matrix, but with a higher amount of biomass at edges and a smooth biomass decline in fragment centers due to a slight edge effect (Fig. 2.1D). However, although a low-contrasting matrix attenuates the microclimatic differences of a patch's edge and interior, this may not neutralize all effects of edge creation.

Temporal effect

The magnitude of biomass loss also depends on the temporal stage at which community modification occurs. In anthropogenic landscapes surrounded by a harsh matrix, we assume that there is a sharp decrease in biomass in the first years after forest fragmentation, due to the mortality of large shade-tolerant trees (Fig. 2.1E). The duration of this biomass-decay

period is context dependent, and it could range between 4 and 80 years (Laurance *et al.*, 1997; Pütz *et al.*, 2014; Dantas de Paula *et al.*, 2015). After the stabilization of shade-tolerant species mortality, biomass can be increased by the proliferation of pioneer and lianas, but insufficiently to compensate for the period of sharp biomass decrease (Fig. 2.1E). We emphasize that our landscape effect hypothesis is based on recently fragmented landscapes and does not predict changes in naturally regenerating areas, due to the absence of empirical data necessary to propose an explanatory model (but see Costa 2015).

Methods for Testing the Landscape Effect Hypothesis

The landscape hypothesis considers the effect of landscape composition and configuration on biomass. To test the proposed hypotheses, an ideal study design should consider collectively and in isolation the effects of edges, habitat amount, habitat isolation, fragment size, and matrix type on biomass stocks. Here, we propose a simpler version of the ideal design to examine only the influence of edge distance and habitat amount, where sample plots are arranged according to a range of edge distances and also spread along a habitat amount gradient (Fig. 2.2A). Our protocol also enables examination of the influence of landscape configuration, by applying a random stratified sampling design (Fig. 2.2B) and/or by statistically controlling collinearity between habitat amount and configuration (see Hadley & Betts, 2016).

When this study protocol is replicated on landscapes with distinct matrix types, with low and high contrast of the focal habitat, we can test our hypothesis that the type of matrix can modulate edge effects and severely affect biomass in small fragments (Fig. 2.1C, D). In this case, sample plots must also be distributed in fragments of different sizes. In both cases, time since edge formation must be controlled, as edge creation is very dynamic (Numata *et al.*, 2009) and could influence the magnitude and extension of the edge effect (Harper *et al.*, 2005). However, if the study's aim is also to account for the time since edge formation to examine biomass trajectory along time (Fig. 2.1E), then edge distance, habitat amount, and matrix type must be controlled or included in the study design. In this regard, we would like to encourage the establishment of collaborative research and international networks to fully

apply the proposed protocol.

Figure 2.2. Suggested sampling protocol to examine the effect of habitat amount and distance to edge on above-ground biomass (AGB) (A). The black point is the AGB sample plot allocated in a linear distance to the nearest patch edge. The area of influence surrounding the plot is the landscape in which habitat amount will be measured. Landscapes must be distributed along a gradient of habitat amount (x axis) and plots allocated in a range of edge distance (y axis). (B) Example of a stratified sample design in which landscapes with similar habitat amount but varying degrees of isolation (i) are randomly selected (red-dashed circles) to compound a gradient of isolation (ii). Here, we did not consider patch shape and matrix heterogeneity for simplification purposes; however, these must be taken into consideration in a complete sample design.

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Supplementary material

Systematic review and data analysis

A systematic review (Pullin & Stewart, 2006, Koricheva *et al.*, 2013) was conducted by searching for peer-reviewed studies that investigated whether vegetation biomass is affected by edge effects in tropical forests. We searched the ISI Web of Science, Scopus, and Scielo databases, using the following search combinations: (“fragment*” or “edge” or “boundary” or “contact”) and (“biomass” or “carbon”) and (“forest” or “tree” or “vegetation”). Terms to refine our search were added, excluding the words “gene” or “microbi*” or “paleo*” or “palaeo*” or “chemi*” or “nano*” or “fungi*” or “beetle*” that appeared in article titles. In Scielo, we searched articles in Spanish using the words “fragment*” or “borde” or “límite” or “contacto” and “biomasa” or “carbono” and “bosque” or “selva” or “árbol” or “vegetación”.

To avoid any publication bias (Koricheva *et al.*, 2013), we included unpublished Masters and PhD thesis data. Only Brazilian platforms of these theses were investigated due to the limitation of general search sources for tropical countries. The platforms used were Banco de Teses da Capes (<http://bancodeteses.capes.gov.br/>) and Biblioteca Digital Brasileira de Teses e Dissertações (BDTD, available at <http://bdtd.ibict.br/>), and the search terms used were as follows: (“fragment*” or “borda” or “contorno” or “contato”) and (“biomassa” or “carbono”) and (“floresta*” or “árvore*” or “vegetação”).

In total, 8,307 titles were selected from all databases. To refine this selection, we considered studies that explicitly estimated biomass from trees at least 2.5 cm in diameter at breast high (because most of the biomass is stocked in this portion of the vegetation; DeWalt & Chave, 2004), and that explicitly evaluated edge effects on biomass (contrasting edge with interior areas). We did not consider studies that analyzed other vegetation types (*e.g.*, grassland, savannas) or forms (*e.g.*, seedlings, shrubs, climbing trees). Literature reviews and studies based on simulations or that used variable proxies of biomass (*e.g.*, basal area, height) were not considered. We excluded these works because our goal was to identify studies that explicitly estimated biomass in an edge effect context. Nevertheless, we do recognize their significance in understanding carbon stocks in tropical forests. Filtering

selection by title resulted in 198 pre-selected works. After reading the abstracts and methodologies of these, only 18 studies were considered to fit all selection parameters, and were thus used for a full inspection.

To avoid missing relevant references, an additional search was conducted in Scopus, examining manuscripts that cited our first list of selected studies. Additionally, all the first authors from the selected papers were contacted for information on additional studies on the subject and missing data from their studies. However, no new studies were added using this search approach. Using this systematic review protocol, we identified a total of nine studies reporting edge effects on vegetation in tropical forests in 82 sites (Table S2.1). A site was defined as a spatially distinct area (*e.g.*, a forest fragment), or class (pioneer or shade-tolerants), or fragment size (mean fragment size as defined by Gould *et al.* 2008: Table S2.1). Thus, a single study can incorporate multiple study sites. All searches were conducted around early July to mid-September 2014 and the authors were contacted in late November 2014.

We classified type of edge effect on AGB based on the statistical results reported, and these were divided into positive (increase), null or negative (decrease) effects. Difference in biomass between interior and edge plots, hereafter Δ AGB, was calculated by subtracting the AGB of edge from that of interior plots. Studies that have reported type of edge effect do not necessarily report AGB values. The site altitudes ranged between 28 and 400 m. Δ AGB values were highly variable (min: -52.3; max: 180.9) in a prevalent narrow range of mean rainfall of approximately 1500 mm/year (min: 1328 mm/year; max: 4000 mm/year). We noticed that three studies were conducted in the Brazilian Amazon (BDFFP fragments).

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Table S2.1. General characteristics of the studies in tropical forests that investigated edge effects on above-ground biomass (AGB). Diameter at breast height (DBH) is the cutoff criterion for inclusion of tree sample. Fragment size and rainfall are represented by means. Edge effects can decrease (-), increase (+), or have no effect (0) on AGB. Edge limit represents the distance to edge where edge influence is assumed to occur and plots were allocated (as a categorical variable). Number of sites in each study that AGB was reported; see Supplementary Information text for a definition of sites.

Forest type	Biome	Effort (ha)	DBH (cm)	Fragment size (ha)	Matrix type	Altitude (m)	Rainfall (mm/year)	Forest succession	Edge effect	Edge limit (m)	Nº sites	Country	Locality	Authors	Year
Wet	Amazon	50.0	10	1-continuous	pasture	100-150	2200	primary	-1	100	0	Brazil	DBFFP	Laurance <i>et al.</i>	1997
Wet	Amazon	50.0	10	1-continuous	pasture	50-80	2700	primary	0	300	1	Brazil	DBFFP	Nascimento & Laurance	2004
Wet	Amazon	50.0	10	1-continuous	pasture	100-150	2200	primary	0 ^b	300	^{4c}	Brazil	DBFFP	Nascimento & Laurance	2006
Wet	Amazon	50.0	10	1-continuous	pasture	100-150	2200	primary	^{1d}	300	^{4c}	Brazil	DBFFP	Nascimento & Laurance	2006
Wet	Amazon	1.8	2.5		various	200-260	2300	primary impacted	0	14300 ^d	30	Peru	Various ^a	Phillips <i>et al.</i>	2006
Wet		1.9	10	170	pasture	58-200	4000	primary/primary harvested	0	300 ^d	6	Costa Rica	Sarapiquí Canton	Schedlbauer <i>et al.</i>	2007
Dry			12.5				1328		-1	60 ^d	1	Puerto Rico	Coast ^e	Gould <i>et al.</i>	2008
Wet			12.5				1992		0	60 ^d	1	Puerto Rico	Lowland ^f	Gould <i>et al.</i>	2008
Wet/dry			12.5	104.5 ^g			1688		-1	60 ^d	1	Puerto Rico	Lowland and coast ^f	Gould <i>et al.</i>	2008
Wet/dry			12.5	23.1 ^g			1688		1	60 ^d	1	Puerto Rico	Lowland and coast ^f	Gould <i>et al.</i>	2008
Wet/dry			12.5	10.9 ^g			1688		-1	60 ^d	1	Puerto Rico	Lowland and coast ^f	Gould <i>et al.</i>	2008
Wet	Atlantic Forest	5.9	10	221.2	sugarcan e	300-400	2000	primary	-1	100	0	Brazil	Usina Serra Grande	de Paula <i>et al.</i>	2011
Wet	Atlantic Forest	2.4	4.8	333.9	various	28-65	1403		-1	300	12	Brazil	Sooretama/Linhares/Jaguaré	Magnago	2013

^a Municipalities of La Torre, Palma Real, Alegria, Tres Islas, Sandoval/Jorge Chavez, Sonene, Puerto Arturo, Lago Valencia, Boca Pariamanu, and Sabaluyoc

^b Edge effect for late successional species

^c Same sites sampled for pioneer and late successional species

^d Study design considering edge distance as a continuous variable; in this case edge limit represent the maximum distance of the transect from an edge

^e Southern and northeastern

^f Central and northeastern

^g Notice that fragments sizes data are means of dry and wet forests from the Puerto Rico coast and lowlands. In the main text, we report edge effects based on the combination of wet/dry forests of Gould *et al.* (2008).

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Table S2.2. Number of studies with negative, null, or positive edge effects on above-ground biomass (AGB) considering different matrix types surrounding forest patches. Δ AGB: difference of AGB between interior and edge plots. In parentheses are the number of sites sampled from the studies. From the 82 sites that reported AGB, only 41 provided information on the surrounding matrix type; see Supplementary Information text for a definition of sites.

	Matrix type			
	<i>Eucalyptus</i>	Pasture	Sugarcane	Various
Edge effect				
Negative		2	1	
Null		3		1
Positive		1 ^a		
Δ AGB	1.1 $\pm$ 42.44 (9)	23.38 $\pm$ 46.21(20)		77.62 $\pm$ 47.04 (12)

CHAPTER 3

Anthropogenic Drivers of Biomass Loss at Neotropical Rainforests

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& Alexandre Adalardo de Oliveira

Schematic diagram:

Abstract

The loss of aboveground biomass in the tropics caused by deforestation is an important degradation process; yet, the underlying mechanisms shaping this process are still poorly understood. Previous studies suggest that landscape structure can influence tree biomass by modulating the extension and magnitude of edge effects and also by limiting the flux of propagules among forest patches. Notably, we expected that forest loss, patch size reduction, increase in isolation, edge and matrix effects to be the main factors acting on biomass loss in tropical forests. We tested those predictions using a large plant-community database (18 503 trees ≥ 10 cm dbh) from 146 sites situated in eight regions in Brazilian and Mexican rainforests. Reductions in biomass stocks were related to changes in the functional composition of plant-communities through the replacement of traits characteristics of old-growth forests by species attributes commonly found in early-successional systems. The loss of large shade-tolerant trees (≥ 40 cm dbh) biomass, the most important component of aboveground biomass, was driven essentially by the interaction between edge effects and forest loss. The biomass of small shade-tolerant trees (≤ 20 cm dbh), that represent the regeneration layer of larger trees, was impacted by the synergism among edge effects, patch size and by the surrounding open matrix area. Our results do not fully confirm the initial predictions, but support that landscape structure interact with patch structure and that processes at both landscape and patch levels regulate biomass stocks in tropical fragmented landscapes, and thus should be considered in carbon emissions estimations derived from deforestation and forest degradation. Moreover, our results imply that biomass conservation in human-modified landscapes can be promoted by hardwood shade-tolerant species enrichment and, complementarily, with adequate landscape planning, including maintaining or increasing forest cover and patch size, and mitigating edge effects through improvements in matrix permeability.

Key-words: carbon stocks; carbon emissions; large trees; landscape composition; landscape configuration;

Introduction

Tropical forests stores 55% of global forest carbon (Pan *et al.*, 2011), configuring it as the major carbon sinks from terrestrial ecosystem (Malhi *et al.*, 2002; Houghton, 2005). Roughly 56% of carbon stored in tropical forests is in live biomass (Pan *et al.*, 2011), split similarly between above and below ground (Malhi *et al.*, 2002). Deforestation of tropical forests largely affects live biomass resulting in 7 to 14% of global anthropogenic CO₂ emissions (Harris *et al.*, 2012; Achard *et al.*, 2014), contributing to the disruption on global carbon cycle (Malhi *et al.*, 2002). About 54% of these deforestation emissions are due to land-use change in Neotropical forests (Harris *et al.*, 2012), which experience losses of about 2 000 trees *per* minute (Rainforest Alliance, 2016). Additionally, carbon emissions due to forest degradation, *e.g.* fragmentation, logging and forest regrowth, are often unaccounted for (*e.g.* Harris *et al.*, 2012) or present great uncertainty (*e.g.* Pan *et al.*, 2011; Achard *et al.*, 2014) in global emissions estimates.

Despite the great importance of biomass on the global carbon cycle and the high level of anthropogenic pressures on tropical forests, the specific mechanisms that modulate biomass loss in these ecosystems remain unclear (Melito *et al.*, in prep.). Although there is little empirical evidence regarding the processes related to biomass loss, it seems that local forest degradation through edge effects and isolation of patches from seed-sources are strong forces influencing plant-communities with ultimate impacts on biomass stocks (Melito *et al.*, in prep.). Edge creation can induce floristic and functional simplification of plants assemblages (Laurance *et al.*, 2006a; Santos *et al.*, 2008; Tabarelli *et al.*, 2008) because it triggers severe microclimatic changes in edge-affected areas, such as increasing wind turbulence, air moisture, light incidence, and temperature (Murcia, 1995; Laurance *et al.*, 2002; Magnago *et al.*, 2015a; Arroyo-Rodríguez *et al.*, 2017), impacting sensitive species and favoring disturbed-adapted ones (Tabarelli *et al.*, 2012). As the effects of habitat fragmentation are not random, some species can be favored (the “winners”) while others will be negatively affected (the “losers”, *sensu* Tabarelli *et al.*, 2012), reductions in recruitment of fragmentation-sensitive species due to dispersal limitation affect plant demography in the long-term (Bruna & Kress, 2002; Howe & Miriti, 2004). Carbon stocks can be depleted when dispersal of large-seeded animal-dispersed species is disrupted by defaunation (Bello *et al.*,

2015; Osuri *et al.*, 2016; Peres *et al.*, 2016) or when seed-sources (*e.g.* large fragments) are far apart, thus limiting dispersal and growth of sensitive species (Magnago *et al.*, 2015b).

Previous studies suggest that landscape composition and configuration can mediate the magnitude and extension of edge effects and seed-flux among habitat patches, and thus accentuate or mitigate biomass loss in human-modified landscapes (Melito *et al.*, in prep.). This “landscape conceptual model” (Fig. 3.1) predicts that below some amount of habitat, the “fragmentation threshold” (*sensu* Andrén, 1994), further reductions on forest cover push the system under a condition where biological flux of seed dispersers of large trees, the major component of biomass stocks (Slik *et al.*, 2013; Lindenmayer & Laurance, 2016), can be severely limited therefore impacting the abundance of these plants and thus the biomass stocks in the long term. Simultaneously, the number and size of habitat patches are reduced in the landscape (Fahrig, 2003) and the patch’s core area becomes more susceptible to edge effects, contributing to reductions in biomass stocks (Magnago *et al.*, 2016) (Fig. 3.1a). Below this fragmentation threshold, habitat configuration is highly variable and minor changes in isolation could severely impact fragmentation-sensitive species (Villard & Metzger 2014), such as shade-tolerant and large trees (Fig. 3.1b). As deforestation intensifies, biological flux may be disrupted (Pardini *et al.*, 2010) and population persistence become dependent on a minimal available habitat amount, the so-called “extinction threshold” (Fahrig, 2002, 2003). Biomass-related traits of forest structure (*e.g.* basal area and diameter; Rocha-Santos *et al.* 2016) and species susceptible to anthropogenic changes (*e.g.* Sapotaceae and Myrtaceae; Rigueira *et al.*, 2013; Lima & Mariano-Neto, 2014) responded non-linearly to forest cover reductions with breakpoints around 30 to 40% of habitat amount, suggesting a similar pattern for biomass stocks (Fig. 3.1a). Another prediction of the “landscape conceptual model” is that matrix type can mediate, by different mechanisms, the effects of patch size and edges on biomass. First, biological flux can be facilitated or limited depending on the degree of matrix permeability (Antongiovanni & Metzger, 2005; Da Silveira *et al.*, 2016). Second, the magnitude and extension of edge effects can be influenced by the surrounding matrix (Tabarelli & Gascon, 2005; Ewers & Didham, 2006; Chaplin-Kramer *et al.*, 2015) through the degree of structural difference among the habitat patch and the matrix (Mesquita *et al.*, 1999; Prevedello & Vieira, 2010). Highly contrasting matrixes (*e.g.* pastures, roads) can both limit movement of forest-dependent dispersers and intensify microclimatic changes at edges, resulting in low biomass within edges influenced by this matrix type. In this scenario, edge

effects can extend into the core areas of small patches resulting in a pervasive biomass loss throughout the patch (Fig. 3.1c). In contrast, patches surrounded by a low contrasting matrix (*e.g.* tree plantations, agroforests) should present smoothed edge effects and high biomass stocks at edges and at the interior of fragment (Fig. 3.1d).

Here we tested the biomass loss predictions of the “landscape conceptual model” using a large plant-community database from eight Neotropical regions. First, we tested the premise that shifts in plant-community composition in the direction of disturbed-adapted species (pioneer) negatively impacted biomass stocks. We thus sought to assess the main drivers of biomass loss in human-modified landscapes in Neotropics searching for synergistic effects of landscape structure parameters (forest cover, open matrix and proximity index) with patch attributes (edge distance and patch size) on biomass. Based on our results we discuss the challenges in sustaining long-term carbon stocks in anthropogenic landscapes.

Fig. 3.1. The “landscape conceptual model” of the influence of landscape and patch structure in aboveground biomass (AGB) in tropical forests based on Melito *et al.* (in prep). (a) Non-linear effect of forest loss on biomass showing the sharp decrease in biomass between the

fragmentation threshold (FT) and the extinction threshold (ET) due to the high mortality of large trees. Although it is predicted, the proliferation of pioneer in a highly deforested landscape, they do not compensate biomass loss by large tree mortality. The small graphic represents the predicted slopes in distinct moments (I, II and III) of the relationship between forest cover and biomass. (b) Patch isolation is predicted to show additive effects on biomass only at intermediate values of forest cover, between the FT and ET. The grey shadow represents the possible trajectories of biomass depending on the degree of habitat isolation. Trajectories closer to the solid line (that symbolizes the independent effect of forest loss) are expected in landscapes showing highly clustered habitat patches thus less affected by habitat configuration. Synergies between patch size and edge distance within a highly contrasting matrix (c) and a low contrasting matrix (d) showing that a highly contrasting matrix increase the magnitude and extension of edge effects that reaches core patch area when fragment size is small.

Methods

Study regions

We surveyed eight regions, four from the Brazilian Atlantic forest and four from Mexico, originally dominated by tropical rainforests (Fig. 3.2, Table 3.1). Our samples include 146 forest sites located in lowland forest areas (0-400 m a.s.l.) with a warm and humid climate. These regions embrace a wide range of human-modified landscapes observed at the tropics, including landscapes with distinct levels of anthropogenic disturbances, spatial arrangements and landscape composition. Although diverse in terms of landscape structure all regions have been suffering strong anthropogenic pressures for at least the past 30 years, time enough for plant-communities responses to fragmentation and forest loss to be detected (Metzger *et al.*, 2009; Laurance *et al.*, 2011) (Table 3.1).

Fig. 3.2. Location of the studied landscapes composed of Neotropical forests in human-dominated landscapes: Tux: Los Tuxtlas ($n = 3$ regions); Lac: Lacandona; Pac: Pacatuba; SGr: Serra Grande; Soo: Sooretama.

Following an latitudinal order, the Los Tuxtlas in Mexico is composed of three regions with distinct levels of deforestation (see Arroyo-Rodríguez *et al.*, 2009 for a complete site description) but all heavily deforested since the 1970's, resulting in a region dominated by a highly contrasting matrix composed of pastures and croplands (Castillo-Campos & Laborde, 2004). The Lacandona region (Mexico) was colonized in the 1970's, but largely deforested between 1984 and 1986 (Aguilar & Mora, 1992) and nowadays forest patches are surrounded by a heterogeneous matrix composed of secondary forests, cattle pastures, crop fields, and human settlements. The Pacatuba-Gargaú and the Usina Serra Grande regions (Brazil) were extensively deforested for the expansion of sugarcane fields, mostly during the 19th century, resulting in forests remnants embedded by a stable and uniform sugarcane matrix. In the Una region (Brazil), shade cocoa plantations pressure natural areas during the 17th to 20th centuries, but deforestation were only accentuated in late 1980's due to declines on cocoa

Table 3.1. Description of the eight studied regions, following a latitudinal order, from Neotropical rainforests. Mean, SD, and range (in parenthesis) values of predictors variables (edge distance, patch size, forest cover, open matrix and proximity index) are presented for each region. See main text for description of each predictor.

Region	Country	Location (lat/long)	Pluviosity (mm/year)	Nº Sites	Effort (ha) ^a	Land-use (years) ^b	Edge distance (m)	Patch size (ha)	Forest cover (%) ^c	Open matrix (%) ^d	Proximity index (log) ^e	Disturbance level
Lacandona	Mexico	16°07'N - 90°53'W	3000	28	0.10	35	22.4-1804.0	2.8-50 000.0	5.1-100	0-88.2	10.2-20	low
Una	Brazil	15°0'S - 39°0'W	1500	16	0.05	30	25.8-373.5	4.4-24 300.0	3.9-93.0	7.9-100	10.7-19.3	intermediate
Sooretama	Brazil	19°04'S - 39°57'W	2000	19	0.10	65	14.0-3922.0	31.6-25 960.0	38.9-100	0-59.4	12.7-19.4	intermediate
Los Tuxtlas 1	Mexico	18°36'N - 94°6'W	3800	15	0.10	60	9.7-553.4	1.1- 1247.0	7.4-99.8	100	9.3-16.3	intermediate
Los Tuxtlas 2	Mexico	18°22'N - 94°47'W	3800	15	0.10	60	11.8-221.6	1.0-75.6	3.3-59.8	100	9.2-13.5	high
Pacatuba	Brazil	6°59'S - 35°5'W	1500	8	0.03	>100	64.8-650.9	28.8-2669.0	53.8-100	2.4-100	12.6-17.1	high
Los Tuxtlas 3	Mexico	18°31'N - 94°49'W	3800	15	0.10	60	11.4-63.8	0.7-13.3	1.1-15.1	100	8.9-11.8	high
Serra Grande	Brazil	8°30'S - 35°50'W	2000	30	0.10/ 0.16 ^f	>100	55.1-667.0	3.5-3930.0	3.4-100	95.1-100	10.5-17.5	high

^a Total area sampled in each site

^b Period when fragmentation started resulting in the present landscape structure

^c Measured at 600 m of radius from centroid patch

^d Measured at 700 m of radius from centroid patch

^e Measured at 900 m of radius from centroid patch

^f We included permanent plots (0.16 ha) and non-permanent plots (0.10 ha) sampled in the region

plantations and increasing forest harvesting (Saracura, 1997), with a subsequent expansion of cattle ranching and agriculture. As a consequence, the Una region is composed by a heterogeneous matrix of cattle pastures, secondary forests, rubber tree and cocoa plantations. Finally, forests from the Linhares-Jaguaré-Sooretama region (Brazil) started being converted to charcoal production, logging and agriculture in the 1950's (Garay & Rizzini, 2004) with the peak of deforestation in the early 1970's. The matrix at the region is currently composed of pastures, *Eucalyptus*, and coffee plantations.

These regions encompass a wide range of forest disturbance levels. Thus, to complemented sites description, the regions were characterized based on a previous classification considering the history of land-use, degree of defaunation, type of matrix and deforestation level (see Table 4.1 and 4.2 in Chapter 4). Regions recently and little deforested, composed of a heterogeneous matrix and well-preserved animal assemblages where classified as low disturbed. In contrast, regions showing a long history of severe deforestation, dominated by a homogeneous and harsh matrix, and presenting a strongly defaunated fauna were denominated as highly disturbed. Intermediate disturbance conditions encompass regions in which the fragmentation process is ongoing, with a mosaic of large and small patches surrounded by high and low contrasting matrix, with a depauperated large-fauna present.

Vegetation sampling

In all regions, only trees presenting diameter at breast height (dbh) ≥ 10 cm were considered in order to standardize the database and because tree biomass is mainly stocked within the arboreal strata (DeWalt & Chave, 2004). All sampled sites within each region were located in areas with similar soil characteristics and topography to avoid the potential confounding effect of these factors. In Lacandona and Los Tuxtlas regions the Gentry's (1982) protocol was used to record all trees in ten 50 x 2 m transects randomly located in the center of each sampled forest patch, totaling 28 and 45 patches, respectively (Arroyo-Rodríguez *et al.*, 2009; Hernández-Ruedas *et al.*, 2014). In the Pacatuba-Gargauí region Gentry's protocol was also applied to establish three parallel plots (50 x 2 m each) separated by 10 m from each other in

each of the eight studied forest patches. In the Usina Serra Grande region two distinct sampling designs were used. In 14 randomly selected forest patches a plot of 100 x 10-m was located at their geometric center (Santos *et al.*, 2008). In six additional forest patches and in 10 forest stands within the largest forest remnant in the area (the Coimbra forest, 3500 ha), a 40 x 40-m plot was located in interior areas (>200 m from the nearest forest edge). In the Una region five 25 x 4-m plots were located in the center of the 16 sampled forest patches, maintaining a minimum distance of 50 m between plots (Rocha-Santos *et al.*, 2016). Finally, in the Sooretama region ten 10 x 10-m plots were sampled in 10 forest interior areas (>300 m from the nearest forest edge; Magnago *et al.*, 2014, 2015b).

Biomass estimation

Because height data was not available for all plots, we estimated aboveground biomass (AGB) using the formula proposed by Chave *et al.* (2005) for tropical moist forests without tree height (Baraloto *et al.*, 2013):

$$AGB = p * \exp(-1.499 + 2.148 \ln(D) + 0.207(\ln(D))^2 - 0.0281(\ln(D))^3)$$

where D is diameter at breast height (cm), and p is wood density in dry weight (g cm^3). This equation was applied to our database because (i) our analysis was developed for a large pantropical dataset which includes Neotropical forests, (ii) the relation between height and diameter are implicit in the equation, and (iii) this same equation was already applied in several studies ensuring its robustness for biomass estimation in tropical moist forests (*e.g.*, Berenguer *et al.*, 2014; Bastin *et al.*, 2015; Osuri *et al.*, 2016). We used The Global Wood Density database, subsection Tropical South America (Chave *et al.*, 2009; Zanne *et al.*, 2009), to estimate wood density for all tree species. We estimated wood density at the species level for 32% of the individuals sampled and for the remaining trees we used the information available at the genus (51%) or family (14%) levels. The mean value of wood density for all tropical species in South America was used for individuals that lacked identification (3%). Aboveground biomass (Mg) was estimated for an area of 0.1 ha to avoid overestimates since sampling efforts in regions were ≤ 0.16 ha.

Functional attributes

We classified tree species based on traits that reflect tree growth, recruitment and survival strategies that are also related to structural and functional changes in plant community composition in fragmented forests (e.g. Santos *et al.*, 2008; Lôbo *et al.*, 2011; Magnago *et al.*, 2014; Benchimol & Peres, 2015). These included classifications based on: (i) plant regeneration strategies - pioneer *species* are those light demanding and fast-growing tree species and typically early colonizers; *shade tolerant* species those late-successional and old-growth forest species that recruit and grow under shaded conditions in the understory; (ii) forest stratification - classification based on maximal potential height with *understory* species with a potential height up to 20 m, *canopy* species with potential height ≥ 21 m and ≤ 30 m, and *emergent* species reaching at least 31 m height; (iii) dispersal mode - *vertebrate-dispersed* species and *abiotical-dispersed* species; (iv) seed size - *small seeded* species as those with seed length ≤ 15 mm and *large seeded* species those with seed length > 15 mm; and (v) wood density - *softwood* species those compounding the 10% percentile of the lower tail distribution of database wood density (≥ 0.41 g m³), while *hardwood* species are those compounding the 10% percentile of the upper tail distribution of database wood density (≤ 0.82 g m³), and the remaining species (> 0.41 and < 0.82) present intermediate wood density (Fig. S1). These ecological classifications were based on information from previous studies within each region (Santos *et al.*, 2008; Arroyo-Rodríguez *et al.*, 2009; Hernández-Ruedas *et al.*, 2014; Magnago *et al.*, 2014, 2015b) and additional literature for other regions (e.g. Lorenzi, 1992, 2008, 2009; Marquette & Vaz, 2007; Amorim & Alves, 2011; Moreau, 2014; SMASP, 2015).

Predictor variables

We considered local factors (edge distance, patch size) and landscape structure parameters (forest cover, open matrix area and proximity index). Edge distance was estimated as the Euclidean distance to the nearest edge from plot and patch size as the area (ha) of the focal patch. We adopted a sample site-landscape approach (Fahrig, 2013) to estimate the percentage of forest cover, open matrix and the proximity index in the landscape-scale surrounding each forest site, considering eleven radii (buffers) from 400 to 1500 m from the centroid of each sampling site. We selected this range of radii because forest structure may be related to processes acting over in different spatial scales (e.g., edge effects, logging, seed

dispersal) (Malhi *et al.*, 2014). We estimated forest cover, *i.e.*, the percentage of old-growth forests based on land cover maps, within each landscape-scale. We classified matrix area as open (plant height < 2 m or areas with low plant-density), shrubby (plants with height up to 6 m), and arboreal (plants or structure with height > 6 m), and then estimated from total area of matrix the percentage compounded by open matrix (hereafter open matrix area). We adapted the proximity index from McGarical & Marks (1994) considering all patches within the radius of the landscape-scale extent (adopted as a search radius), including the patch where the plot is situated. Distances between the plot and the patches were measured from the center of the plot to the closest edge of the patch, except for the focal patch (where the plot is situated), when an arbitrary value of one was adopted. Predictors were estimated using a geographic information system (ArcMap software; ESRI, Redlands, CA, USA) and the “base”, “raster”, “sp” and “maptools” packages from R software v. 3.3.1 (R Core Team, 2016).

Data analyses

The biomass and the density of individuals *per* 0.1 ha were estimated for each functional group and then simple Spearman’s correlations (once some variable did not present normal distribution) were used to explore how functional groups are related to biomass. We used confidence interval to compare the significance of differences among correlations from the same functional group (*e.g.* zoocoric *versus* abiotically dispersal mode) (Zou, 2007; Diedenhofen & Musch, 2015). Additionally, we tested if changes in functional composition affected biomass stocks. For this, we compiled the proportion of trees *per* functional groups by using a Principal Component Analysis (PCA). We thus used the first axis (as summarizing a gradient of floristic composition) from the PCA as a predictor variable and tested its influence on biomass stocks through model selection including a null model. Based on the information-theoretic approach, we selected the model with the best fit using the relative Akaike’s information criterion corrected for small sample sizes (ΔAIC_c ; Burnham & Anderson 2002).

Before we explored the effects of landscape structure and patch attributes on biomass we conducted exploratory analysis of the data and log transformed the predictors edge distance, patch size, and proximity index to avoid model inflation due to a large number of outliers (Zuur *et al.*, 2010). We then used a scale-selection procedure to determine the best scale of biomass response to each predictor measured along different scales, namely forest

cover, open matrix area, and proximity index. We thus performed for each predictor and scale linear mixed models with region and patch ID as random variables and selected the best model fit based on AICc (Burnham & Anderson, 2002). The best model represented the strongest scale of effect of the predictor on biomass, and this selected scale (for each predictor) was then used in further data analysis.

To explore the effect of local and landscape parameters on biomass we considered 9 groups of trees, using a combination of tree size (large and small) with regeneration strategy (shade-tolerant and pioneer). As the definition of large trees is context-dependent (Lindenmayer & Laurance, 2016), we used ≥ 40 cm dbh because this threshold represents just 7% of total trees but 68% of plant-community biomass. We also consider “small trees” (≤ 20 cm dbh) in the analysis because they represent the “regeneration strata” for our database, and also because they are a component of aboveground biomass sensitive to anthropogenic disturbance (Berenguer *et al.*, 2014). Additionally, we calculated the biomass of shade and pioneer for each tree size group. We thus tested the effects of landscape and patch structure on biomass of all trees (total, shade and pioneer), large trees (total, shade and pioneer), and small trees (total, shade and pioneer).

To inspect non-linear relations among forest cover and biomass we build a linear model, a quadratic model and a four-parameter logistic model (Pineiro & Bates, 2000) for each region. Both quadratic and four-parameter logistic models represent non-linear relations with the latter used to identify biological thresholds in recent studies (*e.g.* Morante-Filho *et al.*, 2015; Pessoa *et al.*, 2016; Rocha-Santos *et al.*, 2016). Linear and quadratic models always presented the best fit and were thus used in the rest of the analyses.

All predictors were standardized to a mean of 0 and standard deviation of 1 to compare the relative strength of the predictors (Grueber *et al.*, 2011). We inspected the collinearity among the predictor variables through the variance inflation factor (VIF). Particularly, patch size and proximity index presented strong collinearity (>10 ; Neter *et al.*, 1996) and thus were never included along with the same model. We set models derived directly from our conceptual model and other combinations not explicitly hypothesized by our conceptual model, but that were biologically plausible (*e.g.* forest cover interacting with patch size; see Appendix S3.1). We did not include any triple interactions, except (i) the interaction among edge distance, patch size and open matrix area and (ii) the interaction of

forest cover and proximity index, adding a quadratic term as they represented two of our theoretical hypotheses (Appendix S3.1). We restricted the set of models to those that were biological plausible, avoiding the exploration of all predictors' combinations, to decrease model uncertainty resulted from large number of models relative to the sample size (Burnham & Anderson, 2002; Grueber *et al.*, 2011).

Biomass analysis was conducted in two steps in order to first find the optimal random structure of models and then determine the fixed part (Zuur *et al.*, 2009). We found the optimal random structure of each model by combining several structures (*e.g.* random intercept; random intercept + random slope; random intercept|predictor) always using the region as a random factor. Additionally, we tested the fit of each these model combinations by also adding the patch ID as a random intercept (Appendix S3.1). These models were fitted using the restricted likelihood maximum estimation (REML) as it corrects the estimator for error variance (Burnham & Anderson, 2002), and we choose as the best optimal random structure the models with a $\Delta AICc$ of zero.

After we define the best random structure for each model we refitted the models using the maximum likelihood method (Zuur *et al.*, 2009). We thus proceed to the analysis of the fixed part and tested the relation of landscape structure and patch attributes on biomass. We conducted a model selection including also a null model and considered the models with $\Delta AICc \leq 2$ as equally plausible. When more than one model was considered equally plausible we performed the natural model averaging approach accounting for model uncertainty and to obtain robust parameter estimates by calculating a weighted average of coefficients estimates (Burnham & Anderson, 2002; Grueber *et al.*, 2011). We reported results only of the coefficients in which confidence interval did not overlap zero as these represented reliable effect sizes.

We inspected for spatial auto-correlation using the spline correlogram, a nonparametric estimator of the covariance function (Bjørnstad & Falck, 2001). Confidence intervals of the covariance function was estimated by bootstrapping technic based on 10 000 iterations with a maximal distance of 20 km. All data analysis were performed using R 3.3.1 (R Core Team, 2016) in which we used the package “Hmisc” to fit correlations and “cocor” to compare differences among correlations, “lme4” to fit models, “MuMIn” to model selection and model average, and “ncf” for spatial auto-correlation inspection.

Results

A total of 18 503 trees belonging to 104 families, 418 genera and 1210 species were recorded at the 146 sites located in the Brazilian and Mexican rainforests. Biomass *per* 0.1 ha considering all trees were (mean $\pm$ SD) 57.1 ± 44.1 , from large trees 39.1 ± 43.0 and small trees 5.0 ± 2.3 . Total biomass was strongly related to biomass of large trees (Spearman's correlation: 0.95, $p < 0.01$), specially from large shade-tolerant trees (0.88, $p < 0.01$), and poorly related to biomass of pioneer (0.10, $p < 0.01$) or small trees (-0.15, $p < 0.01$) (Fig. 3.3, Table S3.1). Biomass from species that occupy the canopy and emergent forest layer with vertebrate-dispersed fruits, independent of seed size, and intermediary values of wood density were strongly associated with aboveground biomass (Fig. 3.3, Table S3.1). The same patterns of correlations were observed for large trees (Table S3.1). The biomass of small trees, in contrast, was positively associated with biomass of pioneer trees from the understory, with vertebrate-dispersed fruits from small and large-seeded trees (Table S3.1).

The first axis from the PCA explained 37% of variation among sites and the second axis 17%. Positive values in the first axis were related with shade-tolerant trees inhabiting the emergent and canopy layer bearing large seeds dispersed by vertebrates (Fig. S3.2). In contrast, negative values correspond with sites dominated by pioneer from the understory (Fig. S3.2). Wood density, abiotical dispersal mode and small-seeded trees little contributed to discriminate sites (scores ranging from -0.05 to 0.07). The first axis thus described a gradient of functional traits going from traits commonly associated with disturbed forests (negative scores) to characteristics associated with old-growth forests (positive scores). These first axis was positively related to biomass (Fig. 3.4), showing that shifts in functional composition in direction to disturbed-adapted traits lead to reductions in biomass stocks.

Figure 3.3. Proportion of aboveground biomass *per* tree size (a) and functional traits (b-f) by regions in Neotropical forests. Column of total was calculated considering all regions. Lac: Lacandona, Soo: Sooretama, Tux: Los Tuxtlas (1, 2, and 3), Pac: Pacatuba, SGr: Serra Grande. See the description of regions in Table 3.1

The scales of effect of forest cover, open matrix and proximity index differed among the response variables (Table S3.2). In general, forest cover acted strongly at lower scales (< 700 m), except for large and small pioneer trees (> 1000 m). Open matrix also showed the strongest effects at small scales (< 600 m), but for large pioneer and small trees the scale of

effect can be > 900 m. Pioneers and small trees were more affected by proximity index at small scales (600-700 m) and the remaining response variables at larger scales (1200 m).

Fig. 3.4. Relation between the first axis from a Principal Component Analysis (PCA) and biomass stocks in anthropogenic Neotropical forests. Axis 1 represents a gradient of tree functional traits. Negative values indicate functional traits found in species commonly observed in disturbed forests, whereas positive values are associated with functional traits typically recorded in old-growth forest species.

We did not find any indication of a sigmoidal relation among forest cover and biomass considering all trees, large trees, and small trees (Fig. S3.3). Biomass considering all trees and from shade tolerant species was affected by the interaction among edge distance and forest cover, with increases in biomass following increases in forest cover and distance to edge (Table 3.2, Fig. 3.5a). Biomass of pioneer species considering all trees was affected by the interaction between edge distance and open matrix area (Fig. S3.4), and by the triple interaction of edge distance, patch size and open matrix area (Table S3.3, Fig. S3.5a). In general, biomass of pioneer was low in a combination of (i) high open matrix area and proximity to edge and (ii) low open matrix area and far from edge (Fig S3.4). Contrasting patterns was also observed when fragment size interacted with the amount of open matrix area: the higher biomass of pioneer was observed when the patch was large and open matrix area low or when the patch was small and open matrix area high. Increases in fragment size and edge distance benefited biomass of pioneer trees.

Table 3.2. Ranked linear mixed models ($\Delta\text{AICc} \leq 2$) investigating the influence of landscape structure in biomass stocks in Neotropical forests. For each model, we present the slope coefficients for each predictor term in the models, the degrees of freedom (df), Akaike information criterion corrected for small samples (AICc), difference in AICc from the best model (ΔAICc) and the relative AICc weight (w_i). Coefficients in bold represent effect sizes different from zero by inspection of parameter's confidence intervals. We only show the predictors from the most plausible models, see Appendix S3.1 for all models tested. EG: edge distance; FC: forest cover; OM: open matrix; PI: proximity index; PS: patch size; Shade: shade-tolerant.

Functional trait	EG	PS	FC	OM	PI	EG:PS	EG:FC	EG:OM	PS:OM	EG:PS:OM	df	logLik	AICc	ΔAICc	w_i
All trees	Total	10.65	3.83				12.08				9	-697.7	1414.7	0.0	0.52
	Shade	2.472	10.95				8.921				8	-682.7	1382.4	0.0	0.60
		2.07									7	-537.1	1089.0	0.0	0.18
		3.50	-1.01								8	-536.0	1089.1	0.1	0.16
	Pioneer	1.86		-1.17							8	-536.5	1090.0	1.1	0.10
		0.72	-1.77	1.46		-1.66		3.62	-1.95	-2.93	12	-532.2	1090.8	1.8	0.07
		2.33	-0.53				1.80				8	-537.0	1091.0	2.0	0.07
Large trees (≥ 40 dap)	Total	10.81	2.84				10.32				9	-689.9	1399.1	0.0	0.55
	Shade	9.66	10.18				8.87				9	-670.6	1360.4	0.0	0.91
	Pioneer	2.34		0.31				-1.01			9	-500.9	1021.1	0.0	0.37
		2.86		0.55							7	-503.8	1022.5	1.3	0.19
Small trees (≤ 20 dap)				-0.55	0.19						6	-301.2	615.1	0.0	0.42
	Total			-0.78	0.19						7	-300.7	616.2	1.1	0.24
			0.18	-0.78					0.19		7	-300.7	616.3	1.2	0.23
	Shade	0.12	0.12	-0.23		0.27		-0.12	0.13	0.26	10	-144.0	309.6	0.0	0.58
				-0.51							6	-285.8	584.1	0.0	0.17
		0.31		-0.46				0.18			8	-283.8	584.7	0.5	0.13
	Pioneer			-0.41	0.23						7	-285.3	585.4	1.2	0.09
			0.21	-0.42							7	-285.4	585.6	1.4	0.09
		0.11		-0.47							7	-285.4	585.6	1.5	0.08

Biomass of large trees and large shade-tolerant trees was also influenced by the interaction between the edge distance and forest cover (Table 3.2, Fig. 3.5b), as expected due to the strong correlation with biomass considering all trees (Table S3.1). The isolated effect of edge distance also impacted positively biomass of large shade-tolerant trees (Fig. 3.5c). Distance from edge also increased biomass of large pioneer trees (Fig. S3.6) but in combination with open matrix area we observed two distinct patterns. One is a positive effect of increase in open matrix area on biomass of large pioneer trees when edge distances are less than ~100 m (Fig. S3.7). When the edge distance increases, the sign of the influence of open area shifts and the model predicted negative impacts of open matrix area on biomass of large pioneer.

The open matrix affected negatively the biomass of small trees and small shade-tolerant trees (Table 3.2, Fig. 3.5d). The biomass of shade-tolerant small trees was also affected by the interaction of open matrix area with edge distance and patch size. The biomass was higher when open matrix area was low and distance to edge and patch size was high (Fig S3.8). Although model selection indicated that local factors and landscape structure can impact biomass of small pioneer trees the inspection of the confidence interval from slope coefficients indicate unreliable effect sizes (Table 3.2, Fig. S3.5b).

Fig. 3.5. Influence of landscape composition and patch structure on biomass of large (≥ 40 cm dbh) and small trees (≤ 20 cm dbh) in Neotropical forests. Synergism among forest cover and edge distance on biomass of all trees (a) and large shade-tolerant trees (b). Colors represent predicted biomass (Mg *per* 0.1 ha) by the mixed model at the combination levels of predictors' variables (grey points). Effect of log edge distance on biomass of large shade-tolerant trees (c). Effect of open matrix area on biomass of small shade-tolerant trees (d). Predictors were standardized before data analysis (see text) and zero values correspond to the mean value of the unscaled predictor. Log edge distance (mean $\pm$ SD): 4.5 ± 1.2 (94.2 ± 3.4 m); forest cover (% in 400 m of radius): 50.1 ± 33.7 ; open matrix area (% in 400 m of radius): 70.0 ± 40.1 .

Discussion

Our results bring novel insights about the main drivers of biomass loss in human-modified landscapes. First, we demonstrated that forest degradation is expressed by a shift in plant-community functional composition, replacing communities composed by large, shade-tolerant and zoochoric species typical of old-growth forests by communities dominated by

small, pioneer and understory species, with a consequent decrease in biomass stocks. Second, we revealed that landscape composition can interact with patch structure triggering reductions in biomass stocks. In particular, there were synergistic effects of edge distance with forest cover, edge distance with matrix type, and among edge distance, patch size and matrix type, but they affected in distinct ways the principal component of biomass stocks (large shade-tolerant trees) and the regeneration layer (small shade-tolerant trees).

Composition of Biomass Stocks in Human-Modified Landscapes

Large shade-tolerant trees were the most important component of aboveground biomass in Neotropical forests, reinforcing their crucial role for carbon stocks maintenance in tropical forests. Although represented by few individuals (5%) and species (17%), large shade-tolerant trees corresponded in average to 52% of plant-community biomass. Hyperdominance on carbon stocks by large trees seems to be a widespread pattern on tropical forest, have been reported both on Amazon (Fauset *et al.*, 2015) and African tropical forests (Lewis *et al.*, 2013; Bastin *et al.*, 2015).

Forest loss and fragmentation can lead to sharp declines in abundance and richness of shade-tolerant, late-successional, and large-seeded trees (Laurance *et al.*, 2006b; Michalski *et al.*, 2007; Santos *et al.*, 2008). The replacement of a rich community of hardwood, large-seeded species characteristic of old-growth forests (*i.e.* trees inhabiting the higher forest strata, bearing large-seeds, and with high wood density, as observed in Lacandona), by a poor community of softwood, small-seeded and ecologically-plastic pioneer can lead to long-term impacts on biomass stocks, as observed in the Amazon (Michalski *et al.*, 2007). This process of biotic homogenization and retrogressive succession (*sensu* Santos *et al.* 2008) can be triggered by the collapse of the emergent layer due to large tree mortality (Oliveira *et al.*, 2008) resulting in cascade changes in forest structure (Rocha-Santos *et al.*, 2016). Shifts in plant-community composition driven by the proliferation of fast-growing pioneer can lead to carbon losses up to 34% in tropical forests (Bunker *et al.*, 2005). In the final point of the successive regression, heavily deforested landscapes can reach a new biomass equilibrium where up to 60% of biomass is predicted to be lost configuring it to a degraded stable state (Pütz *et al.*, 2011). This process of floristic and functional simplification of plant-communities

and successive retrogression triggered by habitat loss and fragmentation was already reported for the Atlantic Forest (see Santos *et al.*, 2008; Lôbo *et al.*, 2011b; Magnago *et al.*, 2014; Rocha-Santos *et al.*, 2016), and according to our results appears to be a widespread pattern along the Neotropics.

The Role of Landscape and Patch Structure on Biomass

Forest loss and edge effects were the main drivers of biomass loss in Neotropical forests. Although this synergism was not contemplated in our initial predictions it corroborates our hypothesis that landscape structure can interact with patch attributes and mediate biomass stocks. Forest loss results in landscapes with scattered small patches, poorly connected and embedded in an anthropogenic matrix (Fahrig, 2003). Forest loss can thus reduce population viability through enhanced local extinction risk of sensitive species and decreased probability of recolonization of isolated populations (Fahrig, 2003; Pardini *et al.*, 2010). In deforested landscapes, restricted availability of habitat reduce plant density (Arroyo-Rodríguez *et al.*, 2009) and impact functional diversity, especially by the loss of emergent trees (Benchimol & Peres, 2015), large-seeded hardwood species (Michalski *et al.*, 2007) and large trees (Oliveira *et al.*, 2008).

Microclimatic changes due to edge creation, such as increased wind speed and air temperature (Magnago *et al.*, 2016; Arroyo-Rodríguez *et al.*, 2017), can penetrate deeper in the forest, reaching the central areas of small fragments, and thus leading to the loss of up to 74% of carbon stocks in case of small patches (Magnago *et al.*, 2015b). Populations in these small and poor-quality patches may rely on external seed flux to balance the high degradation-induced mortality due to edge effects (Groeneveld *et al.*, 2009). Yet, forest-dependent birds and mammals can show sharp declines in abundance and richness with forest reduction in tropical forests (*e.g.* Banks-Leite *et al.*, 2014; Morante-Filho *et al.*, 2015), compromising long-scale seed dispersal in deforested landscape. Dispersal limitation of large-seeded species through the loss of large frugivorous are predicted to drive significant carbon reductions in Neotropical forests (Bello *et al.*, 2015; Osuri *et al.*, 2016) with long-term losses up to 37.8% (Peres *et al.*, 2015).

Our results supported the initial prediction of the synergic effects between distance to edge, patch size and matrix harshness on biomass of shade-tolerant, but of small trees instead of large ones. The combination of patch-area and edge effects promoting changes in plant structure and composition (Laurance *et al.*, 2006a; Michalski *et al.*, 2007; Magnago *et al.*, 2014), with ultimate impacts in carbon stocks (Magnago *et al.*, 2016), were already observed in the tropical forests. Yet, the explicit role of the matrix in mediate the severity of forest degradation through the interaction of both patch size and edge distance with consequences in carbon stocks was never tested empirically, as far as we know. Here we showed that small patches surrounded by a matrix dominated by open areas intensify edge effects leading to the reductions in biomass of small shade-tolerant trees. These declines of shade-tolerant trees from the regeneration layer can lead to long-term demographic changes on plant-community by reducing the recruitment of large shade-tolerant trees. The extension of open matrix area was also important for large pioneer trees as it interacted with edge distance (Fig. S3.7). These patterns reinforce that short-lived pioneer might be benefited by forest degradation while long-lived pioneer were harmed by strong edge effects due to the influence of a high-contrasting matrix. The matrix thus plays an important role in mediate biomass stocks in Neotropical forests by acting both on long-lived pioneer as well as on the regeneration layer of shade-tolerant.

Following the “landscape conceptual model” (Fig. 3.1), we initially expected to find more clear effects of patch size, proximity with adjacent patches and forest cover on biomass, but we did not find strong evidences of those relationships (Fig. S3.3). In contrast, a clear pattern emerges, showing the need to consider the interaction of local (*e.g.* edge distance) with landscape (*e.g.* forest cover and matrix type) factors, instead of considering these factors individually. Degradation processes related to forest loss and fragmentation are clearly landscape-level processes (Fahrig 2003), and thus our results reflects the need to understand biomass dynamics in this larger spatial-scale context. Forest degradation can be particularly driven by habitat loss, edge effects, and matrix type, and synergisms between these factors greatly reduce or amplify forest degradation (Tabarelli *et al.*, 2004; Tabarelli & Gascon, 2005). Here we show that these combined effects, especially among forest cover and edge effects, are the main drivers of biomass loss in Neotropical forests.

Moreover, a non-linear response of biomass to habitat loss was predicted by the landscape effect conceptual model, but not observed. This non-linear behavior was expected

in response to the drastic reductions of richness and abundance of sensitive species, such as Sapotaceae (Lima & Mariano-Neto, 2014) and Myrtaceae (Rigueira *et al.*, 2013), as also for key components of forest structure (*e.g.*, palms; Benchimol *et al.*, 2016) and biomass-related traits, such as average diameter and basal area of trees (Rocha-Santos *et al.* 2016). However, the loss of biomass can be more directly related to the loss of forest if species do not respond to fragmentation, as observed for trees in the Peninsular Spain (Montoya *et al.*, 2010). Here we did not find an isolated effect of forest loss on biomass, but this effect may be conditioned to the level of regional disturbance of landscapes. In fact, forest loss only reduced linearly biomass stocks in regions under intermediate disturbance levels, such as Una, Sooretama and Los Tuxtlas 1 (Melito *et al.*, *in prep*; see Chapter 4). This pattern emerged possibly due to the increase variability of local disturbance-related process (*e.g.*, edge effects, logging) that can enhance spatial heterogeneity (Laurance *et al.*, 2009) and plant beta diversity (Socolar *et al.*, 2016), leading to multiple possible successional trajectories of plant-communities (Arroyo-Rodríguez *et al.*, 2015).

Conserving Carbon Stocks in Anthropogenic Tropical Landscapes

The conservation value of a landscape can be depleted when continued anthropogenic disturbances push the system to a degraded state (Melo *et al.*, 2013). Our results show that Neotropical landscapes may be following a trajectory into a degraded state, which considerably reduces the potential of their forest to stock carbon due to synergetic effects of factors acting in the landscape level (forest loss and matrix effects), accentuating local (edge) effects on biomass decay. Estimates of fragmentation-induced carbon emissions, for example, show additional losses to emissions from deforestation of 116 to 237 Tg C y^{-1} , or a ratio of 9 to 24% of annual emissions from global deforestation (Pütz *et al.*, 2014). In the Brazilian Amazon, anthropogenic disturbances were estimated to release roughly 40% of emissions by carbon losses from deforestation (Berenguer *et al.*, 2014).

Although since 2005 the United Nations Framework Convention on Climatic Change (UNFCCC) recognizes additional emissions from forest degradation triggered by anthropogenic disturbances with the release of REDD+ agenda, it is still a major challenge for the scientific community to understand the underlying mechanisms driving emissions from

forest degradation. Here we showed the essential role that landscape composition and patch structure play in mediate biomass stocks, indicating the necessity of landscape planning and mitigation of forest degradation to support carbon stocks in anthropogenic landscapes. To avoid further carbon emissions from forest degradation we suggest conservation initiatives focusing in (i) enhancing (or preserve) forest cover on local scales (~600 m radius), (ii) improving matrix quality to support seed flux from the regional pool and boost rescue effects of small population (Bunker *et al.*, 2005; Haddad *et al.*, 2015), (iii) decreasing the extent and magnitude of edge effects, especially by the management of matrix contrast within 500 m from patch, and (iv) actively restoring fragmented patches by tree enrichment (Berenguer *et al.*, 2014) of hardwood shade-tolerant species.

We also advocate that conservation efforts should not focus in landscapes that have reached a stable degraded state characterized by a simplified biota (Pütz *et al.*, 2011) with low forest cover, edge-dominated, poorly connected landscapes. Instead, management should prioritize landscapes that still retain ecological resilience (Pardini *et al.*, 2010), conservation value, ability to provide ecosystem services (Melo *et al.*, 2013) and potential to afford co-benefits to biodiversity (Strassburg *et al.*, 2010; Magnago *et al.*, 2015b), where local management will show greater effectiveness at lower costs (Tambosi *et al.*, 2014). Moreover, we are in agreement with Chaplin-Kramer *et al.* (2015) that mindfulness must be taken in account with climate policies and carbon trading agendas, such as REDD+, are applied considering that an hectare of forest can be traded by other elsewhere: landscape context matters for biomass stocks and thus should be considered in any policy of carbon conservation and offsetting.

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Supplementary material

Appendix S3.1. Diagram exemplifying the steps of data analyses. Models derived from the previsions of the *landscape effect conceptual model* (step 2, fixed structure) are signaled by an asterisk.

Fig. S3.1. Histogram of wood density highlighting the lower and upper 10 percentile used to classify trees as softwood and hardwood, respectively.

Table S3.1. Spearman's correlations among biomass of distinct trees sizes (all trees, large trees, and small trees) by biomass *per* functional groups (Rgn: regeneration strategy; WD: wood density; Str: vertical stratification; Dsp: dispersal mode; Seed: seed size) in Neotropical forests. Non-significant correlations are not shown. Letters indicate statistically different values among functional traits.

		Biomass		
		Total ^a	Shade ^a	Pioneers ^a
Biomass all trees (≥ 10 cm dbh)	Rgn	Shade	0.88 ^a	1.00 ^a
		Pioneers	0.10 ^b	-0.18 ^b
	WD	Hardwood	0.31 ^a	0.25 ^a
		Intermediate	0.90 ^b	0.78 ^b
		Softwood	0.44 ^a	0.55 ^c
	Str	Emergent	0.66 ^a	0.77 ^a
		Canopy	0.74 ^a	0.74 ^a
		Understory	0.35 ^b	0.24 ^b
	Dsp	Zoocoric	0.87 ^a	0.85 ^a
		Abiotic	0.58 ^b	0.62 ^b
	Seed	Large	0.80 ^a	0.79 ^a
		Small	0.77 ^a	0.74 ^a
Biomass large trees (≥ 40 cm dbh)	Rgn	Shade	0.92 ^a	1.00 ^a
		Pioneers	0.26 ^b	0.06 ^b
	WD	Hardwood	0.43 ^a	0.35 ^a
		Intermediate	0.91 ^b	0.87 ^b
		Softwood	0.55 ^a	0.63 ^c
	Str	Emergent	0.74 ^a	0.80 ^a
		Canopy	0.80 ^a	0.78 ^a
		Understory	0.50 ^b	0.42 ^b
	Dsp	Zoocoric	0.90 ^a	0.86 ^a
		Abiotic	0.67 ^a	0.68 ^b
	Seed	Large	0.84 ^a	0.82 ^a
		Small	0.80 ^a	0.79 ^a
Biomass small trees ≤ 20 cm dbh)	Rgn	Shade	0.39 ^a	1.00
		Pioneers	0.70 ^b	-
	WD	Hardwood	0.65 ^a	0.32 ^a
		Intermediate	0.93 ^b	0.37 ^a
		Softwood	-0.12 ^c	-0.06 ^b
	Str	Emergent	0.39 ^a	0.18 ^a
		Canopy	0.39 ^a	1.00 ^b
		Understory	0.70 ^b	-

Seed	Dsp	Zoocoric	0.80 ^a	0.46 ^a	0.67 ^a
		Abiotic	0.49 ^b	0.15 ^b	0.50 ^b
	Size	Large	0.68 ^a	0.37 ^a	0.57 ^a
		Small	0.73 ^a	0.30 ^a	0.67 ^a

^a Correlations were conducted using biomass from the observed tree size group

Fig. S3.2. Biplot of the principal component analysis (first two axis, respectively PC1 and PC2) showing the general structure of functional groups (in percentage of individuals) in 146 sites at human-modified Neotropical forests. See main text for definition of the functional traits. Interm.WD: trees with intermediary wood density.

Table S3.2. Scale of effect of predictors variables measured from 400 to 1500 radii from the geometric center of plots by tree size (all trees, large trees and small trees) and functional group (shade-tolerant and pioneer). Mean is the approximated mean scale of effect.

Predictor	All trees			Large trees			Small trees		
	Total	Shade	Pioneer	Total	Shade	Pioneer	Total	Shade	Pioneer
Forest cover	400	400	400	600	400	1000	500	700	1300
Open matrix	500	500	600	500	500	900	1200	400	1200
Proximity index	1200	1200	700	1200	1200	600	700	600	600

Fig. S3.3. Biomass of all trees (a), large trees (b), and small trees (c) in response to forest cover (at 400, 500, and 600 m of radius respectively) in Neotropical forests.

Fig. S3.4. Influence of edge distance and open matrix on biomass of pioneer (Mg *per* 0.1 ha) in Neotropical forests. Predictors were standardized before data analysis (see main text). Colors represent predicted biomass by the mixed model at the combination levels of predictors' variables (grey points).

Fig S3.5. Results of natural model-averaged coefficients estimates from linear mixed models of standardized predictor variables effects on biomass of (a) pioneer, (b) small pioneer trees, (c) large pioneer trees, (d) small trees from Neotropical forests. Points are mean slope values, horizontal black lines the standard errors and grey shadows the 95% confidence intervals.

Fig. S3.6. Relationship among log edge distance and biomass of large pioneer trees in Neotropical forests. Predictor was standardized before data analysis (see main text).

Fig. S3.7. Influence of edge distance and patch size on biomass of large pioneer trees (Mg *per* 0.1 ha) in Neotropical forests. Predictors were standardized before data analysis (see main text). Colors represent predicted biomass by the mixed model at the combination levels of predictors' variables (grey points).

Fig. S3.8. Influence of edge distance and patch size on biomass of small shade-tolerant trees (Mg *per* 0.1 ha) in Neotropical forests. Predictors were standardized before data analysis (see main text). Colors represent predicted biomass by the mixed model at the combination levels of predictors' variables (grey points).

CHAPTER 4

Landscape Forest Loss Decreases Tree Biomass in Fragmented Rainforests with Intermediate Disturbance Intensity

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Schematic diagram:

Abstract

Different local disturbances, such as logging and edge effects, can drive the collapse of forest structure in fragmented rainforests. Yet, large uncertainty remains about the effect of landscape-scale forest loss on forest structure, and how this effect varies with disturbance intensity at the regional scale (*e.g.*, regional deforestation, defaunation, matrix harshness). Using a large vegetation dataset (17 166 trees), we tested the effect of forest cover on stem density and tree biomass considering landscapes surrounding 136 forest sites distributed across four Mexican and four Brazilian rainforest regions with different disturbance levels. Such levels ranged from recently and little deforested regions composed of a heterogeneous matrix and well-preserved animal assemblages (29 sites), to old and severely deforested and defaunated regions dominated by a homogeneous and harsh matrix (67 sites). Intermediate disturbance conditions (40 sites) encompass regions where fragmentation process is ongoing, with a mosaic of large and small patches surrounded by high and low contrasting matrix, with a depauperated large-fauna present. Forest cover effects may depend on the spatial extent at which landscape structure best predicts species responses (so-called “scale of effect”). Thus, we assessed the strength of forest cover effects on each response variable across different-sized landscapes (within radii of 400-1500 m from sampled sites). Stem density was only related to forest cover in high disturbed regions, but proliferation of light-demanding pioneer species do not compensate biomass loss due to the extirpation of shade-tolerant species. Yet, forest loss simplified forest structure by decreasing biomass, but this relationship was observed only in regions with intermediate disturbance intensity and showed stronger effects at small scales (< 700 m radii). This novel finding related with the regional effect on biomass loss at intermediate level of disturbance may be related to the high variability in disturbances status or processes (*e.g.*, edge effects, degree of isolation, forest cover) in intermediately disturbed regions, which can promote a high variation in tree biomass among forest sites. Management strategies aimed to sustain carbon stocks should focus on those intermediate disturbance situations, where the potential of biomass response to management is stronger and thus where the delivery of ecosystem services can be optimized.

Keywords: carbon stocks, forest structure, large trees, forest degradation, forest cover, human-modified landscapes, land-use change, tropical forests

Introduction

Tropical forests play a crucial role in climate regulation, especially as carbon sinks (Pan *et al.*, 2011). Yet, they are being rapidly deforested worldwide, with forest losses reaching 5.93 million ha year⁻¹ between 2000 and 2010 (Achard *et al.*, 2014). Neotropical forests lose nearly 2,000 trees *per* minute, and almost half of its original area has been converted to human-modified landscapes (Rainforest Alliance, 2016). The remaining forest patches face numerous local disturbances, including selective logging, edge effects, and defaunation (Malhi *et al.*, 2014; Barlow *et al.*, 2016). Altogether, these threats can reduce tree biomass through the extirpation of large trees (≥ 30 cm of diameter at breast height - dbh; Laurance *et al.*, 1997, 2000; Lindenmayer & Laurance, 2016) – the principal component of aboveground biomass in tropical forests (Bastin *et al.*, 2015; Fauset *et al.*, 2015). Because carbon in tropical forests is mainly stored in aboveground biomass (Schlesinger & Bernhardt, 2015), such biomass loss limits global carbon sinks (Houghton, 2005).

The loss of large trees in fragmented rainforests can promote the proliferation of lianas and pioneer tree species (Santos *et al.*, 2008; Lôbo *et al.*, 2011; Schnitzer & Bongers, 2011; Benchimol & Peres, 2015), but such proliferation does not compensate the biomass that is lost with the extirpation of large trees (Laurance *et al.*, 1997). Nevertheless, because most studies on the topic compare forest structure between forest edges and interiors or among different-sized forest patches (*e.g.* Laurance *et al.*, 2002; Arroyo-Rodríguez & Mandujano, 2006; Hernández-Ruedas *et al.*, 2014), considerable uncertainty remains about the effect of forest loss at larger (landscape and regional) scales on forest structure. In a recent study, Rocha-Santos *et al.* (2016) show that landscape forest loss triggers great losses in local forest structure, but it is still unclear whether this effect varies among regions with different disturbance levels. Understanding the outcome of past and current regional disturbance on forest structure is needed to identify the mechanisms underlying biodiversity erosion and successional pathways in deforested tropical rainforests (Melo *et al.*, 2013; Arroyo-Rodríguez *et al.*, 2016).

Based on the “*fragmentation threshold hypothesis*” (*sensu* Pardini *et al.*, 2010) we can expect habitat configuration (*e.g.*, mean patch size, forest edge density) to have greater impact on forest structure in landscapes or regions with intermediate values (~30-60%) of

forest cover, where configuration has the greatest spatial variability (Villard & Metzger, 2014). This is expected because forest specialists, such as large trees, in landscapes with intermediate levels of forest cover are more susceptible to patch area effects, and thus, more dependent on landscape configuration (Pardini *et al.*, 2010). Additionally, tropical landscapes are highly diverse and composed of both homogeneous (*e.g.*, dominated by pastures and monocultures) and heterogeneous matrices (*e.g.*, composed of different land covers, including secondary forests, small-scale agriculture and human-settlements). Both scale and magnitude of edge effects are known to depend on *matrix* features (Harper *et al.*, 2005; Chaplin-Kramer *et al.*, 2015), being higher in high-contrast matrices (*e.g.*, pastures) than in low-contrast matrices (*e.g.*, tree crops and secondary forests) (Mesquita *et al.*, 1999; Ewers & Didham, 2006). Therefore, the matrix plays an important role in mediating edge-related biomass loss in tropical forests (Chaplin-Kramer *et al.*, 2015). Furthermore, most large trees are long-lived and exhibit lengthy *time lags* in forest structure responses to deforestation and fragmentation (Metzger *et al.*, 2009; Melo *et al.*, 2013). Thus, in contrast with aging regions that have a long history (>100 y) of land-use change (*e.g.*, Santos *et al.*, 2008), forest patches in regions with a relatively short history (<30 years) of human activity still maintain forest structure more similar to those of continuous forests (Hernández-Ruedas *et al.*, 2014). *Defaunation* (*i.e.*, the decline or extirpation of animal populations) can also influence forest structure and composition. Also, it leads to the extirpation of large-seeded, animal-dispersed trees, functional traits known to be associated with old-growth tree species (Osuri *et al.*, 2016), resulting in decreases in carbon storage (Bello *et al.*, 2015; Peres *et al.*, 2016). Therefore, comparing the response of forest structure to changes in landscape forest loss among regions with different disturbance levels (*e.g.*, with different degree of deforestation, defaunation level, matrix contrast and land-use history), it is urgently needed to identify the regional context under which forest structure responses can be greater.

Here, we tested the effect of landscape forest cover (forest cover, hereafter) on tree density and aboveground biomass in 136 study sites distributed across four Mexican and four Brazilian rainforest regions with different histories and levels of disturbance. To accurately evaluate the effect of forest cover on forest structure, we implemented a multi-scale assessment of the strength of such effects on each response variable to detect the “scale of effect”. Meaning, the spatial extent at which landscape structure best predicts species responses (Jackson & Fahrig, 2015). We highlight that we do not intend to compare these

response variables among regions because such differences may be related to different local conditions (*e.g.*, precipitation, dry season length, and soil type) that were not controlled in our sample design (Clark & Clark, 2000; Vieira *et al.*, 2004; Lewis *et al.*, 2013; Chave *et al.*, 2014). Comparisons among regions were made only about the strength of forest structure responses to landscape forest loss.

Therefore, we hypothesized that under low-disturbance scenarios, processes such as edge effects, logging, deforestation, and defaunation do not represent important threats to biodiversity at the regional scale. Thus, contributing to maintaining high ecological resilience (Arroyo-Rodríguez *et al.*, 2015) and similar patterns of well-preserved forests throughout the region (Hernández-Ruedas *et al.*, 2014). We predict low variability forest structure at low disturbed regions (Fig. 4.1a) with no detectable effects of forest loss on biomass and plant density at these areas (Fig. 4.1b, c). Highly-disturbed scenarios, however, results in a pervasive environmental degradation at the regional scale, leading to forest patches composed of tree assemblages severely impoverished and dominated by disturbance-adapted species (Santos *et al.*, 2008). Also, we can expect smaller differences in forest structure among forest sites under this highly-disturbed scenario (Fig. 4.1a) because these species share similar functional attributes, *e.g.*, fast-growing, softwood, and light-demanding species with small seeds dispersed by small animals (Santos *et al.*, 2008; Tabarelli *et al.*, 2010). Increases in forest cover could improve plant density in highly disturbed regions as we expect these communities are below their carrying capacity (Fig. 4.1c). Still, such improvements in tree density would not affect aboveground biomass (Fig. 4.1b). We thus predict greater variability of forest structure responses at intermediate disturbed regions and a stronger dependency on the amount of forest cover to sustain a carbon-rich landscape (Fig. 4.1b). We also expect that forest loss would increase plant density due to the proliferation of fast-growing pioneer triggered by the high mortality and damage of large trees with strong negative impacts in biomass stocks.

Fig. 4.1. Hypotheses for plant structure responses to the regional disturbance level of Neotropical forests. We expect greater variability in forest structure responses in regions under an intermediate disturbance level (a). With significant and positive effects of forest cover on biomass (b) and negative impacts in plant density (c) due to growth of large trees. In (a) we shown centered (mean=0) response variables (biomass and density) in the y-axis to highlight the expected higher variation between regions under distinct disturbance levels, and not differences in the amount of biomass among regions.

Methods

Study regions and sites

We surveyed eight regions, four from Brazil and four from Mexico, originally dominated by tropical rainforests (Fig. 4.1). The regions include a gradient of disturbance level, based on an evaluation of four criteria (degree of deforestation, defaunation level, matrix contrast, and land-use history), considering our personal knowledge of the study regions and published reports (*e.g.*, Dirzo & Miranda, 1990; Faria *et al.*, 2007; Arroyo-Rodríguez *et al.*, 2009; Pardini *et al.*, 2009; Canale *et al.*, 2012; Hernández-Ruedas *et al.*, 2014) (Tables 1 and 2). We categorized the regions in low (LD), intermediate (ID), and high disturbed (HD), with a tendency (from LD to HD) of longer deforestation histories resulting in a lower regional forest cover, more contrasting and homogeneous matrix, and severely depaupered fauna (Table 4.2). Our sample included 136 forest sites; all located in lowland forest areas (0-400 m a.s.l.) with a warm (24-25 °C) and humid climate (Table 4.1).

Fig. 4.1. Map of the eight rainforest regions (four from Mexico and four from Brazil) showing the location of 136 forest sites. Regions were labeled as low disturbed (LD), intermediate disturbed (ID), and high disturbed (HD). Tux: Los Tuxtlas (1,2, and 3); Lac: Lacandona; Pac: Pacatuba; SGr: Serra Grande; Soo: Sooretama. See Table 4.1 for a full description of the regions and Table 4.2 for the classification of disturbance levels.

Under our classification, the best-preserved region (LD), *i.e.* the less-disturbed, is the Mexican portion of the Lacandona rainforest, which conserves the largest remnant of tropical rainforest in the country (~13 000 km²). In LD we studied four continuous forest sites within the Montes Azules Biosphere Reserve (331 200 ha), and 25 forest patches (2 to 188 ha) outside this reserve in the Marqués de Comillas municipality. This municipality was colonized in the 1970's and was mainly deforested between 1984 and 1986 (Aguilar & Mora, 1992). We estimate that approximately 38% of old-growth forest cover (see the “*Explanatory variable*” section) remains nowadays as remnant patches of various sizes embedded in a heterogeneous matrix composed of secondary forests, pastures, field crops, and human settlements. This region has not suffered from a defaunation process, as large terrestrial

mammals (*Mazama americana*, *Tapirus bairdii*, *Pecari tajacu*), including top-predators (*Panthera onca*), primates (*Ateles geoffroyi*, *Alouatta palliata*) and birds (*Ara macao*, *Crax rubra*, *Tinamus major*) are still present even in small forest patches (Arroyo-Rodríguez *et al.*, 2013; Garmendia *et al.*, 2013; Carrara *et al.*, 2015). See further details of this region in Hernández-Ruedas *et al.* (2014).

Following our disturbance gradient, we studied three regions with an intermediate disturbance level: the Una and Sooretama regions in the Brazilian Atlantic forest and the Los Tuxtlas LDL (following Arroyo-Rodríguez *et al.* 2009, hereafter Los Tuxtlas 1) region at Mexico (Fig. 4.1, Table 4.1 and 2). The three regions still maintain large forest reserves: the Una Biological Reserve (~187 km²) and the surrounding Una Wild Life Refuge (~232 km²) at the municipality of Una, the Vale Natural Reserve (~230 km²) and Sooretama Biological Reserve (~278 km²) at the municipalities of Sooretama, Linhares and Jaguaré, and the Los Tuxtlas Tropical Biological Station (700 ha) that is functionally connected with few large private forest patches nearby (200-300 ha). Deforestation at Una area accentuated during late 1980's with the decline of cocoa plantations and an increase in forest harvesting (Saracura, 1997). The subsequent expansion of pastures and agriculture resulted in the disappearance of roughly 75% of forest cover. Remaining forest patches are surrounded by a heterogeneous matrix of pastures, secondary forests, rubber tree, and cocoa plantations. Although a vast area in southern Bahia in Brazil is dominated by extensive shade plantations of cocoa established between the end of 19th and early 20th centuries (Saracura, 1997). This crop arrived at Una more recently (1990's) and has been limited to small patches within the forest mosaic. From this mosaic of scattered fragments, 16 patches (5 to 24 301 ha) were chosen to compound our sample. The Linhares-Jaguaré-Sooretama area remained well preserved until the 1950's, when the region started to be explored for charcoal production, logging and agriculture (Garay & Rizzini, 2004). Forest conversion had its peak by the early 1970's and nowadays, 60% of the original forest cover remains embedded in a heterogeneous matrix composed of pastures, *Eucalyptus*, and coffee plantations, from where we sampled 10 sites (13 to 27 858 ha). Additionally, the Vale Reserve at the Linhares-Jaguaré-Sooretama area still harbors a conserved fauna and is one of the last refuges at the Atlantic Forest to threatened primates (*e.g.* *Alouatta guariba*, *Sapajus robustus*), birds (*Crax blumenbachii*), mammals (*e.g.* *Priodontes maximus*, *Tapirus terrestris*, *Tayassu pecari*) and top-predators (*e.g.* *Puma concolor*, *Panthera onca*) (Alves, 2014; Srbek-Araujo *et al.*, 2014; Srbek-Araujo & Chiarello,

Table 4.1. General characteristics and main disturbance attributes of the studied regions. The regional level of disturbance (see Table 2) was based on land-use history (years since the beginning of the deforestation process), defaunation level (presence of large mammals and birds), degree of deforestation (forest cover in the region), and composition of the anthropogenic matrix.

Area	Country	Location (lat/long)	Pluviosity (mm/year)	Sampling effort (ha) ^a	Disturbance attributes				
					Land-use (years)	Defaunation	Forest cover (%)	Matrix ^b	Classification
Lacandona	Mexico	16°07'N - 90°53'W	3000	29 (0.10)	35	Very low	38	HHe	LD
Los Tuxtlas 1	Mexico	18°36'N - 94°6'W	3800	15 (0.10)	60	High	24	HoP	HD
Una	Brazil	15°0'S - 39°0'W	1500	16 (0.05)	30	High	20	He	
Sooretama	Brazil	19°04'S - 39°57'W	2000	9 (0.10)	65	High	57	He	
Los Tuxtlas 2	Mexico	18°22'N - 94°47'W	3800	15 (0.10)	60	Very high	11	HoP	
Los Tuxtlas 3	Mexico	18°31'N - 94°49'W	3800	15 (0.10)	60	Very high	4	HoP	
Pacatuba	Brasil	6°59'S - 35°5'W	1500	8 (0.03)	>100	Very high	21	HoS	HD
Serra Grande	Brazil	8°30'S - 35°50'W	2000	29 (0.10/0.16) ^c	>101	Very high	12	HoS	

^a Sampling effort refers to the number of forest sites sampled within each study area, and sample size per site.

^b The anthropogenic matrix surrounding forest patches, which can be heterogeneous (He) mostly composed by cattle pastures, plantations, secondary forests, and/or human settlements; or homogeneous dominated by cattle pasture (HoP) or sugarcane (HoS).

^c two sampling efforts were used at Serra Grande, 15 permanent plots of 0.16 ha and 14 non-permanent plots of 0.10 ha.

2016). However, in Los Tuxtlas 1 most large mammals (e.g., *Panthera onca*, *Tapirus bairdii*, *Pecari tajacu*), primates (i.e., *Ateles geoffroyi*), and birds (e.g., *Ara macao*, *Crax rubra*) have been extirpated or maintain very small populations, even within the limits of the forest reserve (Dirzo & Miranda, 1990).

The areas classified as “high disturbance level” include the Los Tuxtlas (IDL and HDL following Arroyo-Rodríguez *et al.* 2009, hereafter Los Tuxtlas 2 and 3) in southeastern Mexico. As well as, the Pacatuba and Serra Grande regions, both located in northwestern Atlantic Forest (Fig. 4.1, Table 4.1 and 2). The Los Tuxtlas region was decreed a Biosphere Reserve in 1998, because of its high and unique biodiversity. The reserve covers an area of 1551.2 km², represents the northern limit of tropical rainforest distribution in the Neotropics, and it has been heavily deforested since the 1970’s, mainly for cattle pasture expansion. This resulted in a landscape composed by small patches (< 10 ha) surrounded by a homogeneous matrix of pastures and croplands (Castillo-Campos & Laborde, 2004) where 30 patches were studied. The Pacatuba and Serra Grande regions also show unique biodiversity. Is considered a center of endemism of the Brazilian Atlantic Forest despite the extensive deforestation for expansion of sugarcane fields in the region, which initiated in the 17th century and were intensified during the 19th century (Ranta *et al.*, 1998; Santos *et al.*, 2008). Deforestation resulted in a loss of 70 to 85% of the regional forest cover, with small forest patches surrounded by a stable and uniform sugarcane matrix. At these intensely human-modified landscapes we studied 8 forest sites (21 to 2637 ha) from the Pacatuba-Gargaú Ecological Corridor, Paraíba state. In addition, 29 sites (4 to 3930 ha) from the Usina Serra Grande – an area belonging to a private sugarcane company in the Alagoas state. The long history of overhunting and habitat loss at Pacatuba and Serra Grande has regionally extirpated all large mammals (*Mazama* spp., *Myrmecophaga tridactyla*, *Tapirus terrestris*, *Tayassu pecari*, *Panthera onca* and *Puma concolor*) and greatly simplified and homogenized the remaining community of medium-mammals (Mendes Pontes *et al.*, 2016). The largest frugivore bird (*Mitu mitu*) was also extinct in the region, whereas other large fruit-eating birds, such as guans (*Penelope*), chachalacas (*Ortalis*), toucans (*Ramphastos*), and aracaris (*Pteroglossus*), maintain reduced populations (Silva & Tabarelli, 2000). As already described above,

the Los Tuxtlas region also present depauperated and even extinct populations, especially of large animals.

Table 4.2. Classification of regions based on scores of regional disturbance level. Scores were attributed considering the sum of points from each level of disturbance characteristics (a). We classified regions as low-disturbed if score was maximum 5, as intermediate-disturbed scores ranging 6 to 10, and high-disturbed regions with a minimum score of 11 (b). Ho: homogeneous and high-contrasting matrix (pastures or sugarcane); He: heterogeneous matrix including low-contrasting land uses (*e.g.* plantations and secondary forests).

(a)

Disturbance levels	Land-use (years)	Defaunation	Forest cover (%)	Matrix	Points
Low	< 30	low	≥ 40	He	1
Intermediate	30-60	high	20-40	He	2
High	> 60	very high	< 20	Ho	3

(b)

Regions	Land-use (years)	Defaunation	Forest cover (%)	Matrix	Score	Classification
Lacandona	2	1	1	1	5	LD
Una	1	2	2	1	6	ID
Sooretama	3	2	1	2	8	ID
Los Tuxtlas 1	3	2	2	3	10	ID
Los Tuxtlas 2	3	2	3	3	11	HD
Pacatuba	3	3	2	3	11	HD
Los Tuxtlas 3	3	3	3	3	12	HD
Serra Grande	3	3	3	3	12	HD

Vegetation sampling

Here we present a brief description of the sampling design adopted in each region. We considered only trees with diameter at breast height (dbh) ≥ 10 cm to standardize the database and because tree biomass is principally stocked within the arboreal strata (DeWalt & Chave, 2004). All sampled sites within each region were located in areas

with similar soil characteristics and topography to avoid potential confounding effects of these factors. In Lacandona and Los Tuxtlas (1 to 3) the Gentry's (1982) protocol was used to record all trees in ten 50 x 2 m transects randomly located in the center of each forest patch, totaling 29 and 45 patches, respectively (Arroyo-Rodríguez *et al.*, 2009; Hernández-Ruedas *et al.*, 2014; Table 4.1). In the Una area (ID) five 25 x 4-m plots were located in the center of each of the 13 forest patches, maintaining a minimum distance of 50 m between plots (Rocha-Santos *et al.*, 2016). In the Sooretama area (ID) ten 10 x 10-m plots were sampled located in 10 forest interior areas (>300 m from the nearest forest edge) (Magnago *et al.*, 2014, 2015a). In the Pacatuba-Gargaú area (HD) the Gentry's protocol was followed to establish in each of the 8 forest patches sampled three parallel plots (50 x 2 m each), 10 m apart from each other. Finally, in the Usina Serra Grande area (HD) two distinct sampling designs were used. In 14 randomly selected forest patches one 100 x 10-m plot was located at their geometric center (Santos *et al.*, 2008). In 6 additional forest patches and in 11 forest stands within the largest forest remnant in the area (the Coimbra forest, 3500 ha), one 40 x 40-m plot was located in interior areas (>200 m from the nearest forest edge) (Table 4.1).

Response variables

We considered the mean and total tree aboveground biomass (Mg), and tree density. All estimated for an area of 0.1 ha *per* site to avoid overestimates since sampling efforts were ≤ 0.1 ha (Table 4.1). We also calculated tree density (ind./0.1 ha) for six classes of dbh (from ≥ 10 to ≥ 60 cm) to validate our assumption that biomass is mainly driven by large trees. We estimated tree biomass using the formula proposed by Chave *et al.* (2005) for tropical moist forests, but following Baraloto *et al.* (2013) we did not consider tree height, as these data were not available for all plots:

$$AGB = p * \exp(-1.499 + 2.148 \ln(D) + 0.207(\ln(D))^2 - 0.0281(\ln(D))^3)$$

where D is diameter at breast height (cm), and p is wood density in dry weight (g cm^{-3}). We obtained wood density for all tree species in the subsection Tropical South

America from The Global Wood Density database (Chave *et al.*, 2009; Zanne *et al.*, 2009). Whenever possible, we included wood density at the species level (32% of sampled individuals). When this information was unavailable, we used the information available at the genus (51%) or family (14%) levels. For non-identified individuals (3%), we used the mean value of wood density for all tropical species in South America. We used this equation because (1) height-diameter relationships are implicit in estimation, (2) it was developed based on a large pantropical dataset, and (3) has been largely applied and tested for biomass estimations in other tropical moist forests (*e.g.*, Berenguer *et al.*, 2014; Bastin *et al.*, 2015; Osuri *et al.*, 2016). Additionally, we classified tree species based on plant regeneration strategies (pioneer and shade tolerant species) and estimated percentage of pioneer stems *per* 0.1 ha (see Appendix S4.1 for full description).

Explanatory variable

We adopted a sample site-landscape approach (Fahrig, 2013) to estimate the percentage of forest cover in the landscape surrounding each forest site, considering 15 radii (buffers) from 100 to 1500 m from the centroid of each sampling site (Fig. 4.2). We selected this range of radii because forest structure may be related to processes acting over different spatial scales (*e.g.*, edge effects, logging, seed dispersal) (Metzger, 2000; Malhi *et al.*, 2014). We estimated forest cover, *i.e.*, the amount of old-growth forests, within each landscape-scale and for each region (regional forest cover) using a geographic information system (ArcMap software; ESRI, Redlands, CA, USA) and the “base”, “raster”, “sp” and “maptools” packages from R software v. 3.2.3 (R Core Team, 2016). Old-growth forests were distinguished of secondary forests through land cover maps produced in previous studies at the regions (*e.g.* Santos *et al.*, 2008; Arroyo-Rodríguez *et al.*, 2009; Hernández-Ruedas *et al.*, 2014; Magnago *et al.*, 2014; Rocha-Santos *et al.*, 2016). The regional forest cover was estimated by summing all old-growth forest pixels from land-use maps from each region divided by the total number of pixels, then standardized as percentage. Mean forest cover across scales was 44% in LD (range = 3.5-100%), 44% in R2 (0.6-100%), and 33% in R4 (0.2-100%) (Fig. S4.1).

Data analyses

We used Spearman's correlation coefficients to test the association between tree density and tree biomass for the six classes of tree dbh (from 10 to 60 cm dbh). We used Levene's test to compare if regions shows distinct variances and test our hypothesis that at medium disturbed landscapes plant structure present greater variability.

We followed the protocol suggested by Jackson & Fahrig (2015) to estimate the scale of forest cover effects on each response variable. For each landscape extent (400 to 1500-m radii), we analyzed the relationship between forest cover and each response variable (biomass and tree density) using an information-theory approach. For LD we fitted Generalized Least Squares model because it is a linear model that allows errors to be correlated and/or present unequal variances, and the fixed structure can be estimated via maximum likelihood (Pinheiro & Bates, 2000; Zuur *et al.*, 2009). For ID and HD we fitted Linear Mixed-Effects models with the regions (three for ID and four to HD, see Table 4.1) as random variables. Then, we constructed 12 models, one for each scale, to analyze the strongest scale of effect of forest cover influence on biomass and tree density inspecting these effects separately for LD, ID and HD. We identified the most plausible models, thus the strongest scales of effect of forest cover, as those with a difference of the Akaike's information criterion corrected for small sample sizes smaller or equal to two ($\Delta AICc \leq 2$) (Jackson & Fahrig, 2015). Then, we included in the model selection a null model that represents a zero effect of forest cover on plant structure to assign if forest cover impacts biomass and tree density in regions under distinct disturbance levels. The same approach was conducted for percentage of pioneer trees to verify if forest structure responses (biomass and tree density) to forest loss may be related with changes in the ratio of pioneer trees in the community.

When the effect of forest cover on plant structure was the most plausible model we validated the best model by inspecting for homogeneity and normality of the residuals. Mantel's tests were used to check for spatial auto-correlation among sites (Mantel, 1967). Biomass at ID and HD and percentage of pioneer at HD presented

positive spatial auto-correlation thus we inserted correlation structures on models to account for spatial dependence among sites (Zuur *et al.*, 2009).

Results

We sampled a total of 17 166 trees belonging to 1170 species, 408 genera, and 104 families. Biomass (Mg/0.1 ha) averaged 37.6 ± 15.4 in LD, 80.8 ± 63.5 in ID, 54.3 ± 33.6 in HD. Biomass variance differed between the disturbance level of areas (Levene's test p -value <0.01 for all comparisons), with ID showing the greater variance, followed by HD, and LD (Fig. 4.3). Mean tree density *per site* was 205.6 ± 32.5 in LD, 86.3 ± 56.0 in ID, and 85.0 ± 38.6 in HD, with all variances considered equal by Levene's test (p -value >0.05 for all comparisons) (Fig. 4.3). Biomass was positively and strongly correlated with density of large trees at least ≥ 40 cm dbh in all regions (LD, ID and HD) (Table S4.1). Percentage of pioneer stems differed among regions averaging $12 \pm 10\%$ in LD, $33 \pm 19\%$ in ID, and $30 \pm 19\%$ in HD.

Fig. 4.3. Centered (mean=0) biomass (a) and density (b) in Neotropical forests with different disturbance levels. Vertical grey bars are the standard deviation ($\sqrt{\sigma^2}$) of the mean highlighting the spread of the data.

Forest cover was positively related to biomass across spatial scales for all regions, but at LD and HD models including forest cover were equally plausible with patterns generated by random (Table S4.2). At landscapes under intermediate disturbance levels (ID), forest loss decreased aboveground biomass (Fig. 4.5, Table S4.2) with the strongest effects at lower scales (≤ 900 m of radius) (Fig. 4.4).

Fig. 4.4. . Multi-scale analysis of the effect of landscape forest cover on biomass (a-c) and stem density (d-e) in rainforest regions with low (LD), intermediate (ID) and high (HD) degree of disturbance. Y-axis are the differences of restricted Akaike Information Criteria ($\Delta AICc$) among each scale with the grey horizontal showing the cutoff criteria ($\Delta AICc < 2$) were models were considered equally plausible. Black points are positive relations among forest cover and the response variable and grey points negative associations.

Tree density was positively related with forest cover at LD between the 400 and 1000 m of radius, above it forest cover decreased tree density (Fig. 4.4). However, these patterns were equally plausible to those caused by random (Table S4.2). At ID forest cover was not related to tree density, regardless of the observed scale (Fig. 4.4, Table S4.2). Increases in forest cover only influenced tree density at HD, especially at

larger scales (≤ 800 m of radius) (Fig. 4.5, Table S4.2). In all regions and scales percentage of pioneer stems increased in landscapes with lower forest (Fig. S4.2, S4.3).

Fig. 4.5. Aboveground biomass (a) and tree density (b) in response to forest cover in regions with intermediate disturbance levels (ID) and high disturbance levels (HD) at Neotropical forests.

Discussion

This study shows novel insights on the pervasive effect of landscape-scale forest loss on Neotropical forest structure across several spatial scales (which vary with the considered region and forest structure parameter), and how this effect varies among regions with different disturbance levels. Particularly, low and high disturbed regions presented weaker correlation between forest cover and tree biomass, while intermediate-disturbed regions presented significant relationships, as deduced from the fragmentation threshold hypothesis. This pattern contributes to understand how and when Anthropocene changes can affect more intensively tropical forests (Malhi *et al.*, 2014). In particular, our findings indicate that forest loss leads to deep changes on forest structure, specifically by the decreases in tree biomass in regions with intermediate disturbance intensity.

Impacts of landscape forest loss on forest structure

Forest cover loss negatively affects biomass in intermediately disturbed regions, but not tree density. Landscape forest loss can affect forest structure through reductions in tree basal area and decreased recruitment of large trees in fragmented rainforests surrounded by low forest cover (*e.g.*, Rocha-Santos *et al.*, 2016). Heavily deforested landscapes are often characterized by a myriad of small forest patches (Fahrig, 2003), presenting a high proportion of edge-affected areas (Riitters *et al.*, 2016). Severe wind turbulence can penetrate up to 400 m into forest interiors, increasing tree mortality and damage of sensitive species, such as large trees (Laurance *et al.*, 2000, 2002). Furthermore, the edge-related desiccation of forest canopy can penetrate into forest interiors up to 2.7 km in heavily deforested landscapes (*i.e.*, 20% forest cover) (Briant *et al.*, 2010), thus increasing the susceptibility of large trees to drought. Combined, these edge-related microclimatic changes can drive biomass losses of 25% (relative to patch interior) within the first 500 m from forest edge (Chaplin-Kramer *et al.*, 2015). In fact, declines of up to 10% in tree biomass can be detected over scales of 1.5 km from the edge (Chaplin-Kramer *et al.*, 2015). At Serra Grande, edge-influenced areas and forest patches retain only one-third of carbon stored at patch interior areas (Dantas de Paula *et al.*, 2011). Drastic decays on biomass stocks (up to 74%) were observed in small patches subject to pervasive edge effects at the Sooretama region (Magnago *et al.*, 2015a). When these small patches are isolated (>2 km) from large fragments (>1600 ha), seed dispersal and growth of sensitive species, such as shade-tolerant large-seeded, can be severely impacted, thus eroding carbon stocks (Magnago *et al.*, 2015a; see also Costa *et al.*, 2012). Additionally, reductions in forest cover are followed by decreases in patch size and expose sensitive species to patch-area effects with negative impacts in plant composition and structure (Arroyo-Rodríguez & Mandujano, 2006; Michalski *et al.*, 2007; Benchimol & Peres, 2015). The combination of patch size and edge effects drive strong abiotic changes at the local level (*e.g.*, higher air humidity, temperature, wind speed) that greatly reduce the potential of tropical forests to store carbon in human-modified landscapes (Magnago *et al.*, 2016).

Therefore, forest loss can trigger cascades effects (*e.g.* edge and patch-area effects) leading to a process of forest degradation with ultimate impacts in tree biomass and carbon stocks.

Biomass loss seems to be weakly related to local variations in tree density. This is in agreement with global models that reveal that tree density is weakly related to carbon storage (Crowther *et al.*, 2015). In our database, biomass was positively and more strongly correlated with density of large trees (> 40 cm dbh), which represented less than 7% of individuals sampled and accounted for 68% of carbon stored. Dominance of carbon stocks by few, large individuals seems to be a widespread pattern among tropical forests (*e.g.*, Lindner, 2010; Bastin *et al.*, 2015; Fauset *et al.*, 2015). Unfortunately, large trees are severely harmed by microclimatic changes on forest edges (Magnago *et al.*, 2015b), presenting increases in mortality up to 40% in edge-affected areas (Laurance *et al.*, 2000). Thus, our findings reinforce the idea that for most tropical forests, the loss of large trees rather than total tree density, strongly determines the loss of tree biomass in fragmented rainforests (Magnago *et al.*, 2015a).

Tree density was weakly related to forest cover in almost all regions, except HD. This can be related to compensatory dynamics (*sensu* Supp & Ernest, 2014), as 12-33% of sampled stems belonged to pioneer species (*i.e.*, early-successional, light demanding and fast-growing tree species), whereas 67-88% were shade tolerant (*i.e.*, old-growth forest species). Considering these two ecological groups show opposing responses to fragmentation and habitat loss (a winner-loser system, *sensu* Tabarelli *et al.*, 2012), community-level properties such as tree density can remain unchanged even in severely disturbed landscapes (Supp & Ernest, 2014). In particular, shade-tolerant species tend to disappear in smaller forest patches and along forest edges due to altered microclimatic conditions. However, pioneer usually proliferate under these environmental conditions (*e.g.*, Laurance *et al.*, 2006; Santos *et al.*, 2008; Arroyo-Rodríguez *et al.*, 2015). Supporting this idea, percentage of pioneer trees, a proxy of forest disturbance (Bongers *et al.*, 2009), increased in landscapes with lower forest cover, suggesting that loss of large trees in more deforested landscapes may allow proliferation of pioneer species (Laurance *et al.*, 2006; Santos *et al.*, 2008). Unlike tree density, compensatory dynamics cannot mask responses in tree biomass because this

community-level attribute is determined by species sharing similar traits (*e.g.*, shade-tolerant, hardwood, large-seeded, zoochoric species; Slik *et al.*, 2013). Hence, showing similar negative responses to forest loss, logging, drought, defaunation, and climate change (Lindenmayer & Laurance, 2016; Osuri *et al.*, 2016). As in regions with high disturbance levels, the process of “retrogressive succession” may be undergoing, as already observed in Serra Grande (*e.g.* Santos *et al.*, 2008; Lôbo *et al.*, 2011). These biotical-impoverished landscapes may lack a diversified regional pool of old-growth species thus failing to promote source-sink dynamics and neighborhood effects in small, fragmentation-sensitive populations. In this scenario, increases in forest cover might facilitate only the proliferation of species typical of early- to intermediate-successional stages (Melo *et al.*, 2013), such as long-lived pioneer, small-seeded dispersed by wind and low wood density (Budowski, 1965). Thus, explaining the positive influence of forest cover on tree density at HD while biomass was unaffected and percentage of pioneer decreased.

The scale of effect of forest cover on biomass was context-dependent, but in general, the influence of forest cover was stronger at small scales (<700m) for both biomass (except at LD) and tree density (except for HD). However, there was a great superposition of forest cover influence among a wide range of scales and significant effects were observed only for biomass at ID and tree density at HD. Species interactions (*e.g.*, competition) and microclimate are processes usually related to small scales (McGill, 2010) and could be affecting biomass in intermediate disturbed regions. Recently, Miguet *et al.* (2016) hypothesized that high-density populations must be close to the site carrying capacity and thus more susceptible to density-dependent effects and immigration from the immediate surroundings. This could explain the smaller scale of effect of biomass at LD (> 700 m) and the greater scale of effect for tree density and percentage of pioneer at high-disturbed regions (>800 m). Where we were supposed to be farther from site carrying capacity and thus receiving immigrants from long-distances.

Differences among regions for tree biomass in the response to forest loss

In agreement with previous theoretical models (Melo *et al.*, 2013; Villard & Metzger, 2014; Arroyo-Rodríguez *et al.*, 2015), our results show forest loss more strongly related to tree biomass in regions with intermediate disturbance intensity than in regions with either very low or very high disturbance intensity. This can be explained by the fact that intermediate levels of disturbance at regional scales can increase local variability of disturbance status and processes (*e.g.*, edge effects, logging, forest isolation). Thereby increasing (i) spatial variation of population and community patterns (Laurance *et al.*, 2009); (ii) compositional differentiation (beta diversity) among communities (Socolar *et al.*, 2016); and (iii) unpredictability of successional trajectories (Arroyo-Rodríguez *et al.*, 2015).

We also highlight that considering only the effect of forest cover may underestimate biomass loss, as the regional pattern of disturbance regime influence the strength of forest structure responses. Our observation is reinforced by the recent findings of Barlow *et al.* (2016) that the conservation and functional value of primary forests are severely impacted by anthropogenic disturbances at local (*e.g.* wildfires, logging) and landscape level (*e.g.* isolation, edge), in addition to forest loss. In our study, high disturbed regions showed great variability in the amount of forest cover across landscape sizes (Fig. S4.1), but this did not reflect in stronger responses of biomass stocks by forest loss. This suggests that long histories of perturbation drive forests to impoverished communities of plant and animals where forest-dependent species are depleted or even extirpated from the landscape. Additionally, the remaining forest patches are subjected to strong forest degradation as a combination of low forest cover and high matrix contrast. In these stable degraded states, increases in forest cover can improve plant density but not the provision of ecosystem services (*e.g.* of carbon sinks), limiting their conservation values (Melo *et al.*, 2013). Thus, the regional context of disturbance level plays an important role in mediate plant-communities responses and provision of ecosystem services in human-modified tropical forests.

Conservation implications

Our findings suggest that management efforts in highly disturbed regions may be relatively unsuccessful to recover biomass, as proposed elsewhere considering biodiversity parameters (Pardini *et al.*, 2010; Melo *et al.*, 2013; Tambosi *et al.*, 2014). Severely fragmented landscapes may reach a certain threshold of disturbance above which tropical forests can collapse (Banks-Leite *et al.*, 2014), inducing a regime shift into a degraded alternative state caused by a regional impoverishment of tree community (Pütz *et al.*, 2011). In this degraded state, dispersion of sensitive species is expected to decline or even be vanished, decreasing the probability of natural regeneration to success (Pütz *et al.*, 2011). Moreover, usually alternative states are characterized by a high resilience (Scheffer & Carpenter, 2003), thus requiring assisted restoration projects to recover tree biomass, making it relatively more costly, both in time and money. Landscapes with an intermediate disturbance are more prompt to management efforts (Melo *et al.*, 2013; Tambosi *et al.*, 2014) and to recover the biodiversity and functionality of communities (Banks-Leite *et al.*, 2014). Above-ground tree biomass has high rates of recovery during secondary succession, especially in humid tropical forests (Poorter *et al.*, 2016). Thus, recovering forest cover (and tree biomass) in regions under intermediate disturbance regime may be carried out through natural regeneration (*e.g.* land abandonment), restoration (with the inclusion of potential large tree species) or afforestation activities (Arroyo-Rodríguez *et al.*, 2015; Poorter *et al.*, 2016). This is in agreement with Melo *et al.* (2013), who propose that maximum levels of ecosystem services, such as carbon storage, will be obtained from regions with moderate levels of disturbance, as they provide a large array of products and services while still maintaining their resilience and most of their original biodiversity. Based on our results, long-term tree biomass maintenance in forest fragments may rely on (1) preventing additional deforestation, (2) increasing forest cover at the landscape scale, (3) maintaining large fragments (“source-patches”) in the landscape to sustain rescue effects, and/or (4) managing matrix quality to mitigate

edge effects, logging and other negative impacts while improving habitat availability for fauna.

Recovering tree biomass is not only crucial for enhancing carbon stocks, but also to protect biodiversity (Grainger *et al.*, 2009). There is a strong synergism among carbon stocks and biodiversity, where carbon-rich landscapes can present high animal species richness (*e.g.*, birds, mammals and amphibians; Strassburg *et al.*, 2010) as well as elevated abundance and richness of endemic and threatened plant species (Magnago *et al.*, 2015a) in contrast to carbon-poor landscapes. Mechanisms for carbon conservation, such as Reduce Emissions from Deforestation and Degradation (REDD++), could then be directed to those carbon-rich landscapes with a free co-benefit to biodiversity (Strassburg *et al.*, 2010; Magnago *et al.*, 2015a). In this sense, our study suggests that economic incentives such as of REDD+ should be directed towards rainforest regions that have suffered intermediate levels of disturbance. Thus, the role of tropical forests in supplying carbon stocks, biodiversity and ecosystem services may be reinforced.

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Supporting Information

Appendix S4.1. Effect of forest cover on pioneer tree species

Following Santos *et al.* (2008) and Groeneveld *et al.* (2009), we classified tree species based on plant regeneration strategies. Specifically, we classified species as pioneer (*i.e.*, early colonizers, light demanding, and fast-growing tree species that recruit and grow principally on gaps of forest edges and open areas), and shade tolerant species (*i.e.*, both late-successional and old-growth forest species that recruit and grow under shaded conditions in the understory). This ecological classification was based on information from previous studies within each region (Santos *et al.*, 2008; Arroyo-Rodríguez *et al.*, 2009; Hernández-Ruedas *et al.*, 2014; Magnago *et al.*, 2014, 2015) and additional literature for other regions (Lorenzi, 1992, 2008, 2009; Marquette & Vaz, 2007; Amorim & Alves, 2011; Moreau, 2014; SMASP, 2015). We then calculated the percentage of pioneer stems within each plot and tested the effect of landscape forest cover on this response variable using the same protocol described in the main text for tree density and tree biomass.

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Table S4.1. Spearman's correlation coefficients for the association between tree density and aboveground biomass for different classes of tree diameter within Neotropical rainforest regions with low level of disturbance (LD), intermediate level of disturbance (ID), and high level of disturbance (HD). Coefficients with asterisk are significant ($p < 0.05$), and those in bold face are the highest values.

Disturbance level	Diameter at breast height (cm)					
	≥10	≥20	≥30	≥40	≥50	≥60
LD	0.07	0.47*	0.68*	0.81*	0.74*	0.69*
MD	-0.17	0.39*	0.60*	0.61*	0.62*	0.67*
HD	-0.31*	0.12	0.40*	0.53*	0.56*	0.58*

Table S4.2. Models testing the relation of forest cover with biomass and tree density across scales (400 to 1500 m of radius from plot centroid) at regions with low (LD), intermediate (ID), and high (HD) levels of disturbance. Only equally plausible models are shown ($\Delta AICc \leq 2$). W_i is model weight.

	Model	df	logLik	$\Delta AICc$	W_i		Model	df	logLik	$\Delta AICc$	W_i
Low disturbance											
Biomass	1400	3	-118.0	0.00	0.13	Density	400	3	-140.0	0.00	0.18
	1300	3	-118.0	0.06	0.13		500	3	-140.0	0.01	0.18
	1500	3	-118.0	0.13	0.12		Null	2	-141.6	0.67	0.13
	1200	3	-118.1	0.26	0.11		600	3	-140.5	0.98	0.11
	1100	3	-118.2	0.57	0.10						
	1000	3	-118.4	0.78	0.09						
	900	3	-118.5	1.02	0.08						
	Null	2	-119.9	1.36	0.07						
	800	3	-118.7	1.40	0.06						
Intermediate disturbance											
Biomass	600	4	-207.9	0.00	0.20	Density	Null	3	-183.8	0.00	0.18
	700	4	-207.9	0.01	0.20		400	4	-183.2	1.27	0.10
	500	4	-208.3	0.73	0.14		500	4	-183.2	1.45	0.09
	800	4	-208.3	0.87	0.13		600	4	-183.3	1.49	0.09
	400	4	-208.6	1.32	0.10		700	4	-183.4	1.67	0.08
	900	4	-208.6	1.38	0.10		800	4	-183.5	1.94	0.07
High disturbance											
Biomass	400	4	-322.8	0.00	0.13	Density	1500	4	-319.5	0.00	0.16
	600	4	-323.0	0.36	0.11		1400	4	-319.6	0.23	0.14
	500	4	-323.0	0.36	0.11		1300	4	-319.8	0.49	0.12
	700	4	-323.2	0.68	0.09		1200	4	-319.8	0.67	0.11
	Null	3	-324.3	0.77	0.09		1100	4	-319.9	0.80	0.11
	800	4	-323.3	0.96	0.08		1000	4	-320.0	1.06	0.09
	900	4	-323.4	1.26	0.07		900	4	-320.2	1.40	0.08
	1000	4	-323.5	1.44	0.06		800	4	-320.4	1.73	0.07
	1100	4	-323.7	1.67	0.06						
	1200	4	-323.7	1.77	0.05						
	1300	4	-323.8	1.88	0.05						
	1400	4	-323.8	2.00	0.05

Figure S4.1. Percentage of forest cover in a gradient of spatial scales (*i.e.*, 100-1500-m landscape radii) within each Neotropical region with increasing degree of disturbance (R1 to R4). The white horizontal line in the boxplot represent the median, the limits of the grey box the 2nd and 3rd quartiles, the vertical lines the 1st and 4th quartiles, and the points are outliers.

Fig. S2. Multi-scale analysis of the effect of landscape forest cover on percentage of pioneer trees in rainforest regions with low (LD), intermediate (MD) and high (HL) degree of disturbance. Y-axis are the differences of restricted Akaike Information Criteria ($\Delta AICc$) among each scale with the grey horizontal showing the cutoff criteria ($\Delta AICc < 2$) were models were considered equally plausible. Grey points are negative relations among forest cover.

Table S4.2. Models testing the relation of forest cover with percentage of pioneer trees across scales (400 to 1500 m of radius from plot centroid) at regions with low (LD), intermediate (ID), and high (HD) levels of disturbance. Only equally plausible models are shown ($\Delta AICc \leq 2$). W_i is model weight.

		df	logLik	AICc	$\Delta AICc$	W_i
<i>Low disturbance</i>						
	400	3	-104.5	216.0	0.00	0.29
	500	3	-105.1	217.2	1.18	0.16
	600	3	-105.2	217.4	1.39	0.14
	700	3	-105.4	217.8	1.81	0.12
<i>Intermediate disturbance</i>						
	1300	4	-213.4	435.7	0.00	0.14
	1200	4	-213.5	435.8	0.07	0.14
	1400	4	-213.5	435.9	0.14	0.13
	1100	4	-213.5	435.9	0.17	0.13
	1000	4	-213.6	436.1	0.35	0.12
	1500	4	-213.6	436.1	0.36	0.12
	900	4	-213.8	436.6	0.84	0.09
	800	4	-214.3	437.5	1.77	0.06
<i>High disturbance</i>						
	1100	4	-274.9	558.4	0.00	0.15
	1200	4	-274.9	558.5	0.03	0.15
	1000	4	-275.0	558.6	0.16	0.14
	900	4	-275.2	559.0	0.58	0.11
	1300	4	-275.2	559.1	0.68	0.11
	800	4	-275.4	559.4	1.00	0.09
	1500	4	-275.4	559.5	1.03	0.09
	1400	4	-275.5	559.6	1.18	0.08

Fig. S4.3. Percentage of pioneer trees in relation of forest cover with in regions with low disturbance levels, intermediate disturbance levels (ID) and high disturbance levels (HD) at Neotropical forests.

General Conclusions

The continuous modification of natural areas might lead to substantial changes in ecosystem functioning especially when it reaches a disturbance threshold, turning out these areas to a degraded state (Melo *et al.*, 2013). The high deforestation rates of tropical forests (7 million ha are lost *per* year - FAO, 2016) may be pushing the system through this threshold. In this scenario, tropical landscapes will be in a near future characterized by intensely deforested landscapes (low forest cover), with low functional connectivity, high edge/interior area ratio, reduced provision of ecosystem services, and little conservation value (Melo *et al.*, 2013). In fact, some human-modified landscapes in the tropics might be already experiencing this degraded state. A critical example is the Brazilian Atlantic forest, which already has lost 84% of its original cover resulting in most landscapes dominated by a constellation of small and poorly connected patches (Ribeiro *et al.*, 2009). Here, we contribute to reinforce this fact, demonstrating the main anthropogenic drivers conducting Neotropical forests to this degraded state of plant-community simplification and low provision of an essential service that is carbon storage.

The **first chapter** brought the general context of the role of tropical forests in global carbon cycle. We explored how deforestation - specially forest degradation - can affect carbon stocks through losses on aboveground biomass. We presented briefly the underlying mechanisms of fragmentation-related forest degradation to give a general overview of the subject, which was further deepened in the following chapters.

In the **second chapter** we highlight the lack of empirical evidence of a pervasive edge effect through tropical forests. This finding disassembles the dominant scientific view that edge effects are the main drivers of biomass loss in tropical forests. The results of our systematic review indicated that landscape structure might modulate edge effects and thus biomass stocks. Inspired by this gap of knowledge in this issue - despite the vast literature about the process of forest fragmentation - we formulated a conceptual model ("*the landscape effect on biomass model*") linking landscape composition and configuration to biomass loss in anthropogenic tropical landscapes.

We constructed a model of how biological flux and both extension and magnitude of edge effects could be influenced by habitat amount, patch isolation, and the synergism among patch size, edge distance, and type of matrix and ultimately impacting biomass stocks. Moreover, we suggested a sampling protocol to test the predictions of our conceptual model.

In the **third chapter** we applied the sampling protocol suggested in the previous chapter to test some of the predictions derived from *the landscape effect on biomass model*. We have found evidence for part of our predictions. First, changes in forest composition through a prevalence of pioneer species from the understory impacted negatively biomass stocks. Shade-tolerant large trees were the principal component of biomass stocks and very sensitive to the synergism between forest loss and edge proximity. This group can be even more affected in long term by changes in both landscape and patch-levels because shade-tolerant small trees are severely affected by the interaction among patch size, edge distance, and open matrix area. Although our results do not completely corroborate the initial predictions of the conceptual model, they support the idea that landscape composition interacts with patch structure and affects processes regulating biomass stocks in anthropogenic tropical forests.

We investigated in the **fourth chapter** if the negative effects of forest loss on biomass were related to the degree of regional disturbance of the landscape. Regions under an intermediate disturbance level promoted the greater variability of vegetation structure responses (tree density and biomass). In these intermediate-disturbed regions forest loss severely impacted biomass stocks but not plant density, which only increased at highly-disturbed regions.

Our study thus brought novel insights about the main drivers of biomass loss in Neotropical forests with practical applications to conservation focusing on carbon stocks. First, we demonstrated that estimates of carbon emissions by forest degradation might be misleading when they do not take into account for the effects of landscape composition and patch structure in its calculations. Recent studies have been demonstrating this limitation of degradation-related carbon estimates when the influence of landscape attributes are not evaluated (*e.g.* Chaplin-Kramer *et al.* 2015, Pütz *et al.* 2014, Magnago *et al.* 2016, Berenguer *et al.* 2014). We endorse this debate

by showing that the synergism of forest loss and edge effects promotes strong carbon losses due to a shift in plant communities by the replacement of typical old-growth species (*e.g.* shade-tolerant, hardwood, large-seeded) to an impoverished early-successional assemblage. This is the first study, as far as we know, showing that this retrogressive succession (*sensu* Santos *et al.*, 2008) is a pervasive ongoing process in Neotropical forests.

Second, that conservation activities to restore, maintain, or enhance carbon sinks must consider the regional context of the landscape. Regions under an intermediate disturbance level should be prioritized in conservation and management planning as they showed the strongest responses of biomass to changes in landscape composition. Thus, we expect that conservation initiatives will be less costly and more effective in these areas (Fig. 4.1). Based on our results we stimulate:

- To prevent additional deforestation;
- To increase forest cover at local scales (< 700 m of radius) since this is the scale with the strongest effect of forest cover on biomass;
- To improve landscape connectivity and matrix suitability to promote species movement for biodiversity supporting seed flux and promote recolonization of vulnerable populations in small patches (Haddad *et al.*, 2015);
- To decrease the contrast of the matrix in areas surrounding forest patches (< 500 m) to soften the extent and magnitude of edge effects;
- To restore actively fragmented patches using tree enrichment (Berenguer *et al.*, 2014) of hardwood shade-tolerant species;
- To maintain large patches of forest (“source-patches”) at landscape scale to maximize the regional species pool and promote rescue effects.

Figure 4.1. Expected relationship between carbon responses (black line) and management costs (red line) at distinct levels of regional disturbance. Management effectiveness should be higher when responses of carbon stocks to regional disturbance are stronger. Green line is the expected trajectory of co-benefits between carbon storage and biodiversity.

REDD and similar funding programs focusing primarily on reducing carbon emissions may mislead great opportunities of low-cost biodiversity conservation (Venter *et al.*, 2009). Carbon-oriented landscape planning and/or programs of payment of ecosystem services such as REDD+ should prioritize regions maximizing both benefits: carbon storage and biodiversity conservation. Even though there is a non-linear relationship between carbon storage and biodiversity conservation (Venter *et al.*, 2009), conserving carbon stocks my substantially benefits biodiversity. It might promote not only the maintenance of increased vertebrate (Strassburg *et al.*, 2010) and plant richness, but also allow the maintenance and conservation of threatened and endemic trees (Magnago *et al.*, 2015; Poorter *et al.*, 2015), (Fig. 4.1). As pointed out by Strassburg *et al.* (2010), is more costly-effective combine efforts to avoid or mitigate both biodiversity crisis and climate change, the biggest challenges from the

Anthropocene. We complement this idea by suggesting that REDD mechanisms and similar programs should prioritize landscapes under anthropogenic pressure but showing the greatest responses to changes in landscape and patch structure, thus implying lower costs to restore ecosystem services and possibly biodiversity. This must be case of regions with a regional intermediate disturbance level (Fig. 4.1) and where we stimulate conservation initiatives should focus.

We expect that our findings can subside for more accurate carbon emissions estimates from forest degradation. Additionally, we hope to contribute to activities of forest management and landscape planning focused in long-term provision of carbon storage in human-modified landscapes.

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