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LARISSA ROCHA SANTOS

EFEITO DA COBERTURA FLORESTAL NA ESTRUTURA, COMPOSIÇÃO E DIVERSIDADE FUNCIONAL REPRODUTIVA DA COMUNIDADE ARBÓREA, EM PAISAGENS DE FLORESTA ATLÂNTICA

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Orientadora: Eliana Cazetta

Co-orientadora: Daniela C. Talora

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Banca Avaliadora:

Dr. Luiz Fernando Silva Magnago

Universidade Federal de Lavras

Dr. Felipe Pimentel Lopes de Melo

Universidade Federal de Pernambuco

Dr. Daniel Piotto

Universidade Federal do Sul da Bahia

Dr. Víctor Arroyo-Rodríguez

Universidad Nacional Autónoma de México

Dra. Eliana Cazetta

Universidade Estadual de Santa Cruz

Orientadora

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"Cipó Caboclo tá subindo na Virola
Chegou a hora do Pinheiro balançar
Sentir o cheiro do mato, da Imburana
Descansar, morrer de sono na sombra da Barriguda
De nada vale tanto esforço do meu canto
Pra nosso espanto tanta mata haja vão matar
Tal Mata Atlântica e a próxima Amazônica
Arvoredos seculares impossível replantar
Que triste sina teve o Cedro, nosso primo
Desde de menino que eu nem gosto de falar
Depois de tanto sofrimento seu destino
Virou tamborete, mesa, cadeira, balcão de bar
Quem por acaso ouviu falar da Sucupira
Parece até mentira que o Jacarandá
Antes de virar poltrona, porta, armário
Mora no dicionário, vida eterna, milenar

Quem hoje é vivo corre perigo
E os inimigos do verde dá sombra ao ar
Que se respira e a clorofila
Das matas virgens destruídas vão lembrar
Que quando chegar a hora
É certo que não demora
Não chame Nossa Senhora
Só quem pode nos salvar é

Caviúna, Cerejeira, Baraúna
Imbuia, Pau-d'arco, Solva
Juazeiro e Jatobá
Gonçalo-Alves, Paraíba, Itaúba
Louro, Ipê, Paracaúba
Peroba, Massaranduba
Carvalho, Mogno, Canela, Imbuzeiro
Catuaba, Janaúba, Aroeira, Araribá
Pau-Ferro, Angico, Amargoso, Gameleira
Andiroba, Copaíba, Pau-Brasil, Jequitibá"

música Matança - Xangai

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ÍNDICE

RESUMO GERAL

Diante do contexto atual de grande demanda de áreas para produção de alimento, seja para agricultura ou pecuária, e para expansão industrial e imobiliária, a perda de habitat pode ser considerada umas das principais ameaças a biodiversidade. A perda de habitat é apontada como causa da redução da abundância e diversidade de plantas, vertebrados e invertebrados, bem como responsável pelo decréscimo da diversidade taxonômica e funcional. No entanto, ainda são raros os estudos que analisa o efeito da cobertura florestal em comunidades arbóreas tropicais pouco estudos, principalmente em relação a estrutura e a composição florística. Este estudo teve como objetivo verificar a influência da redução da cobertura florestal, na estrutura, composição florística e na diversidade funcional das características reprodutivas da comunidade arbórea. Para este fim foram avaliados fragmentos florestais em um gradiente de cobertura florestal que variou de 3 a 93% de floresta em escala de paisagem (1 km de raio e área de aproximadamente de 314 ha) na Floresta Atlântica do Sul da Bahia. Para analisar a estrutura florestal foram utilizados 260 parcelas (total de 2,29 ha) distribuídas em 39 áreas florestais, enquanto que para a composição florística e diversidade funcional foi utilizado um subconjunto com 100 parcelas (total de 1 ha) distribuídas em 20 fragmentos florestais. Dentro das parcelas foram amostrados todos os indivíduos arbóreos com diâmetro a altura do peito igual ou maior a 5 cm, e suas alturas foram mensuradas, além disso, para o subconjunto de 100 parcelas todos os indivíduos também tiveram sua fenologia reprodutiva acompanhada mensalmente e ramos coletados para identificação taxonômica. Após a identificação taxonômica as espécies foram classificadas com relação a estratégia de regeneração, modo de dispersão e tamanho da semente, além de outras características funcionais reprodutivas (síndrome de polinização, biologia floral, sistema reprodutivo e sexual). Os resultados mostraram que a redução da cobertura florestal afetou a estrutura florestal, levando a redução do diâmetro, altura, área basal, ao aumento da abertura do dossel e simplificação da estratificação vertical. Essas mudanças foram mais drásticas em paisagem com cobertura florestal abaixo de um limiar de 35 e 40%. De modo geral, a estrutura florestal dos fragmentos em paisagens com pouca cobertura florestal foi similar a estrutura de florestas secundárias, sugerindo que estes fragmentos podem estar em processo de sucessão retrogressiva, na qual as florestas são conduzidas a padrões similares aos observados em estágios sucessionais iniciais. Também foi mostrado que a redução da cobertura florestal altera a composição florística, levando ao declínio linear da riqueza e abundância de árvores, com perda proeminente de espécies tolerantes à sombra e dispersas bioticamente, e de famílias como Myrtaceae e

Sapotaceae. Além disso, foi demonstrado que a redução da cobertura florestal leva a redução da diversidade funcional das características reprodutivas da comunidade arbórea, e da redundância funcional de grupos e atributos dos traços reprodutivos. Onde as espécies que apresentam atributos funcionais como sistema reprodutivo auto-incompatível e dispersão de sementes por animais foram as mais ameaçadas com a redução da cobertura florestal. Os resultados deste estudo evidenciam que os fragmentos florestais inseridos em paisagens com pouca cobertura florestal passaram por drásticas mudanças, como a simplificação da estrutura vegetal, redução da riqueza e abundância de espécies arbóreas, principalmente as tolerantes á sombra e as que de dispersão, além de redução da diversidade e redundância das características reprodutivas da comunidade arbórea. Essas mudanças demonstram que estes fragmentos podem ser levados a um colapso estrutural, a extinção local de espécies arbóreas e a ruptura de importantes processos ecológicos como a polinização e a dispersão de sementes, sendo assim a persistência dessas florestas a longo prazo pode está comprometida. Devido aos grandes impactos da perda de floresta, é fundamental que os planos de manejo e ações de conservação, considerem o montante de cobertura florestal na paisagem para garantir uma estratégia efetiva de manutenção e regeneração florestal, de conservação de biodiversidade e dos serviços ambientais.

Palavras-chave: biologia floral; composição florística; desmatamento; dispersão; ecologia de paisagem; estrutura florestal; floresta tropical; grupos funcionais; interação planta-animal; perda de habitat; polinização; reprodução da comunidade arbórea; sistema sexual.

ABSTRACT

Currently there is a great demand for land for food production, agriculture, pasture, or industrial expansion, so habitat loss can be considered one of the main threats to biodiversity. Habitat loss is indicated as a cause for the reduction of plant abundance and diversity, vertebrates and invertebrates, and also for taxonomic and functional diversity decreases. This study aimed to verify the influence of forest cover reduction, in forest structure, floristic composition and functional diversity of tree community reproductive characteristics. For this purpose, we used forest fragments in a gradient that varied from 3 to 93% of forest cover at landscape scale (1 km radius and area of approximately 314 ha) in the Atlantic Forest, Southern Bahia. To analyze the forest structure, we used 260 plots (total of 2.29 ha) distributed in 39 forest areas, while for floristic composition and functional diversity we used a subset of 100 plots (total of 1 ha) distributed in 20 forest fragments . Within the plots we sampled all arboreal individuals with diameter at breast height equal to or greater than 5 cm, and their heights were measured. For the subset of 100 plots all individuals we also evaluated the reproductive phenology monthly and branches were collected for taxonomic identification. After taxonomic identification the species were classified in relation to their regeneration strategy, seed dispersial mode and seed size, besides other functional reproductive characteristics (pollination syndrome, floral biology, reproductive and sexual system). The results showed that forest cover reduction affected the forest structure, leading to the reduction of the diameter, height, basal area, the increase of the canopy opening and simplification of vertical stratification. These changes were more drastic in landscapes with forest cover below the threshold of 35 to 40%. In general, the forest structure in deforested landscapes was similar to secondary forests structure, suggesting that these fragments might be in a retrogressive succession process, in which the forests are converted into initial successional stages. It has also been shown that forest cover reduction alters floristic composition, leading to linear decline in tree richness and abundance, with a prominent loss of shade tolerant and biotically dispersed species, and of species from Myrtaceae and Sapotaceae families. In addition, it has been demonstrated that forest cover reduction leads to a decrease in functional diversity of tree community reproductive characteristics, in the functional redundancy of groups and of reproductive traits state. Species that present functional traits state such as self-incompatible reproductive system and seed dispersal by animals were the most threatened with the forest cover reduction. The results of this study show that the forest fragments within landscapes with low forest amount has undergone drastic changes, such as forest structure simplification, reduction of arboreal richness and abundance, mainly habitat-specialists species, besides reduction of functional diversity and functional redundancy of the tree community reproductive traits. These changes demonstrate that these fragments can lead to a structural collapse, the local extinction of tree species and the disruption of important ecological processes such as pollination and seed dispersal, thus the long-term persistence of these forests is compromised. Due to the great impacts of habitat loss, it is fundamental that management plans and conservation actions consider the forest cover amount at the landscape scale to guarantee a effective strategy for forest maintenance and regeneration, and for biodiversity conservation and environmental services.

Keywords: deforestation; dispersal; floral biology; floristic composition; forest structure; functional groups; habitat loss; landscape ecology; plant-animal interaction; pollination; sexual system; tree community reproduction; tropical forest.

INTRODUÇÃO GERAL

Áreas de floresta são de grande importância para a qualidade ambiental que é medida por estoque de floresta e pelos serviços ambientais prestados como água e qualidade do ar, no entanto, o crescimento populacional vem causando desproporcional impacto, principalmente pela redução e fragmentação florestal, dada a necessidade de conversão de áreas florestais em áreas para agricultura e pasto, além do intensivo corte madeireiro (Cropper and Griffiths, 1994; FAO, 2016; Green and Balmford, 2005). A perda de habitat é considerada a principal ameaça a biodiversidade, e vem sendo apontada como causa da extinção de espécies (Barnosky et al., 2011; Pimm et al., 1995; Wright and Muller-Landau, 2006). Essas modificações ambientais são ainda mais críticas quando ocorrem em ambientes de alta diversidade e endemismo como as florestas tropicais, que são muito suscetíveis aos impactos das ações antrópicas já que mais de 80% não estão em áreas de proteção integral (Bender et al., 1998; Brooks et al., 2002; Schmitt et al., 2009). Estudos registraram que a perda de habitat em geral avaliada como a quantidade de floresta na paisagem, leva a profundas mudanças na estrutura da floresta (Murcia, 1995a; Saunders et al., 1991), e a redução da diversidade de muitos táxons de vertebrados (Lindenmayer et al., 2005; Morante-Filho et al., 2015; Pardini et al., 2010), invertebrados (Spiesman and Inouye, 2013; Taki et al., 2010), e plantas (Lima and Mariano-Neto, 2014; Montoya et al., 2010; Rigueira et al., 2013). A relação de perda de diversidade com a redução da cobertura florestal nem sempre é linear. Estudos teóricos mostram que os efeitos da redução da cobertura florestal ficam mais intensos em paisagens com baixa cobertura florestal devido a sinergia dos efeitos da configuração da paisagem, como a redução do tamanho dos fragmentos, aumento do isolamento, e o aumento da suscetibilidade destes ao efeito de borda (Andrén, 1994; Fahrig, 2013, 2003). Sendo assim, essa relação de perda de espécies com a cobertura florestal pode ser não-linear, com a presença de um limiar de extinção, no qual uma pequena mudança no montante de cobertura florestal reflete em uma perda desproporcional e acentuada de espécies (Andrén, 1994; Huggett, 2005). Alguns estudos registraram que o limiar de extinção ocorre em torno de 30% a 50% de cobertura florestal na paisagem, para plantas (Lima and Mariano-Neto, 2014; Montoya et al., 2010; Rigueira et al., 2013), fauna (Banks-Leite et al., 2014; Morante-Filho et al., 2015; Radford et al., 2005).

A perda de cobertura florestal afeta as espécies de forma diferenciada conforme os seus requerimentos ambientais, por exemplo, as espécies habitat-especialistas são mais afetadas do que as habitat-generalistas (Morante-Filho et al., 2015; Pardini et al., 2010). As espécies arbóreas habitat-especialistas, normalmente são representadas pelas espécies tolerantes à sombra, que em geral apresentam maior densidade da madeira, maior porte, e sementes e frutos grandes (Swaine and Whitmore, 1988). Alterações do habitat, como a fragmentação e perda florestal favorecem a proliferação de espécies intolerantes à sombra (Laurance et al., 2006b; Tabarelli et al., 2012) em detrimento das espécies tolerantes à sombra, com sementes grandes e de grande porte (Lima and Mariano-Neto, 2014; Melo et al., 2007; Santos et al., 2008). A perda dessas espécies especialistas pode ser irreversível naturalmente, em um processo no qual as florestas são dominadas persistentemente por espécies generalistas. Este processo conhecido como sucessão retrogressiva, e ocorre principalmente em remanescentes florestais imersos em paisagens altamente antropizadas (Santos et al., 2008; Tabarelli et al., 2008). Essa dominância de espécies generalistas pode levar a homogeneização biótica devido ao aumento da similaridade taxonômica, filogenética e funcional nessas paisagens altamente modificadas pelo homem (Arroyo-Rodríguez et al., 2013; Carneiro et al., 2016; Lôbo et al., 2011; Lopes et al., 2009).

No entanto, o impacto da perda de floresta pode ir além da extinção de espécies e pode acarretar também na perda de funções ecológicas (Valiente-Banuet et al., 2014). Florestas preservadas apresentam alta redundância funcional, ou seja, o conjunto de diversas espécies que desempenham funções ecológicas similares e garantem o funcionamento de importantes processos ecológicos (Laliberté et al., 2010; Mouchet et al., 2010; Tilman, 2001). A alta redundância funcional garante uma alta resiliência contra a perda de funções e serviços ecológicos em casos de alterações antrópicas. Estudos mostram que a perda e fragmentação florestal levam a redução da redundância (Laliberté et al., 2010; Magnago et al., 2014; Smith and Mayfield, 2015) e da diversidade funcional (Benchimol and Peres, 2015; Flynn et al., 2009; Rader et al., 2014). A alta diversidade funcional também é responsável por aumentar a persistência da biodiversidade, pois indica que as espécies apresentam uma maior variedade de características fisiológicas e ecológicas que refletem em diferentes histórias de vida (Fontaine et al., 2006; Mason and Bello, 2013; Tilman, 2001). Sendo assim, florestas em paisagens antropizadas, com baixa diversidade de espécies, apresentam baixa resiliência e diversidade funcional, portanto, são menos capazes de manter biodiversidade e de prestar serviços ambientais, como a polinização e o estoque de carbono (Bello et al., 2015; Hadley and Betts, 2012; Tabarelli et al., 2010a).

Entre as diversas funções florestais importantes se destacam a polinização e a dispersão de sementes, uma vez que em florestas tropicais a necessidade de animais para a reprodução é muito alta, sendo que mais de 97% da comunidade arbórea é polinizada por animais (Bawa et al., 1985; Ollerton et al., 2011) e mais de 90% são dependentes de animais para dispersão de sementes (Jordano, 2016). Estes processos influenciam no sucesso reprodutivo das plantas e, portanto, na regeneração e manutenção florestal (Anderson et al., 2011; Harrison, 2000; Kurten, 2013). Estudos apontam que a polinização e a dispersão de sementes são os processos mais ameaçados com as alterações ambientais, entre os processos envolvidos na regeneração florestal (Neuschulz et al., 2016), provavelmente porque remanescentes florestais em paisagens desflorestada e fragmentada, apresentam alteração nos dois lados dessas interações, devido a redução da diversidade e abundância das plantas (Lôbo et al., 2011; Montoya et al., 2010; Silva and Tabarelli, 2000) e dos potenciais polinizadores e dispersores (Andrén, 1994; Pardini et al., 2010; Potts et al., 2010; Winfree et al., 2011). Uma alta diversidade funcional das características reprodutivas indica maior disponibilidade de recursos (alimento e abrigo) para uma maior gama de animais de diferentes requerimentos ecológicos, aumentando as interações planta-polinizador e planta-dispersor (Biesmeijer, 2006; Decourtye et al., 2010; Fontaine et al., 2006). Ambas as interações são essenciais para manter o funcionamento das florestas, uma vez que o comprometimento dessas interações reduzem o sucesso reprodutivo e o recrutamento de novos indivíduos, alterando a riqueza e dominância das espécies e comprometendo os serviços ambientais (Anderson et al., 2011; Kurten, 2013; Valiente-Banuet et al., 2014).

Diante do fato de grande parte dos remanescentes florestais estarem inserido em paisagens antropizadas e ao crescente desmatamento, é essencial entender as consequências da redução da cobertura florestal em escala de paisagem para direcionar ações de manejo e conservação da biodiversidade. Sendo assim, o objetivo geral desta tese é avaliar a influencia da redução da cobertura florestal em diferentes aspectos das florestas, essenciais para a dinâmica e funcionamento florestal. O primeiro aspecto avaliado foi a estrutura da vegetação, comumente usada para descrever a qualidade do habitat (Banks-Leite et al., 2013), uma vez que afeta a disponibilidade de abrigos, recursos alimentares e a mobilidade da fauna (DeWalt et al., 2003; McElhinny et al., 2006; Palomares, 2001), influenciando a diversidade de aves, mamíferos e artrópodes (Arroyo-Rodríguez et al., 2007; Pardini et al., 2005; Rosenvald et al., 2011; Wettstein and Schmid, 1999) além de influenciar diretamente em importantes serviços ambientais como o estoque de carbono e ciclagem de nutrientes (Bello et al., 2015; Wright, 2010). O segundo aspecto estudado foi a diversidade florística (riqueza, abundância e composição) pois a redução destes componentes da diversidade além também podem aumentar a vulnerabilidade de grupos específicos e levar a ruptura de funções ecológicas e consequentemente de serviços ambientais (Silva and Tabarelli, 2000; Valiente-Banuet et al., 2014). O terceiro e último aspecto estudado foi a diversidade funcional de características reprodutivas da comunidade arbórea, que estão associados diretamente a importantes processos ecológicos como a polinização e dispersão de sementes e consequentemente ao sucesso reprodutivo, e que levam ao processo de recrutamento e manutenção das florestas e dos serviços ambientais prestados (Anderson et al., 2011; Beckman and Rogers, 2013; Harrison, 2000; Kurten, 2013).

OBJETIVOS GERAIS

Esta tese de doutorado apresentou como objetivo geral verificar os efeitos da perda de cobertura florestal em escala de paisagem em importantes aspectos florestais, como a estrutura florestal, a composição florística e a diversidade funcional de características reprodutiva da comunidade arbórea.

Mais especificamente os objetivos desta tese pretendiam verificar qual a influência da porcentagem de cobertura florestal em escala de paisagem:

1 - nas características estruturais da floresta, como diâmetro e altura das árvores, densidade de árvores e de árvores de grande porte, área basal, abertura do dossel e estratificação vertical. E qual o tipo de relação (linear ou não-linear com a presença de um limiar) entre a redução da cobertura florestal e essas características estruturais da floresta;

2 - na composição florística, mais especificamente na riqueza e abundância das espécies arbóreas da comunidade;

3 - nos padrões de importantes famílias (Myrtaceae, Sapotaceae, Fabaceae, Rubiaceae, e Lauraceae) da comunidade arbórea de Floresta Atlântica;

4 - na riqueza e abundância de importantes características funcionais ecológicas, como a estratégia de regeneração, modo de dispersão e tamanho da semente;

5 - nos índices de diversidade funcional ("functional evenness", "functional divergence", "functional diversity") baseado nas características reprodutivas das árvores;

6 - nos grupos funcionais e nas categorias reprodutivas da comunidade arbórea.

A tese está organizada em 3 capítulos, sendo que o primeiro está relacionado com efeito da cobertura florestal na estrutura florestal e visa responder ao primeiro objetivo específico da tese. O segundo capítulo aborda a influencia da cobertura florestal na composição florística e visa responder os objetivos específicos das questões dois, três e quatro. O terceiro capítulo abrange a influencia da cobertura florestal na diversidade funcional das características reprodutivas da comunidade arbórea e procura responder aos as questões cinco e seis dos objetivos específicos.

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CAPÍTULO 1

The shrinkage of a forest: landscape-scale deforestation leading to overall changes in local forest structure

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The shrinkage of a forest: landscape-scale deforestation leading to overall changes in local forest structure

Larissa Rocha-Santos[a], Michaele S. Pessoa[a], Camila R. Cassano[a], Daniela C. Talora[a], Rodrigo L. L. Orihuela[a], Eduardo Mariano-Neto[b], José C. Morante-Filho[a], Deborah Faria[a] and Eliana Cazetta[a]*

[a] Universidade Estadual de Santa Cruz, PPG Ecologia e Conservação da Biodiversidade, Laboratório de Ecologia Aplicada à Conservação, Ilhéus, BA, Brazil

[b] Universidade Federal da Bahia, Departamento de Botânica, Instituto de Biologia, Salvador, BA, Brazil

* Corresponding author at: PPG Ecologia e Conservação da Biodiversidade, Universidade Estadual de Santa Cruz CEP 45662-900, Ilhéus, BA, Brazil. Tel.: +55 73 3680 5537

E-mail adresses: eliana.cazetta@gmail.com (E. Cazetta), rocha_larissa@yahoo.com.br (L. Rocha-Santos)

ABSTRACT

Habitat loss is one of the primary drivers of change in forest biodiversity and ecosystem function worldwide. The synergetic effects of habitat loss and fragmentation might lead to profound impacts on forest structure and composition, conducting forest fragments towards early successional stages (retrogressive succession). In this study, we tested this hypothesis by evaluating how landscape-scale forest loss affects the forest structure. We sampled forest structure descriptors in 40 forest sites in landscapes ranging from 3 to 100% forest cover. Forest cover was negatively related to most of the structural variables, generally in a non-linear manner. In contrast, dead trees and logging were ubiquitous and not related to forest cover. The forest remnants in more deforested landscapes retain early successional forest attributes, with tree assemblages that are less dense, shorter, thinner, with an overall basal area loss, and with increasing canopy openness. This structural degradation indicates that landscape-scale forest loss strongly determines the trajectory of the local forest structure, pushing forests to a retrogressive succession process, which is more likely to occur in deforested landscapes and can lead to functional forest erosion. Our findings indicate that remnants within deforested landscapes may suffer recruitment limitation, primarily of large trees. Additionally, the forest structure characteristics were more severely degraded in landscapes with less than 40% forest cover. In the face of these results, the recommendation is to avoid the reduction of forest cover below this threshold, at which point structural erosion becomes more severe, with predictable negative consequences on biodiversity and ecosystem service maintenance.

Keywords: Extinction threshold, Habitat loss, Landscape changes, Retrogressive succession, Tree community, Tropical forest

1. Introduction

The negative responses of native biota to habitat loss have been largely reported over the last few decades, which is an issue of special concern in tropical forests because they harbor more than 60% of the world's terrestrial species (Brooks et al., 2002; Gardner et al., 2009; Wright and Muller-Landau, 2006). Currently, most of the biota in tropical regions is present in anthropogenic landscapes, in which historical deforestation has reduced large forest tracts that were once continuous into a myriad of small patches that are often isolated from one another by other human-modified land uses (Ribeiro et al., 2009; Wright and Muller-Landau, 2006). Several studies have shown that habitat loss leads to a reduction on species diversity of plants and animals (Andrén, 1994; Bender et al., 1998; Lindenmayer et al., 2005; Montoya et al., 2010).

More recently, researches have highlighted the non-linearity of individual species and entire assemblage responses to habitat loss in the landscape (Banks-Leite et al., 2014; Lima and Mariano-Neto, 2014; Morante-Filho et al., 2015; Rigueira et al., 2013), which may also be associated with a regime shift in the ecosystem (Pardini et al., 2010). Theoretically, there is an extinction threshold at which species losses sharply increase with habitat cover reduction (Fahrig, 2003). Additionally, the extinction probability as deforestation proceeds may be influenced by the habitat configuration, once smaller patches are more likely to harbor non-viable populations and local extinctions are not offset by migrants as isolation effects increase (Andrén, 1994; Villard and Metzger, 2014).

Landscape deforestation, by increasing forest edges amount and number of fragments and decreasing fragment size (Fahrig 2003) can trigger local modifications of the forest structure in the remaining patches (Kapos, 1989; Matlack, 1993; Murcia, 1995b; Saunders et al., 1991). For example, edge effects change the microclimatic conditions, causing tree damage and mortality particularly for emergent and large trees, and also influencing seed predation, germination and establishment, increasing plant species turnover (Fleury and Galetti, 2006, 2004, Oliveira et al., 2008, 2004; Santos et al., 2008). The death of emergent and large trees affects the mean tree diameter, height and basal area, reduces forest biomass and increases the number of canopy gaps, which alter light input into the forest interior (Laurance et al., 2011; Magnago et al., 2015b; Nepstad et al., 1999; Pinto et al., 2010). Moreover, habitat loss and fragmentation can cause the elimination of important animals and the breakdown of animal-plant interactions as a consequence (Cordeiro and Howe, 2003; Jorge et al., 2013). In fragmented landscapes, defaunation tends to occur at higher rates because of the accessibility of these areas to hunters and other synergistic habitat loss effects (Galetti and Dirzo, 2013; Laurance et al., 2011). Seed dispersal, seed predation and seedling trampling are among some of the reported interactions that are compromised in defaunated forests, all of which result in cascading effects on plant regeneration (Jorge et al., 2013; Wright and Duber, 2001).

In addition, those smaller fragments within more deforested landscapes may be subject to the strong negative effects of selective logging, primarily because of the high vulnerability and accessibility of fragments (Echeverría et al., 2007; Liu and Slik, 2014). Large and emergent trees are more subject to logging because they normally have hardwood and more wood volume and therefore more economic value (Oliveira et al., 2004). With increases in large tree deaths, more light input and the scarcity of large fruit dispersion in fragmented landscapes, it is predictable that the loss of one large and emergent tree can be compensated by many small trees (Laurance et al., 1998; Oosterhoorn and Kappelle, 2000), however this change is not able to replace the carbon stock (Bello et al., 2015). The result of these emerging processes is a profound alteration in the forest structure and species composition, driving forest fragments towards early successional stages, or the so-called retrogressive succession (Santos et al., 2008; Tabarelli et al., 2008).

Forest structural changes triggered by the aforementioned disturbances negatively affect biota and can also reduce the potential for carbon storage and hydrological forest cycles (Bello et al., 2015; Wright, 2010). Given that the vegetation structure is usually the primary local component used to describe habitat quality (Banks-Leite et al., 2013), the relation between forest cover loss and vegetation structure in the remnant area can have important implications for understanding the mechanisms driving biota persistence in disturbed landscapes. The forest structure affects fauna mobility (McElhinny et al., 2006) and resource availability (DeWalt et al., 2003; Palomares, 2001), shaping the diversity patterns of many taxonomic groups that can affect the whole forest dynamic (Tews et al., 2004). Overall, forest remnants with greater structural complexity or structural heterogeneity are positively related to bird diversity (Rosenvald et al., 2011; Watson et al., 2004), the presence of primates (Arroyo-Rodríguez et al., 2007), the abundance of small mammals (Pardini et al., 2005), and arthropod diversity (Wettstein and Schmid, 1999).

Given the importance of forest structure on biodiversity maintenance and the paucity of studies at the landscape scale, this study attempts to investigate the influence of forest loss at the landscape scale over forest structural characteristics in a quantitative manner. We also evaluated whether the relation between forest loss and forest structure is linear or if it exhibits a threshold value. To accomplish this goal, we measured the vegetation structural descriptors, the intensity of logging, and the number of dead trees in 40 forest sites across a forest cover gradient (3-100%). We believe that in deforested landscapes the forest fragments will be subjected to retrogressive succession, leading to forest structure shrinkage. Therefore, we predict that the forest cover loss will lead to an increase in the number of dead trees and logging and a reduction in the mean diameter, height, basal area, and density of large trees. Given these changes, we also expect that landscape scale deforestation will lead to an increase in canopy openness, and with more light available, there is a higher density of lower stratum foliage and tree density, particularly because of the increase in small, shade-intolerant individuals at sites with a lower amount of forest cover at the landscape scale.

2. Methods

2.1. Study Area

We conducted this study in the Atlantic Forest of southern Bahia between 15^{o}0' - 16^{o}0'S and 39^{o}0' - 39^{o}30'W. We selected lowland forest fragments that show similar floristic composition, soil type, and topography (Thomas et al., 1998). We avoided sampling montane, sand areas, and the central tabuleiro forest, according to Thomas (2003). The regional climate according to the Koppen classification is hot and moist, without a distinct dry season (Gouvêa, 1969). The mean annual temperature ranges from 23.0 to 24.4°C, and the average rainfall ranges from 1072 to 1656 mm y^{-1}(WorldClim database; Hijmans et al. 2005). The dominant natural vegetation is classified as a Tropical Lowland Rainforest, which is characterized by a clear vertical stratification in the understory, a canopy (trees with 25-30 m) and emergent layers (trees reaching up to 40 m) (Faria et al., 2009; Thomas et al., 1998). Southern Bahia has one of the highest diversities of wood species in the world (Martini et al., 2007; Thomas et al., 1998).

2.2. Sampling Design

The sample site selection was based on the mapping of satellite images (RapidEye from 2009-2010, QuickBird and World View from 2009-2011). The mapping was performed by manually digitizing the land cover features as visually interpreted at a scale of 1:10 000, which is adequate for identifying patches based on differences in color, texture, and shape.

After intensive ground-truthing, we mapped the vegetation and land use over an area of 3,500 km^2. Based on this mapping and on field investigations, we identified 58 potential sampling sites that are located in the forest remnants and surrounded by different amounts of native forest. We performed a stratified sampling to selected 40 sites, maintaining the maximum variation in the amount of forest in the landscape (Fig. 1).

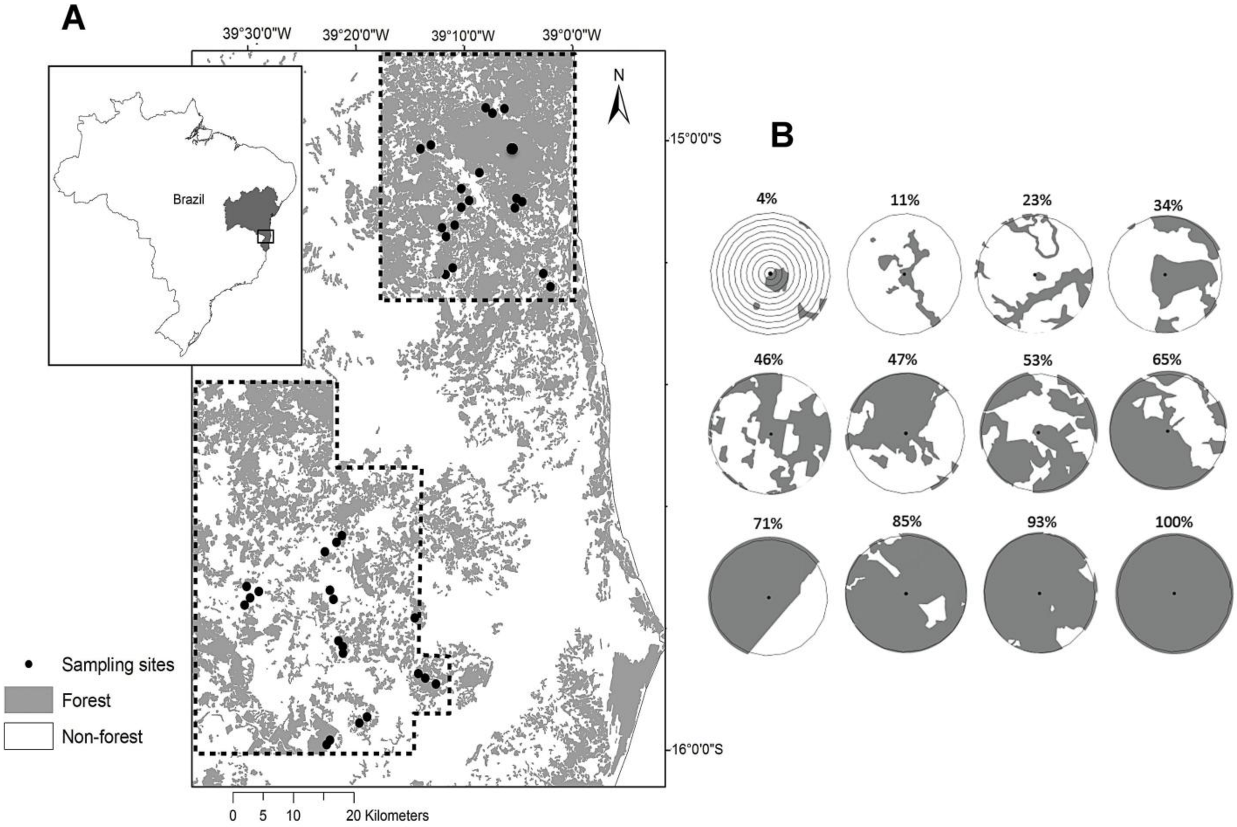

Figure 1 – Map of the study area in southern Bahia, northeastern Brazil. A: Atlantic Forest remnants (gray areas) and the 40 sampling sites (black circles). Dashed lines show the areas that were mapped for this study. Images of areas that are outside of the dashed lines were obtained from the forest cover map "Atlas dos Remanescentes Florestais da Mata Atlântica" with open access (www.sosma.org.br). B: Detail of some sampled landscapes; the first example shows the whole tested radius (100 to 1,000 m) and the others show the most appropriate radius (1,000 m), highlighting the percentage of forest cover (gray areas).

2.3. Vegetation structure

We established 155 sampling plots of 20 x 4 m in 39 forest sites (4 plots/site, except one site with 3 plots) and 105 extra sampling plots of 25 x 4 m in 21 forest (5 plots/site), covering 2.29 ha. These extra plots were collected in a different vegetation study occurring during our own study and were installed in a subset of 20 forest sites included in the range of our previous 39 sites, and uniformly distributed along the gradient of forest cover. The mean sampled area at each site was 572 ± 252 m² (mean ± SD). Because of the different sample size, prior to the analyses we performed linear regressions without the inclusion of the 5 extra plots and the patterns found were maintained. Therefore we opt to include the extra plots to increase sample size and model adjustments. Sampling plots were placed in the center of each site to minimize the edge effects, maintaining a minimum distance of 50 m between plots. Within each plot, we counted and measured the diameter at breast height (DBH) and the heights of all trees with a DBH ≥ 5 cm and with the main trunk totally or partially located within the plot area. We measured the foliage vertical stratification profile by using a technique adapted from Malcolm (1995). The vertical profiles were recorded in three points that were randomly located within each plot by estimating the length (cm) occupied by foliage in an imaginary vertical line in six forest strata (each 5 m interval until 30 m height; see Faria et al. (2009) for further details). We used the mean length value occupied by foliage in each stratum for later analyses. We also estimated the percentage of canopy openness inside the vegetation plots by using hemispherical photographs (Nikon Coolpix4300 digital camera equipped with hemispherical fish-eye lens). Photographs were taken 1.5 m from the ground and analyzed with GLA-Gap Light Analyzer software.

The number of dead trees and selective logging were evaluated in one (100 x 8 m) plot that was set up in each sampling site. Dead trees with diameter at ground level - DGL ≥ 5 cm were recorded as fallen or broken trunks from natural causes. We used the number of dead trees as a proxy of mortality, however we are aware that they do not represent the rate of dead trees (D'Angelo et al., 2004). Selective logging was computed as the number of stumps (logged trees) that had a DGL ≥ 20 cm.

2.4. Forest cover in surrounding landscapes

We adopted the patch-landscape approach (McGarigal and Cushman, 2002) in which the response variables are evaluated within forest patches and landscape attributes (i.e., forest cover) and are measured within a specific area surrounding each site. Each site was based around a central point that was established within forest area, and the proportion of forest cover around that central point was quantified by using ArcGIS software. We delimited buffers of ten different radius sizes, every 100m, the smallest radius size was 100 m (3.14 ha) and the largest was 1,000 m (314 ha). In our estimation, we considered only the amount of native forest and excluded man-made forested land such as cacao (*Theobroma cacao*) and rubber (*Hevea brasiliensis*) plantations. We evaluated which scale presents the maximum relation between forest cover and forest structural characteristics.

2.5. Data Analysis

To evaluate the spatial scales at which the forest cover best explains the forest structure, we compared the coefficient of determination (R^2) between each response variable and the percentage of forest cover in the round landscapes of varying radii. The radius with the highest coefficient of determination values was established as the standard for all subsequent analysis.

We compiled the vertical stratification profile by using a Principal Component Analysis (PCA) and the first axis, which was the synthesis of the gradient of vegetation profile (see Supplementary material Fig. A1), was used as a dependent variable. We performed Pearson correlation tests to evaluate the correlation between all structural variables as follows: mean and maximum DBH, density of all individuals (≥ 5 cm DBH) and large trees (≥ 30 cm DBH), mean and maximum height, basal area, canopy openness, and vertical profile (PC1). Because the maximum diameter was highly correlated ($r > 0.75$) with the mean diameter ($r = 0.77$), large tree density ($r = 0.83$) and basal area ($r = 0.90$), it was excluded from the remaining analyses. The maximum height was also excluded because of the high correlation with the basal area ($r = 0.80$). The large tree density and basal area were also correlated ($r = 0.85$), but we kept both response variables in the analyses because they are commonly used in ecological studies aimed at different questions. For instance, the basal area is one of the key traits used for biomass calculations, and therefore it is used to estimate carbon stocks and fluxes (Baker et al., 2004; Chave et al., 2005; Houghton et al., 2000); on the other side, large trees make up a functional group of the forest that is more sensitive to environmental changes and provides an important resource for fauna (Arroyo-Rodríguez et al., 2007; Clark and Clark, 1992; Laurance et al., 2000; Oliveira et al., 2008).

We used a model selection approach to evaluate the effect of forest cover on several forest structure variables and whether the effect was non-linear. For each dependent variable, we constructed a null model, a linear model representing the constant effect of forest cover over the structure, and three non-linear models, namely a power law model, a four-parameter logistic model (Pinheiro and Bates, 2000), and a piecewise model (Ficetola and Denoël, 2009). These last two models have being used to investigate threshold relations (see Lima and Mariano-Neto, 2014; Swift and Hannon, 2010).

The four-parameter logistic regression is a nonlinear model, expressed by:

$f(x) = d + (a/1+c^{(b-x/c)})$,

where “a”, “b”, “c” and “d” are the four parameters. These parameters control the asymptotes (upper and lower), the inflection point and the velocity at which the model changes between asymptotes. In this case, the upper and lower asymptotes are related to the original values of structure variables that can be sampled with a determined effort and to the remaining values after forest loss. The inflection point is the amount of forest near the change in forest structure values, and the last parameter controls the velocity of forest structure loss. The piecewise model can be adjusted to data that has two distinct regions with different angular coefficients connected by a breakpoint. The breakpoint value was used to estimate the threshold between forest cover at landscape scale and forest structure variables.

We used the Akaike Information Criterion corrected to small samples (AICc) and Akaike information weights (AICc weights) to select the most plausible model (Anderson, 2008). A model was considered to be the best one if it had the lowest AIC value, and its weight was at least two times the weight of the second-best model. Otherwise, models with the highest AICc weights were considered equiprobable, and the decision about the best model was made with residual analyses.

We built routines to adjust logistic models with Gaussian error when necessary, minimizing the model log-likelihood by using numerical optimization (Bolker, 2008). We also calculate AICc, AICc weights and the confidence intervals (CI) of the parameters in all models.

For logistic models, the threshold values were estimated by the inflection point, as represented by the "b" parameter and the confidence interval. During the process of model parameterization, the non-linear models that did not present a convergent solution of parameters in the numerical optimization were excluded from the model selection. We also tested for the difference between the two angular coefficients (Davies test). Whenever the angular coefficients were not different we excluded the piecewise from model selection. All analyses were implemented in R environment (R Development Core Team, 2014) by using the functions ‘’lm’’, “nls” and “anova” of stats package to fit null, linear, and non-linear models. To test the significance of non-linear models we used the functions “segmented” and “davies.test” of segmented package. We performed PCA analysis by using the “rda” function of vegan package and used “mle2” and “confint” in the bbmle package to run the numerical optimization and to calculate confidence intervals, respectively.

3. Results

We sampled 4,556 individual trees (DBH ≥ 5 cm). Forests showed a mean tree diameter ranging from 15.6 to 9.2 cm and a mean tree height between 13.6 and 7.8 m. The overall density of individuals ranged from 3.620 to 1.481 trees/ha and basal area from 68.2 to 17.5m²/ha. The lowest canopy openness was 6% and the highest 24%. The number of dead trees ranged from 75 to 500 dead trees/ha, and selective logging varied from zero to 87 stumps/ha (Table A1).

The 1,000-radius scale showed the highest determination coefficients (R^2) for most forest structural variables (Table 1), and therefore we used 1,000-radius scale to explore the variation in these variables in relation to forest cover. Logging and dead trees presented low R^2 regardless of the scale that was analyzed and then we used the 1,000-radius scale to standardize.

Table 1 – Coefficient of determination (R^2) of forest structure variables as a function of forest cover around each sampled site (100 - 1000 m). The highest value from each structural descriptor showing a significant relationship with forest cover is highlighted in bold.

	100 m	200 m	300 m	400 m	500 m	600 m	700 m	800 m	900 m	1000 m
Diameter	-0.025	0.001	0.031	0.045	0.049	0.053	0.061	0.062	0.059	0.062
Height	0.012	0.101	0.148*	0.210*	0.254*	0.288*	0.310*	0.321*	0.330*	**0.335***
Density of large tree	0.057	0.161*	0.231*	0.284*	0.308*	0.314*	0.324*	0.326*	0.325*	**0.335***
Overall density	0.103	0.250*	0.341*	0.461*	0.546*	0.599*	0.613*	0.625*	0.646*	**0.653***
Basal area	0.080	0.220*	0.330*	0.415*	0.448*	0.464*	0.473*	0.474*	0.472*	**0.475***
Canopy openness	0.031	0.141*	0.192*	0.215*	0.234*	0.264*	0.281*	0.292*	0.301*	**0.307***
Dead trees	0.007	-0.001	-0.018	-0.026	-0.026	-0.025	-0.024	-0.024	-0.023	-0.023
Logging	-0.023	-0.026	-0.024	-0.024	-0.026	-0.026	-0.026	-0.026	-0.026	-0.026

*Value: p<0.01

The PCA first axis (PC1) for foliage vertical profile explained 35% of the total variation and the second axis explained 26%. The PC1 described a gradient of increasing forest density in the lower stratum (understory forest, 0-5 m stratum) with a more open canopy (15-20 m and 20-25 m strata, see Fig. A1), which is a common characteristic of disturbed areas. However, the decreasing PC1 values indicated a denser canopy with a sparse understory, which are usually descriptors that are more commonly associated with old growth remnants.

The forest cover reduction was negatively associated with most of the vegetation structural descriptor (Fig. 2 and Table 2). Forest cover loss lead to an abrupt reduction on both mean diameter and basal area (best fit model: 4-parameter-logistic with inflection points at 35.5% (CI 95% 29.8 - 39.9%) and 39.0% (CI 95% 34.7 - 39.9%) of forest cover, respectively (Fig. 2). The mean height also decreased non-linearly with forest cover loss (best fit model: power law, Fig. 2). Overall and large tree density decay constant with the forest cover (best fit: linear model, Fig. 2). Canopy openness and the vertical stratification profile were both negatively related to forest cover reduction (Fig. 2 and Table 2). Canopy openness was better explained by the power law model (Fig. 2), indicating a greater influx of light to the lower forest strata in forests from more deforested landscapes. The vertical profile (PC1) showed that the mean length occupied by foliage in the low strata increases as forest cover decreases, with an abrupt change in deforested landscapes (best fit model: 4-parameter-logistic with inflection points at 36.8%, CI 95% 17.4 - 40.1%, Fig. 2). This finding illustrates a gradient of decreasing disturbance, in which sites immersed in more deforested landscapes tend to be characterized by an increasing density in the understory strata, as opposed to a landscape with more forest cover that tends to show denser foliage in higher strata > 15 m. In contrast, neither dead trees nor logging pressure was related to forest cover (Fig. 2).

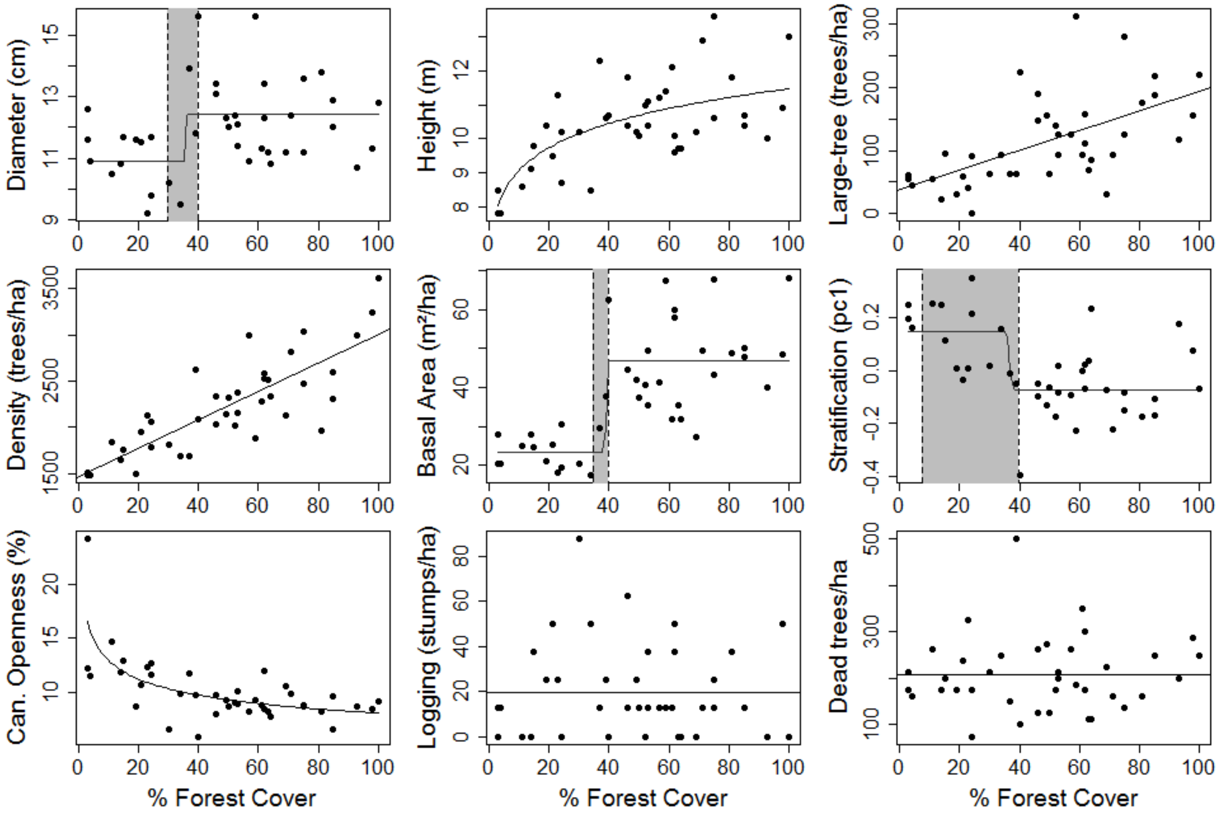

Figure 2 – Relationship between structure variables, dead tree and logging with forest cover at the landscape scale in an Atlantic Forest in southern Bahia, Brazil. The plotted curves represent the most parsimonious models for each study variable. The gray areas represent the breakpoint confidence interval.

Table 2 –Models for explaining the relation between the forest cover and structure variables of vegetation, dead trees and logging. The most parsimonious models are in gray. Models that did

not present the convergence of the likelihood estimate were excluded from the model selection procedure.

Variable	Model	dAICc	df	Weight
Diameter	Logistic	0.0	4	0.93
	Linear	7.0	3	0.03
	Power law	7.4	3	0.02
	Null	7.4	2	0.02
Height	Power law	0.0	3	0.94
	Linear	5.5	3	0.06
	Null	21.3	2	<0.001
Density of large trees	Linear	0.0	3	0.56
	Power law	0.5	3	0.44
	Null	15.0	2	<0.001
Overall density	Linear	0.0	3	0.99
	Power law	8.6	3	0.01
	Null	41.0	2	<0.001
Basal area	Logistic	0.0	4	0.94
	Linear	6.2	3	0.04
	Power law	8.0	3	0.02
	Null	30.4	2	<0.001
Canopy openness	Power law	0.0	3	0.887
	Piecewise	4.1	5	0.112
	Linear	12.7	3	0.002
	Null	25.3	2	<0.001
Vertical stratification	Logistic	0.0	4	0.99
	Linear	9.1	3	0.01
	Null	17.4	2	<0.001
Logging	Null	0.0	2	0.60
	Power law	2.1	3	0.21
	Linear	2.3	3	0.19
Dead trees	Null	0.0	2	0.60
	Power law	2.2	3	0.20
	Linear	2.2	3	0.20

dAICc: difference in AICc from the best model; df: parameter number of the model; w_i: AICc weight.

4. Discussion

Our study has uncovered the following two novel findings with important consequences for landscape conservation in tropical forests. First, landscape-scale deforestation leads to a general shrinkage in the local forest structure in the Brazilian Atlantic Forest. Second, most structural modifications are non-linearly related to forest cover loss, generally with a threshold around 35-40% of forest cover. As landscape-scale deforestation progresses, the forest structure in remnant patches degrades, and as local tree assemblages become less dense, shorter, and thinner, with an overall loss of basal area, there is increasing canopy openness and density in the understory foliage.

A number of studies have shown similar structural changes occurring in small fragments compared with larger or continuous forest remnants. However, this is the first study showing the association between forest structural changes along a gradient of landscape-scale deforestation. Among the structural changes reported in small fragments is the increasing mortality of large and emergent trees (Laurance et al., 2006a, 2000), biomass collapse (Echeverría et al., 2007; Melo et al., 2007; Santos et al., 2008) and overall alterations in microclimatic conditions (Laurance et al., 2002; Pinto et al., 2010). Our results indicate that the consequences of forest fragmentation and loss for a given forest remnant depend ultimately of the amount of forest cover at landscape level. Forest remnants in more forested landscapes retain mature forest attributes, and remnants in deforested landscapes resemble forests in early successional stages. Below, we discuss the possible underlying processes driving the observed patterns and the consequences of our findings for biodiversity and forest functionality.

4.1. Overall forest degradation

Forest degradation is often associated with decreasing biomass (Sasaki et al., 2011; Thompson et al., 2013), and carbon stock (Magnago et al., 2015a). As expected, forest cover reduction at the landscape scale negatively influenced a myriad of forest structural characteristics correlated with forest biomass, such as the mean DBH, height, and, most notably, the basal area. However, our results further indicate that these degraded forests also show a shift in the spatial arrangement of their vertical profile. As deforestation increases, foliage concentrations shift from 15-25 m to 0-5 m; this disturbance is consistent with increased canopy openness (providing more light in the lower forest stratum) in sites from more deforested landscapes. These structural changes are largely triggered by the loss of large trees, as confirmed by the low densities of large individuals in sites from deforested landscapes.

The loss of large trees is a common consequence associated with edge effects (Laurance et al., 2000; Oliveira et al., 2008), logging (Tabarelli et al., 2004) and defaunation (Bello et al., 2015). These processes are expected to increase with forest loss and fragmentation because of the higher perimeter/area ratio in smaller patches (Laurance et al., 2002; Saunders et al., 1991) and also because this forest is more often accessed by humans, facilitating its exploration (Liu and Slik, 2014; Melo et al., 2007; Tabarelli et al., 2012). Therefore, one possible explanation for the structural modifications reported here would be the higher tree mortality in patches that were immersed in more deforested landscapes because of the higher influence of the edge effect and increasing logging pressure. Surprisingly, neither the number of dead trees nor logging was related to the amount of forest cover at the landscape scale in our study sites. This finding suggests that a limited recovery of large trees might be occurring in our landscapes. However, we cannot exclude past mortality differences that might have occurred and our methodology was not designed to detect, even so if crucial ecological processes occurring in pristine areas are operating in deforested landscapes, high large trees would recover.

Tree populations are maintained by seed dispersal, recruitment, and establishment, which are three important, sequential ecological processes in which disruptions can result in limitations to species recovery (Beckman and Rogers, 2013; Fadini et al., 2009). The dispersal rate is likely to be reduced in more deforested landscapes because of the increasing isolation among forest patches (Melo et al., 2006; Zuidema et al., 1996). The absence of large-to-medium mammals can interrupt the dispersal of large seed trees, driving the reduction of their abundance (Beckman and Rogers, 2013; Galetti et al., 2006; Tabarelli et al., 2004). Large seeds associated with slow growth are characteristic of shade-tolerant species, which generally encompass the largest forest trees (Bello et al., 2015; Nascimento et al., 2005; Oliveira et al., 2004; Whitmore, 1989). However, defaunation is widespread in southern Bahia, not as a direct result of habitat loss per se but rather as a consequence of the high hunting pressure that led, for instance, to the local extinction of large mammals such as the tapir *Tapirus terrestris* and the white-lipped peccary *Tayassu pecari* (Canale et al., 2012; Cassano et al., 2012; Jorge et al., 2013). Accordingly, many species of medium and large-sized mammals from our landscapes are extinct or present at very low abundances, therefore seed dispersal limitation mainly of those large-seeded species are likely to occur in all studied landscapes independently of forest amount. The increasing forest canopy openness in more deforested landscapes, changes in the light regime, humidity and other important microclimatic factors can prevent seed germination, recruitment or even the establishment of shade-tolerant species. Among these vulnerable assemblages are many species from large tree species that characterize mature forests while the forest changes favor shade-intolerant species (Harper et al., 2005; Laurance et al., 2006a).

Our results suggest that the overall tree density decreased with forest cover loss. This pattern is contrary to our initial expectation, based on the knowledge that the shift in light regime produced by new gaps is generally followed by an increment in recruitment, turnover, and understory growth (Laurance et al., 2006a, 2002), a process described as a compensatory effect (Harper et al., 2005). Compensatory effects have been reported in areas subject to edge effects and in small forest remnants, which had higher overall tree density than forest interiors and large remnants (Harper et al., 2005; Laurance et al., 2006a). This finding has also been reported in areas recovering from swidden cultivation, in which numerous small trees are replaced by fewer larger trees as the forest ages (Piotto et al., 2009). Similar to our finding, Santos et al. (2008) found an increasing tree density in older forest remnants in a hyper-fragmented landscape of an Atlantic forest in northern Brazil. The absence of a compensatory effect in our studied area is not derived from differential tree deaths, since the number of dead trees is similar among the landscapes, but tree density decay as forest is lost in the landscape. Instead, it could be a reflection of the recruitment limitation that might be occurring in low forest cover landscapes. Again, seed dispersal and/or establishment limitation may explain the absence of compensatory effect. Alternatively, compensatory effect may be constrained by the presence of less fertile soils in more altered landscapes that can reduce growth rates and aboveground biomass accumulation (Liu and Slik, 2014; Moran et al., 2000).

4.2. Retrogressive succession on course

Sampling sites in less forested landscapes showed high structural similarity to secondary forests in the early successional stages, with higher sunlight penetration (high canopy openness) concomitant with a reduction in the density of large trees and loss of above-ground biomass (Faria et al., 2009; Santos et al., 2008). This major degradation of the forest structure indicates a strong change towards retrogressive forest succession. This process was described for small fragments and forest edges in a northern Atlantic forest region, where sugarcane has been grown for over 200 years and represents the primary land-use in forest remnant surroundings (Santos et al., 2008; Tabarelli et al., 2008). However, studies in fragmented Amazonian regions did not find this type of erosion in the fragments so far (Laurance et al., 2011, 2006a; Nascimento et al., 2005), possibly because of the highly forested landscapes and the short time that elapsed between fragmentation and evaluation (from 22 to 32 years).

Retrogressive succession has negative impacts on forest function and ecosystem services, particularly on carbon stocks. For instance, large trees actively fix a greater amount of carbon compared to smaller tress (Stephenson et al., 2014). The largest 10% of trees in the southern Bahia Atlantic forest retain more above-ground carbon than the remaining 90% of trees in the same plot (Schroth et al., 2013). Therefore, the loss of these individuals is likely to compromise cycling processes and carbon stocks (Bello et al., 2015; Osuri et al., 2014; Wright, 2010). Numerous studies have also shown that forest structure disturbance is an important determinant of species richness and/or abundance, which may further interact with patch and landscape characteristics, such as size and connectivity (Banks-Leite et al., 2013; Pardini et al., 2005). Therefore, the signs of retrogressive succession, which are shown here and are more likely to occur in deforested landscapes, can lead to the functional erosion of forest ecosystems, with both local and broad-scale consequences.

4.3. Forest structure threshold

Extinction thresholds were previously reported empirically by several studies on different taxonomic groups (Banks-Leite et al., 2014; Pardini et al., 2010), including two important tree families that are characteristic of the Atlantic rainforest, namely Sapotaceae and Myrtaceae. In both cases, species extinction is exacerbated when landscape forest cover is reduced to less than 30% (Lima and Mariano-Neto, 2014; Rigueira et al., 2013). These thresholds are likely to happen when the amount of habitat reaches a level below which a population cannot sustain itself (Fahrig, 2003). In the present study, important features of forest structure showed a non-linear decay with forest cover reduction, with threshold values ranging from 35 to 39% of the amount of forest in the landscape. Identifying extinction threshold values can be useful for biodiversity conservation (Groffman et al., 2006), as supported by the recent application of these values to guide resource allocation to restore landscapes (Banks-Leite et al., 2014; Pardini et al., 2010). Based on our results, the conservation efforts in our region should be applied to avoid forest reductions below 40%, or, in those deforested landscapes, to use these values as targets for restoration.

5. Conclusions

We have demonstrated that the forest structure is affected by forest cover reduction at the landscape scale. When the forest cover was reduced, we observed changes in forest structure descriptors, such as the diameter, height, density, basal area, canopy openness, and vertical profile. Although the edge effect and logging are undoubtedly drivers of forest structure erosion following tree mortality (Santos et al., 2008; Tabarelli et al., 2008), current the number of dead trees and logging quantities were similar in all sites independent of the forest cover, and thus they did not explain the described erosion pattern. It is possible that other ecological processes, such as seed dispersal, recruitment and establishment limitations, are responsible for the observed forest structure, with the association of a forest cover effect.

The forest remnants from deforested landscapes presented structures that were quite similar to those of secondary forests, suggesting that forest cover loss is driving a retrogressive succession process in the study area. Although many studies are centered on the time of recuperation from disturbance to predicted forest recovery (Laurance et al., 1998; Piotto et al., 2009), it seems that forest remnants in highly deforested landscapes will remain as secondary forests, despite their age (Tabarelli et al., 2008). Our findings support the regime shift proposed by Pardini et al. (2010) in a southeastern Atlantic forest. In both regions of the Atlantic rainforest, there seems to be a forest cover threshold associated with this shift, which started to occur at approximately 35-40% forest cover in our study landscape. In the face of these facts, avoiding the reduction of forest cover below this threshold is strongly recommended because structural erosion becomes more severe, with predictable negative consequences to biodiversity and ecosystem services maintenance.

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APPENDIX A

Appendix A. Supplementary data

Supplementary data can be found online at http://dx.doi.org/10.1016/j.biocon.2016.01.028

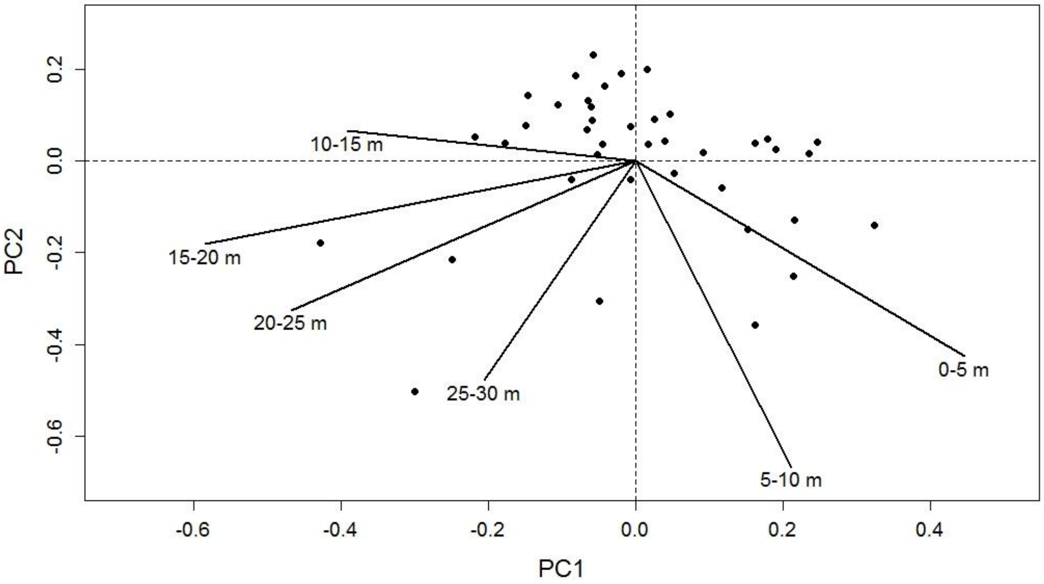

Figure A1 - Biplot of the first two principal components axis (PC1 and PC2, respectively) with all strata of the vertical foliage profile in 40 forest sites that were immersed in landscapes located in southern Bahia, Brazil, and varying from 3 to 100% forest cover. PC1 and PC2 explained 35% and 26% of the variation, respectively.

Table A1 - Correlation matrix, with Pearson correlation tests, among all forest structure variable - mean and maximum diameter (dbh_me; dbh_ma); mean and maximum height (he_me; he_ma); density of large trees (des_ltr); overall density (des_ov); vertical stratification profile (vert_str); canopy openness (can_op); mortality (mort); logging (log). The high correlations between structural variables are highlighted in bold.

	dhb_mean	dbh_max	he_mean	he_max	des_ltr	des_ov	b_area	vert_str	can_op	mort
dbh_max	**0.78****									
he_mean	0.44*	0.55**								
he_max	0.71**	**0.80****	0.56**							
des_ltr	0.64**	**0.87****	0.53**	**0.77****						
des_ov	0.08	0.5*	0.46*	0.46*	0.50*					
b_area	0.72**	**0.93****	0.54**	**0.82****	**0.85****	0.64**				
vert_str	-0.63**	-0.70**	-0.67**	-0.59**	-0.64**	-0.43*	-0.71**			
can_op	0.03	0.11	0.04	-0.05	0.19	0.2	0.18	-0.21		
mort	0.23	0.39	0.35	0.20	0.34	0.42*	0.42*	-0.48*	0.08	
log	-0.04	0.23	-0.09	0.10	0.06	0.26	0.25	-0.19	-0.13	0.40

*$p<0.01$, **$p<0.001$

Table A2 – Values of the mean ± standard deviation (SD), minimum and maximum all the structural descriptors, in addition to mortality and logging, for all 40 sampling sites.

Variables	**Mean (± SD)**	**Min**	**Max**
Mean Diameter	11.9 ± 1.4	9.2	15.6
Maximum Diameter	34.4 ± 7.7	19.1	51.9
Mean Height	10.4 ± 1.3	7.8	13.6
Maximum Height	17.6 ± 2.8	11.1	23.4
Density of large trees	113.4 ± 71.2	0.0	312.5
Overall density	2217.3 ± 509.3	1480.6	3620.0
Basal area	38.5 ± 14.7	17.5	68.2
Canopy openness	10.1 ± 2.9	6.0	24.1
Vertical profile	0.0 ± 0.6	-1.7	1.3
Logging	19.7 ± 20.8	0.0	87.5
Mortality	208.1 ± 79.0	75.0	500.0

CAPÍTULO 2

Functional decay in tree community within tropical fragmented landscapes: effects of landscape-scale forest cover

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Functional decay in tree community within tropical fragmented landscapes: effects of landscape-scale forest cover

Larissa Rocha-Santos[1]*, Maíra Benchimol[1], Margaret M. Mayfield[2], Deborah Faria[1], Michaele S. Pessoa[1], Daniela C. Talora[1], Eduardo Mariano-Neto[3], Eliana Cazetta[1]

[1]Graduate Program in Ecology and Biodiversity Conservation, Applied Ecology and Conservation Lab, State University of Santa Cruz, Ilhéus, Bahia, Brazil. [2]School of Biological Sciences, The University of Queensland, St Lucia Campus, Queensland, Australia. [3]Botany department, Biology institute, Federal University of Bahia, Salvador, Bahia, Brazil.

*rocha_larissa@yahoo.com.br (LRS)

Abstract

As tropical rainforests are cleared, forest remnants are increasingly isolated within agricultural landscapes. Understanding how forest loss impacts on species diversity can, therefore, contribute to identifying the minimum amount of habitat required for biodiversity maintenance in human-modified landscapes. Here, we evaluate how the amount of forest cover, at the landscape scale, affects patterns of species richness, abundance, key functional traits and common taxonomic families of adult trees in twenty Brazilian Atlantic rainforest landscapes. We found that as forest cover decreases, both tree community richness and abundance decline, without exhibiting a threshold. At the family-level, species richness and abundance of the Myrtaceae and Sapotaceae were also negatively impacted by the percent forest remaining at the landscape scale. For functional traits, we found a reduction in shade-tolerant, animal-dispersed and small-seeded species following a decrease in the amount of forest retained in landscapes. These results suggest that the amount of forest in a landscape is driving non-random losses in phylogenetic and functional tree diversity in Brazil's remaining Atlantic rainforests. Our study highlights potential restraints on the conservation value of Atlantic rainforest remnants in deforested landscapes in the future.

Introduction

We are currently in the midst of a massive global extinction event (Barnosky et al., 2011), with the current wave of biodiversity reduction mainly occurring due to habitat loss and habitat modification (Barnosky et al., 2011; Pimm et al., 1995). For plants in particular, studies have shown that the synergistic effects of habitat loss and fragmentation lead to profound changes in patterns of tree species composition (Echeverría et al., 2007; Oliveira et al., 2004), richness (Laurance et al., 2006b; Rigueira et al., 2013; Tabarelli et al., 2010b), functional (Girão et al., 2007; Oliveira et al., 2008; Rocha-santos et al., 2016; Santos et al., 2008) and phylogenetic diversity (Andrade et al., 2015; Arroyo-Rodríguez et al., 2012; Lôbo et al., 2011; Santos et al., 2014), with landscape configuration and edge effects commonly identified as the key drivers of floristic decay in tropical rainforests.

The amount of forest cover at the landscape-scale is currently considered an important driver of biological change, and a meaningful proxy for habitat loss (Fahrig, 2003). The 'habitat amount hypothesis' (Fahrig, 2013), in fact, posits that "patch size" and remnant "isolation" can be replaced by a single predictor variable – the amount of the remnant habitat found across a landscape. Moreover, the fragmentation threshold hypothesis (Andrén, 1994; Pardini et al., 2010) suggests that the amount of forest in the landscape is an important driver of species diversity, and that when forest remnants are in landscapes within higher percentages of total overall forest cover (> 50%) they are prone to maintain higher diversity than those in landscapes with less total forest cover. Under this hypothesis, patch size is also thought to contribute to biodiversity maintenance in landscapes with intermediate levels of forest cover (>30 and <50%), whereas below this threshold (30%) an abrupt, non-linear loss of diversity is expected to occur regardless of patch size (Pardini et al., 2010). Both theories have been accepted by the landscape ecology and conservation communities (but see (Haddad et al., 2017)), leading to the widely held belief that the amount of forest within a landscape is an effective way of measuring habitat loss and fragmentation, which is easier and more widely accessible information than patch size and isolation (Fahrig, 2013).

Investigating the species extinction thresholds, *i.e.*, the minimum amount of habitat area at a landscape scale required for a species to persist, has gained prominence in recently proposed conservation management strategies for human modified tropical landscapes. Yet few studies have evaluated the effects of habitat loss on the occurrence of extinction thresholds for plants at family (Lima and Mariano-Neto, 2014; Rigueira et al., 2013), or community levels [19]. Theoretical models, have previously fail to predict extinction thresholds for community responses to landscape modification mainly due to the specific functional traits of different species composing it (King et al., 2011; King and Baker, 2010). Therefore, more studies are needed to determine if thresholds hold across families and communities or when taking into account species' functional attributes.

Apart from examining landscape-level thresholds in species richness, several studies have investigated phylogenetic and functional diversity patterns to assess how biological communities respond to different levels of anthropogenic disturbances [13,21,22]. In fact, both approaches are increasingly common due to the growing emphasis on the idea that richness patterns alone can lead to incorrect interpretations of the effects of habitat loss and fragmentation on biodiversity [23–25]. Investigating phylogenetic associations, like families, can improve studies by allowing similar ecological species to be considered together, acting as a proxy for phylogenetic and functional diversity [26].

Ecologists recognize that studying functional traits or functional groups can provide valuable information regarding ecosystem processes, function and evolutionary history in human-altered landscapes (Tilman et al., 1997). For instance, species with functional traits of habitat-specialists are frequently more negatively impacted by forest loss across landscapes, in contrast to generalist species (Morante-Filho et al., 2015; Pardini et al., 2010). The disproportionate loss of some plant functional traits in fragmented forest landscapes, like shade-tolerant and large-seeded species (Melo et al., 2007; Murcia, 1995a; Thier and Wesenberg, 2016), can have detrimental effects on food availability (Pessoa et al., 2016), shelter for native animals (Arroyo-Rodríguez et al., 2007), and biomass accumulation (Baker et al., 2004; Bello et al., 2015). In tropical forests, late successional plants – mainly shade-tolerant species, including representative families such as Myrtaceae, Sapotaceae and Rubiaceae – are usually negatively affected by forest cover loss, whereas shade-intolerant pioneer families can be positively influenced by forest cover loss (Andrade et al., 2015; Lima and Mariano-Neto, 2014; Tabarelli et al., 2010b). Despite functional traits and groups have received growing attention in studies of community ecology and conservation biology (Hooper et al., 2005), there is still a lack of information on the functional responses of tree assemblages in relation to forest cover thresholds in fragmented forest landscapes (but see (Montoya et al., 2008)).

Here, we investigated how tree community, families, and functional traits are affected by forest cover reduction in contrasting landscapes across the Brazilian Atlantic rainforest region. Southern Bahia State is home to some represented largest remnants of Atlantic forest in northeastern Brazil and has a recent history of fragmentation (late twentieth century (Saracura, 1997)). In this region, we evaluated whether loss of landscape-scale forest cover corresponds to a functional decay (i.e., a collapse in taxonomic and functional diversity) in forest remnant plant assemblages. To do this, we performed floristic surveys at twenty forest remnants found across a gradient of landscape-scale native forest cover, ranging from 3% to 93% forest cover around focal forest remnants. First, we evaluated the similarity of tree species composition among sites. Then, we investigated the relationship between forest cover and tree species richness and abundance, using a model selection approach to evaluate whether these relationships were linearly or non-linear, and in case of non-linear results, we then identified potential "thresholds" of species and functional diversity loss. We further assessed the diversity patterns for the most common tree families in our surveys (Myrtaceae, Sapotaceae, Fabaceae, Rubiaceae, and Lauraceae). Finally, we explored the richness and abundance of species with three key functional tree traits (regeneration strategy, dispersal mode, and seed size). We hypothesized that forest cover amount would be a strong driver of tree community attributes in our study area. Specifically, we expect that: (*i*) highly deforested landscapes are more similar to each other in terms of species composition, following the floristic differentiation hypothesis (Arroyo-Rodríguez et al., 2013); (ii) both species richness and abundance is exhibited to reflect a nonlinear pattern and be greater in landscapes with more forest cover, following the predictions from the Habitat Amount Hypothesis (Fahrig, 2013) and; (*iii*) the most common families will vary in response to a landscape-wide loss of forests according to family specific requirements; (*iv*) species richness and abundance of shade-intolerant, small-seeded and abiotic-dispersed species (seeds dispersed by anemochory or autochory) will decrease in landscapes with more forest cover, due to the prevalence of disturbance-adapted species within these functional traits (Laurance et al., 2006a; Tabarelli et al., 2010b); whereas large-seeded, shade-tolerant and biotic-dispersed species will be less common in landscapes with less forest cover given that such species are known to be vulnerable to forest loss and fragmentation (Santos et al., 2008; Tabarelli et al., 2008).

Methods

Study area

We conducted this study in twenty forest sites of the Brazilian Atlantic rainforest in southern Bahia ($15^0$0' - $16^0$0' S and $39^0$0' – $39^0$30' W), which harbors one of the highest diversities of wood plant species in the world (Martini et al., 2007; Thomas et al., 1998). All sampled forest sites were located across a gradient of landscape-scale forest fragmentation, in tropical lowland rainforests fragments (Oliveira-Filho and Fontes, 2000), surrounded by a matrix of agroforestry, pastures, rubber, or eucalyptus plantations (Cassano et al., 2008; Faria et al., 2009). Sample sites were at least in medium to advanced stages of secondary succession and were variable in size, but only forest sites larger than 3ha were included. Deforestation occurred in all fragments at about the same time, starting in the mid 1980’s, increasing during the cocoa crisis of the 1990’s. The whole study region’s climate is classified as *Af*, hot and moist, without a distinct dry season (Gouvêa, 1969), according to the Koppen classification, and has an annual average temperature of 24 °C and rainfall of ~1,500 mm y^{-1} (Mori et al., 1983).

Sampling design

We firstly mapped the forest coverage across an area of 3,500 km^2, between the Jequitinhonha and Contas Rivers. This region is formed by the same soil, topography, and vegetation types (Thomas et al., 1998). Regions dominated by Montane Forest (mostly in the northwest, at elevations of 500 m a.s.l. or higher) and Restinga Forests (mostly in southeast) were excluded to avoid these distinct vegetation and soil types. Using high-resolution satellite images (RapidEye, with tiles from 2009 to 2010, and QuickBird and WorldView from 2009 to 2011) of this study region, we created a map by visual interpretation of land cover features at a scale of 1:10,000, which is adequate for identifying patches based on the visual inspection of differences in color, texture, shape, location, and context. To characterize each landscape we quantified the percent forest cover around each site from the center of each forest site (using ARCGIS). We considered only mature and secondary native forests in our estimations of forest cover, excluding shade cocoa and rubber plantations. Although we recognize that agroforests can enhance habitat availability and forest connectivity between forest sites (Cassano et al., 2012), they differ even from regrowth forests considerably in our high-resolution images and since only a small number of surveyed sites were embedded within an agroforestry mosaic we excluded these sites. All selected forest sites were classified according to vegetation types following the typologies provided by the Brazilian Institute of Geography and Statistics (IBGE, 2006). Once patches were identified, we delimited them as polygons and digitally mapped them using ArcGIS software.

From the above map we selected all possible forest sites (total of 58), that spanned a range of landscape-scale forest covers and ground-truthed them all. All selected sites were checked to ensure that they were composed of our focal forest type (tropical lowland rainforests) and that no sites were less than 1 km from any other. Ground truthing also involved determining which sites were accessible and for which we could obtain formal consent from land-owners to survey (for details see (Morante-Filho et al., 2015)). Of the sites that fit these criteria post ground truthing, we used a stratified sampling approach to select 20 focal forest sites from across the full range of forest cover classes. We then adopted a patch-landscape approach, in which the response variables were evaluated within forest sites and the landscape variable (here represented by forest cover) were measured within a specific area around each sampling site (Tischendorf and Fahrig, 2000). The four spatial scales we used to assess landscape forest cover were: 500, 1,000, 1,500 and 2,000 m radii circles, which captured total landscape areas of 78,5 ha, 314 ha, 706,5 ha and 1256 ha, respectively. These scales were chosen based on similar studies from the literature, and because they seem to appropriately account for relevant landscape factors for seed dispersal (Jackson and Fahrig, 2015), pollination functions (Winfree et al., 2007) and plant structure (Rocha-santos et al., 2016).

Floristic surveys and species classification

We established five 4 x 25 m forest-plots (0.01 ha) close to the center of each selected forest remnant. Plots were positioned at least 50 m apart from each other and from the nearest forest edge, whenever possible (85% of the total). In each forest-plot, we measured and identified all live trees (including arboreal palms) with a diameter at breast height (DBH = 1.30m above ground) of ≥ 5 cm and that had at least 10% of the main trunk partially within plot boundaries. Identifications were performed by experienced botanists to the lowest possible taxonomic level, according to the APG III (2009) classification, based on herbaria collections of Brazilian Institutes located in the Bahia state (CEPEC/Ceplac, UESC and UFBA).

For all surveyed species, we obtained trait values for three categorical functional traits: regeneration strategy, dispersal mode and seed size. Trait data were gathered from published literature (Barroso et al., 1999; Lorenzi, 2002; Mariano-Neto, 2004) and authors' experience with species in the study region. We selected these traits given their known association with important life-history traits in tropical forest systems. Specifically, regeneration strategy is associated with tree recruitment, establishment and survival (Oliveira et al., 2004; Swaine and Whitmore, 1988); dispersal mode is important for the maintenance and spreading of viable populations (Hammond et al., 1996); and seed size is correlated to a range of important processes including seed dispersal, germination success and seedling survival (Armstrong and Westoby, 1993; Foster and Susan, 1986). To each species that we could identify to at least the family level and with available information, we assigned states for each functional trait. Even though some family traits are labile, we were able to assign traits in some specific cases in which the species were not identified, but for which fruits were collected, or when the whole family presented the same trait in all Atlantic forest biome (for instance, in Atlantic forest all Myrtaceae species are biotically-dispersed [58,59]; all Sapotaceae species are shade-tolerant (Lima and Mariano-Neto, 2014); and Melastomataceae species are typically shade-intolerant (Faria et al., 2009; Lôbo et al., 2011; Piotto et al., 2009; Rocha-santos and Talora, 2012)). For regeneration strategy we classified species as shade-tolerant or shade-intolerant (Whitmore, 1989). For dispersal mode, species were classified as vertebrate biotic-dispersed or abiotic-dispersed (seeds dispersed by anemochory or autochory- free fall or propelled explosively by fruit opening). For seed size, data were gathered as a continuous trait and then species were classified as having small seeds (seeds smaller or equal to 1.2 cm of diameter) or large seeds (seeds larger than 1.2 cm diameter). This criterion considers the patterns of seed consumption by frugivores in tropical forests, in which seeds smaller than 1.2 cm are eaten by small birds (including those from Turdidae family), and above this size by large-bodied bird and mammal species (Bello et al., 2015; Côrtes et al., 2009; Galetti et al., 2013). Based on overall representativeness (number of species) we conducted analyses considering the most common families, separately: Fabaceae, Myrtaceae, Sapotaceae, Rubiaceae, and Lauraceae. Fabaceae is often the most abundant family in floristic surveys across the Atlantic Forest region (Mori et al., 1983; Rocha-santos and Talora, 2012; Thomas et al., 2009). Myrtaceae, Sapotaceae and Rubiaceae are composed of shade-tolerant species typical of most preserved areas in the Atlantic Forest (Lima and Mariano-Neto, 2014; Rigueira et al., 2013; Rocha-santos and Talora, 2012; Tabarelli et al., 1999), are of great importance as food resources for native animals (Canale et al., 2016; Oliveira et al., 2010; Tabarelli et al., 1999), and are among the most diverse families in this part of Brazil (Mariano-Neto, 2004; Mori et al., 1983; Thomas et al., 2009). Lauraceae is abundant and highly diverse in the Atlantic Forest region (Mori et al., 1983; Piotto et al., 2009; Rocha-santos and Talora, 2012), also representing important animal food resources (Tabarelli et al., 1999).

Ethics statement

Field work was carried out on private properties with permits from each landowner. We did not perform any other activities that required specific government permissions.

Data analysis

To assess the relationship between forest cover and tree community, we started by comparing the four selected landscape scales to identify the scale that best captured variation in diversity in this study. To do this, we used the software Focus (Holland et al., 2004) to assess Spearman's rank test (r) at each of our four pre-established landscape scales (500, 1,000, 1,500 and 2,000 m radii) and determine which scale ranks highest for each response variable (richness and abundance patterns, overall and for each functional trait and family). We used the total number of individuals per fragment as a measure of abundance. We detected that 1,000 m scale showed the highest coefficient values for the majority of richness (86%) and abundance (57%) models, so we used this radius for forest cover estimates for all subsequent analyses.

To investigate the potential spatial dependence on the patterns of species richness and abundance, we applied a semivariogram (see (Diggle and Ribeiro, 2007)), a spatial technique widely applied to examine and identify spatial dependency and the spatial structure of that dependency. We included spatial covariates in statistical models, by performing 1,000 Montecarlo simulations to construct a confidence envelope of a complete spatial random distribution of the data and infer the existence and type of spatial trend. We thus performed a Detrended Correspondence Analysis (DCA) on the quantitative species composition, to evaluate patterns of similarity among our contrasted surveyed landscapes. Semivariograms were executed in the "geoR" package (Ribeiro and Diggle, 2016) in R (R Development Core Team, 2013).

We proceeded with a model selection approach to evaluate the type of relationship (linear or non-linear) that best explains responses of species richness and abundance to forest cover amount. Specifically, we ran separate model comparisons for the following groups of species: (*i*) overall community, (*ii*) the most common families (Fabaceae, Myrtaceae, Sapotaceae, Rubiaceae and Lauraceae), and (*iii)* each functional trait (regeneration strategy, dispersal mode, and seed size). For each of these groups, we tested four models: (1) null (constant); (2) linear; and two non-linear, (3) power law (Pinheiro and Bates, 2000), and (4) four-parameter logistic (Crawley, 2007). The four-parameter logistic model has been widely used to investigate threshold relationships in fragmented tropical forest landscapes (Banks-Leite et al., 2014; Lima and Mariano-Neto, 2014). When the four-parameter logistic was selected as the best fit model we calculated the threshold value. The four parameters control the upper and lower asymptotes, the velocity in which the model changes between asymptotes, and the inflection point, which represents the amount of forest cover nearby the rapid change in forest richness and composition values (Rocha-santos et al., 2016). For all variables exhibiting spatial correlation, we performed spatial linear models (SLMs), which account for spatial autocorrelation (F. Dormann et al., 2007). In those cases, we tested only three models, because SLMs analyses unsuccessfully adjust logistic models, so this option was excluded from the model selection approach. In all cases, we determined the parsimonious models by selecting all those showing dAIC (delta Akaike Information Criterion) value ≤ 2.00 (Burnham and Anderson, 2002). We built routines to adjust non-linear model parameters, minimizing the model's log-likelihood using numerical optimization (Bolker, 2008), wAICc (weight Akaike Information Criterion corrected) and confidence intervals. During our model parameterization procedure, we excluded those models that did not show convergent solutions during numerical optimization. In all those cases in which the null model appeared amongst the parsimonious models, we assumed that no other model best explained the specific pattern than the chance. All analyses were implemented in R (R Development Core Team, 2013) using the "bbmle", "nlme", "spdep" and "lme4" packages (Bolker, 2014; Pinheiro and Bates, 2000).

Given that a great number of studies highlighted the role of edge effect as a local driver of changes in tree diversity, composition and functioning in tropical fragmented landscapes (Harper et al., 2005; Magnago et al., 2015b), we also performed analysis including the average linear distance from all five forest-plots to the nearest edge. For this, we performed Generalized Linear Models (GLMs), Generalized Additive Models (GAMs) or SLMs, according to the forest cover relationship type, and thus examined the effects of forest cover and edge distance to each community attribute investigated in our study. We ran GLMs if the linear model was a parsimonious model, GAMs were used when non-linear models were found to be most parsimonious, or SLMs when the variable showed spatial correlation. We used the same model selection approach described above to test these different landscapes metrics. For each community attribute, we tested four models: the null, only forest cover, only forest edge, and forest cover plus forest edge. Forest cover and forest edge distance were log transformed. The analyses were implemented in R using the "MuMIn", "mgcv", " lmmfit" and "bbmle" packages (Bartón, 2009; Bolker, 2014).

Results

We recorded a total of 1,955 individuals belonging to 512 species and 53 families across a total sampled area of 1 ha (divided equally among 20 sites). 80.07% of surveyed individuals were identified to species level (410 species), 15.23% to genus (78 species), and 4.68% to family level (24 species). We were able to assign regeneration strategies to 89.8% of surveyed species, dispersal strategies for 95.9% of surveyed species, and seed size for 66.3% of all zoochoric species. Of the 66% of species with seed size data, 48.1% came from published sources and 18.2% from direct measurement from field collected seeds (see classification on S1 Table). Across the three traits, we assigned trait values to 98.4% of surveyed individuals.

The number of individuals in each forest site ranged from 60 to 129 (mean ± SD, 98 ± 17.5), and the number of species varied from 32 to 85 (57 ± 14.2). The five common families considered separately in this study were the most species rich in our survey: Myrtaceae (84 species), Fabaceae (65), Rubiaceae (32), Sapotaceae (32), and Lauraceae (25; see S1 Table).

Spatial correlation

Out of the fourteen response variables tested (richness and abundance of tree communities and species with specific functional traits), only three showed significant spatial correlation - overall community abundance, abundance of biotic-dispersed species and abundance of small-seeded species, with remnants located less than 30 km from other remnants being more similar to each other than expected by chance (see S1 Fig).

Forest cover influence on tree communities

The first DCA axis explained 59% of variance in community composition (p <0.001). Tree species composition was highly dissimilar in less forested landscapes (Fig. 1). Overall, tree species richness and abundance were linearly related to forest cover amount, with our model predicting that every 10% reduction leads to a loss of 46 tree species and 83 individual trees. Non-linear models were also among the most parsimonious for species richness (Fig. 2, S2 Table). At the family-level, we found a reduction in Myrtaceae and Sapotaceae species richness as forest cover decreased, within a 1000 m radius area, in linear and non-linear ways (linear and power law models selected), respectively (Fig. 3). Lauraceae richness and abundance showed a sharp decrease with an inflection point of 29% (CI 95% 17.7-43.3%) of forest cover, based on the logistic model. Conversely, forest cover amount did not influence Rubiaceae and Fabaceae species richness (null model selected) (Fig. 3, S2 Table).

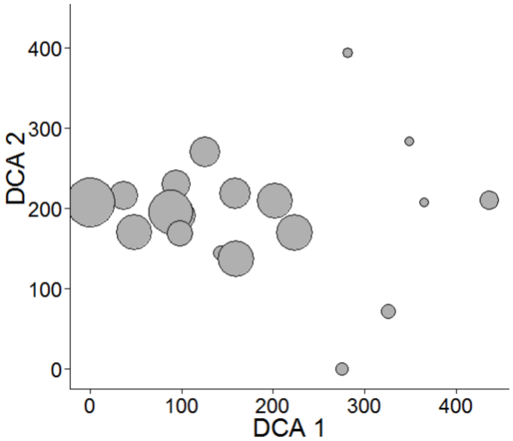

Fig. 1 Detrended Correspondence Analysis (DCA) ordinations on the quantitative tree species composition.

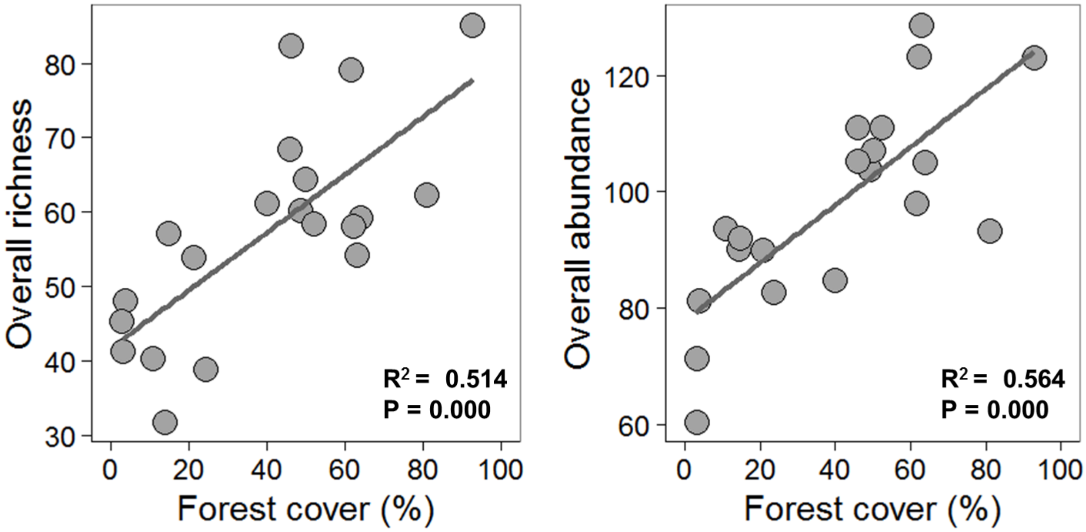

Fig. 2 Relationships between forest cover amount with the overall species richness and overall abundance (number of individuals). Plotted curves represent all well-supported models (null, linear, power-law and logistic model) identified with AICc for each relationship. Logistic models were excluded for spatial linear models (see text for details).

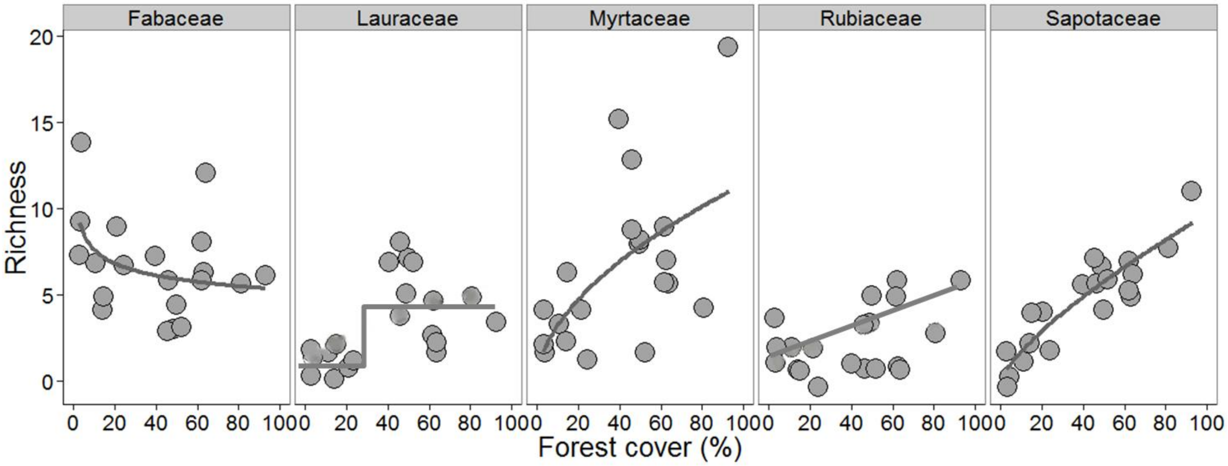

Fig. 3 Relationships between forest cover with the species richness for each of the most common families recorded (Myrtaceae - Myr, Fabaceae - Fab, Lauraceae - Lau, Rubiaceae - Rub and Sapotaceae - Sap). Plotted curves represent all well-supported models (null, linear, power-law and logistic model) for each relationship.

Considering the functional traits examined in this study, we found that forest cover reduction was associated with a decrease in shade-tolerant and biotic-dispersed species richness and abundance, with both linear and non-linear models explaining richness patterns, whereas the power-law best described the abundance patterns of those groups. Small-seeded species richness was also non-linearly affected by forest cover, with fewer of these species detected in sites surrounded by less forest (power law model selected). Forest cover did not affect the richness and abundance of shade-intolerant, abiotic-dispersed and large-seeded species and the abundance of small-seeded species, given that the null model was selected (Fig. 4 and 5, S3 Table).

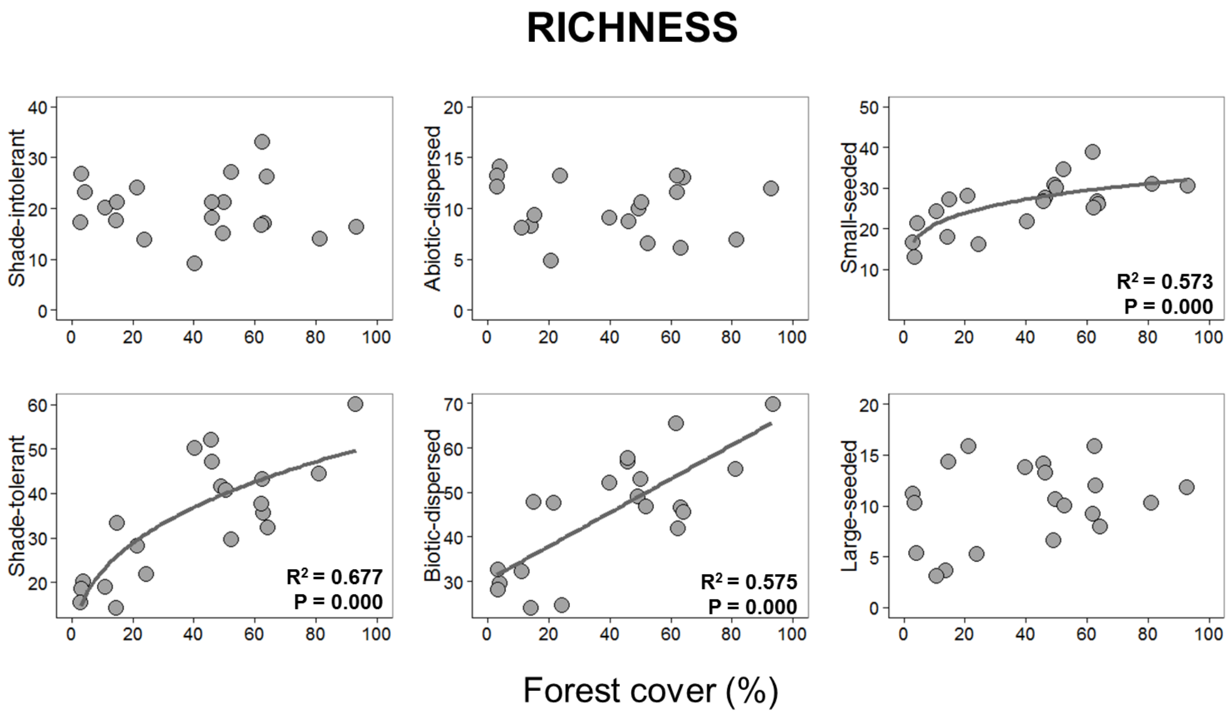

Fig. 4 Relationships between forest cover amount with the species richness of shade-intolerant, shade-intolerance, abiotic-dispersed, biotic-dispersed, small-seeded and large-seeded species. Plotted curves represent of all well-supported models (null, linear, power-law and logistic model) identified with AICc for each relationship.

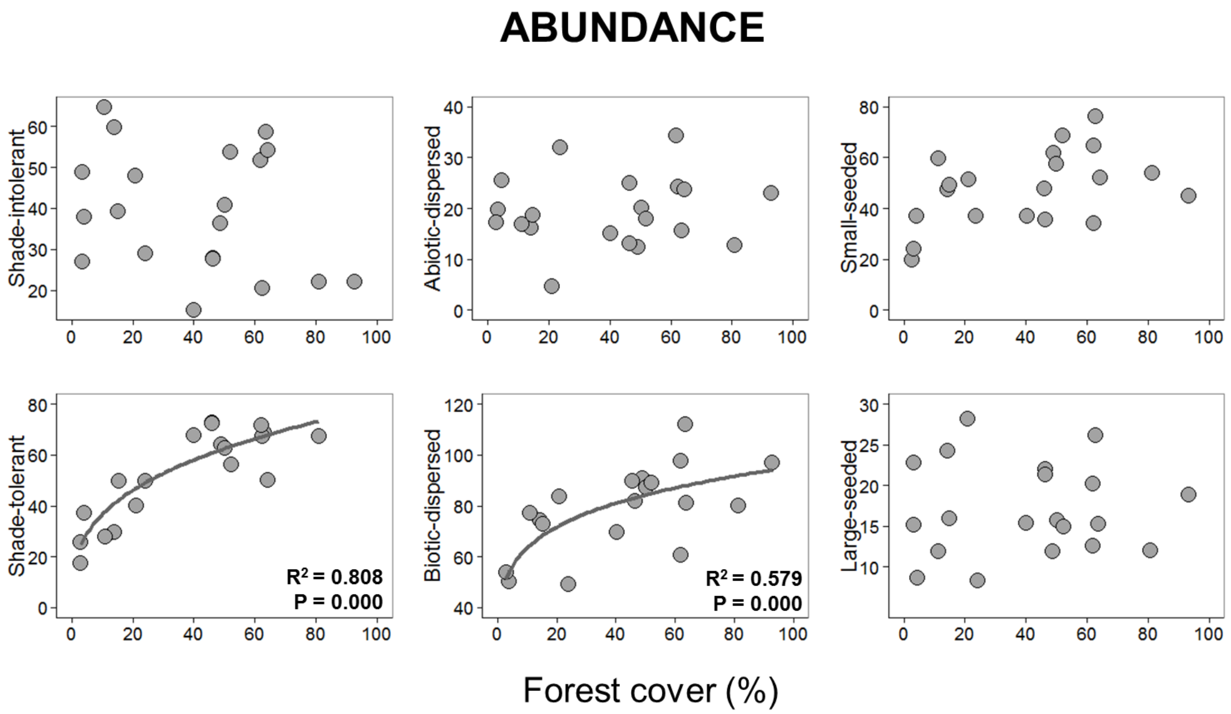

Fig. 5 Relationships between forest cover amount with the abundance of shade-intolerant, shade-intolerance, abiotic-dispersed, biotic-dispersed, small-seeded and large-seeded species. Plotted curves represent of all well-supported models (null, linear, power-law and logistic model) identified with AICc for each relationship. Logistic models were excluded for spatial linear models (see text for details).

Forest cover or edge distance?

When we conducted model selection analyses including forest cover amount (in a 1000 m radius) and nearest edge distance, we found that forest cover was the only variable included in the best model explaining the patterns for both overall community richness and abundance (S4 Table), with lower tree richness and abundance being recorded in forest sites within more deforested landscapes (Table 1). Likewise, at the family level, there were fewer Fabaceae species in remnants surrounded by lower amount of forest cover. The abundance of Fabaceae increased with forest cover reduction and edge proximity, whereas the species richness and abundance of Myrtaceae and Sapotaceae decreased only with forest cover reduction (Table 1 and S4 Table). By contrast, richness and abundance of Rubiaceae and Lauraceae were not associated with forest cover but were lower closer to forest edges (Table 1 and S4 Table).

Table 1 - Coefficients and significance of the most parsimonious model (determined by AICc) for richness and abundance of the overall tree community and for the most important families in our study.

Parameter	Richness		Abundance	
	Edge distance	Cover amount	Edge distance	Cover amount
Overall[1,3]	+0.28	+0.23*	-	+4.16***
Myrtaceae[1,1]	-	+1.10***	-	+1.13***
Fabaceae[2,2]	-	NS	+14.78**	+41.81***
Lauraceae[2,2]	+6.33**	-	+7.02***	-
Rubiaceae[1,1]	+1.15*	-	+0.96*	-
Sapotaceae[1,1]	-	+1.71***	-	+1.82***

[1]GLM test (estimate); [2]GAM test (Chi square value); [3]SLM test (t-value). The first and second number refers to the test used for species richness and abundance, respectively. When the null model was parsimonious we indicate using dash sign (-). Significance values: * p ≤0.05; ** p≤0.01;*** p≤0.001. NS: non-significant results.

For functional traits, the number of shade-tolerant, biotic-dispersed and small-seeded species was reduced in forest sites surrounded by lower amount of native forest, with this parameter alone included in the best model for these three trait classifications (Table 2 and S5 Table). Neither distance to edge nor percentage of forest cover were associated with the richness of shade-intolerant, large-seeded, and abiotic-dispersed species. For abundance patterns, the models containing only forest cover and forest cover plus edge distance were the most parsimonious for shade-tolerant and biotic-dispersed, whereas shade-intolerant, abiotic-dispersed, small- and large-seeded were not substantially associated with forest cover or distance to edge (Table 2 and S5 Table).

Table 2 - **Coefficients and significance of the best parsimonious model explaining patterns of species richness and abundance for each tree functional trait examined in our study.**

Parameter	Richness		Abundance	
	Edge distance	Cover amount	Edge distance	Cover amount
Shade-intolerant[1,1]	-	-	-	NS
Shade-tolerant[1,2]	-	+0.78***	-	+109.5***
Biotic-dispersed[1,2]	-	+0.52***	NS	+17.58***
Abiotic-dispersed[1,3]	-	-	-	-
Small-seeded[2,3]	-	+16.72***	NS	-
Large-seeded[1,1]	-	NS	-	-

[1]GLM test (estimate); [2]GAM test (Chi square value); [3]SLM test (t-value). The first and second number refers to the test used for species richness and abundance, respectively. When the null model was parsimonious we indicate using dash sign (-). Significance values: *** p≤0.001. NS: non-significant results

Discussion

Our study demonstrates the powerful detrimental influence of landscape-scale forest cover loss on floristic diversity within Atlantic rainforest remnants. Specifically, we found that tree species richness and abundance, within remaining rainforest patches, significantly declined across a gradient of declining forest cover at the landscape scale. Additionally, our results suggest that tree communities persisting in severely deforested landscapes have experienced profound functional changes in tree community composition, with a directional loss in the number of shade-tolerant and biotically-dispersed species, and in the number of species within the most common families, such Myrtaceae and Sapotaceae, native to this tropical forest region.

Overall tree community responses

Landscapes embedded within the highest deforestation levels showed the highest floristic differentiation among surveyed forest sites, evidence that deforested landscapes are maintaining high β-diversity (Arroyo-Rodríguez et al., 2013). Additionally, the amount of forest cover at the landscape-scale, a proxy for habitat amount, was linearly related to the overall richness and abundance of trees in the surveyed forest sites. Our knowledge regarding the role of landscape-scale forest cover affecting tree communities is still scarce, but few studies have consistently reported negative effects on species richness and abundance patterns (Andrade et al., 2015; Bascompte and Rodriguez, 2001; Lima and Mariano-Neto, 2014; Montoya et al., 2008; Rigueira et al., 2013). We did not detect an extinction threshold for tree communities in our landscapes, using a 1000 m radius, as forest cover triggered a linear decay in both tree species richness and overall abundance. Indeed, extinction thresholds were less detectable at community level, since many species showing different ecological requirements were coupled together. Conversely, some studies have found a clear breakpoint in the relationship between forest cover and species richness when looking at families or functional traits (Lima and Mariano-Neto, 2014; Morante-Filho et al., 2015; Swift and Hannon, 2010).

Distance to forest edge at local scales was not a key predictor of overall tree species richness or abundance, a finding that contrasts with other studies in fragmented tropical forests (see (Benchimol and Peres, 2015; Lôbo et al., 2011; Oliveira et al., 2004)). Thus, our findings suggest that the amount of forest cover (1000 m radius) influenced the overall erosion of tree communities in anthropogenic landscapes, indicating a greater influence of habitat loss on the shaping of remaining tree communities. Our study therefore reinforces the importance of considering the amount of forest cover at landscape scales when accessing rainforest plant communities. As recent theory (Fahrig, 2013) and empirical studies support this conclusion (Melo et al., 2017), it is becoming increasingly clear that researchers should include this variable in future biodiversity studies in fragmented tropical landscapes. Thus conservation managers should consider this key landscape variable in management decisions for maintaining high diversity of flora assemblages in human modified landscapes.

Tree family responses

When looking at dominant families individually, we also found a pronounced reduction in the species richness and abundance of common families along a gradient of decreasing forest cover within 1000m of survey sites. This pattern was strongest for Myrtaceae and Sapotaceae. These families are composed predominantly of shade-tolerant and zoochoric (animal dispersed) species, playing key roles for forest functionality in tropical forests (Rigueira et al., 2013; Rocha-santos and Talora, 2012; Tabarelli et al., 1999). The observed response patterns for Myrtaceae and Sapotaceae were quite similar to those for the overall tree community, that is, a strong decline along the forest cover gradient. In contrast, Fabaceae species richness was not affected by changes in forest cover amount, which may not be surprising given that this family includes both shade-tolerant and shade-intolerant species, many of which are known disturbance affiliates. Thus, the opposing response of these contrasting groups is likely to underlie the overall lack of response in this family. For Rubiaceae and Lauraceae, the proximity to forest edge seems to be an important factor leading to a decline in species richness and abundance. It probably indicates that these families are more susceptible to the effects of microenvironmental changes induced by edge effects.

An extinction threshold (around 29% forest cover) was only evident for Lauraceae in our study, despite past evidence of similar thresholds for Myrtaceae and Sapotaceae around 30% forest cover to adults trees in other Atlantic Forest landscapes (Lima and Mariano-Neto, 2014; Rigueira et al., 2013). These families are major sources of fleshy fruits in Atlantic forests, most providing important food resources for the native fauna (Galetti, 1996; Tabarelli et al., 1999). Thus, declines of such species may lead to reduced resources for many vertebrate species persisting in forest remnants, and perhaps driving extinction cascades across trophic levels. This is further supported by past evidence of reductions in fruit biomass previously recorded in our study area (Pessoa et al., 2016).

Functional traits responses

We detected an unequal decline of functional traits along gradients of forest cover amount in a 1000 m radius, but not to forest edge distance. Interestingly, shade-tolerant species were among the most vulnerable group of trees examined in our study, with both species richness and abundance of this group declining with reduced forest cover. Shade-tolerant trees are among the most common species in well preserved tropical rainforests, comprising ~98% of all species in Amazonian old-growth forests (Laurance et al., 2006b). Indeed, the shade-tolerant group, which is mainly composed of late-successional species with high wood densities and higher maximum heights, is known to be more sensitive to anthropogenic changes at local (forest structure) and large-scales (landscape disturbance) than shade-intolerant species (Bongers et al., 2009; Whitmore, 1989). Our results showed that the abundance of shade-intolerant species was maintained along our forest cover gradient, a surprising outcome as we expected a compensatory effect in which sensitive groups (including shade-tolerant species) were replaced by many individuals of favored groups, as found previously in other studies (Harper et al., 2005; Laurance et al., 2006a). We also did not observe a proliferation of disturbance-loving pioneer species, as reported in other Amazonian (Benchimol and Peres, 2015; Laurance et al., 2006b) and Atlantic forest fragmented landscapes (Santos et al., 2008; Tabarelli et al., 1999). However, due to the drastic reduction of shade-tolerant species in more deforested areas, the remaining species are mainly represented by disturbance affiliated species. Land-use history may be an important factor explaining the observed patterns in this study. For instance, unlike many regions of the Atlantic rainforest in Brazil, our landscapes were cleared quite recently (late twentieth century (Dias and Araújo, 2016)) and do not have an extensive history of slash-and-burn agriculture. Such distinct long-term land use histories may lead to differences, for instance, in the extinction debts observed among regions.

Forest cover loss at landscape scale triggered a significant reduction of biotic-dispersed species reduction but not to forest edge distance. This group has previously been shown to be highly vulnerable to fragmentation and deforestation given its dependence on animal vectors for seed dispersal (Tabarelli and Peres, 2002). In extensively deforested landscapes, isolation among fragments generally increases, and such spatial disruptions of landscape structure lead to decreases in the likelihood of biotic dispersion among fragments (Melo et al., 2006; Tabarelli and Peres, 2002) - a situation that might be aggravated in our region where large dispersers have been driven to near or complete extinction (Canale et al., 2012; Cassano et al., 2012). However, forest sites embedded within shade-cocoa matrix plantations can obtain higher turnover of animal dispersers, given that agroforestry mosaics enhance habitat availability and forest connectivity between forest sites (Cassano et al., 2012). The reduction in biotic-dispersed and shade-tolerant species, important resources for frugivorous birds and mammals (Arroyo-Rodríguez et al., 2007; Oliveira et al., 2010; Tabarelli and Peres, 2002), may have important consequences for forest dynamics. For instance, the loss of these species may drive changes to plant-animal interactions resulting in disruptions of vital functional services, such as seed dispersal and regeneration (Cordeiro and Howe, 2001; Galetti et al., 2006; Valiente-Banuet et al., 2014). In contrast, abiotic-dispersed species were not affected by forest cover amount (at least within a 1000m radius) or forest edge distance. The similar distribution of these species across our forest sites suggests that wind and autochory dispersal may not be strongly influenced by the extent of forest within the landscape. Trees in deforested landscapes, as well as in small fragments, are likely to be more susceptible to wind action (Laurance et al., 2000). While such conditions can increase dispersal distances by wind, seeds dispersed beyond forest patches can be limited by a lack of suitable establishment and recruitment sites in the surrounding matrix. In temperate forests, where wind action is stronger, past studies have found that reduction of forest cover amount across landscapes is negatively related to species richness of wind-dispersed species (Montoya et al., 2008). Conversely, no effect was detected for this group within a highly fragmented tropical landscape in northeastern Brazil (Santos et al., 2008, 2007; Tabarelli et al., 1999).

Surprisingly, we found that small-seeded species also declined in terms of species richness (but not in abundance) as forest cover amount declined. Conversely, the presence of large-seeded species was constant along the forest cover gradient. In our study area, large-seeded species represented 23% (± 18%) and 17% (± 12%) of the community species and abundance, respectively. These values are similar to the ones previously recorded in 31 Atlantic forest patches, where 21% of the tree species had large seeds (Bello et al., 2015). Some of the large-seeded species are still found in deforested fragments, including *Virola gardneri, V. officinalis,* and *Pouteria bangii*. However, the presence of adults of these species may reflect an extinction debit, in which the reproduction and establishment of such species might be compromised by new environmental conditions, while adults are able to persist having established under previously more amenable conditions. Extinction debt was not evident in patterns of species richness of herbaceous vegetation in savanna (Alofs et al., 2014). Herbaceous or young vegetation, however, often responds faster to forest cover loss than tropical arboreal species, for which extinction debts are expected (Rigueira et al., 2013). Our results suggest that the dispersal process has been hampered by reductions in forest cover amount across Brazil's Atlantic forests, including the dispersal of small-seeded species, a pattern that is likely reinforced by the decline of frugivorous birds (Morante-Filho et al., 2015) and very low densities of large and medium mammals in the study region (Canale et al., 2012; Cassano et al., 2012). This latter demise is regionally attributed to a high and widespread hunting pressure (Canale et al., 2012), a process that is further aggravated by overall forest loss that is an important driver of defaunation (Dirzo et al., 2014).

Conclusion

The change in species composition recorded in this study indicates that species loss is highly selective, with greater directional reduction with decreasing forest cover within a 1000m area in the number of shade-tolerant, biotic-dispersed and small-seeded species than shade intolerant, abiotically dispersed, and large-seeded species. Such floristic changes also show that the loss of shade-tolerant species is not being offset by increased numbers of shade-intolerant species. This suggests that Atlantic forest remnants in fragmented landscapes are changing in structural and compositional ways, linearly related to forest cover amount, whereas the distance to the nearest edge at landscape scales seems to play a secondary role, affecting only some families such as Rubiaceae and Lauraceae. Changes in specific functional traits suggest further negative impacts on the frugivorous animals that rely on these plant communities (Tabarelli et al., 1999), while reductions in abundance is likely to decrease the capacity of these forest remnants to store carbon in the future (Stephenson et al., 2014). Species changes may just be the beginning, reflecting initial shifts that will drive more extreme long-term modifications of forest pattern and process to other organisms and ecological functions. For instance, the declines in frugivorous-bird abundance and richness that have been recorded in our study area, may, in part, be driven by a lack of fruit producing trees in these rainforest remnants (Morante-Filho et al., 2015; Pessoa et al., 2016). Likewise, increases in the rate of seed predation by invertebrates of an important palm species (*Euterpe edulis*) (Soares et al., 2015) may result from changes in tree diversity in remnants, something which may drive even greater changes to forest structure in the future (Rocha-santos et al., 2016). These changes can lead to forest dynamics and ecosystem service disruptions, such as dispersal and pollination services. This study therefore highlights the importance of maintaining forest cover at landscape-scales as a means to prevent further changes in tree composition that are likely to drive cascading effects on the total biodiversity and ecosystem functioning of this important tropical region.

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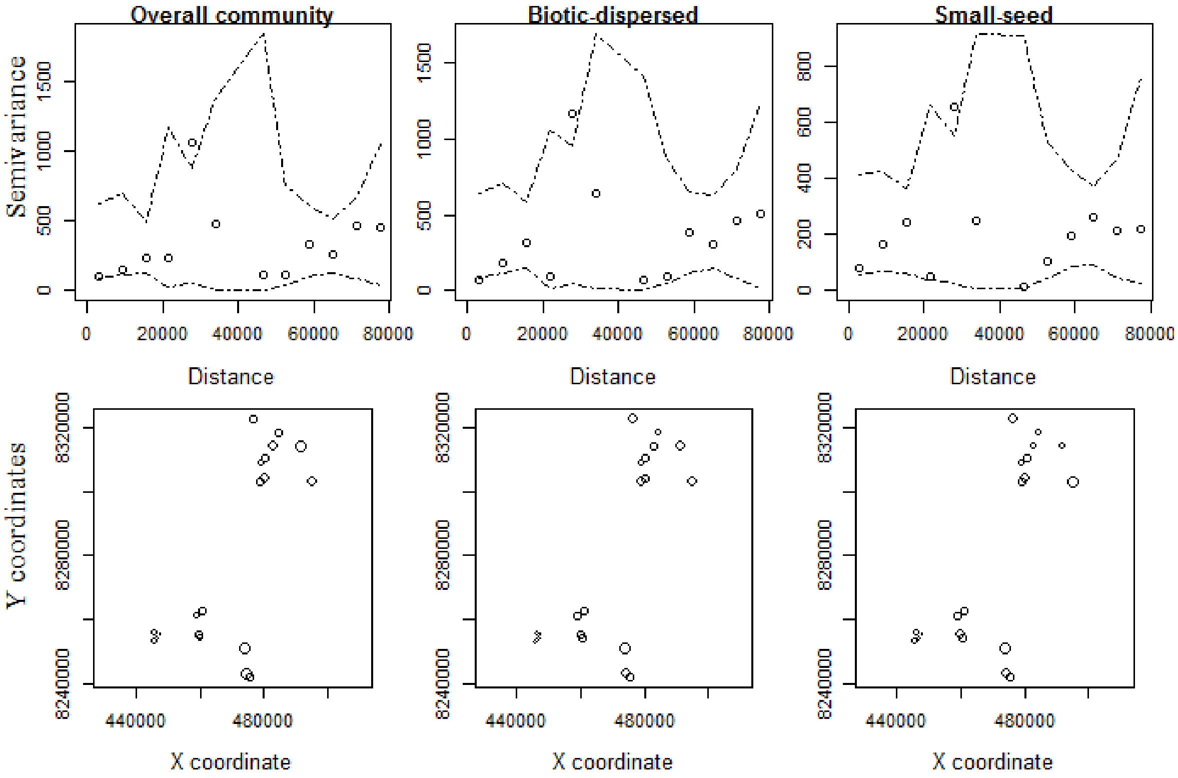
Supporting information



S1 Fig - Spatial correlation of species richness and abundance patterns. Semivariograms of variables with spatial dependence: abundance of overall community, biotic-dispersed species and of small-seeded species. On the bottom, circles are sized proportional to the number of individuals in each landscape.

S1 Table - Frequency of tree species and their respective classification on regeneration strategy, dispersion mode, and seed size, within 20 forest sites with different forest cover amount in northeastern Brazil.

FAMILIES AND SPECIES	Regen.	Disp.	Seed	Nº ind.
Achariaceae				**5**
Carpotroche brasiliensis	ST	BI	LS	5
Anacardiaceae				**51**
Astronium graveolens	ST	AB	NC	4
Tapirira guianensis	SI	BI	SS	37
Thyrsodium spruceanum	SI	BI	SS	10
Annonaceae				**55**
Annona cacans	SI	BI	SS	2
Annona glabra	ST	BI	SS	3
Annona leptopetala	SI	BI	SS	3
Annona muricata	ST	BI	NC	2
Annona neolaurifolia	SI	BI	SS	10
Annona salzmannii	SI	BI	SS	1
Annona sylvatica	NC	BI	NC	2
Annonaceae 5	NC	BI	NC	1
Guatteria australis	SI	BI	SS	8
Guatteria oligocarpa	SI	BI	SS	3
Guatteria pogonopus	SI	BI	SS	2
Hornschuchia obliqua	SI	BI	NC	2
Pseudoxandra bahiensis	SI	BI	NC	3
Rollinia sp1	NC	BI	NC	1
Rollinia sp2	NC	BI	NC	1
Xylopia aromatica	SI	BI	SS	6
Xylopia frutescens	SI	BI	SS	1
Xylopia ochrantha	SI	BI	NC	1
Xylopia sericea	SI	BI	SS	3
Apocynaceae				**44**
Aspidosperma discolor	ST	AB	NC	6
Aspidosperma illustre	ST	AB	NC	1
Aspidosperma parvifolium	ST	AB	NC	2
Aspidosperma spruceanum	ST	AB	NC	1
Geissospermum laeve	SI	BI	SS	2
Himatanthus articulatus	SI	AB	NC	2
Himatanthus bracteatus	SI	AB	NC	14

Himatanthus phagedaenicus	SI	AB	NC	1
Lacmellea bahiensis	ST	BI	SS	5
Macoubea guianensis	SI	BI	SS	1
Malouetia cestroides	SI	NC	NC	2
Rauvolfia grandiflora	SI	BI	SS	3
Tabernaemontana brasiliensis	SI	BI	NC	1
Tabernaemontana salzmannii	ST	BI	SS	3
Araliaceae				**16**
Schefflera morototoni	SI	BI	SS	16
Arecaceae				**111**
Allagoptera caudescens	SI	BI	LS	35
Bactris ferruginea	SI	BI	LS	3
Bactris setosa	SI	BI	LS	1
Euterpe edulis	ST	BI	SS	51
Syagrus botryophora	SI	BI	LS	21
Bignoniaceae				**17**
Bignoniaceae 1	NC	AB	NC	1
Handroanthus chrysotrichus	ST	AB	NC	4
Handroanthus impetiginosus	SI	AB	NC	4
Jacaranda jasminoides	ST	AB	NC	1
Jacaranda puberula	ST	AB	NC	1
Jacaranda sp2	NC	AB	NC	2
Tabebuia cassinoides	SI	AB	NC	1
Tabebuia elliptica	SI	AB	NC	3
Boraginaceae				**30**
Cordia anabaptista	SI	BI	SS	2
Cordia ecalyculata	SI	BI	SS	15
Cordia glabrifolia	SI	BI	NC	1
Cordia membranacea	SI	BI	NC	2
Cordia mucronata	SI	BI	NC	1
Cordia polycephala	SI	BI	SS	1
Cordia sp3	SI	BI	NC	1
Cordia taguahyensis	SI	BI	SS	2
Cordia toqueve	SI	BI	SS	4
Cordia trachyphylla	SI	BI	NC	1
Burseraceae				**35**
Protium aracouchini	ST	BI	SS	4
Protium heptaphyllum	ST	BI	SS	18
Protium icicariba	ST	BI	NC	3
Protium sp1	ST	BI	NC	1
Protium warmingiana	ST	BI	SS	6
Tetragastris catuaba	ST	BI	NC	3

Calophyllaceae				**1**
Kielmeyera elata	ST	NC	NC	1
Caricaceae				1
Jacaratia heptaphylla	SI	BI	SS	1
Caryocaraceae				1
Caryocar edule	*ST*	BI	LS	1
Celastraceae				**9**
Cheiloclinium cognatum	ST	BI	LS	3
Maytenus distichophylla	SI	BI	SS	2
Maytenus obtusifolia	ST	BI	NC	1
Maytenus patens	SI	BI	NC	2
Tontelea mauritioides	ST	BI	NC	1
Chrysobalanaceae				**27**
Couepia belemii	ST	BI	NC	3
Couepia impressa	ST	BI	NC	2
Couepia monteclarensis	ST	BI	NC	3
Hirtella hebeclada	SI	BI	SS	1
Licania discolor	ST	BI	SS	1
Licania hoehnei	ST	BI	NC	1
Licania lamentanda	ST	BI	LS	5
Licania littoralis	ST	BI	SS	1
Licania naviculistipula	ST	BI	NC	1
Parinari alvimii	ST	BI	SS	5
Parinari sp1	ST	BI	NC	4
Clusiaceae				**18**
Garcinia gardneriana	SI	BI	SS	1
Garcinia macrophylla	SI	BI	LS	5
Symphonia globulifera	SI	BI	LS	2
Tovomita brevistaminea	ST	BI	NC	1
Tovomita choisyana	ST	BI	NC	2
Tovomita mangle	ST	BI	SS	7
Combretaceae				**4**
Buchenavia sp1	NC	BI	NC	1
Combretum sp1	NC	BI	SS	1
Terminalia brasiliensis	ST	AB	NC	2
Dichapetalaceae				**3**
Stephanopodium blanchetianum	ST	BI	SS	2
Stephanopodium organense	ST	BI	NC	1
Ebenaceae				1
Diospyros sp1	SI	BI	NC	1
Elaeocarpaceae				**8**
Sloanea guianensis	ST	BI	SS	6

Sloanea obtusifolia	ST	BI	SS	1
Sloanea sp1	ST	BI	NC	1
Erythroxylaceae				**2**
Erythroxylum martii	SI	BI	SS	1
Erythroxylum squamatum	SI	BI	SS	1
Euphorbiaceae				**62**
Actinostemon appendiculatus	ST	AB	NC	4
Actinostemon verticillatus	ST	AB	NC	2
Alchornea glandulosa	SI	BI	SS	1
Alchornea triplinervia	ST	BI	SS	3
Aparisthmium cordatum	SI	AB	NC	3
Croton floribundus	SI	AB	NC	3
Croton macrobothrys	SI	AB	NC	3
Euphorbiaceae 2	NC	NC	NC	2
Euphorbiaceae 4	NC	NC	NC	1
Euphorbiaceae 6	NC	NC	NC	1
Euphorbiaceae 7	NC	NC	NC	3
Glycydendron amazonicum	SI	BI	SS	4
Hevea brasiliensis	SI	AB	NC	5
Mabea brasiliensis	SI	AB	NC	4
Mabea piriri	SI	AB	NC	4
Ophthalmoblapton crassipes	ST	BI	NC	5
Ophthalmoblapton pedunculare	ST	BI	SS	1
Pausandra megalophylla	ST	AB	NC	1
Sapium glandulosum	ST	AB	NC	3
Sebastiania gaudichaudii	SI	AB	NC	2
Sebastiania jacobinensis	SI	AB	NC	1
Senefeldera multiflora	ST	AB	NC	5
Tetrorchidium rubrivenium	SI	BI	SS	1
Fabaceae				**234**
Abarema turbinata	NC	NC	NC	1
Aeschynomene sensitiva	NC	NC	NC	1
Albizia pedicellaris	SI	AB	NC	9
Andira anthelmia	ST	BI	LS	1
Andira fraxinifolia	SI	BI	LS	1
Andira legalis	ST	BI	LS	1
Andira lewisii	ST	BI	LS	1
Andira marauensis	ST	NC	NC	2
Andira sp1	NC	NC	NC	1
Andira sp2	NC	NC	NC	1
Andira sp3	NC	NC	NC	1
Arapatiella emarginata	ST	AB	NC	1

Arapatiella psilophylla	ST	AB	NC	14
Bauhinia sp1	NC	AB	NC	2
Bowdichia virgilioides	ST	AB	NC	2
Calliandra calycina	ST	AB	NC	1
Chamaecrista amorimii	ST	AB	NC	2
Chamaecrista bahiae	ST	AB	NC	9
Chamaecrista duartei	ST	AB	NC	9
Copaifera langsdorffii	ST	BI	LS	2
Copaifera trapezifolia	ST	BI	LS	2
Dialium guianense	ST	BI	SS	16
Diplotropis incexis	SI	AB	NC	1
Dipteryx sp1	NC	AB	NC	1
Enterolobium monjollo	SI	AB	NC	2
Exostyles venusta	ST	AB	NC	1
Hymenaea aurea	ST	BI	NC	1
Hymenaea oblongifolia	ST	BI	SS	2
Hymenolobium janeirense	SI	NC	NC	1
Inga capitata	SI	BI	SS	4
Inga cylindrica	SI	BI	SS	2
Inga luschnathiana	SI	BI	NC	1
Inga sp1	SI	BI	NC	1
Inga sp2	SI	BI	NC	3
Inga sp3	SI	BI	NC	1
Inga striata	SI	BI	SS	4
Inga thibaudiana	SI	BI	LS	8
Inga vera	SI	BI	SS	21
Machaerium hirtum	SI	AB	NC	1
Macrolobium latifolium	ST	AB	NC	7
Melanoxylon brauna	ST	AB	NC	5
Mimosa sp1	NC	AB	NC	1
Moldenhawera blanchetiana	ST	AB	NC	4
Moldenhawera floribunda	ST	AB	NC	2
Parkia pendula	ST	AB	NC	5
Peltogyne confertiflora	SI	AB	NC	14
Peltogyne sp1	ST	AB	NC	2
Piptadenia gonoacantha	SI	AB	NC	3
Piptadenia paniculata	SI	AB	NC	3
Plathymenia foliolosa	ST	AB	NC	5
Poincianella pluviosa	SI	AB	NC	5
Pterocarpus rohrii	ST	AB	NC	9
Senegalia sp1	NC	AB	NC	4
Senna multijuga	SI	AB	NC	3
Stryphnodendron pulcherrimum	SI	AB	NC	4

Swartzia macrostachya	ST	BI	LS	1
Swartzia oblata	ST	BI	LS	2
Swartzia polita	ST	BI	LS	4
Swartzia simplex	ST	BI	LS	3
Tachigali densiflora	SI	AB	NC	4
Tachigali paratyensis	SI	AB	NC	4
Vatairea heteroptera	ST	AB	NC	2
Vataireopsis araroba	ST	AB	NC	1
Zollernia glabra	ST	BI	SS	1
Zollernia latifolia	ST	BI	SS	1
Humiriaceae				**6**
Humiria balsamifera	ST	BI	NC	2
Schistostemon retusum	ST	BI	LS	2
Vantanea bahiaensis	SI	BI	SS	1
Vantanea compacta	ST	BI	SS	1
Hypericaceae				**3**
Vismia baccifera	SI	BI	SS	1
Vismia guianensis	SI	BI	SS	1
Vismia latifolia	SI	BI	SS	1
Icacinaceae				1
Emmotum nitens	ST	BI	SS	1
Lauraceae				**91**
Aniba intermedia	SI	BI	SS	5
Beilschmiedia linharensis	ST	BI	SS	1
Cryptocarya mandioccana	ST	BI	NC	3
Lauraceae sp2	NC	BI	NC	1
Lauraceae sp3	NC	BI	NC	1
Lauraceae sp4	NC	BI	NC	2
Licaria bahiana	SI	BI	SS	8
Licaria guianensis	SI	BI	LS	10
Nectandra membranacea	ST	BI	SS	11
Nectandra purpurea	ST	BI	NC	1
Nectandra sp1	NC	BI	NC	7
Ocotea aciphylla	ST	BI	LS	3
Ocotea cernua	ST	BI	NC	1
Ocotea divaricata	ST	BI	NC	5
Ocotea elegans	SI	BI	SS	5
Ocotea indecora	SI	BI	SS	5
Ocotea insignis	ST	BI	LS	1
Ocotea longifolia	SI	BI	SS	2
Ocotea macrophylla	ST	BI	NC	2
Ocotea montana	ST	BI	NC	1

Ocotea notata	ST	BI	NC	1
Ocotea oppositifolia	ST	BI	NC	4
Ocotea percoriacea	ST	BI	NC	2
Ocotea puberula	SI	BI	SS	8
Ocotea sp1	NC	BI	NC	1
Lecythidaceae				**62**
Eschweilera ovata	SI	BI	LS	50
Lecythis lurida	ST	BI	LS	5
Lecythis pisonis	ST	BI	LS	7
Malpighiaceae				**20**
Byrsonima alvimii	ST	BI	SS	2
Byrsonima fanshawei	ST	BI	NC	2
Byrsonima laxiflora	ST	BI	SS	1
Byrsonima sericea	SI	BI	SS	12
Byrsonima stipulacea	SI	BI	SS	3
Malvaceae				**65**
Apeiba albiflora	SI	BI	SS	1
Apeiba tibourbou	SI	AB	NC	4
Basiloxylon brasiliensis	SI	AB	NC	1
Ceiba sp1	NC	AB	NC	1
Eriotheca globosa	ST	AB	NC	5
Eriotheca macrophylla	ST	AB	NC	35
Hydrogaster trinervis	SI	AB	NC	1
Luehea divaricata	SI	AB	NC	4
Pavonia makoyana	ST	AB	NC	1
Pavonia morii	ST	AB	NC	2
Quararibea sp1	NC	BI	NC	1
Quararibea turbinata	SI	BI	LS	1
Sterculia apetala	ST	AB	NC	8
Melastomataceae				**59**
Henriettea succosa	SI	BI	SS	16
Melastomataceae 1	SI	BI	NC	1
Miconia amoena	SI	BI	SS	3
Miconia centrodesma	SI	BI	SS	6
Miconia dorsaliporosa	SI	BI	SS	4
Miconia hypoleuca	SI	BI	SS	7
Miconia minutiflora	SI	BI	SS	2
Miconia mirabilis	SI	BI	SS	3
Miconia prasina	SI	BI	SS	10
Miconia speciosa	SI	BI	SS	1
Tibouchina francavillana	SI	AB	NC	5
Tibouchina sp1	SI	AB	NC	1

Meliaceae				**21**
Guarea blanchetii	ST	BI	SS	7
Trichilia casaretti	ST	BI	SS	1
Trichilia elegans	ST	BI	SS	5
Trichilia lepidota	SI	BI	LS	4
Trichilia silvatica	ST	BI	SS	4
Moraceae				**145**
Artocarpus heterophyllus	SI	BI	LS	5
Brosimum guianense	SI	BI	SS	6
Brosimum rubescens	ST	BI	SS	13
Clarisia biflora	SI	BI	NC	3
Clarisia ilicifolia	SI	BI	SS	2
Ficus americana	ST	BI	NC	1
Ficus christianii	ST	BI	NC	2
Ficus hirsuta	SI	BI	SS	1
Ficus insipida	ST	BI	SS	2
Ficus sp1	NC	BI	NC	1
Helicostylis tomentosa	SI	BI	SS	99
Maclura tinctoria	ST	BI	SS	2
Sorocea bonplandii	ST	BI	SS	1
Sorocea guilleminiana	ST	BI	SS	7
Myristicaceae				**30**
Virola gardneri	ST	BI	LS	15
Virola officinalis	ST	BI	LS	15
Myrtaceae				**166**
Calyptranthes sp1	NC	BI	NC	1
Calyptranthes sp4	NC	BI	NC	1
Campomanesia dichotoma	SI	BI	SS	2
Campomanesia laurifolia	ST	BI	SS	3
Eugenia adenantha	SI	BI	NC	3
Eugenia astringens	ST	BI	NC	1
Eugenia ayacuchae	ST	BI	NC	3
Eugenia candolleana	ST	BI	SS	1
Eugenia excelsa	ST	BI	NC	3
Eugenia florida	ST	BI	SS	1
Eugenia itapemirimensis	ST	BI	SS	1
Eugenia lacistema	ST	BI	NC	1
Eugenia luschnathiana	ST	BI	SS	1
Eugenia magnifica	ST	BI	NC	8
Eugenia melanogyna	ST	BI	LS	3
Eugenia pauciflora	ST	BI	SS	1
Eugenia pisiformis	ST	BI	SS	1

Eugenia platyphylla	ST	BI	NC	4
Eugenia plicata	ST	BI	NC	1
Eugenia prasina	SI	BI	NC	3
Eugenia pruniformis	ST	BI	SS	2
Eugenia rostrata	ST	BI	NC	1
Eugenia schottiana	ST	BI	NC	7
Eugenia sp1	ST	BI	NC	1
Eugenia sp10	ST	BI	SS	5
Eugenia sp11	ST	BI	NC	1
Eugenia sp13	ST	BI	LS	1
Eugenia sp15	ST	BI	NC	1
Eugenia sp17	ST	BI	NC	1
Eugenia sp22	ST	BI	NC	1
Eugenia sp23	ST	BI	NC	2
Eugenia sp25	ST	BI	NC	1
Eugenia sp28	ST	BI	NC	1
Eugenia sp5	ST	BI	NC	1
Eugenia sp6	ST	BI	NC	1
Eugenia sp7	ST	BI	NC	1
Eugenia sp9	ST	BI	NC	1
Eugenia subterminalis	ST	BI	SS	3
Eugenia umbellata	ST	BI	SS	1
Gomidesia fenzliana	ST	BI	SS	1
Marlierea excoriata	ST	BI	NC	2
Marlierea obversa	ST	BI	SS	5
Marlierea racemosa	ST	BI	SS	1
Marlierea rufa	ST	BI	SS	3
Marlierea sp1	ST	BI	NC	1
Marlierea sp2	ST	BI	SS	1
Marlierea sp3	ST	BI	NC	1
Marlierea sp4	ST	BI	NC	1
Marlierea sucrei	ST	BI	SS	5
Myrcia anceps	ST	BI	NC	1
Myrcia calyptranthoides	ST	BI	NC	1
Myrcia carvalhoi	ST	BI	SS	1
Myrcia eximia	ST	BI	NC	1
Myrcia gigantea	ST	BI	SS	3
Myrcia pseudomarlierea	ST	BI	NC	1
Myrcia racemosa	ST	BI	SS	6
Myrcia sp1	ST	BI	NC	1
Myrcia sp11	ST	BI	NC	1
Myrcia sp12	ST	BI	NC	3
Myrcia sp14	ST	BI	NC	2

Myrcia sp18	ST	BI	NC	1
Myrcia sp20	ST	BI	NC	1
Myrcia sp24	ST	BI	NC	1
Myrcia sp25	ST	BI	NC	1
Myrcia sp27	ST	BI	NC	1
Myrcia sp28	ST	BI	NC	1
Myrcia sp3	ST	BI	NC	2
Myrcia sp9	ST	BI	NC	3
Myrcia splendens	SI	BI	SS	15
Myrcia sylvatica	SI	BI	SS	2
Myrcia vittoriana	ST	BI	SS	1
Myrciaria guaquiea	ST	BI	SS	2
Myrtaceae 15	ST	BI	NC	1
Myrtaceae 32	ST	BI	NC	1
Myrtaceae 34	ST	BI	NC	1
Myrtaceae 35	ST	BI	NC	1
Myrtaceae 5	ST	BI	NC	1
Neomitranthes langsdorfii	ST	BI	NC	2
Plinia callosa	ST	BI	NC	3
Plinia edulis	ST	BI	LS	1
Plinia grandifolia	ST	BI	SS	1
Plinia muricata	ST	BI	NC	2
Plinia rara	ST	BI	NC	2
Plinia sp1	ST	BI	NC	1
Nyctaginaceae				**102**
Guapira hirsuta	ST	BI	NC	11
Guapira laxiflora	ST	BI	SS	9
Guapira nitida	ST	BI	SS	56
Guapira obtusata	ST	BI	NC	1
Guapira opposita	ST	BI	SS	8
Guapira sp1	NC	BI	NC	1
Neea duckei	ST	BI	NC	2
Neea floribunda	ST	BI	SS	1
Neea macrophylla	ST	BI	SS	4
Neea madeirana	ST	BI	NC	2
Neea verticillata	ST	BI	NC	7
Olacaceae				**16**
Aptandra sp1	NC	NC	NC	1
Aptandra tubicina	ST	BI	NC	4
Heisteria ovata	ST	BI	NC	1
Heisteria perianthomega	ST	BI	SS	5
Heisteria sp2	NC	BI	LS	1

Schoepfia brasiliensis	ST	BI	NC	1
Tetrastilydium brasiliense	ST	BI	NC	2
Tetrastylidium grandifolium	ST	BI	LS	1
Peraceae				**32**
Chaetocarpus echinocarpus	SI		NC	1
Pera glabrata	SI		SS	5
Pogonophora schomburgkiana	SI		NC	26
Phyllanthaceae				**3**
Hyeronima alchorneoides	SI	BI	SS	2
Margaritaria nobilis	ST	BI	SS	1
Picramniaceae				**1**
Picramnia glazioviana	NC	NC	NC	1
Polygonaceae				**9**
Coccoloba arborescens	SI	BI	NC	1
Coccoloba bullata	ST	BI	NC	2
Coccoloba glaziovii	SI	BI	NC	1
Coccoloba oblonga	SI	BI	NC	1
Coccoloba rosea	ST	BI	SS	3
Coccoloba sp1	NC	BI	NC	1
Primulaceae				**2**
Myrsine coriacea	SI	BI	SS	1
Myrsine guianensis	SI	NC	NC	1
Proteaceae				**3**
Roupala sp1	NC	AB	NC	3
Quiinaceae				**1**
Quiina glaziovii	ST	BI	SS	1
Rubiaceae				**67**
Alseis floribunda	SI	AB	NC	1
Alseis latifolia	ST	AB	NC	1
Amaioua guianensis	ST	BI	SS	3
Bathysa mendoncaei	ST	BI	NC	4
Bathysa sp1	NC	BI	NC	1
Chomelia pedunculosa	ST	BI	SS	2
Cordiera bahiensis	ST	BI	NC	1
Cordiera sp1	NC	BI	NC	1
Coussarea carvalhoi	ST	BI	NC	5
Coussarea ilheotica	ST	BI	SS	4
Faramea biflora	ST	BI	SS	1
Guettarda platyphylla	ST	BI	NC	1
Guettarda sp1	NC	BI	NC	1
Guettarda viburnoides	ST	BI	SS	1
Ixora muelleri	ST	BI	SS	3

Palicourea blanchetiana	ST	BI	SS	1
Posoqueria latifolia	ST	BI	SS	2
Psychotria bahiensis	ST	BI	NC	1
Psychotria mapourioides	ST	BI	SS	9
Psychotria sp1	ST	BI	NC	1
Psychotria tenerior	ST	BI	NC	2
Psychotria vellosiana	ST	BI	SS	2
Randia nitida	ST	BI	NC	1
Rubiaceae 1	ST	BI	NC	2
Rubiaceae 2	ST	BI	NC	1
Rubiaceae 4	ST	BI	NC	3
Rubiaceae 6	ST	BI	NC	2
Rubiaceae 7	ST	BI	NC	1
Rudgea involucrata	ST	BI	SS	1
Rudgea pachyphylla	ST	BI	NC	1
Simira glaziovii	SI	AB	NC	4
Tocoyena bullata	ST	BI	NC	3
Rutaceae				**17**
Almeidea caerulea	ST	AB	NC	1
Conchocarpus macrophyllus	ST	NC	NC	1
Dictyoloma vandellianum	ST	AB	NC	1
Hortia arborea	ST	BI	SS	2
Pilocarpus grandiflorus	SI	AB	NC	1
Pilocarpus sp1	ST	AB	NC	1
Pilocarpus spicatus	ST	AB	NC	1
Rutaceae 1	NC	NC	NC	1
Zanthoxylum nemorale	ST	BI	NC	1
Zanthoxylum rhoifolium	SI	BI	SS	7
Salicaceae				**46**
Banara brasiliensis	SI	BI	SS	1
Casearia arborea	SI	BI	NC	3
Casearia bahiensis	ST	BI	NC	3
Casearia commersoniana	ST	BI	SS	25
Casearia silvestris	SI	BI	SS	9
Casearia sp1	NC	BI	NC	1
Macrothumia kuhlmannii	SI	BI	NC	2
Salicaceae 1	NC	BI	NC	1
Salicaceae 2	NC	BI	NC	1
Sapindaceae				**34**
Allophylus edulis	ST	BI	SS	7
Allophylus sericeus	SI	BI	SS	2
Cupania impressinervia	ST	BI	SS	2

Cupania oblongifolia	ST	BI	SS	1
Cupania racemosa	SI	BI	SS	1
Cupania rugosa	SI	BI	NC	2
Cupania scrobiculata	SI	BI	SS	1
Cupania sp2	NC	BI	SS	1
Cupania sp4	NC	BI	NC	2
Cupania tenuivalvis	ST	BI	NC	1
Cupania torta	ST	BI	NC	5
Matayba discolor	SI	BI	SS	1
Matayba guianensis	ST	BI	SS	1
Matayba juglandifolia	SI	BI	NC	1
Sapindaceae 1	NC	NC	NC	2
Scyphonychium multiflorum	ST	AB	NC	1
Talisia cerasina	SI	BI	SS	2
Talisia esculenta	ST	BI	SS	1
Sapotaceae				**129**
Chrysophyllum gonocarpum	ST	BI	SS	2
Chrysophyllum lucentifolium	ST	BI	NC	1
Chrysophyllum splendens	ST	BI	SS	13
Diploon cuspidatum	ST	BI	SS	3
Ecclinusa ramiflora	ST	BI	SS	22
Manilkara longifolia	ST	BI	SS	2
Manilkara maxima	ST	BI	SS	4
Manilkara multifida	ST	BI	NC	2
Manilkara salzmannii	ST	BI	SS	6
Micropholis crassipedicellata	ST	BI	SS	4
Micropholis gardneriana	ST	BI	SS	14
Micropholis guyanensis	ST	BI	SS	1
Pouteria atlantica	ST	BI	NC	2
Pouteria bangii	ST	BI	LS	12
Pouteria bapeba	ST	BI	SS	1
Pouteria bilocularis	ST	BI	NC	1
Pouteria grandiflora	ST	BI	LS	10
Pouteria guianensis	ST	BI	LS	1
Pouteria macahensis	ST	BI	NC	1
Pouteria macrophylla	ST	BI	SS	5
Pouteria microstrigosa	ST	BI	NC	1
Pouteria peduncularis	ST	BI	LS	2
Pouteria procera	ST	BI	SS	2
Pouteria reticulata	ST	BI	LS	4
Pouteria sp1	NC	BI	NC	1
Pouteria sp3	NC	BI	NC	1
Pouteria sp4	NC	BI	NC	2

Pouteria venosa	ST	BI	LS	2
Pradosia kuhlmannii	ST	BI	NC	1
Pradosia lactescens	ST	BI	SS	3
Pradosia sp2	ST	BI	NC	1
Sapotaceae sp3	ST	BI	NC	2
Simaroubaceae				**2**
Simarouba amara	ST	BI	SS	2
Siparunaceae				**9**
Siparuna guianensis	*ST*	BI	SS	9
Solanaceae				**4**
Aureliana fasciculata	SI	BI	SS	1
Solanum sooretamum	SI	BI	SS	1
Solanum sp2	NC	BI	SS	2
Urticaceae				**26**
Cecropia cecropiifolia	SI	BI	LS	1
Cecropia hololeuca	SI	BI	SS	2
Cecropia pachystachya	SI	BI	SS	2
Pourouma guianensis	SI	BI	SS	1
Pourouma mollis	SI	BI	SS	6
Pourouma velutina	SI	BI	SS	14
Violaceae				**48**
Paypayrola blanchetiana	ST	AB	NC	4
Paypayrola sp1	ST	AB	NC	1
Rinorea guianensis	ST	AB	NC	43
Total				1955

Legend: regeneration strategy (ST: shade-tolerant, SI: shade-intolerant), dispersal mode (AB: abiotic-dispersed, BI: biotic-dispersed) and seed size (SS: small-seeded, LS: large-seeded). NC: no classification.

S2 Table - Ranking selection of best models explaining species richness and abundance of trees in function of forest cover amount at landscape-scale, for overall community and for the most important families. Models that did not present convergence on the likelihood estimates were excluded from the model selection procedure. The most parsimonious models (linear – Li, logistic – Lo, null – Nu and power-law – Po) are highlight in gray.

Var.	Richness				Abundance			
	Model	dAICc	df	w_i	Model	dAICc	df	w_i
Ov	Li	0.0	3	0.6	Li	0.0	5	0.99
	Lo	1.7	4	0.2	Nu	15.2	4	0.00
	Po	2.0	3	0.2	Po	24.0	5	<0.001
	Nu	12.7	2	<0.001				
Mry	Po	0.0	3	0.52	Li	0.0	3	0.48
	Li	0.3	3	0.45	Po	0.7	3	0.35
	Nu	5.5	2	0.03	Lo	2.2	4	0.16
					Nu	7.4	2	0.01
Fab	Po	0.0	3	0.52	Nu	0.0	2	0.50
	Nu	0.9	2	0.32	Po	1.8	3	0.21
	Li	2.4	3	0.16	Li	2.0	3	0.19
					Lo	3.2	4	0.10
Lau	Lo	0.0	4	0.91	Lo	0.0	4	0.72
	Po	5.4	3	0.06	Po	3.0	3	0.16
	Li	7.3	3	0.02	Li	4.4	3	0.08
	Nu	10.3	2	0.01	Nu	5.5	2	0.05
Rub	Li	0.0	3	0.57	Li	0.0	3	0.33
	Nu	1.9	2	0.22	Lo	0.4	4	0.27
	Po	2.0	3	0.21	Nu	0.6	2	0.24
					Po	1.4	3	0.16
Sap	Po	0.0	3	0.56	Li	0.0	3	0.57
	Li	0.4	3	0.44	Po	0.5	3	0.43
	Nu	30.6	2	<0.001	Nu	24.8	2	<0.001

Legend: Variables (Var.); overall (Ov); Mrytaceae (Mry); Rubiaceae (Rub); Sapotaceae (Sap); Fabaceae (Fab); Lauraceae (lau); difference in AICc from the best model (dAIC); parameter number of the model (df); AICc weight (wi).

S3 Table - Ranking selection of best models explaining species richness and abundance of trees in function of forest cover amount at landscape-scale, for each functional trait. Models that did not present convergence on the likelihood estimates were excluded from the model selection procedure. The most parsimonious models (linear – Li, logistic – Lo, null – Nu and power-law – Po) are highlight in gray.

	Richness				**Abundance**			
Var.	Model	dAICc	df	w_i	Model	dAICc	df	w_i
Si	Nu	0.0	2	0.6	Nu	0.0	2	0.5
	Po	2.3	3	0.2	Li	1.3	3	0.3
	Li	2.5	3	0.2	Po	2.1	3	0.2
St	Po	0.0	3	0.5	Po	0.0	3	0.9
	Li	0.8	3	0.3	Li	3.6	3	0.1
	Lo	2.0	4	0.2	Nu	29.2	2	<0.001
	Nu	18.4	2	<0.001				
Ad	Nu	0.0	2	0.6	Nu	0.0	4	0.8
	Po	2.5	3	0.2	Li	3.4	5	0.2
	Li	2.8	3	0.1	Po	15.7	5	<0.001
	Lo	4.0	4	0.1				
Bd	Li	0.0	3	0.6	Po	0.0	3	0.8
	Po	0.8	3	0.4	Li	3.7	3	0.1
	Nu	15.4	2	<0.001	Lo	4.1	4	0.1
					Nu	12.9	2	0.0
Ls	Nu	0.0	2	0.4	Nu	0.0	2	0.6
	Po	0.7	3	0.3	Po	2.7	3	0.2
	Li	0.8	3	0.3	Li	2.8	3	0.2
					Lo	6.0	4	0.0
Ss	Po	0.0	3	0.6	Li	0.0	5	0.7
	Li	2.3	3	0.2	Nu	1.4	4	0.3
	Lo	2.8	4	0.2	Po	15.5	5	<0.001
	Nu	12.8	2	0.0				

Legend: Variable (Var.); shade-intolerant (Si); shade-tolerant (St); abiotic-dispersed (Ad); biotic-dispersed (Bd); large-seeded (Ls); small-seeded (Ss); difference in AICc from the best model (dAIC); parameter number of the model (df); AICc weight (w_i).

S4 Table - **Ranking selection of best models explaining the richness and abundance of overall community and the most important families recorded for this study in function of forest cover amount and distance of nearest edge.** The most parsimonious (Nu - null; Co - Forest cover; Ed - Forest edge distance; Co + Ed - Forest cover plus edge distance) models are shown in gray.

Var.	Models	RICHNESS			Models	ABUNDANCE		
		dAIC	df	w_i		dAIC	df	w_i
Ov [1,3]	Co + Ed	0.0	3.0	0.50	Co	0.0	5.0	0.78
	Co	1.0	2.0	0.30	Co + Ed	3.3	6.0	0.15
	Ed	1.9	2.0	0.20	Ed	4.7	5.0	0.07
	Nu	31.2	1.0	0.00	Nu	15.2	4.0	0.00
Mry [1,1]	Co	0.0	2.0	0.75	Co	0.0	2.0	0.74
	Co + Ed	2.5	3.0	0.22	Co + Ed	2.3	3.0	0.24
	Ed	6.1	2.0	0.04	Ed	7.6	2.0	0.02
	Nu	20.2	1.0	0.00	Nu	27.9	1.0	0.00
Fab [2,2]	Co	0.0	2.1	0.46	Co + Ed	0.0	12.1	0.99
	Nu	1.6	1.0	0.21	Co	10.0	9.4	0.01
	Co + Ed	1.9	6.1	0.18	Ed	27.4	7.5	0.00
	Ed	2.1	4.1	0.16	Nu	50.8	1.0	0.00
Lau [2,2]	Ed	0.0	7.3	0.56	Ed	0.0	8.0	0.68
	Co + Ed	1.7	8.2	0.24	Co + Ed	1.6	9.0	0.31
	Co	2.0	5.0	0.21	Co	8.4	6.2	0.01
	Nu	19.5	1.0	0.00	Nu	41.1	1.0	0.00
Rub [1,1]	Ed	0.0	2.0	0.63	Ed	0.0	2.0	0.62
	Co + Ed	2.3	3.0	0.20	Co + Ed	2.6	3.0	0.17
	Nu	3.9	1.0	0.09	Co	3.6	2.0	0.10
	Co	4.2	2.0	0.08	Nu	3.7	1.0	0.10
Sap [1,1]	Co	0.0	2.0	0.80	Co	0.0	2.0	0.80
	Co + Ed	2.8	3.0	0.20	Co + Ed	2.7	3.0	0.21
	Ed	10.8	2.0	0.00	Ed	18.6	2.0	0.00
	Nu	28.9	1.0	0.00	Nu	44.7	1.0	0.00

[1] GLMM test; [2] GAMM test; [3] SLM test. The first number refers to the test used for richness and the second for abundance. Values of difference in AICc from the best model (dAIC); parameter number of the model (df); AICc weight (wi).

S5 Table - Ranking selection of best models explaining the richness and abundance of each functional trait in function of forest cover amount and distance of nearest edge. The most parsimonious models (Nu - null; Co - Forest cover; Ed - Forest edge distance; Co + Ed - Forest cover plus edge distance) are shown in gray.

Var.	Models	RICHNESS			Models	ABUNDANCE		
		dAIC	df	w_i		dAIC	df	w_i
Si [1,1]	Nu	0.0	1.0	0.52	Co	0.0	2.0	0.41
	Co	1.8	2.0	0.21	Ed	1.0	2.0	0.25
	Ed	2.4	2.0	0.15	Nu	1.2	1.0	0.23
	Co + Ed	3.0	3.0	0.12	Co + Ed	2.7	3.0	0.11
St [1,2]	Co	0.0	2.0	0.77	Co	0.0	7.3	0.59
	Co + Ed	2.4	3.0	0.23	Co + Ed	0.7	12.7	0.41
	Ed	21.6	2.0	0.00	Ed	14.5	7.9	0.00
	Nu	65.6	1.0	0.00	Nu	116.5	1.0	0.00
Ad [1,3]	Nu	0.0	1.0	0.58	Nu	0.0	4.0	0.73
	Co	2.2	2.0	0.20	Co	3.4	5.0	0.13
	Ed	2.4	2.0	0.17	Ed	3.5	5.0	0.13
	Co +Ed	4.9	3.0	0.05	Co + Ed	7.6	6.0	0.02
Bd [1,2]	Co	0.0	2.0	0.55	Co + Ed	0.0	4.3	0.71
	Co + Ed	0.5	3.0	0.43	Co	1.8	5.0	0.29
	Ed	6.7	2.0	0.02	Ed	15.0	2.0	0.00
	Nu	40.6	1.0	0.00	Nu	49.8	1.0	0.00
Ls [1,1]	Co	0.0	2.0	0.36	Nu	0.0	1.0	0.59
	Nu	0.3	1.0	0.30	Ed	2.3	2.0	0.19
	Ed	0.7	2.0	0.25	Co	2.4	2.0	0.18
	Co + Ed	2.7	3.0	0.09	Co + Ed	5.1	3.0	0.05
Ss [2,3]	Co	0.0	2.0	0.41	Ed	0.0	5.0	0.38
	Co + Ed	0.2	3.1	0.36	Co	0.1	5.0	0.37
	Ed	1.1	2.0	0.23	Nu	1.5	4.0	0.19
	Nu	16.1	1.0	0.00	Co + Ed	3.6	6.0	0.06

[1]GLMM test; [2]GAMM test; [3]SLM test. The first number refers to the test used for richness and the second for abundance. Values of difference in AICc from the best model (dAIC); parameter number of the model (df); AICc weight (w_i).

CAPÍTULO 3

Erosion of tree reproductive functional diversity in fragmented tropical landscapes

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Erosion of tree reproductive functional diversity in fragmented tropical landscapes

Larissa Rocha-Santos[1*]; Margaret M. Mayfield[2]; Ariadna Lopes[3]; Michaele S. Pessoa[1]; Daniela C. Talora[1]; Deborah Faria[1]; Eliana Cazetta[1]

[1] Graduate Program in Ecology and Biodiversity Conservation, Applied Ecology and Conservation Lab, State University of Santa Cruz, highway Jorge Amado, 45662-900, Ilhéus, BA, Brazil.
[2] School of Biological Sciences, The University of Queensland, St Lucia Campus, 4072, Australia
[3] Department of Botany, State University of Pernambuco, highway Prof. Moraes Rego, 50670-901, Recife - PE, Brazil.

* Corresponding author: e-mail: rocha_larissa@yahoo.com.br

Summary

1. Productive activities such as agriculture and cattle ranching are rapidly reducing forest cover worldwide, especially in the tropics. Such forest loss can have a negative impact on affects different aspects of biodiversity, altering patterns of species composition, forest structure and taxonomic diversity. Yet, its effect on ecosystem functioning is largely unknown. Tree reproductive functionality processes such as pollination and seed dispersion can lead to a rupture in the regeneration process and forest dynamics. In the present study we evaluated the influence of landscape-scale forest loss on functional diversity of tree reproductive traits.

2. Tree community of 20 forest sites of tropical Atlantic rainforest in northeastern Brazil, with different percentages of forest cover (3 to 93%) had their functional traits classified as floral biology, pollination and dispersion syndromes, sexual and reproductive system. This information was used to calculate indices of functional diversity, evenness and divergence, and we then related each index to the amount of forest cover at the landscape scale.

3. Functional diversity decreased linearly with the reduction of forest cover, but functional evenness and divergence were not related to forest amount. Functional-groups richness was similar among landscapes, but redundancy between some groups was lower in areas with lower forest cover. Forest loss affected the redundancy of some trait states, with self-incompatible reproductive system and animal seed-dispersal being the most sensitive traits to forest loss.

4. *Synthesis*. Forest loss leads to changes in tree functional reproductive characteristics, where common reproductive traits of generalist species (such as open or inconspicuous flowers, pollinated by small bees and other insects) are being reduced by forest loss. Our results show that the tree community reproduction may be compromised, mainly for species dependent on plant-pollinator and plant-dispersers interaction. The reproductive success is impaired, leading to profound changes such as the decrease of food resources, alteration on floristic composition and fauna diversity, and even to changes in ecological processes which may compromise regeneration and forest maintenance in remnants with low forest cover amount.

Key-words: sexual system, reproductive system, floral biology, pollination, seed dispersion, plant-animal interaction, tree reproduction, habitat loss.

Introduction

Human activities modify natural environments, especially by forest loss and fragmentation, due to the expansion of industrial and agricultural activities (Wright, 2010). New ecosystems arise from these changes in which the remaining forest patches are immersed in anthropogenic landscapes (Hobbs et al., 2009; Tabarelli et al., 2012). The fast rates of habitat conversion are one of the main drivers of species extinction (Gibbs et al., 2010; Green and Balmford, 2005). However, the consequences of habitat loss and fragmentation go beyond species extinction (Gibson et al., 2013; Lôbo et al., 2011), also affecting phylogenetic and functional diversity (Andrade et al., 2015; Laliberté et al., 2010; Santos et al., 2014) and species interaction (Valient-Banuet 2015), which in turn may compromise ecological processes and ecosystem functions.

The local species extinction does not necessarily imply in the loss of ecological functions, since functional redundancy is an important community attribute, in which a set of species might similarly contribute to an ecosystem function (Laliberté et al., 2010; Mouchet et al., 2010). High functional redundancy provides high ecosystem resilience against the loss of ecosystem functions and services. However, an increasing number of studies has shown that environmental changes have led to a functional redundancy decay (Laliberté et al., 2010; Magnago et al., 2014; Smith and Mayfield, 2015) mainly due to the reduction of particular functional traits shared by species more vulnerable to habitat modification (Carneiro et al., 2016), in general, typical traits of specialist species (Matthews et al., 2014; Pardini et al., 2010), such as large seeded (Freitas et al., 2013), shade tolerance (Rocha-santos et al., 2017), large flowers (Girão et al., 2007), and vertebrate pollination (Girão et al., 2007). These changes in the representativeness of functional traits and in functional diversity and redundancy as a consequence, contribute to a decay in forest functionality, by reducing processes such as carbon storage (Bello et al., 2015), pollination (Hadley and Betts, 2012), and seed dispersal (McConkey & O'Farrill 2016).

Among ecosystem functions, some of the most important for forest maintenance and regeneration are pollination and seed dispersal. Several studies indicate that both are highly sensitive to environmental changes (Eckert et al., 2010; Kearns et al., 1998; Kurten, 2013), being recently indicated as the most threatened processes among multiple processes involved in forest regeneration such as seed predation, recruitment, and herbivory (Neuschulz et al., 2016). One possible explanation is that they are affected by changes in both flora and fauna composition, since they involve interactions between plant-pollinator and plant-disperser (Neuschulz et al., 2016; Spiesman and Inouye, 2013). It is evident that habitat loss leads to a reduction in the tree community richness and abundance (Montoya et al., 2010; Rocha-santos et al., 2017), pollinator community such as bees and other diverse insects (Grass et al., 2014; Spiesman and Inouye, 2013; Taki et al., 2010) and seed dispersers community (Morante-Filho et al., 2015; Pardini et al., 2010). However, there is still a lack of information on the effects of habitat loss and fragmentation on plant reproductive functions. Some studies have shown the negative effects of forest fragmentation on reproductive traits, such as type and floral reward, pollinator syndrome, and sexual and reproductive system (Girão et al., 2007; Lopes et al., 2009). However, these studies used a simplified functional index (based on Shannon and Simpson diversity indices). Studies covering plant traits related to pollination and seed dispersion, in general, used the number of functional traits observed to evaluated contrasting environments such as deforested versus forested areas (Mayfield et al., 2006, 2005). Only recently the influence of forest cover reduction was evaluated using a consolidated functional diversity index and robust set of traits however the forest cover gradient was restricted to landscapes with less than 28% of forest coverage (Carneiro et al., 2016). Thus, there is an urgently need to evaluate how forest loss affects the reproductive traits using a more robust approach.

In this scenario, the importance of understanding the different aspects of functional diversity of tree community reproductive traits is clear, which can help to predict maintainability and permanence of species in anthropogenic landscapes, and therefore the viability of some ecosystem services such as pollination and seed dispersal. Thus, our main objective was to assess the functional diversity of reproductive traits from tree communities in a gradient of forest cover reduction at landscape scale in Atlantic Forest fragments, northeastern Brazil. More specifically, our main questions were: 1- How does functional diversity indices (evenness, divergence, functional diversity) of reproductive traits are influenced by forest cover reduction at the landscape scale, and what is the relationship type (linear or non-linear)?; 2- Is there evidence that some reproductive functional groups of tree community are more affected by forest cover amount?; and 3- How does the categories of reproductive traits of tree community vary with forest cover loss? We expect that sites with lower forest cover will present lower functional diversity and redundancy, since previous studies in the same area showed changes in floristic composition, and a reduction in tree abundance and richness due to forest cover loss, and that this effect occurs unequally among ecological groups (Rocha-santos et al., 2017). We expect that all functional diversity components (diversity, redundancy, divergence) will be positively related with forest cover amount in the landscape, and that the type of relationship will be predominantly non-linear. We also expect that functional groups and reproductive traits will be affected by forest cover amount, in which sites with less forest cover amount will have fewer reproductive traits and functional groups, and these will have less redundancy (they will be represented by a small number of species).

Methodology

Study landscape

This study was conducted in Atlantic forest sites in the northeast region of Brazil ($15^00'$ - $16^00'$ S and $39^00'$ – $39^030'$ W). This region of Brazil is a biodiversity hotspot (Myers et al., 2000), with high levels of plant and animal endemism but particularly remarkable tree diversity, with up to 400 species of trees per hectare (Martini et al., 2007; Thomas et al., 1998). The region has a stable tropical climate lacking any significant seasonal climate variation. The annual average temperature for the region is 24°C with average annual rainfall of ~1500 mm y^{-1} (Mori et al., 1983; Thomas et al., 1998).

Forest sites for our study were spread across a 3,500 km^2 area, which we mapped for land uses and vegetation cover using satellite images (RapidEye from 2009-2010, QuickBird and World View from 2009-2011) at a scale of 1:10,000, which is adequate for identifying patches based on the visual inspection of differences in color, texture and shape. All forest sites have similar soils, topography, and vegetation type (tropical lowland Atlantic rainforest), for this we excluded Montane Forest regions (mostly in the northwest, at elevations of 500 m a.s.l. or higher) and Restinga Forests (mostly in southeast). We adopted a patch-landscape approach, in which the response variables were evaluated within forest sites and the landscape variable (here represented by forest cover) were measured within a specific area around each sampling site (Tischendorf and Fahrig, 2000). To characterize each landscape we quantified the percent forest cover around each site from the center of each forest site, using multiple buffers of different radius size (400, 600, 800, and 1000 m) in the ArcGIS software. We considered as forest cover all mature and secondary native forests, but excluding plantations (such as cocoa, rubber, and eucalyptus). Although we recognize that agroforests (mainly shade cocoa plantation) can be habitat for some tree species, pollinators and seed dispersers (Cassano et al., 2012; Sambuichi, 2002), only a small number of surveyed sites were embedded within an agroforestry mosaic, so we excluded this sites. From this map we selected all possible forest sites (total of 58) keeping a minimum distance of 1 km from any other, they varied in size but only forest sites larger than 3ha were included. They were ground-truthed to determine which sites were accessible and for which we could obtain formal consent from land-owners to survey. Using this pool of appropriate forest sites we performed a stratified sampling and selected 20 sites from across the full range of forest cover classes at landscape scale. This random sample ranged from 92.8% forest cover to 2.5% forest cover within the 1km buffer (Figure 1), and all fragments suffer deforestation at about the same time, due the cocoa crisis of the 1990's (for details see Rocha-santos *et al.* 2017).

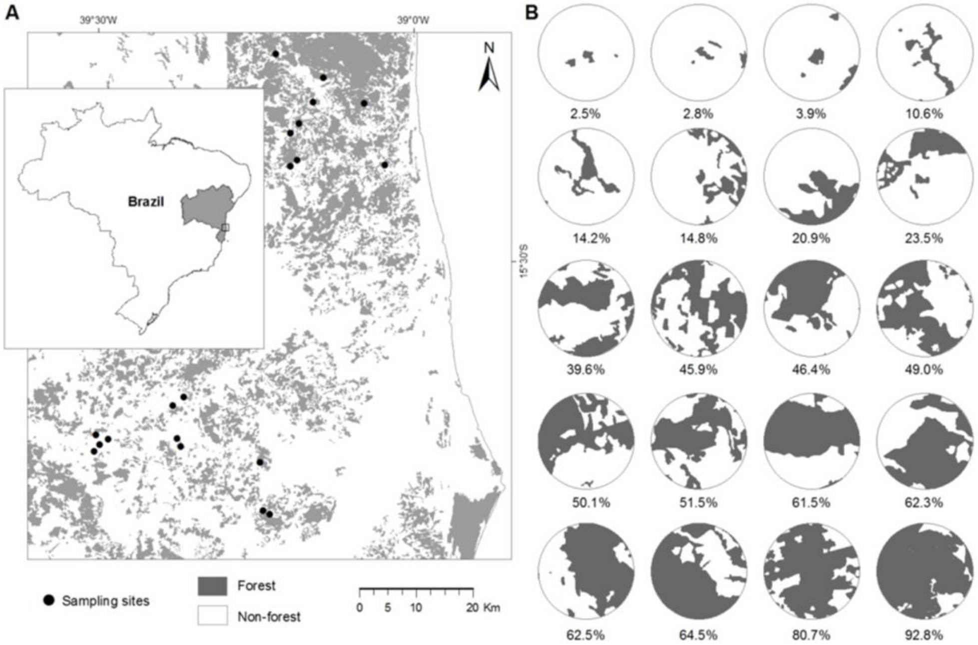

Figure 1 – Map of the study area in southern Bahia, Brazil. A: Atlantic Forest remnants (gray areas) and the 20 sampling forest sites (black circles). B: Details of some sampled landscapes within 1000 m radius. The images of study areas were obtained from forest cover map "Atlas dos Remanescentes Florestais da Mata Atlântica" with open access (SOS Mata Atlântica, n.d.).

Vegetation Sample

In each site we established five forest-plots of 100m² (25 x 4m), close to the center of each selected forest site and with at least 50m distance from forest edge, from each other and from the nearest forest edge, whenever possible (85% of the total). Within each forest-plot, we counted all trees with the diameter at breast height ≥ 5 cm that had at least 10% of the main trunk partially within plot boundaries. All Individuals had a branch sampled for taxonomic identification and their reproductive phenology was evaluated every month from February 2013 to January 2014. Flower and fruits samples were collected from trees that reproduced during this period, to help with species identification and for direct measurements of reproductive functional traits. The taxonomic identification was carried out to the lowest possible taxonomic level, according to the APG III (2009) classification, by consulting the most relevant herbaria of Bahia state (CEPEC/Ceplac, UESC and UFBA), with assistance of botanic experts (see Rocha-santos *et al.* 2017 for details).

Reproductive Functional traits

We surveyed 1955 individual trees belonging to 512 species from 53 families. The species richness ranged from 32 to 85 species and the abundance from 60 to 129 individuals per forest site (database from Rocha-santos *et al.* 2017). All species were classified into 11 categories according to five major classes of reproductive traits: (1) pollination system, (2) floral biology, (3) sexual system, (4) reproductive system, and (5) seed characteristic (Table 1). These classes were adapted from Girão *et al.* (2007), Lopes *et al.* (2009), Soares et al. (2014), Tabarelli et al. (2010), and Rocha-santos *et al.* (2017). The species classification in different trait states within each reproductive category was based on (1) field observations and measurements of collected flowers and fruits; (2) scientific papers, theses, dissertations and books (such as Kimmel et al., 2010; Lorenzi, 2002; Morellato, 1991; Ribeiro et al., 1999; Yamamoto et al., 2007); (3) Virtual Herbarium entries including photo and voucher information (e.g. Kew Royal Botanic Garden, The New York Botanic Garden, Neotropical Herbarium Specimens, Flora do Brasil); and (4) authors' knowledge.

As the Atlantic forest has high richness and endemism rates, especially in the study region (Martini et al., 2007) round 18% of surveyed species were removed from analyses mainly because they could not be identified to species level and were not fertile during the study period, leading to no information on their reproductive traits. Thus the effective species pool was 422 species. We only included categories whose data were available for at least 50% (Laliberté et al., 2010). The available data percentage varied from 51 to 97% for the 10 examined reproductive traits (Table 1).

Table 1 - Reproductive categories and associated traits measured, with the respective percentage of species with category values available in this study. Table adapted from Girão et al. (2007), Lopes et al. (2009), Soares et al. (2014) and Tabarelli et al. (2010).

Reproductive Categories	% sp	Trait States
1. Pollination system	74.6	bat; small bee ; large bee; beetle; bird; butterfly; diverse small insects (DSI); fly; hummingbird; moth (excluding hawkmoth); Sphingid (hawkmoth); non-flying mammal; wasp; wind

2. Floral biology		
2.1. Size	91.7	diameter size (mm)
2.2. Reward	64.9	nectar; oil; pollen; brood or mating places/floral tissues (BMFT); without resource
2.3. Type	91.7	brush; flag; inconspicuous (very small flower, ≤4 mm); open/dish; camera; tube
2.4. Color	91.9	white; red; pale color (greenish, yellowish, green, cream); yellow; orange; purple; pink
2.5. Anthesis period	66.6	diurnal; nocturnal
2.6. flowering duration	73.5	brief (until 1 month); intermediate (>1 and ≤5); extended (≥6 months)
3. Sexual system	96.9	dioecious; hermaphrodites; heterostylous; monoecious
4. Reproductive system	51.4	self-compatible; self-incompatible; agamospermic; outcrossing
5. Seed characteristic		
5.1. Seed Size	69.6	small seed (≤1.2 cm of diameter); large seed (>1.2 cm diameter)
5.2 Dispersal mode	98.3	autochory ; anemochory; zoochory

Data Analysis

We compared the coefficient of determination (R^2) from regression analyses of functional diversity indices for each forest cover radius (i.e., 400, 600, 800, 1000 m), to determine which buffer radii explained functional diversity patterns (see Table S1). These scales are likely appropriate for capturing the relevant landscape factors for seed dispersal and pollination functions (Jackson and Fahrig, 2015; Winfree et al., 2007). The 1000 m radius had highest r^2 value, furthermore 1000 m radius was the best scale for capture the forest cover effect on floristic composition (Rocha-santos et al., 2017), forest structure (Rocha-santos et al., 2016) on previous study at the same studied sites, so we use data from the 1000 m radius for all analyses presented below.

To answer question 1, we used three important indices to access the different aspects of functional diversity, the functional diversity index (FD), the functional evenness (Feve) and the functional divergence (FDiv) (Clark et al., 2012; Mouchet et al., 2010; Villéger, 2008). The FD was calculated for each forest site, based on total branch length of a trait dendrogram generated using a similarity matrix of functional traits, as proposed by Petchey & Gaston (2002). This index is considered good in predicting ecosystem functioning, because it has logical statistical properties (Flynn et al., 2009; Petchey and Gaston, 2006). Because we had continuous and categorical traits in our study, we used the flexible Gower similarity matrix (Laliberté et al., 2010; Laliberté and Legendre, 2010). We used presence–absence data to proceed with unweighted the paired-group clustering method using arithmetic averages, that is a recommended clustering method (Podani and Schmera, 2006), and performed the analysis excluding the unnecessary root segments of the tree dendrogram (Petchey and Gaston, 2006). The Feve and Fdiv indices were weighted by abundance. The matrix of these three indices were calculated considering all species (422 sp) and all categories of the 10 reproductive traits (Table 1) and the analysis was performed using "PD" package (Laliberté and Legendre, 2010) and "Picante" package (Kembel et al., 2010) of R (R Development Core Team, 2013).

To evaluate the relationship type among the functional indices obtained for each forest site and forest cover, we used a model selection approach. We tested four models: 1) a null model; 2) a linear model, representing the constant effect of forest cover, and two non-linear models, 3) the power-law, 4) and a four-parameter logistic model (Pinheiro and Bates, 2000). The power law model was used because it was consistent with some patterns we observed in a visual inspection of the scatter plots. This model has been also widely used to investigate nonlinear relationships (Pessoa et al., 2016; Rocha-santos et al., 2017; Rybicki and Hanski, 2013). The four-parameter logistic model has being used to investigate threshold relationships (see Lima and Mariano-Neto, 2014; Swift and Hannon, 2010). We select the most plausible model based on Akaike's information criterion (AIC). The model with lowest AIC value was considered most plausible, and when the difference in the AIC between the lowest two models was smaller than 2, we considered both plausible (Anderson, 2008). We built routines to adjust logistic model parameters minimizing the models log-likelihood using numerical optimization (Bolker, 2008). During model parameterization process, models that did not show convergent solution of parameters in numerical optimization were excluded from model selection. The analyses were implemented in R software, using the "bbmle" and "nlme" packages (Bolker, 2014).

In order to answer question 2, we identified the functional groups, using a dendrogram based on other Gower similarity matrix by reproductive trait (Laliberté and Legendre, 2010; Petchey and Gaston, 2006). The similarity matrix used for this analysis was structured on four mainly reproductive traits (with two possible categories each) and for species that had information for at least 3 of 4 traits evaluated (337 species total). The categories of this four mainly reproductive traits were grouped as follows: (1) pollination system was grouped in generalist pollinators (categories included were small bees, butterflies, diverse small insects, flies, moths, and wind) or specialists pollinators (bats, large-bees, beetles, wasp, birds, Sphingids, and non-flying mammals), *sensu* Kang and Bawa, (2003) and Lopes et al., (2009); (2) sexual system was separated in hermaphrodites (hermaphrodite and heterostylous) or no-hermaphrodites (monoecious and dioecious); (3) reproductive system was grouped in self-compatible (agamospermic and self-compatible) or self-incompatible (outcrossing and self-incompatible); and (4) dispersion mode was represented by abiotic (autochory and anemochory) or biotic dispersion (zoochory).

Functional groups, were selected from the dendrogram described above that was visually examined to identify main functional groups, and avoid biologically nonsensical groupings (Hooper et al., 2001; Laliberté et al., 2010; Smith and Mayfield, 2015). The species were divided into 19 functional groups, however, two of these were excluded from further analysis because they were not consistent groups (formed by species with different reproductive characteristics, or very small groups, composed of only 3 species, see Appendix 1). Thus we used these 17 groups to calculate functional group richness - the number of functional groups within each landscape, and functional group redundancy - the number of species into each reproductive group (Laliberté et al., 2010). We used linear regressions to determine if there was a relationship between functional group richness and redundancy (number of species in each functional group) and forest cover within 1000 m radii sites. We performed the analysis using "PD" package (Laliberté and Legendre, 2010) and "Picante" package (Kembel et al., 2010) of R (R Development Core Team, 2013).

To answer question 3, we investigated the effect of forest cover on some important categories of reproductive traits (categories present in most sites and with enough number of species), such as some categories of pollination system (bat, bird, small and large bees), reproductive system (self-compatible and incompatible), and sexual system (dioecious and hermaphrodites).

Results

The reproductive traits were represented by all range of categories. For pollination system the most common category was small/medium bees (vector pollination of 106 sp that, representing 33.7% of all species classified in this category) and DSI (98 sp or 31.1%). The most common flower type was inconspicuous (156 sp or 40.5%) and tube (76 sp or 19.7%) whereas the most frequent flower color was pale (170 sp or 43.8%) and white (143 sp or 36.9%). The most common flowering period was intermediate (201 sp or 64.8%), whereas the reward was nectar (160 sp or 58.4%) and the anthesis period was diurnal (247 sp or 87.6%). The most representative sexual system was hermaphrodite (281 sp or 68.7%) and the reproductive system was self-incompatible (97 sp or 44.7%). The most common seed characters were small seeds (156 sp or 66.5%) and zoochoric dispersal (332 sp or 76.3%).

Functional diversity indices

Different functional indices had distinct relationships with forest loss. The forest cover amount at landscape scale was positively and linearly related to FD index, showing that forest sites at low forest amount have less functional diversity (Fig. 2 and Table S2). However, forest cover amount did not affect Feve indicating that sites with different forest cover amount have similar distribution of species in niche space, therefore, similar effectiveness use of resources available range (Fig. 2 and Table S2). Forest cover amount was not correlated to Fdiv index, since the null model was between the plausible models, demonstrating that the sites had similar functional divergence, so, similar functional redundancy regardless forest cover at landscape scale (Fig. 2 and Table S2).

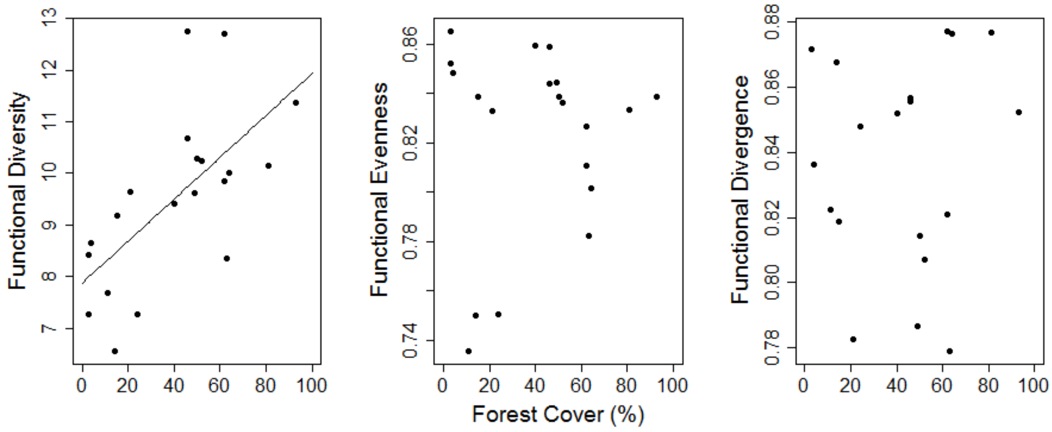

Figure 2 - Relationship between the forest cover amount and functional indices of tree reproductive traits in Atlantic rainforest in southern Bahia, Brazil. Only one of plausible models were plotted, the simplest model (less parameter). Plotted curve represent well-supported model (null, linear, power-law and logistic models) identified with AICc for each relationship. In the case of more than one plausible model, the model with the lowest number of parameters was plotted.

Functional Groups

The most common group was GnHIZ (formed by species with generalist pollination, no-hermaphrodite, self-incompatible and zoochoric), followed by the GHZ (generalist pollination, hermaphrodite and zoochoric) and GHIZ (generalist pollination, hermaphrodite, self-incompatible and zoochoric) with 70, 53 and 41 species respectively. Regardless of forest cover amount, these groups were presented in all sampled forest sites. Whereas, the most rare groups were GnHCZ (generalist pollination, no-hermaphrodite, self-compatible and zoochoric) and GnHZ (generalist pollination, no-hermaphrodite and zoochoric) with five species each, but both groups are composed by common species, presented in 95% forest sites. The less frequent group among the sampled forest sites were SHCZ (specialist pollination, hermaphrodite, self-compatible and zoochoric) and SnHIZ (specialist pollination, no-hermaphrodite, self-incompatible and zoochoric), present in only 7 and 9 forest sites, respectively (Table S3).

Forest cover amount at landscape scale was not related to functional group richness ($R^2 = 0.054$; $p = 0.163$), as group richness was high in all forest sites with at least 10 out of 17 groups (Figure 3). When looking into each functional group, we found evidence that forest cover amount affected some particular groups. Forest cover reduction was positively related to decrease of functional group redundancy (number of species within each group) only for GHIZ (formed by species with generalist pollinators, hermaphroditic, self-incompatible and zoochory), GHZ (generalists, hermaphrodite and zoochory) and GnHIZ group (generalists, non-hermaphrodite, self-incompatible and zoochory (Figure 4, Table S3). Results were quite similar if functional group redundancy was calculated by number of individuals rather than species (Table S3).

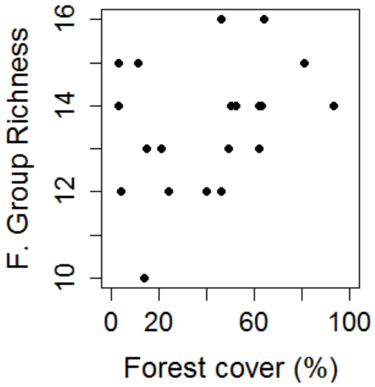

Figure 3 - Relationship between functional group richness (number of functional groups) and the percentage of forest cover at landscape-scale, in Atlantic rain forest, Brazil.

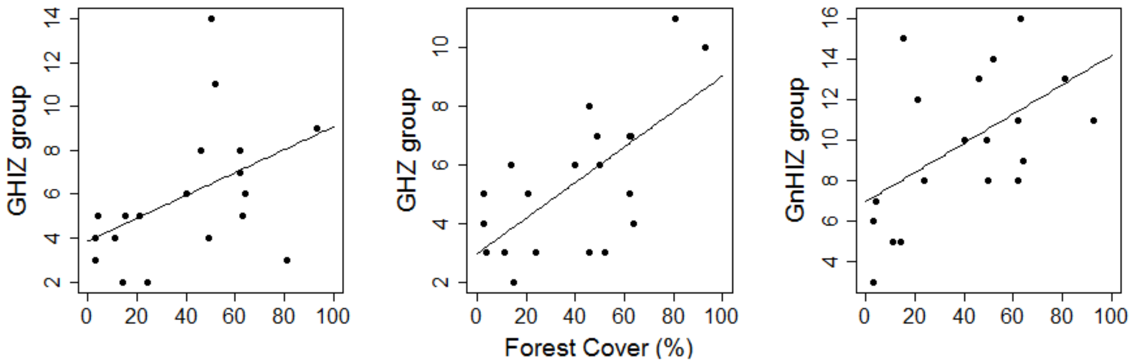

Figure 4 - Relationship between the forest cover and functional group redundancy (number of species) for the three groups significantly influenced by the forest cover amount. Groups: GHIZ (generalists, hermaphrodite, self-incompatible and zoochory), GHZ (generalists, hermaphrodite and zoochory) and GnHIZ (generalists, non-hermaphrodite, self-incompatible and zoochory).

Categories of reproductive traits

Forest cover amount was related to 17 reproductive trait states of different categories from 32 traits tested (Table S4). Among the pollination vectors only species pollinated by small bees, DIS and moths were significantly less common in landscapes with less forest cover ($r^2 = 0.21$ and $p = 0.021$, $r^2= 0.20$ and $p = 0.019$, $r^2=0.51$ and $p < 0.001$, respectively). Forest cover reduction was also related to the decrease of species with floral types such as inconspicuous, open and tube ($r^2 = 0.25$ and $p = 0.015$, $r^2=0.46$ and $p < 0.001$, $r^2 = 0.20$ and $p = 0.025$, respectively), with floral rewards such nectar and pollen ($r^2= 0.16$ and $p = 0.044$, $r^2= 0.39$ and $p = 0.002$, respectively), and with all flowering period, brief ($r^2= 0.53$, $p <0.001$); intermediate ($r^2= 0.24$, $p = 0.016$), extended ($r^2= 0.42$, $p <0.001$). Furthermore, as forest cover decreased, so did the presence of self-incompatible species ($r^2= 0.20$, $p = 0.025$), dioecious ($r^2= 0.15$, $p = 0.048$), monoecious ($r^2= 0.17$, $p = 0.039$), hermaphroditic ($r^2= 0.51$, $p <0.001$), small seed ($r^2= 0.37$, $p = 0.003$), and zoochory ($r^2= 0.55$, $p <0.001$; Table S4).

Discussion

Our study shows that the effect of landscape-scale forest loss go beyond species loss, and also affect the functional diversity of tree reproductive traits within Atlantic rainforest remnants. Additionally, our results suggest that the interactions between plant-pollinators and plant-dispersers may be compromised in less forested landscapes, since the most affected reproductive plant traits were self-incompatible reproductive system and zoochoric seed-dispersal. Change in diversity and redundancy of reproductive traits may imply in a reduction in tree reproductive success, and consequently in profound modifications in the establishment, regeneration and maintenance of forests in the long term. The production of essential food-resources for fauna might be affected and therefore, forests health, resilience and the environmental services provided by them.

Overall community reproductive traits

In general, our forest sites are dominated by floral traits typical from generalist species, such as very small flowers with pale coloration, easy access to pollinators, pollinated by small bees and others insects. In tropical forests, many species have simple floral characteristic that allow the access of several pollinator vectors, such as bees, small insects, moths and butterflies (Bawa, 1990). The dominance of these reproductive traits was also observed in other Atlantic forest areas (Araújo et al., 2009; Lopes et al., 2009), even in different environmental conditions such as small fragments, edge areas and conserved forests (Girão et al., 2007; Lopes et al., 2009). Although most species are hermaphrodite, which increases the reproductive probability compared to dioecious species, the most common reproductive system was the self-incompatibility, in which is necessary the presence of more than one reproductive individual of the species, and the action of pollinator agents to perform the outcrossing (Aguilar et al., 2006). This type of reproductive system is efficient in the long term, as it guarantees outcrossing that increases the genetic variability and consequently population viability (Bawa, 1990; Bawa et al., 1985). However, it also increases the vulnerability to anthropogenic disturbances due to the necessary requirement of animal vectors for pollination, especially bees and small insects that are also highly affected by environmental changes (Eckert et al., 2010; Rader et al., 2014; Williams and Winfree, 2013).

Functional diversity x Forest cover

Forest cover loss has led to a reduction in functional diversity, in which the species presented a smaller variety of reproductive functional traits. Studies involving multiple functional plant traits (Benchimol and Peres, 2015; Flynn et al., 2009; Laliberté et al., 2010), pollinators (Grass et al., 2014; Taki et al., 2007), or seed dispersers (Flynn et al., 2009), also evidence the reduction of functional diversity due to environmental changes such as fragmentation, forest cover loss or land-use intensification. However, studies with multiple functional traits usually involves contrasting functions (e.g. fruit length, litter size, growth form, leaf area) making it difficult to tease apart the effects of habitat disturbance on such different processes (Trisos et al., 2014). Functional diversity reduction in our forest sites embedded in landscapes with low forest coverage, occurs mainly due to low frequency or absence of certain reproductive traits, so the permanence of species with these traits may also being affect due the low representativeness of pollinators and reduction on the reproductive success (Anderson et al., 2011). The efficiency reduction in pollination and seed dispersal leads to changes in the community floristic composition, usually leading to lower richness, lower diversity and greater dominance (Fontaine et al., 2006; Kurten, 2013).

Our results show that forest cover loss decreases tree species richness (Rocha-santos et al., 2017) and functional diversity but show no effect on functional evenness and divergence. These results highlight that for the investigated functional traits, heterogeneity and redundancy are similar among sites. This may occur because the plant-pollinator and plant-disperser interaction networks have been shown to be highly nested and asymmetrical, in which most generalist plant and animal species interact among themselves and specialist species interact only with generalists (Bascompte et al., 2003). These traits are responsible for cohesive networks with a dense core of interactions that is resistant to habitat loss, and that can provide alternative ways for rare species to persist to forest perturbations (Bascompte et al., 2003). Thus, even the less forested sites are able to maintain the redundancy of reproductive traits, since generalist species and therefore, resistant to environmental changes, are responsible for most of the interactions.

Functional Groups x Forest Cover

Most of the functional groups (59%) were represented in all the studied landscapes, and the groups formed by specialized pollinators (with zoochoric dispersion, independent of sexual and reproductive systems) were the least frequent. Even forest sites embedded in low forest cover landscapes maintained functional group richness, but the redundancy of some of those groups were reduced. The groups formed by species pollinated by generalist vectors, self-incompatible, hermaphrodite or non-hermaphrodite and zoochoric dispersed, presented a reduced redundancy, that is, they were represented by a smaller number of species and individuals. Forest cover amount was not related to group's redundancy of species pollinated by specialist vectors; however, this was probably because of the low occurrence of these groups in all landscapes. An evidence of this is that 10 out of the 17 formed groups were represented by species pollinated by generalist vectors and only 6 by specialist vectors. Studies have shown that plants pollinated by specialist and generalist vectors were equally susceptible to the effects of fragmentation, with similar pollination rates and reproductive success (Aguilar et al., 2006; Aizen et al., 2002). However, our results indicate that groups which depend on plant-animal interactions for pollination and seed dispersal (because they are self-incompatible and zoochorous, respectively) are more vulnerable to habitat loss. Studies suggest that in self-incompatible plants the effects of fragmentation are more intense than in self-compatible ones, with lower pollination rates and reproductive success (Aguilar et al., 2006; Aizen et al., 2002). In addition, studies have shown that the absence of seed dispersers can lead to increased seedling aggregation around parent trees (Kurten, 2013), which reduces the probability of survival due to increased competition, predation and pathogens (Clark and Clark, 1984; Connell, 1971; Janzen, 1970). Therefore, these groups are more vulnerable to local extinction because in sites with low forest at landscape they present less redundancy and therefore less resilience, besides being subject to a lower rate of pollination, seed dispersal and reproductive success.

Categories of reproductive traits x Forest Cover

Forest cover reduction decreases reproductive traits related to interaction between generalist species, such as simple flowers (inconspicuous and open), with less elaborate resources (nectar and pollen), pollinated by generalist vectors (small bees, DIS and moths), and dispersed by small animals (small seeds and zoochoric). This shows that even generalist species are suffering reduction in deforested landscapes, and that this reduction probably has already occurred for the species specialists in all landscapes, including those with high percentage of forest cover. Different from what occurred in fragmented environments, where more altered habitats (edge area, small fragments) show an increase in traits associated with generalist vectors and generalist pollination systems in relation to more conserved forests (Girão et al., 2007; Lopes et al., 2009), our forest sites with less forest cover in the landscape scale showed a reduction of these generalist traits and maintained constant specialist traits.. The reduction of generalist traits may indicate that the cohesive core formed by the interactions between generalist species present in the mutualistic networks as plant-pollinator and plant-disperser

(Bascompte et al., 2003) may have already been affected by the forest cover reduction. In addition, the significant species reduction of all flowering periods (brief, intermediate and extended) in sites with low forest cover also indicate that the pollinators have less floral resource in general, which in turn, can sustain a smaller abundance of pollinators and thus threaten the pollination process (Biesmeijer, 2006; Decourtye et al., 2010; Kremen and Ricketts, 2000).

Conclusion

Our study shows that forest cover reduction leads to changes in the reproductive characteristics of the tree community, reducing the functional diversity of overall community, the redundancy of some functional groups and some reproductive characteristics. It was also evident that forest cover reduction strongly affects species with self-incompatible system and zoochoric seed dispersal. Even the common reproductive traits of generalist species (such as open or inconspicuous flowers) that lead to pollination by generalist species (small bees and other insects) are being reduced by forest cover loss. These results show that the reproduction of the tree community may be compromised, leading to profound changes in remnants with low forest cover at landscapes scale. These changes can range from the reduction of food resources to fauna, alteration of forest structure and floristic composition, reduction of fauna diversity and richness, even to changes in ecological processes such as pollination and seed dispersal (Anderson et al., 2011; Kurten, 2013). Therefore, these changes lead us to uncertainty about the permanence of these species and these remnants in the long term as the environment quality is being compromised, with predictable effects on community resilience, reinforcing the need of good management actions.

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Supplementary Material

Table S1 – Determination coefficients (R^2) among percentage of forest cover within landscapes at different buffer sizes, in relation to each functional index. Highest significant values from each functional index are highlighted in bold.

Functional Index	Cover 400 m		Cover 600 m		Cover 800 m		Cover 1000m	
	R²	**P**	**R²**	**P**	**R²**	**p**	**R²**	**p**
Func. Diversity	0.285	0.009*	0.307	0.007*	0.305	0.007*	**0.348**	0.004*
Func. Evenness	0.172	0.037*	0.228	0.018*	0.255	0.013*	**0.300**	0.007*
Func. Divergence	-0.041	0.631	-0.025	0.521	-0.021	0.548	**-0.003**	0.656

* Significative value ($p \leq 0.05$)

Table S2 - Ranking selection of best models explaining functional diversity indices in function of forest cover amount at landscape-scale. Models that did not present convergence on the likelihood estimates were excluded from the model selection procedure. The most parsimonious models (linear – Li, logistic – Lo, null – Nu and power-law – Po) are highlight in gray.

Parameter	**Model**	**dAICc**	**df**	**wi**
Functional evenness	null	0	2	0.66
	linear	2.6	3	0.18
	power law	2.8	3	0.17
Functional divergence	null	0	2	0.599
	power law	2.3	3	0.189
	linear	2.8	3	0.148
	logistic	4.5	4	0.064
Functional diversity	logistic	0	4	0.4564
	linear	0.8	3	0.3071
	power law	1.4	3	0.2317
	null	9.1	2	0.0047

Legend: difference in AICc from the best model (dAICc); parameter number of the model (df); AICc weight (wi).

Table S3 - Number of specie and individuals within each forest site sampled, and the relationship between the forest cover amount and the functional group redundancy (number the species and individuals in each group), with the corresponding determination coefficients (R^2). Acronyms that comprise functional groups: G= generalist pollinator or S= specialist pollinator; H= hermaphrodite or nH= non-hermaphrodite; C= self-compatible or I= self-incompatible; A= anemochory specie or Z= zoochory specie.

Forest cover	GHA	GHCZ	GHIA	GHIZ	GHZ	GnHCA	GnHCZ	GnHIA	GnHIZ	nHIZ	SHA	SHCZ	SHIA	SHIZ	SHZ	SnHIZ	GnHZ
3	1 / 2	1 / 4	1 / 2	3 / 4	5 / 6	1 / 1	1 / 2	2 / 3	6 / 9	0 / 0	2 / 2	0 / 0	1 / 1	2 / 2	3 / 3	1 / 2	1 / 1
3	2 / 3	1 / 3	1 / 1	4 / 9	4 / 5	0 / 0	1 / 5	1 / 1	3 / 3	1 / 1	1 / 2	0 / 0	2 / 4	2 / 3	6 / 8	0 / 0	3 / 4
4	6 / 11	2 / 5	0 / 0	5 / 6	3 / 5	0 / 0	1 / 1	1 / 1	7 / 14	2 / 4	2 / 5	0 / 0	0 / 0	0 / 0	1 / 1	1 / 1	2 / 3
11	1 / 3	3 / 12	1 / 1	4 / 10	3 / 4	1 / 1	2 / 5	1 / 6	5 / 10	0 / 0	3 / 5	1 / 1	1 / 1	3 / 20	5 / 5	0 / 0	1 / 3
14	0 / 0	3 / 5	0 / 0	2 / 5	6 / 13	0 / 0	1 / 14	2 / 5	5 / 24	0 / 0	2 / 2	0 / 0	2 / 4	0 / 0	3 / 8	0 / 0	2 / 3
15	1 / 1	4 / 10	0 / 0	5 / 6	2 / 2	1 / 1	0 / 0	2 / 6	15 / 19	1 / 2	1 / 4	1 / 1	0 / 0	1 / 1	3 / 4	0 / 0	1 / 10
21	0 / 0	3 / 3	0 / 0	5 / 5	5 / 10	0 / 0	3 / 13	1 / 1	12 / 17	3 / 4	2 / 2	2 / 3	0 / 0	2 / 2	5 / 12	1 / 1	1 / 4
24	2 / 5	1 / 1	0 / 0	2 / 2	3 / 3	0 / 0	1 / 3	2 / 4	8 / 25	1 / 5	2 / 2	0 / 0	2 / 2	0 / 0	2 / 2	0 / 0	1 / 1
40	0 / 0	3 / 3	0 / 0	6 / 7	6 / 9	2 / 3	1 / 3	1 / 2	10 / 18	3 / 3	1 / 1	0 / 0	0 / 0	0 / 0	4 / 5	1 / 1	1 / 4
46	1 / 1	6 / 7	1 / 1	8 / 14	8 / 10	0 / 0	2 / 3	0 / 0	13 / 23	4 / 10	1 / 1	0 / 0	1 / 1	0 / 0	0 / 0	1 / 1	1 / 4
46	2 / 2	4 / 5	5 / 5	8 / 10	3 / 5	1 / 1	2 / 3	1 / 2	13 / 17	5 / 10	3 / 4	0 / 0	2 / 2	2 / 4	3 / 3	1 / 1	1 / 2
49	1 / 1	3 / 5	2 / 2	4 / 5	7 / 11	0 / 0	3 / 4	1 / 1	10 / 16	2 / 7	1 / 2	0 / 0	2 / 2	0 / 0	2 / 3	0 / 0	2 / 15
50	0 / 0	3 / 5	2 / 6	14 / 20	6 / 8	2 / 3	1 / 14	2 / 5	8 / 10	2 / 2	2 / 3	0 / 0	1 / 1	0 / 0	1 / 1	1 / 1	2 / 7
52	1 / 2	3 / 6	2 / 8	11 / 20	3 / 13	1 / 1	2 / 5	1 / 1	14 / 19	2 / 2	1 / 1	0 / 0	0 / 0	3 / 3	2 / 2	0 / 0	2 / 11
62	0 / 0	4 / 5	5 / 8	7 / 10	7 / 9	1 / 1	1 / 3	0 / 0	11 / 17	4 / 7	3 / 12	1 / 1	0 / 0	4 / 8	13 / 17	0 / 0	1 / 5
62	1 / 2	2 / 3	1 / 1	8 / 10	5 / 8	0 / 0	2 / 4	1 / 1	8 / 13	0 / 0	4 / 12	1 / 2	1 / 1	1 / 1	2 / 2	0 / 0	1 / 1
63	1 / 1	2 / 2	1 / 1	5 / 12	7 / 12	0 / 0	2 / 4	1 / 5	16 / 31	1 / 1	0 / 0	0 / 0	1 / 1	1 / 1	1 / 1	1 / 1	2 / 34
64	1 / 3	5 / 10	2 / 2	6 / 16	4 / 5	1 / 1	1 / 3	1 / 1	9 / 14	2 / 2	4 / 10	1 / 1	2 / 5	2 / 9	6 / 8	0 / 0	1 / 1
81	1 / 1	5 / 5	1 / 1	3 / 4	11 / 14	1 / 2	2 / 2	1 / 1	13 / 20	3 / 6	1 / 1	0 / 0	1 / 2	1 / 2	4 / 4	0 / 0	1 / 3
93	1 / 1	0 / 0	1 / 1	9 / 13	10 / 12	1 / 3	1 / 6	1 / 1	11 / 14	2 / 2	2 / 4	1 / 1	0 / 0	2 / 4	3 / 5	2 / 2	0 / 0
Regression: Species number x Fores cover																	
R^2 values	0.053	-0.009	0.103	0.167	0.418	0.009	-0.006	0.12	0.251	0.108	-0.05	-0.047	-0.043	-0.041	-0.052	-0.019	0.111
p values	0.165	0.624	0.088	0.040*	0.002*	0.292	0.64	0.071	0.014*	0.083	0.761	0.704	0.646	0.623	0.797	0.561	0.08
Regression: Individuals number x Fores cover																	
R^2 values	0.103	-0.001	0.054	0.158	0.28	0.149	-0.052	0.093	0.021	0.011	-0.004	-0.05	-0.049	-0.055	-0.055	-0.052	-0.029
p values	0.089	0.664	0.164	0.051	0.009*	0.049*	0.798	0.11	0.249	0.286	0.651	0.76	0.737	0.935	0.953	0.803	0.513

Table S4 - Relationship between forest cover amount and the number of species for some reproductive traits categories, with the corresponding determination coefficients (R^2).

		R^2	p
Pollination system	Bats	0.069	0.1349
	Birds	-0.04	0.5893
	Dsi	0.202	0.0255*
	Beetles	0.002	0.3236
	Flies	-0.013	0.5992
	large bees	-0.04	0.6055
	Moths	0.51	<0.001*
	small bees	0.216	0.0214*
	Sphingid	0.099	0.0931
	Wasp	-0.056	0.9746
	Wind	-0.036	0.5711
Floral biology	Nectar	0.158	0.044*
	Oil	0.055	0.161
	Pollen	0.393	0.002*
	BMFT	-0.047	0.717
	without resource	-0.035	0.564
	Inconspicuous	0.25	0.015*

	open/dish	0.464	<0.001*
	Tube	0.202	0.0254*
	Brief	0.526	<0.001*
	Intermediate	0.239	0.016*
	Extended	0.416	<0.001*
Sexual system	Hermaphrodite	0.51	<0.001*
	Dioecious	0.151	0.049*
	Monoecious	0.169	0.039*
Reproductive system	self-incompatible	0.224	0.0193*
	self-compatible	0.045	0.1838
Seed size	small seeds	0.368	0.003*
	large seeds	0.074	0.127
Seed dispersion	Zoochory	0.51	<0.001*
	Autochory	-0.029	0.5115
	Anemochory	-0.056	0.9737

* Significative value ($p \leq 0.05$)

CONCLUSÕES GERAIS

Essa tese contribuiu para melhorar a compreensão dos impactos da perda de habitat em diferentes aspectos da floresta Atlântica do sul da Bahia, tendo como principais conclusões:

1 - A redução de cobertura florestal em escala de paisagem leva a um encolhimento na estrutura florestal, onde as florestas se tornam menos densas, mais baixas, mais finas, com maiores aberturas de dossel e com folhagem mais concentrada no sub-bosque.

2 - As modificações na estrutura florestal são mais severas em paisagens com montantes de cobertura abaixo do limiar, que ocorreu em torno dos 40% de cobertura florestal na paisagem.

3 - Fragmentos florestais em paisagens mais florestadas retém características estruturais similares a florestas maduras, enquanto que fragmentos em paisagens com baixas porcentagens de cobertura florestal são mais similares a estrutura de florestas secundárias.

4 - A perda de cobertura florestal também leva a alterações na composição florística, com redução da riqueza e abundância de espécies arbóreas. De modo geral, a redução de 10% da cobertura florestal leva a redução de 46 espécies e 83 indivíduos arbóreos.

5 - A perda das espécies não foi aleatória, ela ocorreu de forma mais acentuada para a espécies tolerantes à sombra, espécies com dispersão de semente por animais, e para espécies das famílias Myrtaceae e Sapotaceae.

6 - A redução da cobertura florestal leva ao decréscimo da diversidade funcional das características reprodutivas da comunidade arbórea, da redundância funcional de alguns grupos e traços reprodutivos.

7 - Características reprodutivas que indicam a necessidade de animais para a polinização (reprodução auto-incompatível) e para a dispersão de sementes (zoocoria) são as mais afetadas com a redução da cobertura florestal.

Essas alterações registradas na estrutura, na composição florística e diversidade funcional desencadeiam uma cascata de efeitos, como redução de recursos essenciais para a fauna (como abrigo e alimento), comprometimento de importantes processos ecológicos como a polinização, dispersão de sementes e estoque de carbono, reduzindo a resiliência dos fragmentos florestais remanescentes. Todas essas mudanças mostram que fragmentos em paisagens de baixa cobertura florestal podem ter importantes gargalos para o recrutamento de novos indivíduos, manutenção florestal, e recuperação após distúrbio e portanto não serem capazes de se manter a longo prazo.