FABIO ANTONIO RIBEIRO MATOS

IMPACTOS DA FRAGMENTAÇÃO NA DIVERSIDADE FILOGENÉTICA, FUNCIONAL E CO-BENEFÍCIOS NA FLORESTA TROPICAL ATLÂNTICA

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

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APROVADA: 7 de março de 2016.

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João Augusto Alves Meira Neto
(Orientador)

“Quem caminha sozinho pode até chegar mais rápido, mas aquele que vai acompanhado, com certeza vai mais longe”

Clarice Lispector

Eu dedico esta tese à David Edwards,

Luiz Magnago e Mônica P. da Silva.

Sem vocês teria sido impossível!

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SUMÁRIO

RESUMO

MATOS, Fabio Antonio Ribeiro, D.Sc., Universidade Federal de Viçosa, março de 2016. **Impactos da fragmentação na diversidade filogenética, functional e co-benefícios na Floresta Tropical Atlântica**. Orientador: João Augusto Alves Meira-Neto. Coorientadores: Luiz Fernando Silva Magnago e David P. Edwards.

A fragmentação de habitat e a degradação das florestas tropicais causadas por mudanças no uso da terra, são as principais ameaças à biodiversidade e a emissões de carbono antropogênico. Consequentemente, o desenvolvimento de políticas adequadas de conservação requer uma compreensão de como as comunidades são afetadas pelas mudanças antropogênicas das paisagens. Para investigar os efeitos da fragmentação e possíveis co-benefícios entre carbono e biodiversidade em florestas em renegeração, focamos nas espécies arbóreas, tendo três objetivos gerais: (i) verificar os efeitos da configuração e composição das paisagens e o efeito de borda sobre a diversidade filogenética; (ii) avaliar o impacto da fragmentação sobre a diversidade funcional; (iii) verificar a existência de co-benefícios entre biodiversidade e o estoque de carbono para aplicação de mecanismos de conservação, por meio do mercado de carbono (*Reducing Emissions from Deforestation and Forest Degradation* - REDD+), utilizando como modelo florestas em regeneração. Nosso estudo foi desenvolvido na floresta tropical brasileira conhecida como Florestas de Tabuleiro. Para o objetivo geral (i), amostramos 27 fragmentos de diferentes tamanhos, formas e graus de isolamento, com um total de 280 parcelas de 10mx10m, sendo que, para 12 destes fragmentos também alocamos 120 parcelas de igual tamanho no ambiente de borda. Para o objetivo geral (ii) utilizamos os mesmos 27 fragmentos descrito para o objetivo (i), contudo, sem o ambiente de borda. Para o objetivo (iii), utilizamos 27 fragmentos de floresta primária, 11 fragmentos de florestas em regeneração e 11 pastos de criação de gado, totalizando 490 parcelas de 10mx10m. Em cada parcela coletamos todos os indivíduos arbóreos, com diâmetro à altura do peito (DAP; a 1,30 metros acima do solo) ≥4.8 cm de diâmetro. De acordo com cada objetivo deste estudo, os indivíduos amostrados foram classificados em espécies endêmicas da Floresta Atlântica, ameaçadas de extinção (Lista Vermelha da IUCN), quanto às suas características funcionais, como também calculados suas respectiva densidade de madeira e carbono. A diversidade filogenética-PD foi positivamente relacionada ao aumento da porcentagem de cobertura florestal. A distância filogenética entre pares de indivíduos que co-ocorrem (SES.MPD), diminuiu com o aumento da irregularidade dos fragmentos e com a densidade de fragmentos nas paisagens. PD foi maior no interior do que no ambiente de borda, enquanto SES.MNTD, foi menor no interior do que nos ambientes de borda. Em termos da diversidade funcional, o isolamento gerou uma redução da regularidade funcional e aumento da divergência funcional. Além disso, grandes fragmentos apresentaram uma menor uniformidade funcional, enquanto a dispersão funcional diminuiu com aumento da cobertura florestal. Encontramos também, que paisagens com maior densidade de fragmentos apresentaram maiores valores de densidade da madeira. Em termos de co-benefícios, encontramos positivas relações entre o carbono das árvores com todas as métricas de biodiversidade utilizadas neste estudo. Temos como conclusões

principais que: (i) a composição das paisagens e o efeito de borda altera a diversidade filogenética das espécies arbóreas estocadas nos remanescentes de floresta. Por outro lado, paisagens fragmentadas possuem a capacidade de manter elevada história evolutiva, dada a retenção de diversidade filogenética, através de uma gama de métricas de configuração das paisagens; (ii) o isolamento aumentou a diferenciação de nicho através do incremento de espécies adaptadas ao distúrbio. Métricas de composição das paisagens geraram um incremento da co-ocorrência de espécies funcionalmente semelhantes; e (iii) existem fortes co-benefícios entre o estoque de carbono e a biodiversidade em florestas em regeneração, mesmo estas estando isoladas de grandes blocos florestais.

ABSTRACT

MATOS, Fabio Antonio Ribeiro, D.Sc., Universidade Federal de Viçosa, march, 2016. **Impact of fragmentation on phylogenetic and functional diversity, and cobenefits in a Tropical Atlantic Rain Forest**. Adviser: João Augusto Alves Meira-Neto. Co-advisers: Luiz Fernando S. Magnago e David P. Edwards.

Fragmentation and degradation of tropical forests caused by changes in land use are among the main causes of biodiversity loss and emissions of greenhouse gases. Consequently, the development of appropriate conservation policies requires an understanding of how communities are affected by anthropogenic changes of landscapes. To investigate the effects of fragmentation and possible cobenefits between carbon storage and biodiversity conservation in forest regeneration, we focus on tree species, with three general objectives: (i) verify effects of configuration and composition of the landscapes and the edge effect on the phylogenetic diversity; (ii) evaluate the fragmentation impact on the functional diversity; (iii) verify the existence of cobenefits between carbon storage and tree-biodiversity to application of conservation mechanisms, through the carbon market (Reducing Emissions from Deforestation and Forest Degradation - REDD +), in forest regeneration. Our experiment was developed in a fragmented landscape of a type of Brazilian Atlantic Forest known as Tableland Forest. For the first objective (i), we sampled 27 fragments of different sizes, shapes and isolation levels, with 280 plots of 10 m x 10 m. For the second objective (ii), we used the same 27 fragments without edge plots. For the third objective (iii), we used 27 fragments of primary forest, 11 fragments in regeneration and 11 in cattle pastures, totaling 490 plots of 10 m x 10 m. In each plot we collect all trees with a diameter at breast height (DBH, 1.30 meters above the ground) ≥4.8 cm in diameter. According to each objective of this study, from the sampled individuals we identified the endemic species of the Atlantic Forest, the threatened species (IUCN Red List), their functional characteristics and calculated their respective wood density and carbon storage. Phylogenetic diversity-PD was significantly and positively associated with an increased

percentage of forest cover. The phylogenetic distance between individuals that co-occur (SES.MPD) reduced with increasing irregularity of fragments and fragments density in the landscape. PD was higher on the fragments interiors than on the edge habitat, while SES.MNTD was lower on the fragments interiors than on the edge habitat. In terms of the functional diversity, the isolation led to a reduction of functional regularity and increased functional divergence. In addition, the larger the fragments, the lower the functional uniformity; while functional dispersion decreases as percentage of forest cover increases. We also found that landscapes with higher density of fragments have higher values of wood density. In terms of co-benefits, we find positive relationship between the carbon storage and all the biodiversity metrics used in this study. Finally we have remarkable conclusions about Brazilian Rainforest fragmentation and cobenefits, being: (i) the composition of landscapes and edge effects alter the phylogenetic diversity of the tree species stored in forest remnants. Moreover, fragmented landscapes have the ability to maintain high evolutionary history, given the phylogenetic diversity retention, across a range metrics of configuration of landscapes; (ii) isolation increased the niche differentiation through the increase of species adapted to disturbance. The metric of landscapes composition increases with the co-occurrence of functionally similar species; and (iii) there are strong cobenefits between carbon storage and biodiversity in forests regeneration, even if isolated from large forest blocks.

I – Introdução Geral

As florestas tropicais, desempenham importantes papéis, como controle da invasão biológica (Kennedy *et al*., 2002), sequestro e estoque de carbono em sua biomassa (Lewis, 2006; Laurance, 2008), regulação climática (Anderson-Teixeira *et al*., 2012), além de fornecer recursos madeireiros, não madeireiros, alimentícios (e.g., pesca, caça frutos e sementes) e culturais (e.g., estético, artístico, científico e espiritual), para mais de 800 milhões de pessoas que vivem nestes ecossistemas (Chomitz *et al*., 2007). Apesar disto, devido a atividades antrópicas, estas florestas estão entre umas das mais ameaçadas do globo, especialmente pela exploração irregular e desordenada de seus recursos naturais, fragmentação de habitats, uso e ocupação desordenada do solo (Gibbs *et al*., 2010; Hansen *et al*., 2013; Magnago *et al*., 2014; Magnago *et al*., 2015a; Lewis, Edwards & Galbraith, 2015).

A fragmentação de habitat ocorre pelo processo de transformação de áreas anteriormente contínuas, em manchas isoladas do habitat original, geralmente ladeadas por áreas transformadas por ação antrópica (Wilcove *et al*., 1986; Fahrig, 2003; Bennett & Saunders, 2010). Desta forma, o processo de fragmentação pode ser caracterizado por conduzir modificações na configuração e composição das paisagens. Dentre os efeitos da fragmentação na configuração das paisagens, podemos citar: (i) aumento na irregularidade da forma (Hill & Curran, 2003); e (ii) aumento do isolamento (Ewers & Didham, 2006); enquanto que os efeitos geralmente descritos para características de composição são: (iii) redução da área do fragmento (Ewers & Didham, 2006; Magnago *et al*., 2014); e (iv) aumento da densidade de fragmentos nas paisagens (Bennett & Saunders 2010; Boscolo & Petzger, 2011). Em adição, posteriormente ao processo de fragmentação o principal efeito indireto é o aumento da área de borda dos remanescentes florestais (i.e., efeito de borda; Fahrig, 2003; Ewers & Didham, 2006).

A fragmentação, é considerada uma das maiores ameaças à biodiversidade, com redução da riqueza de espécies e alterações na composição das comunidades (Magnago *et al*., 2014), redução da densidade da madeira (Laurance *et al.* 2006) e estoque de carbono (Pütz *et al*. 2014; Berenguer *et al*. 2014; Magnago *et al*., 2015a). Em adição, a redução da área do fragmento aumenta os efeitos de borda, conduzindo mudanças abióticas e bióticas que interferem na estrutura e funcionamento dos ecossistemas (Laurance *et al.* 2006; Magnago *et al*., 2014). Dentre os efeitos abióticos, temos o aumento da temperatura e redução da umidade relativa do ar (Magnago *et al*., 2015b). Em termos dos efeitos bióticos, temos o aumento da taxa de mortalidade de árvores e da densidade de lianas (Laurance *et al*. 2002), bem como a substituição de espécies tardias por espécies pioneiras com baixa densidade da madeira (Laurance *et al*. 2006; Pütz *et al*. 2011). Por fim, além da fragmentação e efeito de borda, a criação de fragmentos com forma mais irregular e o aumento do isolamento entre remanescentes florestais afetam negativamente a ocorrência das espécies (Boscolo & Metzger *et al*., 2011), com profundos efeitos sobre as relações planta-dispersores (Laurance *et al*., 2011; Hagen *et al*., 2012).

Apesar de ter sido realizado considerável esforço nas últimas décadas para a compreensão do efeito da fragmentação (i.e., métricas de configuração e composição das paisagens) sobre a biodiversidade, a maioria dos estudos foram centrados na dimensão taxonômica da biodiversidade (e.g., riqueza de espécies, diversidade de espécies; Fahrig, 2003; Sodhi & Ehrlich 2010; Tscharntke *et al*., 2012). Como os efeitos da variação ambiental, incluindo o produzido pelo processo de fragmentação, são mediados por características das espécies (e.g., limitações fisiológicas, necessidades de habitat, habilidades na dispersão), considerações sobre a diversidade taxonômica só podem fornecer uma impressão incompleta sobre as consequências das atividades humanas sobre a biodiversidade em escala local ou regional. Por conseguinte, a inclusão de atributos de espécies, tais como funções ecológicas ou histórias evolutivas, em avaliações da biodiversidade, pode fornecer maior subsidío na tomada de decisões visando a conservação da biodiversidade em paisagens altamente fragmentadas de floresta tropical.

Estimativas da biodiversidade, com base na história evolutiva e funções ecológicas das espécies, descrevem a dimensão da diversidade filogenética e a dimensão da diversidade funcional. A priorização de distinção evolutiva para planejamento de conservação, pode nos ajudar a preservar o máximo da diversidade filogenética em fragmentos remanescentes (Mace, Gittleman & Purvis, 2003; Redding & Mooers, 2006; Isaac *et al.,* 2007). Por outro lado, a conservação da diversidade filogenética diminui a chance de se perder fenótipos únicos e características ecológicas importantes (Jetz *et al*., 2014), proporcionando benefícios para o funcionamento e estabilidade dos ecossistemas (Dinnage *et al.,* 2012; Cadotte, 2013). Diversidade funcional mede a variabilidade dos atributos funcionais entre espécies dentro de uma comunidade (Petchey e Gaston, 2006), permitindo compreender os impactos da fragmentação florestal sobre os papéis que as espécies desempenham dentro das comunidades. Com a conservação de elevada diversidade funcional, espera-se que seja mantido dentro dos ecossistemas um grande número de espécies funcionalmente distintas, bem como o provisionamento de serviços ecossistêmicos, através de uma variedade de mecanismos (Tilman *et al*., 1997; O`Gorman *et al*., 2011).

Além da elevada biodiversidade, as florestas tropicais são responsáveis por ~32% da produção primária global (Field *et al*., 1998), abrigando os maiores estoques de carbono acima do solo (Lewis, 2006; Laurance, 2008). No entanto, estas regiões são cada vez mais dominadas por atividades humanas (Lewis, Edwards & Galbraith, 2015), tendo experimentado a degradação dramática via extração de madeira e desmatamento para a agricultura (Gibbs *et al*., 2010; Hansen *et al*., 2013). Estes diferentes tipos de distúrbios combinados, são importantes fontes de emissões de carbono antropogênicos, perdendo apenas para a queima de combustíveis fósseis (Fearnside & Laurence, 2004; Bonan, 2008; Van der Werf, 2009). As emissões de dióxido de carbono e outros gases de efeito estufa podem conduzir a mudanças climáticas, agravando a perda de biodiversidade global no futuro (Thomas *et al*., 2004). Apesar dos impactos negativos na biodiversidade e no clima, existe um déficit substancial no financiamento disponível para deter as perdas de biodiversidade e carbono (McCarthy *et al*., 2012).

Considerando que os recursos financeiros disponíveis para combater as alterações climáticas e a perda de biodiversidade são limitados, há uma necessidade urgente de identificar ações que visem, simultaneamente, ambas as questões (Miles & Kapos, 2008; McCarthy *et al*, 2012). Um potencial emergente para pagamento de carbono baseado em serviços ecossistêmicos é o mecanismo proposto pelas Nações Unidas: a redução das emissões por desmatamento e degradação florestal (*Reduced Emissions from Deforestation and Degradation*; REDD+), com o '+' incluindo pagamentos para melhorias do estoque de carbono das florestas, simultaneamente, protegendo a biodiversidade como um co-benefício gratuito da proteção do estoque de carbono.

Para que o mecanismo REDD+ ofereça co-benefícios, é essencial que sejam identificadas as atividades que conservem carbono e possuam uma forte relação entre carbono e biodiversidade. Contudo, a maioria dos trabalhos tem focado no potencial de co-benefícios através da prevenção do desmatamento (Miles & Kapos, 2008; Venter *et al*., 2009; Phelps, Webb & Adams 2012) e impactos associados à fragmentação das florestas (Magnago *et al*., 2015a). Desta forma, se fazem necessários estudos que indiquem os potenciais estoques de carbono e co-benefícios para as florestas em regeneração após distúrbio, uma vez que estas representam uma elevada porcentagem das paisagens de florestas tropicais.

Neste estudo, avaliamos o efeito da fragmentação em comunidades de árvores sobre a sua diversidade funcional e filogenética, bem como, os possíveis mecanismos de co-benefícios entre carbono e biodiversidade para florestas em regeneração. Este estudo foi conduzido na altamente fragmentada e ameaçada floresta Atlântica brasileira, um *hotspot* de biodiversidade, aonde 300 espécies de árvores são encontrados em apenas um hectare de floresta (Rolim & Chiarello 2004; Saiter *et al*., 2011). Este estudo foi dividido em três capítulos. No **primeiro capítulo**, avaliamos o efeito da configuração das paisagens, composição e efeito de borda na diversidade filogenética de árvores. No **segundo capítulo,** investigamos os impactos da fragmentação florestal sobre a diversidade funcional de árvores. No **terceiro capítulo**, avaliamos se florestas em regeneração em paisagens altamente fragmentadas podem oferecer co-benefícios entre carbono e biodiversidade.

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III. CAPÍTULO I

Effects of landscape configuration, composition and edges on phylogenetic diversity of trees in a highly fragmented tropical forest

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Summary

1. Fragmentation of tropical forests is a major driver of the global extinction crisis. A key question is understanding how fragmentation impacts phylogenetic diversity, which summarises the total evolutionary history shared across species within a community. Conserving phylogenetic diversity decreases the potential of losing unique ecological and phenotypic traits, and plays important roles in maintaining ecosystem function and stability.
2. Our study was conducted in forest patches within the Brazilian Atlantic forest, which is both highly fragmented and a global hotspot of threatened biodiversity. We focus on trees to evaluate the impacts of landscape configuration and landscape composition, as well as fragment size and edge effects, on phylogenetic diversity.
3. We found that PD, a measure of phylogenetic richness, MPD, a measure of the phylogenetic distance between individuals in a community in deep evolutionary time, and MNTD, a measure of distance between individuals in a community at the intra-familial and intra-generic level, were not affected by landscape configuration. However, among the metrics of landscape composition, PD was significantly and positively related to increasing percentage of forest cover. Additionally, phylogenetic distance between pairs of co-occurring individuals (SES.MPD) reduced with fragment irregularity (i.e. more edge effected) and fragment density in the landscape, indicating more phylogenetic clustering.
4. We also found a gradient of fragmentation impacts on PD, from small to large fragments and edge versus interior habitats: with increasing

fragment size, we found a reduction of PD in interiors, but no change at edges. Additionally, PD was higher in fragment interiors than at edges, whereas SES.MNTD, which accounts for variation in species richness, was lower in interiors than at edges, indicating phylogenetic overdispersion in fragment interiors versus phylogenetic clustering at edges.

5. *Synthesis.* Landscape composition and edge effects cause changes to the evolutionary history within fragments, but fragmented landscapes still retain high evolutionary history given the retention of phylogenetic diversity across a range of landscape configurations. Protecting large patches and those within landscapes that retain much forest cover, as well as extending forest cover via forest restoration to enhance patch area, connectivity and density, are key conservation goals.

Key-words: Habitat fragmentation, habitat loss, landscape structure, phylogenetic structure, edge effect, tableland Atlantic rain forest

Tweetable Abstract: Tree evolutionary history is best saved in large, connected forest patches in the threatened Brazilian Atlantic forest

Introduction

Human modification of tropical landscapes is one of the greatest threats to global biodiversity (Morris 2010; Ellis *et al*. 2010; Lewis, Edwards & Galbraith 2015). Over 100 Mha of tropical forest was converted to farmland between 1980 and 2012 (Gibbs *et al*. 2010; Hansen *et al*. 2013), driving a dramatic loss of species in cleared areas (Gibson *et al*. 2011). What remains is a landscape dominated by fragmentation processes, with 25% of remaining rainforest in the Amazon and Congo Basins and 91% in the Brazilian Atlantic forest within 1 km of an edge (Haddad *et al*. 2015). Remaining tropical forests are increasingly isolated, persist in increasingly smaller and more irregular patches, and have greater edge effects (Fahrig 2003; Laurance *et al.* 2006; Arroyo-Rodríguez *et al.* 2013; Magnago *et al*. 2014).

Fragmentation drives both shifts in forest structure and biodiversity. There is an increase in the abundance of trees with low wood density (Laurance *et al.* 2006) that drive a decay in functional diversity in just three decades since isolation (Benchimol & Peres 2015), while edge effects that penetrate into the forest, from wind to woody vines, increase tree mortality (Laurance *et al*. 2002). Fragments thus have reduced carbon stocks compared to contiguous forest (Putz *et al*. 2014; Berenguer *et al*. 2014), particularly at fragment edges (Magnago *et al*. 2015a; Haddad *et al*. 2015). In turn, fragmentation drives the loss of species richness and changes in species composition when compared to contiguous habitat (Laurance *et al*. 2006; Laurance *et al*. 2007; Arroyo-Rodríguez *et al*. 2013; Magnago *et al*. 2014), in smaller versus larger fragments (Laurance *et al*. 2011), at edges versus interiors (Magnago *et al*. 2014), and in more isolated patches (Fahrig 2003; Magnago *et al*. 2015b). These changes are typified by the replacement of rare interior forest species with edge-tolerant generalist species (Arroyo-Rodríguez *et al*. 2013; Carrara *et al*. 2015) and exotic species (Turner 1996).

While much of the knowledge of the effects of fragmentation on biodiversity is based on species richness, abundance, and composition, it is also important to understand the impacts of fragmentation on phylogenetic diversity—the total evolutionary history shared across all species within a community (Arroyo-Rodríguez *et al*. 2012; Winter, Devictor & Schweiger 2013; Cisneros, Fagan & Willig 2015a; Frishkoff *et al*. 2014). Incorporating measures of evolutionary distinctiveness into conservation planning can help us to preserve as much of the tree of life as possible (Mace, Gittleman & Purvis 2003; Redding & Mooers 2006; Isaac *et al.* 2007), while conserving phylogenetic diversity decreases the chance of losing unique phenotypic and ecological traits (Jetz *et al*. 2014), and provides benefits for ecosystem function and stability (Dinnage *et al.* 2012; Cadotte 2013).

Reviewing the literature, we identified seven studies that used phylogenetic metrics to evaluate the effects of forest fragmentation in tropical communities (Table 1). Of these studies, two showed that forest fragments have lower phylogenetic diversity than contiguous landscapes (Santos *et al.* 2014; Munguía-Rosas *et al.* 2014). Four investigated the effect of fragment area and/or amount of forest cover on phylogenetic diversity and phylogenetic structure with conflicting findings: With declining fragment size or percentage forest, bats in Caribbean lowlands, Costa Rica, lost phylogenetic diversity (Cisneros, Fagan & Willig 2015a), trees in the Brazilian Atlantic both lost (Andrade *et al*. 2015) and retained (Santos *et al*. 2010) phylogenetic diversity, and trees in Los Tuxtlas, Mexico, retained phylogenetic diversity (Arroyo-Rodríguez *et al*. *et al*. 2012). Finally, two studies investigated the impact of edges on tree phylogenetic diversity, one revealing reductions at fragment edges (Santos *et al*. 2010), the other no difference between edge and interior (Benitez-Malvido *et al.* 2014).

Beyond the impacts of fragment area and edge effects, the degree of isolation from other fragments and fragment shape are also likely to determine impacts on phylogenetic diversity. This is because the retention of species in fragments is influenced by the level of isolation (Boscolo & Metzger 2011; Magnago *et al*. 2015b) and the shape of fragments (Hill & Curran 2003). However, we identified just one study that investigated the impacts of isolation and fragment shape (Cisneros, Fagan & Willig 2015a). Cisneros, Fagan & Willig (2015a) found that the phylogenetic diversity of bats increased as proximity between forest patches and shape irregularity of patches decreased. A key question therefore is how the phylogenetic diversity of tree communities is affected by fragment isolation and shape.

Trees are critical for habitat structure (Boscolo & Metzger 2011; Pardini *et al*. 2010; Magnago *et al*. 2014), carbon storage (Laurance 2004; Nascimento & Laurance 2004; Magnago *et al*. 2015b), as well as their high diversity (Banks-

Leite *et al*. 2014). Given this and the importance of phylogenetic diversity for conservation and ecosystem functioning, in this study we answer the fundamental question of how configuration and composition metrics affect phylogenetic diversity and structure of trees. We also investigate the impact of edge effects on phylogenetic diversity and structure. We do so in the biodiversity hotspot of the Brazilian Atlantic forest, where the landscape is largely fragmented (Haddad *et al.* 2015) and around 300 tree species are found in just one hectare of forest (Rolim & Chiarello 2004; Saiter *et al*. 2011), making it one of the biologically most important biomes on Earth.

Materials and methods

Study sites

Our 220 km long study area was conducted in Espírito Santo (19°3'48.02" S and 39°58'58.52" W) northwards to southern Bahia (17°43'29.30" S and 39°44'26.60" W), east Brazil (Fig. 1 and see Table S1 for details). Remaining forests in the region are highly fragmented, situated in a matrix of cattle pastures, and plantations of *Eucalyptus* spp., sugar cane, coffee, and papaya (Rolim *et al*. 2005). These forest areas are included in the Atlantic Forest domain (IBGE 1987; also termed Tableland forest, Rizzini 1979), typified by large flat areas rising slowly from 20 to 200 m a.s.l., and according to the Brazilian vegetation classification are Lowland Rain Forest (IBGE 1987). The prevailing climate is wet tropical (Köppen climate classification), with low rainfall from April to September followed by high precipitation from October to March, and with minimal variation in climate across sampling sites: precipitation ranges from 1,228 mm yr^{-1} in Espírito Santo (Peixoto & Gentry 1990) to ~1,403 mm yr^{-1} in Bahia (Gouvêa 1969), with similar average temperatures in the dry season (Espírito Santo ~15.6°C; Bahia ~14°C) and the wet season (Espírito Santo ~27.4°C; Bahia ~23°C).

Historically, the studied landscape remained well preserved until the 1950's. Thereafter, Espírito Santo and Bahia experienced rampant clearcut logging and charcoal production, followed by agriculture (Garay & Rizzini 2004). The main deforestation period in our study area was between 1950s and early 1970s (Simonelli 2007; Magnago *et al*. 2015b), with conversion of forests primarily to sugar cane and cattle pastures. Because our fragments were 40 to

60 years old when sampled, extinction debts of some long-lived tree species are likely still to be paid. However, tree species composition in the interior of smaller fragment alters rapidly (most within the first 10 years since isolation) to reflect a more disturbed community (Laurance *et al*. 1998; Laurance *et al*. 2002; Laurance *et al*. 2006), indicating that our time since isolation is sufficient to detect many important impacts of fragmentation.

Data collection

Fieldwork was conducted between January 2008 and July 2014 in 27 forest fragments that ranged in area from 13 to 23,480 ha (see Table S1 in the Supplementary Methods). Within each fragment, we sampled one transect (except for the second largest fragment of 17,716 ha in which we sampled two transects separated by 4 km), positioned ≥200 m from the forest edge (28 transects in total; see Fig. 1 and Table S1). Additionally, within 11 of these fragments again spanning 13 to 23,480 ha, we sampled one transect (again, two transects separated by 4 km were sampled in the 17,716 ha fragment) each positioned ~5 m from the forest edge and each paired with the plot sampled in the interior of the same fragment (see Magnago *et al*. 2014 and Table S1). We thus have a dataset of 28 interior transects, and 12 edge transects (paired with 12 of the 28 interior transects). On each transect, we sampled 10 plots of 10 m x 10 m (0.1 ha) located at 20 m intervals along each transect, totaling 400 plots (4 ha). We only sampled primary forests, with no evidence of recent logging, although we cannot rule out the occurrence of limited logging several decades ago.

Within each plot, we sampled all individuals living and rooted within our plots with diameter at breast height (DBH; 1.30 metres above ground height) ≥4.8 cm. Individuals that were not identified at the site were collected and classified into morphospecies, subsequently identified by morphological comparison in the Herbarium of Vale (CVRD) or botanical experts for their families. The botanical material collected in reproductive stage was deposited in the Herbarium of the Federal University of Viçosa, Minas Gerais (VIC) and CVRD.

Data analysis

Metrics of fragmentation

We investigate both the configuration (i.e. geometric arrangement, isolation and position of elements [fragments or matrix] within the landscape) and composition (i.e. quality or quantity of elements [fragments or matrix] that compose the landscape) of our focal forest fragments within the study area (Cisneros, Fagan & Willig 2015a; Cisneros, Fagan & Willig 2015b). We identify the configuration and composition characteristics of landscapes using the vegetation map of the Brazilian Atlantic forest (reference year 2005; www.sosma.org.br and www.inpe.br), developed by SOS Mata Atlântica/INPE (2015). This dataset depicts the spatial distribution of the main forest formations within this biome (see also Supplementary Methods, Text S1), and has been used to describe landscape structure via forest loss and fragmentation (Ribeiro *et al*. 2009) and to generate estimates of carbon loss due to habitat fragmentation (Pütz *et al*. 2014). We first divided our landscape into forest (i.e. only Tableland forest) and non-forest (i.e. all other types of natural and non-natural formations). Second, we created a buffer of 5 km around each of the 27 sampled fragments, due to the high level of fragmentation and isolation within our landscapes (see Magnago *et al*. 2014; Magnago *et al*. 2015 and Table S3). However, omission and commission errors were detected after comparison with available very-high optical spatial resolution satellite data from 2012 (World Imagery 2015b), these were then manually corrected to obtain the most accurate spatial delineation of the forest fragments within each 5 km buffer. All forest fragments were then converted to raster format using the same spatial resolution (30 meters) used to generate the vegetation map of this biome.

Fragmentation metrics were computed within the area defined by the 5 km buffer around each forest fragment and using the implementation given in FRAGSTATS (v 4.2; McGarigal *et al*. 2012; except ‘source distance’ see below). Furthermore, all metrics were computed using the eight-cell neighbourhood rule and considering a search radius of 5 km. For each fragment we measured five metrics related to landscape configuration (see Table S2 in the supplementary material for full details of each metric): (1) forest shape index - measures the level of shape complexity on a per fragment basis. A low number, indicates fragments are more regular and thus have less edge effects; (2) landscape shape index - measures the degree of shape complexity of all fragments belonging to the same class (forest) across a landscape. For a given forest area, a low number means that fragments within a landscape are on average more regularly shaped and thus have less edge effects; (3) forest nearest neighbour - gives the Euclidean distance to the nearest neighbour forest patch. A low number suggests less isolation; (4) mean forest nearest neighbour – gives the average value of the forest nearest neighbour metric when considering all forest fragments within each buffer; and (5) source distance – measures distance to the nearest forest patch having an area of at least 1,000 ha, with a low number suggesting less isolation. This metric was computed with ArcGis (v 10.1) using as a base the vegetation map of Brazilian Atlantic forest (SOS Mata Atlântica/INPE (2015) (Table S2).

For each fragment, we additionally measured three metrics of landscape composition again using the implementation given in FRAGSTATS (see Table S2 for full details of each metric): (6) forest patch size – measures the area of the focal fragment; (7) forest cover – measures the percentage of the landscape covered by forest, with a high number reflecting largest remaining forest cover; and (8) forest patch density – measures the number of fragments in 100 hectares within each landscape.

Phylogeny construction

For the preparation of our phylogenetic tree, we constructed a list of all our family/genus/species according to APG III (2009). In the program Phylocom version 4.2 (Webb *et al*. 2008), we then used the PHYLOMATIC function to return the phylogenetic hypothesis for the relationship between our 72 families, 273 genera and 604 species sampled in 6,802 tree individuals, using the new modified megatree R20120829mod.new for vascular plants from Gastauer & Meira-Neto (in press). In our phylogenetic hypothesis more than two species per family or more than two genera of an unresolved family in R20120829mod.new were inserted as polytomies. Finally, to estimate the lengths of branches in millions of years for our ultrametric phylogenetic tree, we used the file "ages_exp", (Gastauer & Meira-Neto, in press) and the BLADJ algorithm in Phylocom program version 4.2 (Webb *et al*. 2008, see Fig. S1).

Measures of phylogenetic diversity and structure

From our phylogenetic hypothesis we calculate six phylogenetic metrics weighted by the abundance:

1) *PD* (phylogenetic diversity) - the sum of evolutionary history in a community (Faith 1992). This metric is given in millions of years.

2) *SES.PD* (the standard effect size (SES) of PD) – PD is positively related with species richness (Swenson 2014). Thus, SES.PD was calculated by comparing observed PD with that of null communities of equal species richness (Swenson 2014). Positive values of SES.PD indicate higher PD than expected by chance for a given species richness, while negative values indicate lower PD than expected by chance.

3) *MPD* (mean pairwise distance) – mean phylogenetic distance between all combinations of pairs of individuals (given in millions of years; Webb *et al*. 2000). High values suggest greater evolutionary distance between pairs of individuals sampled and negative values decrease this distance.

4) *SES.MPD* (the standard effect size (SES) of MPD) – MPD corrected for species richness. Positive values indicate that the co-occurrence of pairs of individuals which are phylogenetically close is greater than expected by chance (phylogenetic clustering) and negative values that pairs co-occuring individuals are phylogenetic more distant than expected by chance (*phylogenetic overdispersion)* (Webb *et al*. 2000; Webb *et al*. 2002).

5) *MNTD* (mean nearest taxon distance) – mean phylogenetic distance between an individual and the most closely related (non-conspecific) individual (given in millions of years; Webb *et al*. 2000). Low levels suggest that closely related pairs of individuals (non-conspecific) co-occur and high values that they do not.

6) *SES.MNTD* (the standard effect size (SES) of MNTD) - MNTD corrected for species richness. High values indicate the co-occurrence of individuals more closely related than expected by chance given the species richness (phylogenetic clustering) and negative values that the co-occurrence of related individuals is lower than expected by chance (*phylogenetic overdispersion)* (Webb *et al*. 2000; Webb *et al*. 2002).

We calculated these six metrics using “picante” package (Kembel *et al*. 2010) in R, version 3.2.1 (R Development Core Team. 2015). For the standard effect size (SES) calculations, our tree was compared with 10,000 null model randomizations using the algorithm "phylogeny pool", with the result for

SES.MPD and SES.MNTD multiplied by -1 (Swenson 2014). The applied null model randomizes the identity of species occurring in each sample, however maintains constant species richness and abundance within each transect. It Assuming therefore, that all species are equally likely to occur in any fragment in the landscape (Arroyo-Rodríguez *et al*. 2012).

Statistical analyses

We analysed the effects of landscape configuration and composition on each phylogenetic metric using Generalized Linear Models, with Gaussian error and an identity link (normality was tested and confirmed by the Shapiro Wilk test), as implemented in the 'glm' function from *stats* package. For each metric of phylogenetic diversity (PD, MPD and MNTD), phylogenetic structure (SES.PD, SES.MPD and SES.MNTD) and species richness, we then used the "dredge" function in the MuMIn package to find all possible combinations among our landscape variables for the global model. The model with the lowest Akaike Information Criterion of Second Order (∆AICc, indicated for small sample sizes) was selected as the best model (Burnham *et al*. 2011). Log transformations were used to reduce the variance heterogeneity for forest shape index, source distance and forest patch size measurements. Lastly, given that predictor landscape variables may have high multi-collinearity (Boscolo & Metzger 2011), we used the variance inflation factor (VIF) to identify any correlated variables (i.e. VIF values ≥10); however, because VIF values ranged from 2.90 (i.e. forest patch size) to 10 (i.e. forest cover), we did not remove any variable.

Additionally, we investigated the impacts of fragment area and edge effects on metrics of phylogenetic diversity, phylogenetic structure and species richness. We considered two predictor variables: (i) fragment size in log scaled and (ii) habitat type with two levels (edge and interior). We also consider the possible interactions between these two predictor variables (see Magnago *et al*. 2014 for details). These analyzes were conducted using Generalized Linear Mixed Model (GLMM), with site as a random variable (Bolker *et al*. 2009). The GLMM was built using the function "lmer" in the package *lme4*, with Gaussian error and an identity link. After creating each model, we applied the "dredge" function in the package MuMIn and our best model was considered the one with value of ∆AICc = 0. All statistical analyses were performed in R, version 3.2.1 (R Development Core Team. 2015).

Results

We recorded 6,802 Individuals of 604 tree species, spanning 273 genera and 72 families according to the classification of the Angiosperm Phylogeny Group's III (2009) across our 28 interior transects and 12 edge transects.

Impacts of landscape configuration on phylogenetic diversity

Our fragments varied substantially in terms of their configuration, with between a seven- and 13,000-fold variation in minimum and maximum values (Table S3). However, none of our phylogenetic diversity metrics (i.e. PD; MPD and MNTD) was affected by any characteristics of landscape configuration according to our best models (in which ΔAICc=0; Tables 2 and S4).

For phylogenetic structure (i.e. SES.PD, SES.MPD and SES.MNTD), our best models (Tables 2 and S4) showed that SES.MPD was negatively affected by increasing landscape shape index (t = -2.553, P < 0.017, Fig. 2a), indicating that increasing irregularity of landscapes leads to an increase in the co-occurrence of pairs of individuals more distant phylogenetically (*phylogenetic overdispersion).* In addition, our best models indicated a marginally significant negative effect of forest shape index on SES.MPD (t = -1.721, P = 0.098, Fig. 2b).

In relation to species richness, no landscape configuration metric significantly explained the number of species in fragments, according to our best model (Tables 2 and S4). Finally, across all thirty-six selected models (ΔAICc<2; Table S4), landscape shape index and source distance (both seven times) were the most frequently selected variables, with forest shape index and forest nearest neighbour (both four times) the next most frequently selected variables.

Impacts of landscape composition on phylogenetic diversity

Our fragments varied substantially in terms of their composition, with between a five- and 1,800-fold variation in minimum and maximum values (Table S3). Considering only the best model (Tables 2 and S4), phylogenetic diversity (PD) was positively related to forest cover (t = 4.394, P < 0.0001, Fig. 3a), indicating that landscapes with higher forest cover retain a larger amount of evolutionary history in their remaining forests. We also found that with increasing forest patch density there was a marginally significant decrease of MPD (t = -1.719, P = 0.097, Fig. 3b).

Considering our best models of phylogenetic structure (Tables 2 and S4), we found a positive effect of increasing forest patch density on SES.MPD (t = 3.391, P < 0.0002, Fig. 3c), indicating that co-occurring individuals are more closely related than expected by chance (phylogenetic clustering). In contrast, we found a marginally significant negative effect of forest cover on SES.MNTD (t = -1.793, P = 0.084, Fig. 3d).

In terms of species richness, our best models (Tables 2 and S4) indicate a positive effect of forest cover (t = 4.436, P < 0.0001, Fig. S2). In addition, we found a positive and marginally significant effect of forest patch density of landscapes on species richness (t = 1.823, P = 0.081). Lastly, across all thirty-six selected models (ΔAICc<2; Table S4), forest patch density (15 times) and forest cover (11 times) were frequently selected, whereas forest patch size was only selected twice. Thus, metrics of phylogenetic diversity are most frequently impacted by forest cover and forest patch density.

Impacts of fragment size and edge-effects on phylogenetic diversity

Considering our best model (Tables 3 and S5), phylogenetic diversity (PD) was significantly affected by the interaction between fragment size and interior versus edge of the fragments (t = -3.470, P < 0.004, Fig. 4a): with increasing fragment size, we found a reduction of PD in interiors (F = 6.685, P < 0.027, Fig. 4a), but no significant change of PD at edges (F = 2.530, P = 0.142, Fig. 4a). PD was significantly greater in fragment interiors than fragment edges (t = 3.773, P < 0.002, Fig. 4b).

In terms of phylogenetic structure, our landscapes were little affected by habitat type and were not affected by fragment size (Tables 3 and S5). SES.MNTD was lower in interior than in edge locations (t = -2.672, P < 0.020, Fig. 4c), indicating phylogenetic overdispersion inside fragment versus phylogenetic clustering at edges.

In addition, we found that species richness was significantly affected by the interaction between the size of the fragments and interior versus edge of the sampled transects (t = 1.842, P < 0.010, Fig. S3a): with increasing fragment size, there was a reduction in species richness in interiors (F = 7.420, P < 0.021, Fig.

S3a), but no significant change at edges (F = 1.852, P = 0.203, Fig. S3a). Species richness was significantly higher in fragment interiors than in fragment edges (t = 3.045, P < 0.005; Fig. S3b).

Finally, across all seventeen selected models (ΔAICc<2; Table S5), only habitat (edge vs interior) was frequently selected (10 times), with forest fragment size (5 times) the next most frequently selected. The interaction between fragment size and habitat type (edge vs interior; three times) was rarely selected.

Discussion

Forest fragmentation is a major driver of the global extinction crisis (Haddad *et al*. 2015; Lewis, Edwards & Galbraith 2015). A key question is how the degree of isolation and shape of forest fragments impacts phylogenetic diversity. Saving phylogenetic diversity prevents the loss of evolutionarily unique species (Purvis *et al*. 2000; Vamosi *et al*. 2008), conserves as much of the tree of life as possible (Mace, Gittleman & Purvis 2003; Redding & Mooers 2006; Isaac *et al.* 2007) and underpins the retention of key ecosystem services and functions (Cadotte, Cardinale & Oakley 2008; Cadotte 2013). Focusing on trees communities within the globally threatened Brazilian Atlantic forest, we find that with increasing forest cover there was higher retention of phylogenetic diversity and that with more irregular fragments (i.e. more edge effected) and with increased density of fragments in the landscape was a reduction in the phylogenetic distance between pairs of co-occurring individuals (SES.MPD, more clustering). Fragmentation can thus lead to profound changes in the evolutionary history stored in these remaining fragments (Santos *et al*. 2014; Munguía-Rosas *et al*. 2014). There was, however, no significant impact of the configuration characteristics of fragments and landscapes (i.e. shape and isolation) on phylogenetic diversity (PD, MPD and MNTD), suggesting that fragments remaining in these landscapes still retain important regional tree evolutionary history, as well as important ecosystem functions (Magnago *et al*. 2014; Magnago *et al*. 2015b).

Impacts of landscape configuration on phylogenetic diversity

That no phylogenetic diversity metric was affected by the configuration of landscape features suggests that recently fragmented landscapes (i.e. <100 years) have not led to profound changes in the phylogenetic diversity. These new findings indicate the possibility that landscape configuration has not promoted profound changes in productivity of trees (Cadotte *et al*. 2013) and ecosystem stability (Cadotte, Dinnage & Tilman 2012). However, landscape configuration affected the phylogenetic diversity of bats in Costa Rica, with decreased phylogenetic diversity with increased isolation (Cisneros, Fagan & Willig 2015a). Presumably bats have more rapid relaxation following fragmentation than do trees, and consequently, while phylogenetic diversity of trees is presently retained even in isolated and edge dominated fragments, over centennial timescales, this could slowly degrade if isolation is not reversed.

Phylogenetic structure within fragments was affected by landscape configuration, with higher landscape shape index (more edge effects) causing individuals of co-occurring species to be more distantly related than expected by chance (i.e. SES.MPD<0; Fig. 2a). Firstly, increasing complexity of landscape form could filter individuals of tree species from across the entire phylogenetic tree, but not whole clades (Arroyo-Rodríguez *et al*. 2012). Secondly, more edge effects could facilitate the spill-over of individuals of species from fragment edges (Hill & Curran 2003) and the non-forest matrix (Cook *et al*. 2002; Cisneros, Fagan & Willig 2015a), which in many cases are likely to have evolved from different lineages than forest interior trees. Both possibilities are supported by the fact that with increasing complexity of the landscape, the remaining forests are more susceptible to the impacts of edge effects (Ranta *et al*. 1998; Hill & Curran 2003; Ewers & Didham 2006).

Impacts of landscape composition on phylogenetic diversity

Phylogenetic diversity (PD) was higher in landscapes with more forest cover (Fig. 3a), but this might be partially explained by increases in species richness (see Table 2 and Figure S2; *Faith* 1992; Swenson 2014). However, the loss of evolutionary history to reduced forest cover in the threatened Brazilian Atlantic forest is also supported by the fact that MPD of species in the Rubiaceae increases with more forest cover (Andrade *et al*. 2015; but see Arroyo-Rodríguez *et al*. 2012), and more generally, that increasing habitat loss drives profound changes in species composition, functional groups and carbon storage (Laurance *et al*. 2006; Tabarelli *et al*. 2010; Magnago *et al*. 2014; Magnago *et al*. 2015b).

Phylogenetic structure within fragments was also affected by landscape composition, with lower forest patch density (more isolation and edge effects; Fahrig 2003) causing individuals of co-occurring species to be more phylogenetically dispersed (i.e. SES.MPD<0; Fig. 3c). As with the impacts of higher edge effects on SES.MPD (Fig. 2a), it seems likely that more disturbance filters individuals of tree species from across the entire phylogenetic tree, but not whole clades (Arroyo-Rodríguez *et al*. 2012), and that phylogenetically unique species (versus those from forest interiors) colonize from fragment edges (Hill & Curran 2003) and the non-forest matrix (Cook *et al*. 2002; Cisneros, Fagan & Willig 2015a). Additionally, increased isolation also limits the dispersion of seed between remaining forests, decreasing similarity in species composition between isolated forest patches (Hubbell 2001; Chave 2008; Duque *et al*. 2009), and possibly leading to lower similarity of evolutionary characteristics between species.

Impacts of fragment size and edge-effects on phylogenetic diversity

PD was higher in the interior of smaller fragments than in the interior of large fragments (Fig. 4a), whereas other studies either found no impact of area on phylogenetic diversity for trees (Santos *et al*. 2010; Arroyo-Rodríguez *et al*. 2012) or higher phylogenetic diversity of bats in larger fragments (Cisneros, Fagan & Willig 2015a). While we sampled higher species richness in the interiors of small than of large fragments (see Table 3; Fig. S3a and Magnago *et al*. 2014), differences are also likely to reflect changes in the evolutionary history of species presents, which exhibit lower functional redundancy, more disturbance-adapted species, and low prevalence of zoochoric fruit, fleshy fruit and medium seeds (Magnago *et al*. 2014).

We found lower PD at edges than interiors (Fig. 4b; Santos *et al*. 2010, but see Benítez-Malvido *et al*. 2014). In our fragments, edge effects change microclimatic conditions (Magnago *et al*. 2015a), reduce species richness (see Fig. S3b; see also Laurance *et al*. 2006) and alter functionality (Magnago *et al*. 2014). Thus while reductions in species richness again likely part explain the loss of PD, reductions are also underpinned by other ecological factors.

Lastly, we found higher SES.MNTD at edges than interiors (Fig. 4c), indicating that the evolutionary distance between species pairs of individuals within family or genera is less than expected by chance. Because edge effects reduce community dissimilarity (Laurance *et al*. 2006) and important functional groups (Lopes *et al*. 2009; Magnago *et al*. 2014), the next individual sampled is likely a close relative of at least one kind of individual already sampled. However, recent work in the Brazilian Atlantic forest (Santos *et al*. 2010) and Mexican dry forest (Benítez-Malvido *et al*. 2014) found no impact of edge effects on the phylogenetic structure of tree, suggesting that they were predominantly assembled by stochastic processes (Hubbell 2001).

Conclusions and conservation implications

Tropical forests are suffering dramatic levels of deforestation (Gibbs *et al*. 2010; Hansen *et al*. 2013) and fragmentation (Haddard *et al*. 2015), with landscape features such as shape, isolation, and density of fragments limiting ecological processes and change the evolutionary characteristics of communities (Laurance *et al*. 2002; Fahrig 2003; Laurance *et al*. 2006; Ewers & Didham 2006; Haddad *et al*. 2015). However, these features did not affect the phylogenetic diversity of trees, while reduced forest cover has led to loss of evolutionary history. On the one hand, this underscores the importance of protecting large forest blocks and/or many fragments in a landscape that retains much forest cover (Pardini *et al*. 2010; Gibson *et al*. 2011; Arroyo-Rodríguez *et al*. 2012). On the other hand, this suggests that where the vast majority of forest cover has been lost there is limited benefit of protecting the few remaining patches for retention of phylogenetic diversity and potentially that dispersal (rescue effects) is limited in such highly fragmented landscapes. These results suggest that conservation must seek to extend forest cover via forest restoration to enhance patch area, patch connectivity and/or patch density in highly threatened regions, such as the Brazilian Atlantic and Tropical Andes.

From a conservation perspective, it is encouraging that phylogenetic structure (SES.MPD) was positively affected by increasing fragmentation effects. When compared to fragments in a more natural state (i.e., larger blocks, less isolated, lower edge effects), edge effected and/or isolated fragments are able to retain a range of evolutionary histories resulting in phylogenetic overdispersion. Future studies should investigate the quality of these changes in light of resource availability for fauna (Magnago *et al*. 2014), the matrices in which the remnants are immersed (Cisneros, Fagan & Willig 2015a), and how phylogenetic structure changes following forest restoration.

Finally, our results underscore the potential conservation value of small fragments (especially within landscapes that retain much forest cover), which harboured more phylogenetic diversity in their interiors than did the interiors of larger patches. Such fragments could represent important sources of seeds of evolutionarily distinct species for restoration projects, as well as stepping-stones for dispersal between larger, viable patches.

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Tables

Table 1 - Studies investigating the phylogenetic diversity and phylogenetic structure in the tropics through fragmentation effects. Phylogenetic metric abbreviations: MPD, mean phylogenetic distance; MNTD, mean nearest taxon phylogenetic distance; NRI, net related index; NTI, nearest taxon index; Rao`s Q, Rao's quadratic entropy; PSV, phylogenetic species variability metric; PSE, phylogenetic species evenness metric; PS, phylogenetic structure of PSV and PSE.

Taxon	Geographic region	Fragmentation metric (s)	Phylogenetic metric (s)	Study
Trees	Brazilian Atlantic forest	Area, edge	MPD, MNTD, NRI, NTI	Santos *et al.*, 2010
Trees	Mexico - Los Tuxtlas	Area, % cover	MPD, MNTD, NRI, NTI	Arroyo-Rodríguez *et al.*, 2012
Trees	Brazilian Amazon forest	Contiguous *vs.* fragmented forest	MPD, NRI	Santos *et al.*, 2014
Bats	Costa Rica - Caribbean lowlands	Area, edge, % cover, isolation, shape, matrix type	Rao's Q	Cisneros, Fagan & Willig, 2014
Trees	Mexico - Yucatan Peninsula	Contiguous *vs.* fragmented forest	MPD, MNTD, NRI, NTI	Munguía-Rosas *et al.*, 2014
Trees	Mexico - western coast of Jalisco	Edge, matrix type	PSV, PSE, PS	Benítez-Malvido *et al.*, 2014
Trees	Brazilian Atlantic forest	% cover	MPD, MNTD, NRI, NTI	Andrade *et al.*, 2015

Table 2 - Results for the generalized linear models for the impacts of landscape configuration and composition metrics of landscapes on the phylogenetic diversity and phylogenetic structure. We present only the best models according to Akaike information criterion corrected for small samples (∆AICc=0). SES.PD = standardized value of phylogenetic diversity (PD); MPD = mean phylogenetic distance (millions of years); SES.MPD = standardized value of MPD; MNTD = Mean nearest taxon phylogenetic distance (millions of years) and SES.MNTD = standardized value of MNTD.

Model	Parameter	Estimate	SE	*t* value	*P* value
PD	Intercept	3607.82	140.83	25.62	0.0001
	Forest cover (%)	28.19	6.41	4.39	0.0001
SES. PD	Intercept	-0.09	0.16	-0.57	0.572
MPD	Intercept	215.76	3.41	63.22	0.0001
	Forest patch density (in 100 ha)	-17.56	10.22	-1.72	0.097
SES. MPD	Intercept	-0.19	0.69	-0.28	0.783
	Forest shape index (log)	-2.42	1.41	-1.72	0.098
	Landscape shape index	-0.18	0.07	-2.55	0.017
	Forest patch density (in 100 ha)	5.44	1.60	3.39	0.002
MNTD	Intercept	82.76	1.44	57.55	0.0001
SES. MNTD	Intercept	0.01	0.28	0.04	0.972
	Forest cover (%)	-0.02	0.01	-1.79	0.084
Species richness	Intercept	55.44	5.64	9.84	0.0001
	Forest cover (%)	0.65	0.15	4.43	0.0001
	Forest patch density (in 100 ha)	26.11	14.35	1.82	0.081

Table 3 - Results for the generalized linear mixed model for the impacts of fragment size and fragment location (edge vs. interior). We present only the best models according to Akaike information criterion corrected for small samples (∆AICc=0). SES.PD = standardized value of phylogenetic diversity (PD); MPD = mean phylogenetic distance (millions of years); SES.MPD = standardized value of MPD; MNTD = mean nearest taxon phylogenetic distance (millions of years) and SES.MNTD = standardized value of MNTD. Habitats = edge and interior.

Model	**Parameter**	**Estimate**	**SE**	***t* value**	***p* value**
PD	Intercept	3866.35	257.27	15.03	0.0001
	Forest patch size (log(ha)) : Habitats (Interior)	-394.23	113.62	-3.47	0.004
	Habitats (Interior)	1240.75	328.85	3.77	0.002
SES. PD	Intercept	-0.13	0.20	-0.64	0.536
MPD	Intercept	208.88	1.47	142.40	0.0001
SES. MPD	Intercept	1.28	0.22	5.74	0.0001
MNTD	Intercept	76.48	2.01	38.03	0.0001
	Habitats (Interior)	5.14	2.84	1.81	0.083
SES.MNTD	Intercept	0.16	0.21	0.76	0.453
	Habitats (Interior)	-0.79	0.30	-2.67	0.020
Species richness	Intercept	69.40	6.65	10.44	0.0001
	Forest patch size (log(ha)) : Habitats (Interior)	-8.98	2.30	1.84	0.010
	Habitats (Interior)	28.64	9.40	3.05	0.005
	Forest patch size (log(ha))	4.22	3.25	-2.76	0.078

Figures (High resolution files available if accepted for publication)

Figure 1

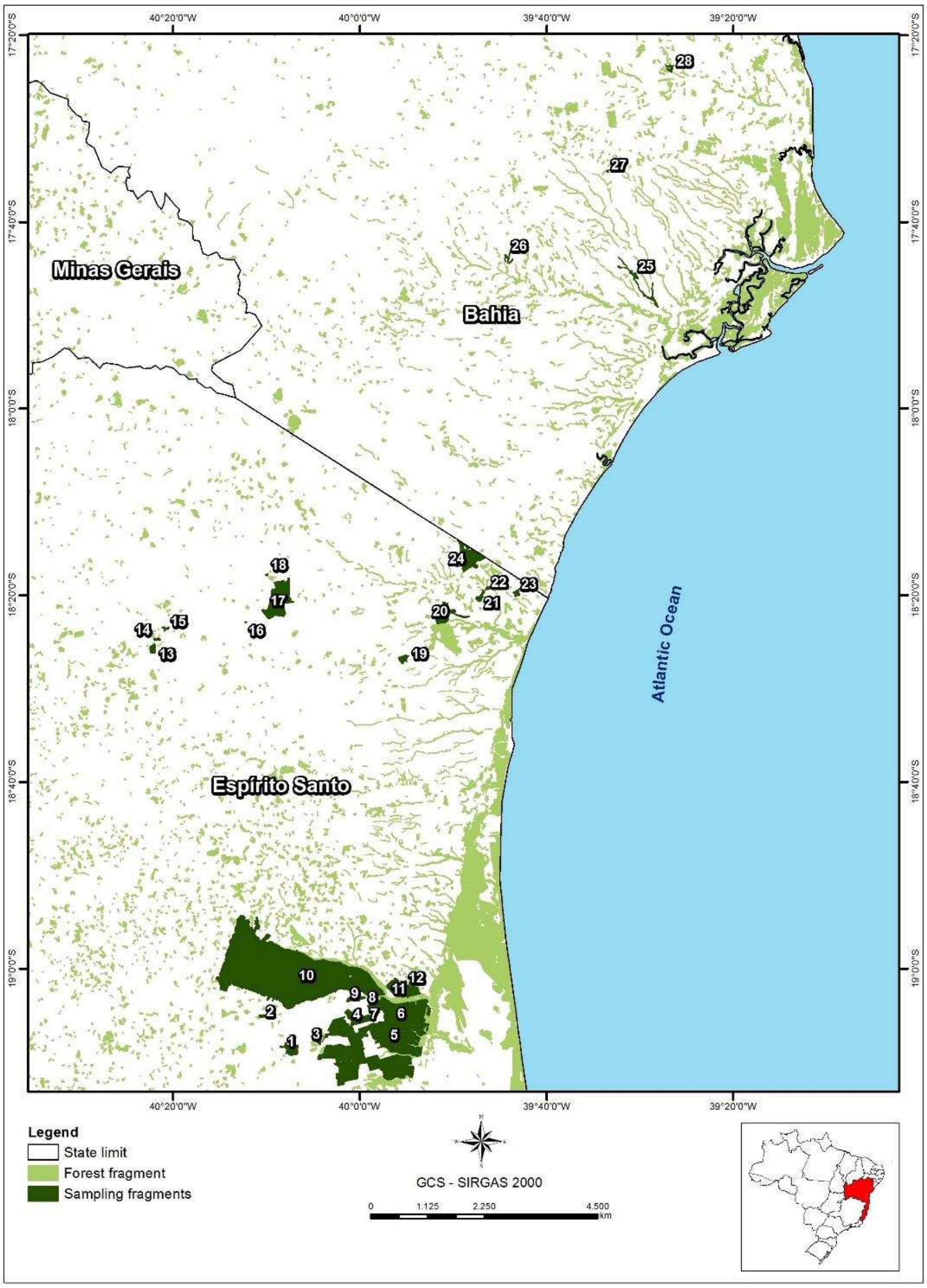

Fig. 1 - Study area and forest fragments sampled in the Brazilian Atlantic Forest. Size of each fragment and their coordinates can be seen in Table S1.

Figure 2

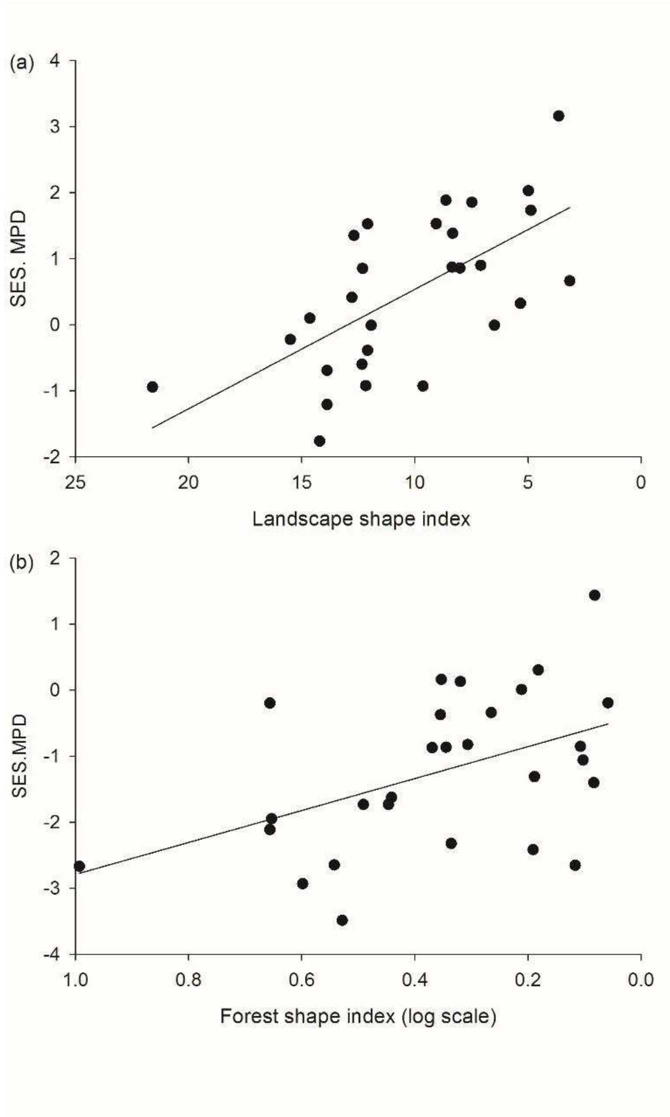

Fig. 2 - Effect of landscape shape index (a) and forest shape index (b) on the phylogenetic structure (SES.MPD), analyzed in 28 transects sampled in the Brazilian Atlantic forest. The values for graph were obtained after the summation of the raw residuals with the expected values for variable (y), assuming average value for the variable (partial residuals plots). The x-axes of (a) and (b) have been reversed to aid interpretation: *lower* values indicate less edge effects.

Figure 3

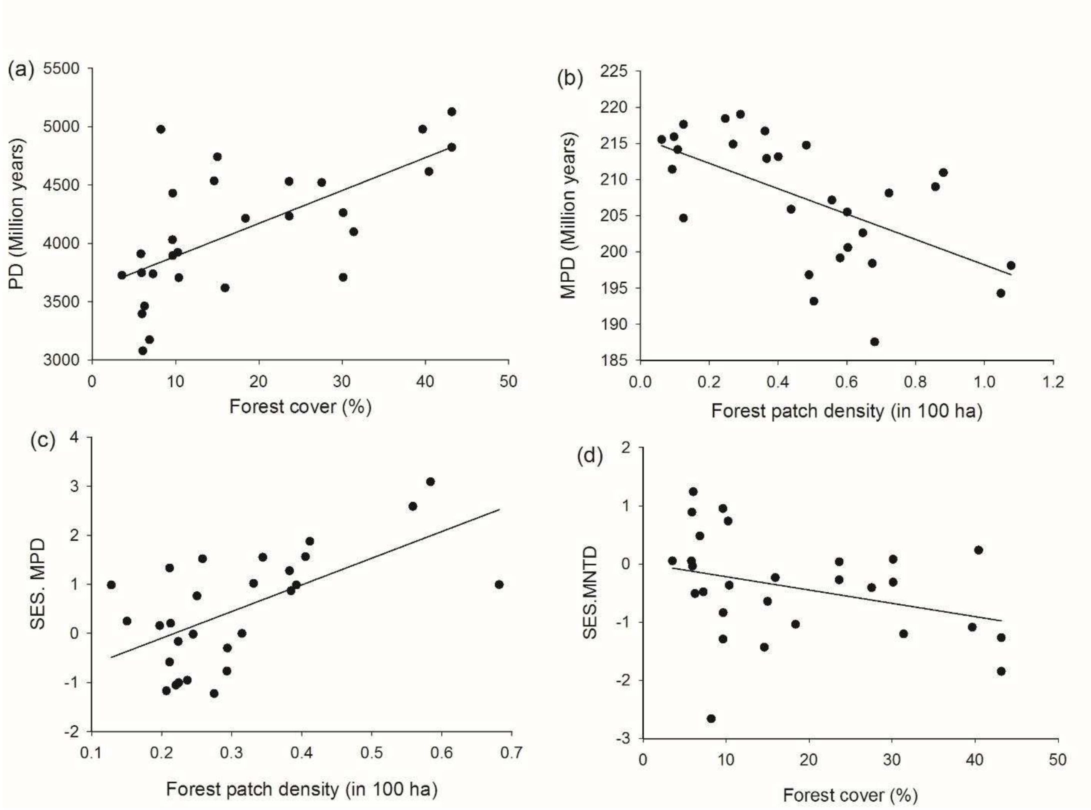

Fig. 3 - Relationship between landscape composition, and phylogenetic diversity and structure. (a) The effect of forest cover (%) on PD; (b) the effect of forest patch density (in 100 ha) on MPD; (c) the effect of forest patch density (in 100 ha) on SES.MPD; and (d) the effect of forest cover (%) on SES.MNTD. The values for each graph were obtained after the summation of the raw residuals whit the expected values for each variable, assuming average values for other variables (partial residuals plots).

Figure 4

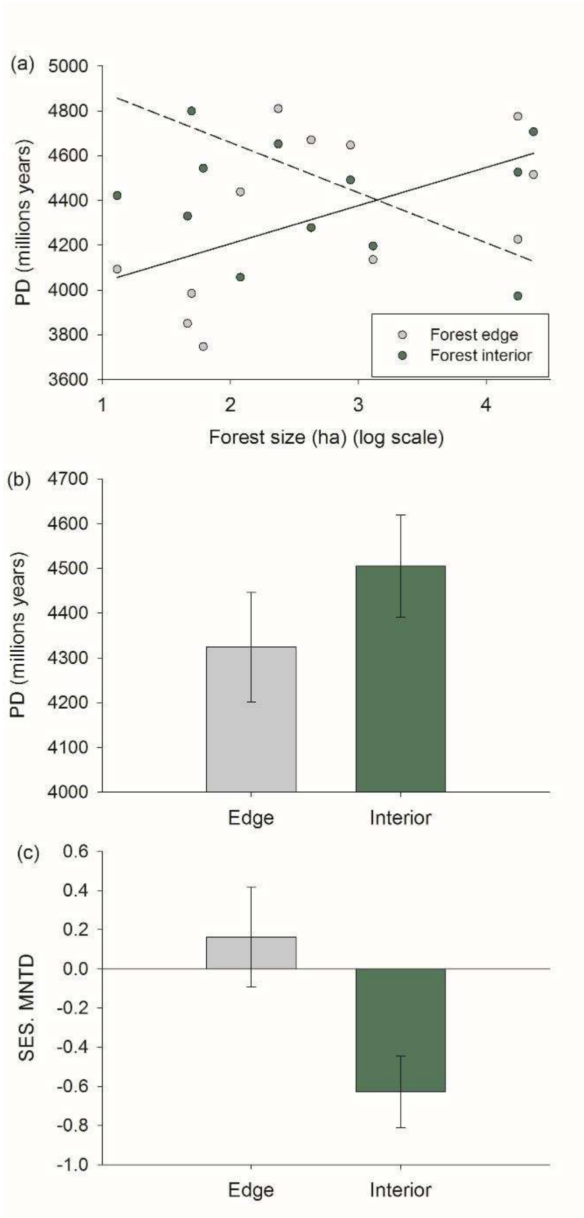

Fig. 4 - Relationship between fragment area and location (i.e. edge vs. interior) with phylogenetic diversity and structure sampled in 24 transects of the Atlantic forest. (a) The effect of the interaction between fragment size and habitat on phylogenetic diversity PD, partial residuals plots; (b) the effect of habitat on phylogenetic diversity PD; and (c) the effect of habitat on phylogenetic structure SES.MNTD. Continuous line (forest edge) and dashed line (forest interior); circles represent values obtained after summation of raw residuals with the expected values for each variable, assuming average values for other covariates; errors bars represent standard errors.

IV. CAPÍTULO II

Impacts of forest fragmentation on the functional diversity of trees: roles of landscape configuration and composition in the Brazilian Atlantic forest

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ABSTRACT
Forests fragmentation is one of the main causes of global biodiversity loss, impacting the distribution of functional traits within communities. Conserving functional diversity decreases the loss of phenotypic characteristics that play important roles in ecosystem processes. We evaluate the impacts of landscape configuration (i.e., shape and isolation) and landscape composition (i.e., area, cover and patch density) on (i) functional diversity, (ii) functionally unique species; and (iii) the richness and abundance of functional characteristics of trees in 27 fragments within the threatened Brazilian Atlantic forest. We used four functional diversity metrics commonly used in conservation studies (i.e., functional richness, evenness, divergence and dispersion). In terms of landscape configuration, higher forest shape index (irregularity promoting edge effects) reduced functional divergence and functional dispersion, while increasing isolation negatively impacted functional evenness and positively impacted functional divergence. In terms of landscape composition, smaller fragments had higher functional evenness and lower forest cover led to increased functional dispersion. We also found that increasing forest patch density reduced the richness and abundance of species adapted to disturbance and increased species with high wood density. Finally, there was no impact of landscape characteristics on functionally unique species. These results suggest that higher isolation increases niche differentiation via increase of species adapted to disturbance, while landscape composition increased niche homogenization. In highly threatened tropical regions, conservation must seek to expand connectivity, forest cover or increase patch density between patches via secondary forest restoration to reverse the negative impacts of fragmentation and retain key functional traits and processes.

Key-words: Habitat fragmentation, landscape structure, functional structure, functional trait attributes, wood density, tableland Atlantic rain forest

Introduction

Tropical forests are increasingly human-dominated (Lewis et al., 2015): the conversion of more than 1.5 million hectares of tropical forest to agriculture between 1980 and 2012 (Gibbs et al., 2010; Hansen et al., 2013) plus the associated fragmentation of remaining forests represent the main drivers of global biodiversity loss and ecosystem degradation (Morris, 2010; Ellis et al., 2010). So severe are these processes that 25% of the vast Congo and Amazon basins and 91% of the Brazilian Atlantic forest are within 1 km of an edge (Haddad et al., 2015). Fragmentation creates landscapes with forest patches of different sizes, shapes and isolation levels (Fahrig, 2003; Ewers and Didham, 2006). In turn, each patch is affected by abiotic changes especially at edges, including increased wind, temperature and desiccation (Laurance et al., 2002; Magnago et al., 2015a), and with big implications for species persistence and their movement between fragments (Vieira et al., 2009; Boscolo and Metzger, 2011; Laurance et al., 2011). Given predictions that forest fragmentation will increase (Haddad et al., 2015; Lewis et al., 2015), understanding the effects that these 'new landscapes' have on biodiversity is crucial.

Species richness, community composition and phylogenetic diversity are strongly influenced by fragmentation (Magnago et al., 2014, Santos et al., 2010; Andrade et al., 2015; Cisneros et al., 2015a). Reducing fragment area and increasing edge effects both tend to result in the loss of species (Ewers and Didham, 2006; Magnago et al., 2014) and changes in species composition (Laurance et al., 2002; Hill and Curran, 2003; Magnago et al., 2014; Benchimol and Peres, 2015), often via shifts in resource availability (e.g., food for fauna; Lopes et al., 2009). These changes are typified by the replacement of rare interior forest species with edge-tolerant generalist species (Arroyo-Rodríguez et al., 2013; Carrara et al., 2015) and exotic species (Turner, 1996). Fragmentation also tends to most strongly negatively impact those species that are most evolutionarily distinct (Purvis et al., 2000; Vamosi and Wilson, 2008).

It is also important to understand the impacts of forest fragmentation on the roles that species play within communities to shape ecological processes. Functional diversity measures the variability of functional attributes among species within a community (Petchey and Gaston, 2006), generally using attributes that affect the performance of the species in a community (Díaz and Cabido, 2001; Pérez-Harguindeguy et al., 2013). It has the advantage over approaches that compare abundances of members of different functional guilds (Azhar et al., 2013; Gilroy et al., 2015) in accounting for within-guild variation between species (such as concurrent differences in body size and beak morphology; Edwards et al., 2013). Conserving high functional diversity is expected to both retain functionally unique species (O`Gorman et al., 2011) and the provisioning of ecosystem services via a variety of mechanisms (Tilman et al., 1997; Petchey and Gaston 2006; Cardinale et al., 2012; Hooper et al., 2005). For instance, functional diversity was a better predictor of variation in above-ground biomass, and thus carbon storage, than was species richness in manipulative experiments in European grasslands (Petchey et al., 2004).

Recent studies investigating the impacts of tropical forest fragmentation on functional diversity (FD) have tended to focus on area, forest cover, and edge impacts across an array of taxa. In terms of area effects, results are contrasting: in Los Tuxtlas, Mexico, the FD of copro-necrophagous beetles was lower in small than in larger fragments (Barragán et al., 2011), as was the FD of mammals in a global meta-analysis (Ahumada et al., 2011), whereas FD was higher in small than in larger fragments for trees in the Brazilian Atlantic forest (Magnago et al., 2014) and bats in Costa Rica (Cisneros et al., 2015a). In terms of forest cover effects, in the Brazilian Atlantic forest, the FD of birds was higher with smaller percentage of forest cover (De Coster at al., 2015). Lastly, FD of tree species in the Brazilian Atlantic forest was lower at the edge than in the interior of the fragments (Magnago et al., 2014), and FD of pollination systems gradually decreased from forest interior to edges (Lopes et al., 2009).

Beyond the impacts of fragment area and edge effects, the degree of isolation from other fragments (Boscolo and Metzger, 2011; Magnago et al., 2015b) and fragment shape (Hill and Curran, 2003) influence species retention in fragments and, therefore, are also likely to determine impacts on functional diversity. However, to our knowledge there is just one study investigating the impacts of isolation and fragment shape on FD (Cisneros et al., 2015) revealing that the FD of bats increases when shape irregularity decreases (i.e., less edge to interior ratio) and proximity (i.e., connectivity) increases between fragments. A key question therefore is how the functional diversity of tree communities is affected by the shape and isolation of fragments, since these communities are critical for habitat structure (Boscolo and Metzger, 2011; Pardini et al., 2010; Magnago et al., 2014), carbon storage (Laurance, 2004; Nascimento and

Laurance, 2004; Magnago et al., 2015b), as well as their high diversity (Banks-Leite et al., 2014).

In this study, we examined the effects of configuration and composition of landscapes on the functional diversity of trees on 27 fragments of the threatened Brazilian Atlantic forest (Myers et al., 2000). The Atlantic forest retains just 11% of its original forest cover (Ribeiro et al., 2009), which nevertheless provides vital habitat and resources for much threatened fauna (Moran and Catterall, 2010; Magnago et al., 2014), considerable primary production (Barber, 2007) and carbon stocks (Pütz et al., 2014), and thus co-benefits between carbon and biodiversity (Magnago et al., 2015b). Our study had three specific objectives: (1) to evaluate the effect of configuration and composition of landscapes on four functional diversity indices; (2) to evaluate the effect of configuration and composition of landscapes on functionally unique species; and (3) to determine how metrics of configuration and composition affect the richness and abundance of functional characteristics of trees vulnerable to fragmentation.

Materials and methods

Study sites

Our study area was based in Espírito Santo (19° 3'48.02" S and 39°58'58.52" W) northwards to southern Bahia (17°43'29.30" S and 39°44'26.60" W), east Brazil (Fig. 1; see Table A1), which contains a landscape matrix composed of cattle pastures, plantations of *Eucalyptus* spp., sugar cane, coffee, and papaya, and forest fragments (Rolim et al., 2005). The prevailing climate is wet tropical (Köppen climate classification), with low rainfall from April to September followed by high precipitation from October to March, and with minimal variation in climate across sampling sites: precipitation ranges from 1,228 mm yr^{-1} in Espírito Santo (Peixoto and Gentry, 1990) to ~1,403 mm yr^{-1} in Bahia (Gouvêa, 1969), with similar average temperatures in the dry season (Espírito Santo ~15.6°C; Bahia ~14°C) and the wet season (Espírito Santo ~27.4°C; Bahia ~23°C). The predominant soil in the study area is Yellow Podzolic (IBGE, 1987; Magnago et al., 2015b).

These forest areas are included in the Atlantic Forest domain (IBGE, 1987), typified by large flat areas rising slowly from 20 to 200 m a.s.l., and according to the Brazilian vegetation classification are Lowland Rain Forest

(IBGE, 1987). These areas are of high conservation value, as these landscapes despite having fragments of different shapes, sizes and levels of isolation (Fig.1 and Table A2), still have high biodiversity (Chiarello, 1999; Rolim and Chiarello, 2004; Magnago et al., 2014) and strong carbon storage and biodiversity co-benefits (Magnago et al., 2015b).

Historically, the studied landscape remained well preserved until the 1950's. Thereafter, Espírito Santo and Bahia experienced rampant clear-cut logging and charcoal production, followed by agriculture (Garay and Rizzini, 2004). The main deforestation period in our study area was thus between 1950s and early 1970s (Magnago et al. 2015b), with conversion of forests primarily to sugar cane and cattle pastures. Because our fragments were 40 to 60 years old when sampled, extinction debts of some long-lived tree species are likely still to be paid. However, trees species composition in the interior of smaller fragment alters rapidly (most within the first 10 years since isolation) to reflect a more disturbed community (Laurance et al., 1998; Laurance et al., 2002; Laurance et al., 2006), indicating that our time since isolation is sufficient to detect many important impacts of fragmentation.

Data collection

Fieldwork was conducted between January 2008 and July 2014 in 27 forest fragments with areas ranging from 13 to 23 480 ha (Table A1; Matos et al., in review). Within each fragment, we sampled one transect (except for the second largest fragment of 17 716 ha in which we sampled two transects separated by 4 km), positioned at least 200 m from the forest edge (28 transects in total; see Fig. 1 and Table A1). On each transect, we sampled 10 square plots (10 m x 10 m; 0.1 ha combined) located at 20 m intervals along each transect, totaling 280 plots (2.8 ha). We only sampled primary forests, with no evidence of recent logging, although we cannot rule out the occurrence of limited degradation several decades ago.

Within each plot, we sampled all individuals living and rooted within our plots with diameter at breast height (DBH) of ≥4.8 cm at 1.3 meters above ground height. Individuals that were not identified at the site were collected and classified into morphospecies, subsequently identified by morphological comparison in the Herbarium of the Vale (CVRD) or botanical experts for their families (e.g. Myrtaceae and Sapotaceae). The botanical material collected in reproductive stage was deposited in the Herbarium of the Federal University of Viçosa, Minas Gerais (VIC) and CVRD, Espírito Santo.

Metrics of fragmentation

We investigate both the configuration (i.e., geometric arrangement, isolation and position of elements within the landscape) and composition (i.e., type or quantity of elements that compose the landscape) of our forest fragments within the study area (Cisneros et al., 2015). Following Matos et al. (in review), we identify the configuration and composition characteristics of landscapes using a vegetation map of the Brazilian Atlantic forest (reference year 2015; www.sosma.org.br and www.inpe.br). This dataset depicts the spatial distribution of the main forest formations within this biome, and has been used to describe landscape structure via forest loss and fragmentation (Ribeiro et al., 2009) and to generate estimates of carbon loss due to habitat fragmentation (Pütz et al., 2014). See Text A1 for further details.

Fragmentation metrics were computed as in Matos *et al*. (in review), i.e., encompassing an area defined by a 5 km buffer around each forest fragment and using the implementation given in FRAGSTATS (v 4.2; McGarigal et al., 2012; except 'source distance' see below). Furthermore, all metrics were computed using the eight-cell neighbourhood rule and considering a search radius of 5 km. For each fragment we measured four metrics related to landscape configuration (see Table A3): (1) forest shape index - measures the level of shape complexity on a fragment basis, with a low number indicating that fragments are more regular and thus have less edge effects; (2) forest nearest neighbour - gives the Euclidean distance to the nearest neighbour forest patch, with a low number suggesting less isolation; (3) mean forest nearest neighbour – gives the average value of the forest nearest neighbour metric when considering all forest fragments within each buffer; and (4) source distance – measures distance to the nearest forest patch having an area of at least 1,000 ha, with lower values suggesting less isolation. This metric was computed with ArcGis (v 10.1) using as a base the vegetation map of Brazilian Atlantic forest (SOS Mata Atlântica/INPE, 2015) (Table A3).

For each fragment, we additionally measured three metrics of landscape composition again using the implementation given in FRAGSTATS (see Table S3 for full details of each metric): (5) forest patch size – measures the area of the focal fragment; (6) forest cover – measures the percentage of the landscape covered by forest, with a high number reflecting largest remaining forest cover; and (7) forest patch density – measures the number of fragments in 100 hectares within each landscape.

Functional trait matrix

We examined six traits related to: quantity and type of food resource (1. fruit size [mm], 2. seed size [mm], and 3. fruit type, categorized into fleshy or non-fleshy fruits; Coombe, 1976; Magnago et al., 2014); fruit dispersal syndrome (4. zoochoric or non-zoochoric dispersion; Magnago et al., 2014); forest structure (5. succession group, categorized as pioneer, initial secondary or later secondary; Borges et al., 2009; Magnago et al., 2014), and carbon storage (6. wood density in dry weight [g cm^{-3}]; Magnago et al., 2014; 2015b). See Text A2 for full details.

Among the 538 species sampled, 4% representing 0.5% of the total abundance (i.e., 24 of 4 847 individuals) were removed from the analysis because they were identified to morphospecies level or could not have functional characteristics obtained.

Measures of functional diversity

We used the function '*dbFD*' function (FD package; Laliberté et al., 2015) in R version 3.2.1 (R Development Core Team 2015) to calculate four functional diversity metrics: (1) functional richness (FRic), which measures the volume of trait space occupied by a community. High FRic suggests a high use of resources, whereas a low value of FRic suggests that some traits are missing from communities resulting in poor use of resources; (2) functional evenness (FEve), which describes the uniformity of distribution of abundance of species in the occupied functional trait space. A community with high FEve has a symmetric abundance distribution throughout functional space, indicating the absence of dominance by specific functional groups and suggesting that resources are being used efficiently by the community; (3) functional divergence (FDiv), which quantifies the divergence in the distribution of abundance in the volume of traits. When FDiv is high, there are high levels of niche differentiation, indicating low competition for resource; and finally (4) functional dispersion (FDis), which estimates the dispersion of species in functional trait space, considering species' relative abundances. Higher values of FDis suggest that the remaining forests have a high functional richness and/or divergence, since this index incorporates features of both functional metrics. The functional diversity indices FRic, FEve and FDiv have been proposed by Villéger et al., (2008) and FDis proposed by Laliberté and Legendre, (2010). Both indices have been widely used in studies investigating the effect of fragmentation on bird communities (De Coster et al., 2015), mammals (Ahumada et al., 2011), beetles (Barragán et al., 2011) and trees (Magnago et al., 2014) in tropical forests.

Measures of null model

Measures of functional diversity are sensitive to underlying species richness (Pavoine and Bonsall, 2011; Schuldt et al., 2014). Hence we determine whether changes in functional diversity resulting from landscape configuration and composition were higher or lower than one would expect by chance, by calculating the standardized effect size (ses) of our four metrics of functional diversity (FRic, FEve, FDiv and FDis). The ses measures the number of standard deviations between the observed values and expected. Thus, ses takes the following form: *[(observed – mean expected) / standard deviation of expected]*, where *observed* values are obtained from the sampled data, *expected mean* is the average of 999 randomizations and *standard deviation of expected* is the standard deviation of the 999 simulated communities. We used the independent swap algorithm (Gotelli, 2000), to maintain species richness and species frequency occurrence in the 999 communities. These analysis were run in R version 3.2.1 (R Development Core Team. 2015) according to script from (Swenson, 2014). A negative value indicates that the fragmented forest has lower FD than expected by chance, whereas a positive value denotes higher FD than expected by chance.

Measures of functionally unique species

We adapted the Evolutionary Distinction (ED) index, which measures how much a given species is distinguished from other species in a phylogeny (phylogenetic diversity), to be used in a functional context (Thuiller et al., 2014). First, we constructed a functional dendrogram according to the functional traits of trees (see Text A2 for complete details of functional traits). To build a functional dendrogram, we used the Gower`s distance (Pavoine et al., 2009) to create a distance matrix from continuous and categorical functional traits, and the UPGMA clustering method. We then used the '*as.phylo'* function available in the R *ape* package to transform the functional dendrogram into a tree of class *phylo*. Finally, we applied the function '*fair.proportion*' available in *picante* package to calculate ED of each species present in the functional dendrogram. The fair proportion method (Isaac et al., 2007) is given by the sum of the branch lengths among all the nodes from the tip to the root, divided by the number of species subtending each branch.

Statistical analyses

We analysed the effects of landscape configuration and composition on each metric of functional diversity (FRic, FEve, FDiv and FDis), functional structure (ses FRic, sesFEve, sesFDiv and sesFDis), functionally unique species and functional traits. We used generalized linear models (GLM), with Gaussian error and an identity link (normality was tested and confirmed by the Shapiro Wilk test), in the 'glm' function from *stats* package. For count data (e.g. the abundance of categorical functional traits; see Text A2) we used GLM, with a Poisson error distribution and a log link function, and negative binomial distributions with log link functions when the data showed significant overdispersion. These models were made using the 'glmmadmb' function from the package *glmmADMB*. We used the 'dredge' function from *MuMIn* package to test all possible combinations of the fragmentation metrics (i.e., configuration and composition) included in the global model. To select our best model we used an information theoretical approach based on the Akaike Information Criterion of Second Order (ΔAICc), which is indicated for small sample sizes, and the best model was indicated by the lowest ΔAICc value (Burnham et al., 2011). Log transformations were used to reduce the variance heterogeneity for forest shape index, source distance and forest patch size measurements. Lastly, given that predictor landscape variables may have high multi-colinearity (Boscolo and Metzger, 2011), we used the variance inflation factor (VIF) to identify any correlated variables (i.e., VIF values ≥10; Benchimol and Peres, 2015); however, because VIF values ranged from 2.90 (i.e., forest patch size) to 10 (i.e., forest cover), we did not remove any variable.

Results

Impacts of landscape configuration on functional diversity

Considering only our best model (in which ∆AICc=0; Tables 1 and A4), functional evenness (FEve) was significantly (α = 0.05) and negatively related to forest nearest neighbour (t = -2.648, *P* = 0.0138; Fig. 2a), indicating that increasing isolation of fragments generated high irregularity of distribution of species abundances within the trait space. Functional divergence (FDiv) showed a significant negative relationship with forest shape index (t = -2.130, *P* = 0.0432; Fig. 2b) and was significantly higher in fragments with the highest level of isolation (i.e., forest nearest neighbor) (t = 2.223, *P* = 0.0355; Fig. 2c). Finally, we found that increasing irregularity of the fragments (i.e., forest shape index) reduced functional dispersion (FDis) (t = -3.781, *P* = 0.0009; Fig. 2d).

In terms of the best models explaining functional structure (Tables 1 and A4), we found that with increasing irregularity of fragments (i.e., forest shape index) there was a significant decrease in sesFRic (t = -2.487, *P* = 0.0199; Fig. 3a), suggesting that highly irregular fragments are less FRic than expected for communities assembled with random processes. sesFEve was significantly lower than expected by chance in areas with higher values of forest nearest neighbour (t = -2.917, *P* = 0.0074; Fig. 3b). sesFDiv was significantly lower than expected by chance in areas with higher forest shape index (t = -2.161, *P* = 0.0405; Fig. 3c), and larger than expected by chance with increased level of isolation between the remaining forests within landscapes (i.e., mean forest nearest neighbor) (t = 2.137, *P* = 0.0426; Fig. 3d). Lastly, we found that sesFDis was lower than expected by chance with increasing irregularity of fragments (i.e., shape forest index) (t = -4.014, *P* = 0.0005; Fig. 3e).

In terms of functionally unique species, we found no effect of landscape configuration according to our selection of models (which ∆AICc=0; Table A5). Instead the null model was the best model.

We found that configuration characteristics of landscapes (see Table A3) significantly affected the richness and abundance of three functional traits (in which ∆AICc=0; Tables 2, A6, A7, A8 and A9), but that fruit diameter, seed diameter, and wood density were not affected (Tables 2, A6 and A9). In terms of species richness, higher forest shape index caused a significant reduction of non-zoochoric dispersers (Table 2; Fig. A1-a), while increasing source distance (i.e., distance to fragments ≥1000 ha) increased the richness of initial secondary but reduced the richness of later secondary species (Table 2; Fig. A1b-c). In terms of abundance, higher forest shape index had a positive effect on the abundance of species with fleshy fruits (Fig. A2a), but a negative effect on the abundance of species with non-fleshy fruits and non-zoochoric dispersion (Table 2; Fig. A2b-c). Higher forest nearest neighbor reduced the abundance of species with zoochoric dispersion, and increased the abundance of pioneer species (Fig. A2e-f). Finally, increased source distance was negatively related to the abundance of species with fleshy fruits, zoochoric dispersion, and later secondary (Fig. A2g-i), whereas it was positively related to the abundance of pioneer and initial secondary species (Table 2; Fig. A2j-k).

Impacts of landscape composition on functional diversity

According to our best models of functional diversity (in which ΔAICc=0; Tables 1 and A4), FEve was negatively related to forest patch size (t = -2.632, *P* = 0.0143; Fig. 4a), indicating that the evenness of traits is less heterogeneous in larger than smaller fragments. We also found that increasing the percentage of forest cover reduced FDis (t = -3.214, *P* = 0.0036; Fig. 4b).

In terms of functional structure, according to our best model (Tables 1 and A4), sesFEve was negatively related to fragment area (t = -2.623, *P* = 0.0146; Fig. 4c) and sesFDis was negatively related to forest cover (t = -3.772, *P* = 0.0009; Fig. 4d). This suggests that larger fragments and increased forest cover have lower values of sesFEve and sesFDis than expected for communities assembled at random processes.

Considering our best models for functionally unique species, we found no effect of composition of the landscape (which ΔAICc=0; Table A5). Instead the null model was the best model.

Evaluating the effect of landscape composition (see Table A3) on the richness and abundance of functional traits (in which ΔAICc=0; Tables 2, A6, A7 A8 and A9), we found that fruit and seed diameter were not affected by any of our landscapes composition metrics (Tables 2, A6). In terms species richness, increasing forest cover led to increasing richness of tree species with fleshy fruits, zoochoric dispersion and later secondary species (Table 2; Fig. A3a-c), while increasing forest patch size and forest patch density led to decreasing richness of pioneer species and to increasing richness of later secondary species, respectively (Table 2; Fig. A3d-e). Finally, in terms of abundance, increased forest cover led to a reduction in the abundance of non-zoochoric dispersing species (Table 2; Fig. A4a), while forest patch density was negatively related to the abundance of initial secondary species but positively related to wood density (Table 2; Fig. A4b-c).

Discussion

Understanding the effects of forest fragmentation on functional diversity will enable us to design conservation strategies that help to maximise the provision of key ecosystem functions and services (Tilman et al., 1997; Petchey and Gaston, 2006; Cadotte et al., 2011). Our results demonstrate that functionally unique species were not impacted by any of our landscapes metrics of configuration and composition, indicating that even remote, isolated, small and/or edge-effected fragments can harbor functionally unique species. Considering the effects of landscape configuration on functional diversity, we found that increased isolation led to a reduction of functional evenness and increased functional divergence. Moreover, and taking into account the impact of landscape compositional characteristics, lower functional evenness was associated with larger forest patches and lower functional dispersion with increased forest cover. Finally, landscapes with higher forest patch density may be important reservoirs of biodiversity and carbon storage, since they retain trees with higher values of the wood density and later secondary species, but fewer species adapted to disturbance. These results suggest that characteristics of landscape configuration (i.e., increasing isolation) leads to a loss of functional redundancy, but do not promote fewer functions than areas with less isolation, while the impact of changing landscape composition (i.e., increasing area, forest cover and forest patch density) increase functional similarity between species, suggesting higher interaction with fauna and capacity for carbon storage (see Bello *et al*. 2015).

Impacts of landscape configuration on functional diversity

Functional diversity can be influenced by species richness (Pavoine and Bonsall, 2011; Schuldt et al., 2014). After correcting for the potentially confounding impacts of species richness, we found that functional richness (sesFRic), functional divergence (sesFDiv) and functional dispersion (sesFDis) were low (i.e., ses<0) in fragments with higher forest shape index (i.e., high edge effect; Hill and Curran, 2003; Ewers and Didham, 2006). This suggests niche homogenization among species sharing similar functional characteristics (Mouchet et al., 2010; Magnago et al., 2014; De Coster et al., 2015). Unexpectedly, however, homogenization was caused by (1) increased abundance of species with fleshy fruits, and (2) decreased richness of species with non-zoochoric dispersion, reductions in the abundance of species with non-fleshy fruits and abundance of initial secondary species (i.e., species adapted to disturbance; Hill and Curran, 2003; Magnago et al. 2014). One potential explanation is that our most edge-effected (irregular) fragments were also those with a larger size (see Fig. A5), and thus that size is more important than shape in driving functional responses.

In contrast, fragments with the highest level of isolation (i.e., forest nearest neighbor) had lower functional evenness (FEve and sesFEve, thus independent of species richness) and higher functional divergence (FDiv, but not sesFDiv). These patterns suggest higher niche differentiation with greater isolation, caused by the loss of functional redundancy (i.e., later secondary species) and the increase in species adapted to disturbance (i.e., pioneers species), which may generate negative interactions with fauna and the erosion of ecosystem services over time (Girão et al., 2007; Magnago et al., 2014). A possible explanation is that increasing isolation limits seed dispersal among remaining forest fragments (Hubbell, 2001; Duque et al., 2009), leading to increased floristic differentiation between species in highly fragmented landscapes (Arroyo-Rodríguez et al., 2013). Increased floristic differentiation is predicted by the landscape-divergence hypothesis, in which anthropogenic-induced changes lead to different successional trajectories, changing species composition and functional characteristics of trees (Laurance et al., 2007; Arroyo-Rodríguez et al., 2013; Sfair et al., 2016).

In addition to the level of isolation, we found that with increasing source distance (i.e., distance to fragments ≥1000 ha) there was an increase in the richness of initial secondary species and reduced richness of later secondary species. Similarly, we found a decrease in abundance of fleshy fruits, zoochoric dispersion and later secondary species and an increase in abundance of pioneer species and initial secondary species. These results suggest that the loss of large forest blocks across the landscape can lead to the reduction of important ecosystem functions through the loss of later secondary species and increasing richness and abundance of resilient species (i.e., adapted to disturbance), as well as loss of important resources for fauna (Girão et al., 2007; Magnago et al., 2014).

Impacts of landscape composition on functional diversity

The presence of large forest blocks reduced functional evenness (FEve and sesFEve) and higher percentage of forest cover decreased functional dispersion (FDis and sesFDis), independent of the number of species sampled. These results indicate strong functional redundancy between species that share similar functional characteristics in highly forested landscapes (Mouchet et al., 2010; Magnago et al., 2014; De Coster et al., 2015). Increased redundancy for FEve and FDis within functional space was caused by reducing the species richness of pioneers and the abundance of non-zoochoric species, and increasing the richness of species with fleshy fruits, zoochoric and later secondary traits. In support of these findings, studies investigating the effect of fragment area on the community of trees in the Brazilian Atlantic forest (Magnago et al., 2014) and of forest cover on the functional diversity of birds (De Coster et al., 2015) showed an increase in functional redundancy with increasing fragment area and forest cover driven by increases in functional traits that have important interactions with fauna.

Finally, with increasing forest patch density there was an increase in the species richness of later secondary and high wood density trees, but reduced abundance of initial secondary species. This suggests that fragmented landscapes that retain high densities of fragments can play an important role in the conservation of carbon storage and co-benefits between carbon storage and biodiversity (Magnago et al., 2014; 2015b). This is very important in highly fragmented landscapes such as those found in the Brazilian Atlantic forest, where ~80% of remaining forest fragments have an area of less than 50 ha (Ribeiro et al., 2009).

Conclusions and conservation implications

Changes to tree functional diversity caused by the configuration and composition of fragmented landscapes have important implications for the conservation of highly fragmented tropical landscapes, including the globally threatened Brazilian Atlantic, Tropical Andes, and Himalaya forests (Armenteras et al., 2003; Kumar and Ram, 2005; Ribeiro et al., 2009; Magnago et al., 2014; De Coster et al., 2015). There are both positive and negative impacts for conservation associated with these changes. We found high functional redundancy even in highly edge-effected areas (i.e., high forest shape index) as well as in areas with large forest blocks. This was driven by the high availability of tree species with important traits for fauna and composed of later secondary species, suggesting that these habitats are important for conservation, plus offer favorable sources of seed dispersal for secondary forest enrichment in adjacent degraded areas (Chazdon et al., 2009).

However, increasing isolation among remaining forest fragments drives lower functional evenness and increased functional divergence, possibly caused by floristic differentiation promoted by the isolation process (Arroyo-Rodríguez et al., 2013). Such isolation limits the persistence of animal species (Prugh *et al*. 2008; Vieira et al., 2009; Boscolo and Metzger, 2011), likely drives long-term reductions in capacity to store carbon (Bello et al., 2015; Peres et al., 2016), and consequently, isolated fragments may have a lower potential to offer strong co-benefits between carbon and biodiversity (Magnago et al., 2015b). Furthermore, while reductions in forest patch size and forest cover promote higher functional evenness and dispersion (and thus losses of functional redundancy), this is driven by reductions of fleshy fruit, zoochoric dispersed, and later secondary species and by increases of trees adapted to disturbance (i.e., changing quality, but not quantity of functions; De Coster et al., 2015). Future studies should investigate the long-term effect of these functional changes on ecological processes. For instance, Banks-Leite et al., (2014) showed that it is important to recover or maintain forest cover in the Atlantic forest above 30% of native habitat to prevent the loss of endemic species and associated ecological processes.

Finally, these results suggest that where the vast majority of forest cover and connectivity has been lost there is limited benefit of protecting the few remaining patches for the retention of functional diversity, and that such isolated locations could represent poor conservation investment if found in regions where much contiguous forest cover remains (see also Matos *et al*. in review for similar results for phylogenetic diversity). Nevertheless, in highly threatened regions where most contiguous forest is already gone, including the Brazilian Atlantic and Tropical Andean forests (Ribeiro et al., 2009; Haddad et al., 2015), then conservation must seek to expand forest cover, increase patch density, and/or connectivity between patches via secondary forest restoration to reverse the negative impacts of fragmentation processes. This is likely to be an important option for recovering carbon stocks—via promoting species with higher wood density—and maintaining biodiversity within such highly fragmented and threatened regions, potentially offering strong co-benefits between carbon and biodiversity under REDD+ (Magnago et al. 2015b).

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Tables

Table 1. Results of fitting generalized linear models to assess the impact of landscape configuration and composition metrics on functional diversity and functional structure. We present only the best models according to Akaike information criterion corrected for small samples (ΔAICc=0). FRic = functional richness; FEve = functional evenness; FDiv = functional divergence and FDis = functional dispersion. ses = standardized effect size of the four functional diversity metrics.

Model	Parameter	Estimate	SE	*t* value	P(>t)
FRic	Intercept	2.452	0.149	16.470	0.0001
sesFRic	Intercept	-0.288	0.410	-0.702	0.4894
	Forest shape index (log)	-1.376	0.553	-2.487	0.0199
	Source distance (km) (log)	0.274	0.143	1.921	0.0662
FEve	Intercept	0.720	0.024	29.931	0.0001
	Forest nearest neighbour (m)	-0.0001	0.00004	-2.648	0.0138
	Forest patch size (ha) (log)	-0.021	0.008	-2.632	0.0143
sesFEve	Intercept	1.568	0.560	2.801	0.0097
	Forest nearest neighbour (m)	-0.003	0.001	-2.917	0.0074
	Forest patch size (ha) (log)	-0.489	0.186	-2.623	0.0146
FDiv	Intercept	0.813	0.013	62.714	0.0001
	Forest shape index (log)	-0.052	0.024	-2.130	0.0432
	Forest nearest neighbour (m)	0.0001	0.00003	2.223	0.0355
sesFDiv	Intercept	-0.195	0.364	-0.536	0.5966
	Forest shape index (log)	-1.241	0.574	-2.161	0.0405
	Mean forest nearest neighbour (m)	0.001	0.001	2.137	0.0426
FDis	Intercept	2.530	0.074	34.396	0.0001
	Forest shape index (log)	-0.529	0.140	-3.781	0.0009
	Forest cover (⁄)	-0.008	0.002	-3.214	0.0036
sesFDis	Intercept	1.195	0.313	3.820	0.0008
	Forest shape index (log)	-2.388	0.595	-4.014	0.0005
	Forest cover (⁄)	-0.039	0.010	-3.772	0.0009

Table 2. Results of fitting generalized linear models to assess the impacts of landscape configuration and composition metrics on the richness and the abundance of our six functional traits. We present only the best models according to Akaike information criterion corrected for small samples (∆AICc=0).

Model	**Parameter**	**Estimate**	**SE**	***t* value**	**P(>t)**
Fruit diameter	Intercept	21.655	0.612	35.380	0.0001
Seed diameter	Intercept	10.345	0.209	49.480	0.0001
Model	**Parameter**	**Estimate**	**SE**	**z value**	**P(>z)**
Species richnnes					
Fleshy fruits	Intercept	3.488	0.072	48.390	0.0001
	Forest cover (⁄)	0.013	0.003	4.290	0.0001
Non-fleshy fruits	Intercept	0.405	0.154	2.620	0.0087
Zoochoric dispersion	Intercept	3.826	0.063	61.230	0.0001
	Forest cover (⁄)	0.012	0.003	4.420	0.0001
Non-zoochoric dispersion	Intercept	3.193	0.092	34.720	0.0001
	Forest shape index (log)	-1.086	0.250	-4.340	0.0001
Pioneers	Intercept	2.246	0.275	8.170	0.0001
	Forest patch size (ha) (log)	-0.312	0.118	-2.650	0.0081
Initial secondary	Intercept	2.792	0.116	24.050	0.0001
	Source distance (km) (log)	0.113	0.048	2.340	0.0001
Later secondary	Intercept	3.838	0.183	20.970	0.0001
	Source distance (km) (log)	-0.170	0.057	-2.970	0.003
	Forest cover (⁄)	0.008	0.004	2.200	0.028
	Forest patch density (in 100 ha)	0.790	0.243	3.250	0.0012

Model	Parameter	Estimate	SE	z value	P(>z)
Species abundance					
Fleshy fruits	Intercept	4.565	0.169	26.980	0.0001
	Forest shape index (log)	0.467	0.212	2.200	0.0277
	Source distance (km) (log)	-0.159	0.060	-2.640	0.0084
Non-fleshy fruits	Intercept	4.687	0.083	56.650	0.0001
	Forest shape index (log)	-0.530	0.209	-2.540	0.011
Zoochoric dispersion	Intercept	5.231	0.109	47.830	0.0001
	Forest nearest neighbour (m)	-0.001	0.0003	-2.450	0.014
	Source distance (km) (log)	-0.123	0.050	-2.480	0.013
Non-zoochoric dispersion	Intercept	4.485	0.126	35.680	0.0001
	Forest shape index (log)	-1.442	0.303	-4.750	0.0002
	Forest cover (⁄)	-0.014	0.005	-2.770	0.0055
Pioneers	Intercept	1.175	0.396	2.970	0.003
	Forest nearest neighbour (m)	0.001	0.001	2.280	0.0224
	Source distance (km) (log)	0.481	0.150	3.220	0.0013
Initial secondary	Intercept	3.552	0.222	15.990	0.001
	Forest shape index (log)	-0.595	0.239	-2.490	0.013
	Source distance (km) (log)	0.335	0.063	5.340	0.0001
	Forest patch density (in 100 ha)	-0.980	0.423	-2.310	0.021
Later secondary	Intercept	5.319	0.119	44.610	0.0001
	Forest nearest neighbou (m)	-0.001	0.0003	-1.800	0.072
	Source distance (km) (log)	-0.236	0.055	-4.280	0.0001
Model	**Parameter**	**Estimate**	**SE**	***t* value**	**P(>t)**
Wood density	Intercept	0.628	0.023	27.799	0.0001
	Source distance (km) (log)	-0.016	0.008	-1.961	0.0611
	Forest patch density (in 100 ha)	0.142	0.054	2.619	0.0148

Figures (High resolution files available if accepted for publication)

Figure 1

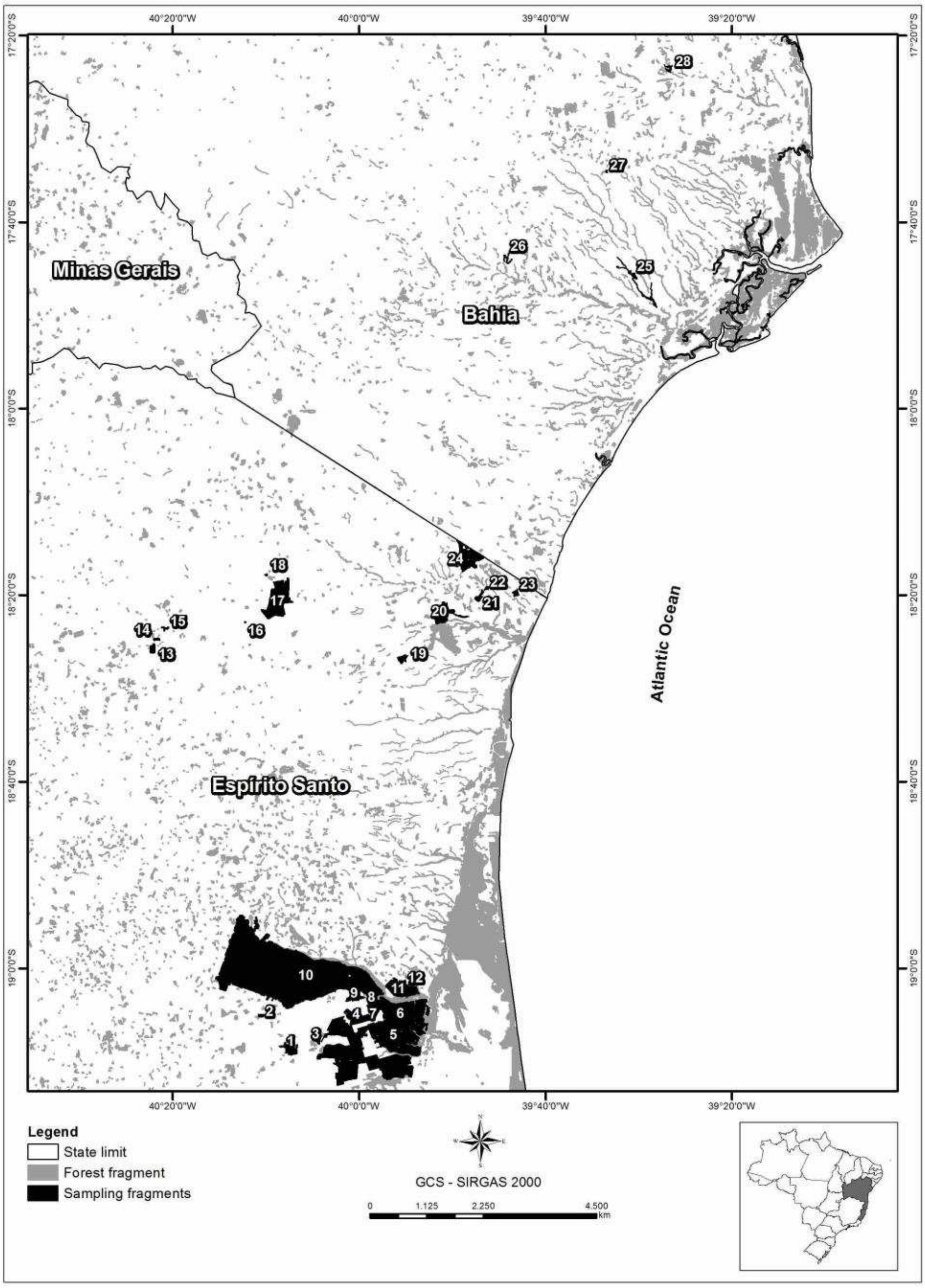

Fig. 1. Study area and forest fragments sampled in the Brazilian Atlantic Forest. Size of each fragment and their coordinates can be seen in Table A1.

Figure 2

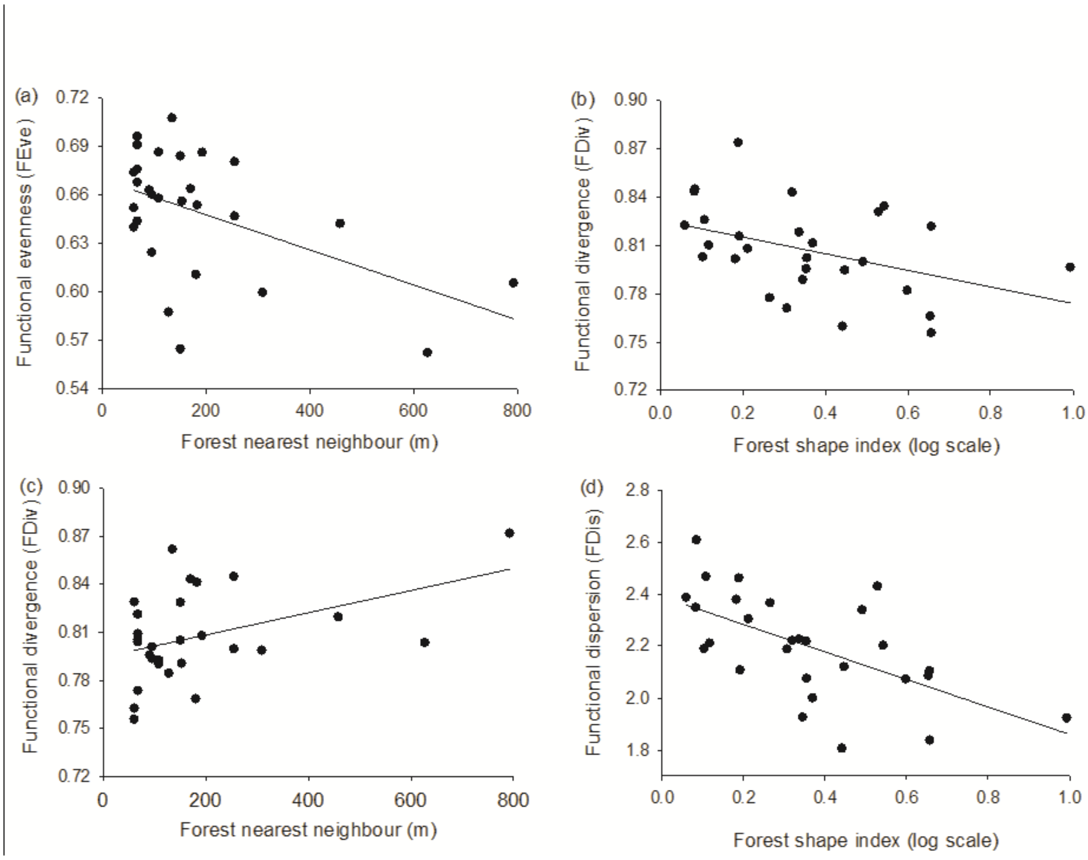

Fig. 2. Effects of landscape configuration on functional diversity metrics. (a) Effect of forest nearest neighbour on functional evenness (FEve); (b) effect of forest shape index on functional divergence (FDiv); (c) effect of forest nearest neighbour on functional divergence (FDiv); and (d) effect of forest shape index on functional dispersion (FDis). The values for graph were obtained after the summation of the raw residuals with the expected values for variable (y), assuming average values for the other covariates (partial residuals plots).

Figure 3

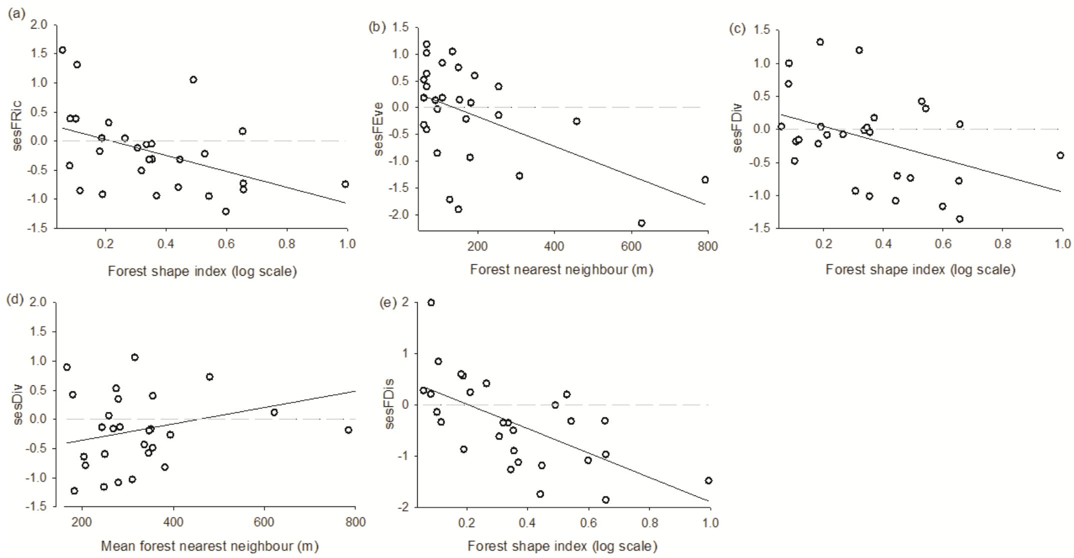

Fig. 3. Effects of landscape configuration on functional structure metrics. (a) Effect of forest shape index on sesFRic; (b) effect of forest nearest neighbour on sesFEve; (c) effect of forest shape index on sesFDiv; (d) effect of mean forest nearest neighbor on sesFDiv; and (e) effect of forest shape index on sesFDis. The values for graph were obtained after the summation of the raw residuals with the expected values for variable (y), assuming average values for the other covariates (partial residuals plots).

Figure 4

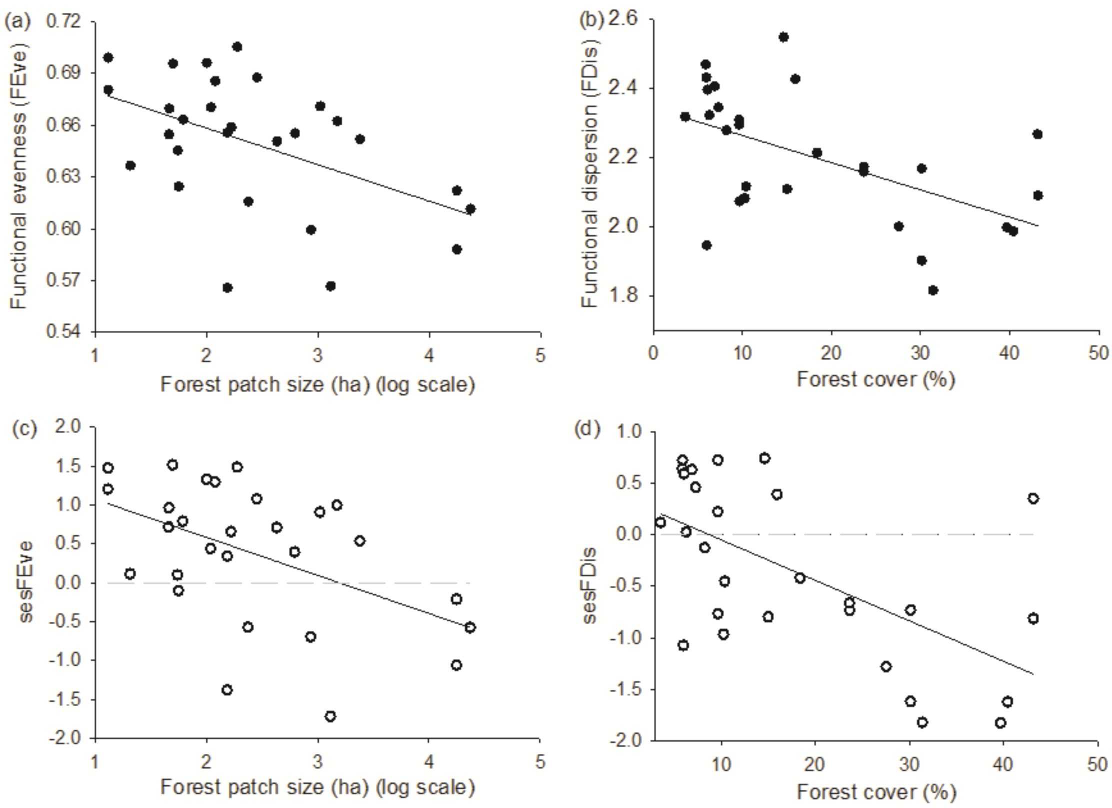

Fig. 4. Effects of landscape composition on functional diversity and functional structure metrics. (a) Effect of forest patch size on functional evenness (FEve); (b) effect of forest cover on functional dispersion (FDis); (c) effect of forest patch size on sesFEve; and (d) effect of forest cover on sesFDis. The values for graph were obtained after the summation of the raw residuals with the expected values for variable (y), assuming average values for the other covariates (partial residuals plots).

V. CAPÍTULO III

Does natural forest regeneration offer important carbon-biodiversity co-benefits in a highly fragmented landscape?

Abstract

Tropical forests store large amounts of carbon and have high biodiversity, but they are being degraded at alarming rates. Given the rapid conversion of rainforest and associated release of carbon dioxide, and the massive shortfall in funding for biodiversity conservation, we urgently need to seek mechanisms that can simultaneously stem both carbon and biodiversity losses. One potential is for carbon-based payments for ecosystem services (e.g., United Nations, Reducing Emissions from Deforestation and Forest Degradation, REDD+) to protect biodiversity as a co-benefit for free. Here, we investigated whether carbon enhancements via natural forest regeneration offer such co-benefits focusing for the first time in the highly fragmented Brazilian Atlantic forest and on tree diversity. After four decades of regeneration, patches of secondary forest that were isolated from mature forest had recovered 25% of the carbon stocks of a primary forest. Over this period, secondary forest recovered high floristic similarity with primary forests, high richness and abundance of endemic and IUCN red list species, and resulting from this recovery of species richness, high phylogenetic and functional diversity. There were positive relationships between carbon stock and tree diversity recovery, suggesting that there is potential for co-benefits under REDD+. This indicates that more emphasis should be placed on the regeneration of secondary tropical forests by carbon-based funding initiatives that even isolated patches of secondary forest could help to mitigate the biodiversity extinction crisis by recovering important species and improving landscape connectivity.

Key-words: biodiversity value, biomass, ecosystems services, forest management, fragment isolation, REDD+, threatened species, endemic species

Introduction

Tropical forests account for ~32% of global primary production (Field *et al*., 1998), harboring the largest above-ground carbon stocks (Lewis, 2006; Laurance, 2008) and highest levels of biodiversity (Gardner, 2010). However, these regions are increasingly human-dominated (Lewis, Edwards & Galbraith, 2015), having experienced dramatic degradation via selective logging and fire, deforestation for agriculture (more than 1.5 million km^2 between 1980 and 2012; Gibbs *et al.*, 2010; Hansen *et al*., 2013), and resulting fragmentation of remaining forests (Haddad *et al*., 2015). Combined, these land-use driving climate change, increasing anthropogenic carbon emissions (Fearnside & Laurance, 2004; Bonan, 2008; Van der Werf, 2009), and causing massive loss of global biodiversity (Morris, 2010; Ellis *et al*., 2010; Pimm *et al*., 2014).

In addition to the loss of carbon stocks and biodiversity via land-use change, resulting increases in emissions of carbon dioxide—second only to the burning of fossil fuels as the key emitter of greenhouse gases (Berenguer *et al*., 2014; Pütz *et al*., 2014)—have the potential to change irreversibly the global climate. Greenhouse gas emissions thus exacerbate the current global biodiversity crisis via temperature increases, severe heatwaves, and severe droughts (Herrera-Montes & Brokaw, 2010; Cortés-Gómez *et al.,* 201; Scheffers *et al*., 201). Because the financial resources available to tackle climate change and biodiversity loss are limited, there is an urgent need to identify actions that simultaneously address both issues (Miles & Kapos, 2008; McCarthy *et al*., 2012). One emerging potential is for carbon-based payments for ecosystem services—such as the United Nations, Reducing Emissions from Deforestation and Forest Degradation (REDD+) mechanism, with the '+' including payments for enhancements of forest carbon stocks—to simultaneously protect biodiversity as a free co-benefit of carbon protection.

For REDD+ to offer co-benefits, we must identify carbon-saving activities within locations that offer a strong positive congruence between carbon stocks and biodiversity, and to direct investment to such locations. Most work has thus far focused on the potential for co-benefits via preventing deforestation (Miles & Kapos, 2008; Venter *et al*., 2009; (Phelps, Webb & Adams 2012) and associated impacts within forest fragments (Magnago *al*., 2015). Given severe losses of species richness, functional diversity and phylogenetic diversity following conversion (for examples, Gibson *et al*., 2011; Edwards *et al*., 2013 Ibis;

Magnago *et al*., 2014, Santos *et al.*, 2010; Andrade *et al*., 2015; Cisneros et al., 2015; Edwards et al. 2015), potential co-benefits are often clear. Another important potential is for natural regeneration of secondary forest to recover the loss of carbon stocks, forest cover, and biodiversity, and ultimately to reverse drastic climate change by sequestering carbon from the atmosphere (Thomas *et al.,* 2004; Poorter *et al*., 2016).

Assessing above-ground biomass (AGB) recovery of lowland Neotropical secondary forests, Poorter *et al*., (2016) demonstrated that after 20 years since land abandonment, the carbon-absorption rate in secondary forests was 11 times the uptake rate of old-growth forests, and that AGB stocks take a median of 66 years to recover 90% of old-growth AGB levels. In the Tropical Andes, after 30 years of secondary succession approximately half of old-growth AGB had been restored (Gilroy *et al*., 2015). Within secondary forests, there can also be substantial recovery of ant, bird, dung beetle, butterfly and bat diversity, amongst others (Barlow *et al*., 2007; Chazdon *et al*., 2008; Bihn *et al*., 2008; Gilroy *et al*, 2014; Hernández-Ordóñez, Urbina-Cardona & Martínez Ramos, 2015). This suggests that important carbon and biodiversity co-benefits could accrue if REDD+ is used to enhance the rate with which marginal farmland is abandoned and thus the natural recovery of secondary forests. However, to our knowledge, only two studies have formally quantified the rate of carbon and biodiversity recovery and thus accrual of co-benefits, revealing strong positive links between the amount of AGB and bird, dung beetle, and amphibian recovery in the Tropical Andes (Gilroy *et al*., 2014; Basham et al. in revision).

Trees are critical for habitat structure (Boscolo & Metzger 2011; Pardini et al. 2010; Magnago et al. 2014), carbon storage (Laurance 2004; Nascimento & Laurance 2004; Magnago et al. 2015), as well as their high diversity (Banks-Leite *et al*. 2014). A key question, therefore, is whether carbon enhancements under REDD+ can offer carbon and tree diversity co-benefits. Recent studies evaluating the effect of secondary forests on tree diversity demonstrate an increase in species richness, functional diversity (Lohbeck *et al*., 2012), and changes in the phylogenetic structure (Letcher, 2009). However, none considered the rate of recovery of carbon and biodiversity, preventing a direct assessment of the potential for co-benefits.

In this study, we focus on the question of whether secondary forest regrowth offers carbon and tree diversity co-benefits in the threatened Brazilian

Atlantic forest (Myers et al., 2000). The Atlantic forest retains just 11% of its original forest cover (Ribeiro et al., 2009), with natural regeneration of forest to enlarge and reconnect patches frequently cited as a vital management technique for reducing extinction risk and returning ecosystem functions and services to this highly degraded region. We answer this question by sampling tree carbon and diversity across a full landscape transition from cattle pasture through various ages of secondary forest after abandonment, and we contrast the values of these landscapes against primary forest controls.

Materials and methods

Study area

Our 340 km long study area was based in the state of Espírito Santo (20°10'9.04"S and 40°13'47.63"W) to southern Bahia (17°15'41.00"S and 39°29'43.00"W), east Brazil (Fig. S1 and see Table S1 for details). Remaining forests in the region are highly fragmented (Magnago *et al*., 2015), situated in a landscape matrix of cattle pastures, and plantations of *Eucalyptus* spp., sugar cane, coffee, and papaya (Rolim *et al*. 2005). These forest areas are included in the Atlantic Forest domain (IBGE 1987; also termed Tableland forest, Rizzini 1979), typified by large flat areas rising slowly from 20 to 200 m a.s.l., and according to the Brazilian vegetation classification are Lowland Rain Forest (IBGE 1987).

Tree sampling locations

Fieldwork was conducted between January 2008 and January 2016 across the main habitat types (primary forest, secondary forest and cattle pasture). Primary forest fragments ranged in area from 13 to 23,480 ha (see Table S1), with no evidence of recent logging, although we cannot rule out the occurrence of limited logging several decades ago.

The formation of secondary forests in tropical regions is strongly attributed to expansion of the agricultural frontier for cattle pasture, plus associated logging and mining (Gibbs *et al.*, 2010; Hansen *et al*., 2013; Lewis, Edwards & Galbraith, 2015). We define secondary forests as those that had suffered significant anthropogenic change, via severe logging, mining, roads, plus opening of glades within the highly-degraded habitat for cattle grazing. Thus our secondary forests were not entirely converted to pasture, but have regrown within a heavily degraded matrix. These secondary forests differ from old-growth by visibly altering forest structure, with smaller trees, lower canopy height, and infestation of lianas (Chazdon *et al*., 2007; Dupuy, Leyequien & Lópes-Martínez, 2012; Roeder, Holscher & Kossmann-Ferraz, 2012), making it possible to identify them in the field.

In our study area, all 11 sampled secondary forest fragments ranged between 10 and 346 ha in area with approximate time of regeneration since recovery from intensive degradation of 18 to 46 years. All of our secondary forest fragments were immersed in extensive areas of pasture cattle without connectivity to primary fragments forest, with a great distance (18 to 29.4 km) to large blocks of forest (≥1,000 hectares; see table S1 for details). The estimated time of secondary succession is derived from data on two levels: (1) we use aerial images taken annually starting in the years 1969 to 1971 at 3,800 meters altitude and available from the Instituto Estadual de Meio Ambiente–IEMA (http://www.meioambiente.es.gov.br) to determine the approximate year in which the landscapes of the sampled secondary fragments began to be degraded and isolated by large expanses of cattle pasture. Besides the intense removal of wood, these secondary fragments were used as cattle resting areas, increasing the intensity of disturbance (*personal communication*). (2) We use the Google Earth Pro database to determine whether these fragments underwent a more severe disturbance (i.e., clear-cutting of vegetation), or remained as observed in the images provided by IEMA, until the year in which plots were allocated for this study. Finally, as none of the sampled fragments have changed in shape (i.e., total vegetation cut), compared with reference images (i.e., IEMA), we subtract the approximate year that these fragments were degraded and isolated in cattle pasture areas by the year in which the plots were allocated in field to derive our approximate time of secondary forest succession forest in years.

The distance of secondary forest patches (km) from large forest blocks (herein 'source distance'), which may act as sources of seeds and important ecological processes (White et al., 2004; Kormann *et al*., 2016), was computed with ArcGis (v 10.1) using as a base the vegetation map of Brazilian Atlantic forest (SOS Mata Atlântica/INPE 2015), with a low value suggesting less isolation (see Matos et al., in review). For full methodological details of calculating secondary forest age and source distance, see supplementary methods (Text A2).

Finally, we sampled areas of active cattle pasture that were not abandoned or in the early stages of regeneration. We focus on cattle farming because it represents 35% of agricultural land and 22% of the area within the city limits of 13 urban centers in the two study states (Espírito Santo and Bahia; see table S2 for full details).

Tree sampling methods

Within each habitat type, we sampled one transect per forest patch or cattle farm (except for the second largest fragment of primary forest [17,716 ha] in which we sampled two transects separated by 4 km; see Fig. S1 and Table S1). We thus have a dataset of 27 primary forest transects, 11 secondary forest transects and 11 cattle pasture transects. On each transect, we sampled 10 plots of 10 m x 10 m (0.1 ha) located at 20 m intervals along each transect, with the plots positioned ≥200 m from the forest edge, totaling 270 plots (2.7 ha) in primary forest, 150 plots (1.5 ha) in secondary forest and 120 plots (1.2 ha) in cattle pasture.

Within each plot, we sampled all tree individuals living and rooted within our plots with diameter at breast height (DBH; 1.30 meters above ground height) ≥4.8 cm. Individuals that straddled the plot edge were counted as being within the plot if at least half of the trunk was inside the plot. For tree individuals that were not identified at the site, we collected leaves and any reproductive parts, these were then classified into morphospecies and subsequently identified by morphological comparison in the Herbarium of Vale (CVRD) or by botanical experts for their families. The botanical material collected in reproductive stage was deposited in the Herbarium of the Federal University of Viçosa, Minas Gerais (VIC) and CVRD.

Above-ground carbon stock

We estimate the amount of above-ground biomass (AGB) in each tree individual, using Chave *et al*., (2005) equation for moist forest stands. We assume that 50% of AGB of each individual is represented by carbon (Laurance *et al*., 1997; Malhi *et al*., 2004; Chave *et al*., 2005; Paula *et al*., 2011; Lima *et al*., 2013; Magnago *et al*., 2015).

Wood density in dry weight (g cm^{-3}) was obtained from Global Wood Density database (GWD) (available in: http://dx.doi.org/10.5061/dryad.234/1;

Chave *et al*., 2009; Zanne *et al*., 2009). When a species was identified at the genus level or was not present in the GWD database, we used the average density of wood for all species of the same genus in the database (for more details see Flores and Coomes, 2011; Hawes *et al*., 2012; Magnago *et al*., 2014; Magnago *et al*., 2015).

Phylogeny construction

For the preparation of our phylogenetic tree, we constructed a list of all our family/genus/species according to APG III (2009). In the program Phylocom version 4.2 (Webb *et al*. 2008), we then used the PHYLOMATIC function to return the phylogenetic hypothesis for the relationship between our 66 families, 263 genera and 576 species sampled in 5,970 tree individuals, using the new modified megatree R20120829mod.new for vascular plants from Gastauer & Meira-Neto (in press). In our phylogenetic hypothesis more than two species per family or more than two genera of an unresolved family in R20120829mod.new were inserted as polytomies. Finally, to estimate the lengths of branches in millions of years for our ultrametric phylogenetic tree, we used the file "ages_exp", (Gastauer & Meira-Neto, in press) and the BLADJ algorithm in Phylocom program version 4.2 (Webb *et al*. 2008).

Functional trait matrix

We examined six traits related to: quantity and type of food resource (1. fruit size [mm], 2. seed size [mm], and 3. fruit type, categorized into fleshy or non-fleshy fruits; Coombe, 1976; Magnago *et al*., 2014); fruit dispersal syndrome (4. zoochoric or non-zoochoric dispersion; Magnago *et al*., 2014); forest structure (5. succession group, categorized as pioneer, initial secondary or later secondary; Borges *et al*., 2009; Magnago *et al*., 2014), and carbon storage (6. wood density in dry weight [g cm^{-3}]; Magnago *et al*., 2014; 2015). See Text A2 for full details.

Among the 576 species sampled, 5.55% representing 0.7% of the total abundance (i.e., 44 of 5,970 individuals) were removed from the analysis of functional diversity and phylogenetic construction (described above) because they were only identified to morphospecies level.

Functional dendrogram construction

We build one functional dendrogram for all individuals of trees sampled in the primary forest, secondary forest and cattle pasture using functional characteristics described above. Gower`s distance (Pavoine e*t al*., 2009) was used to create a distance matrix from continuous and categorical functional traits (see Text A1 for information about the functional traits), and the UPGMA clustering method. To verify the loss of information when we transform the distance matrix into a dendrogram, we correlated the original matrix and the dendrogram cophenetic matrix, however we did not find great loss of information (r = 0.927). Lastly, we used the '*as.phylo'* function available on R *ape* package to transform the functional dendrogram into a tree of class *phylo*. These analyzes were performed in R version 3.2.1 (R Development Core Team 2015).

Tree conservation value

We considered a broad metrics of biodiversity, phylogenetic diversity and functional diversity to determine tree conservation value.

Biodiversity

(1) Forest community structure: To calculate forest community structure, we applied a non-metric multidimensional scaling (MDS) ordination analysis to identify changes in community structure (see Magnago *et al*., 2014, Magnago *et al*., 2015). We evaluated changes in the structure between habitat types using raw species abundance data from each transect (i.e., primary forest, secondary forest and cattle pasture), with the Sorensen (Bray–Curtis) distance metric. We considered the MDS results arising from tree species abundance data as a measure of community structure (Barlow *et al*., 2010). This analysis was developed in R version 3.2.1 (R Development Core Team 2015)

(2) Similarity to primary forest: We evaluated changes in the similarity of tree communities between the habitat types using Chao-Sørensen abundance-based similarity index, with raw species abundance data from each transect (Gilroy *et al*., 2014). We opted for the use of Chao-Sørensen abundance-based because similarity based on the classic Sørensen index is sensitive to the sample size (Chao *et al*., 2005). This analysis was developed in EstimateS version 9.1.0 (Colwell, 2013).

(3) Species richness and abundance: We evaluated changes in species richness between the different types of habitat using the raw number of species from each transect. We evaluated changes in the species abundance between the habitats types using raw number of individuals from each transect.

(5) Richness and abundance of endemic species: To classify the species endemic to the Atlantic Forest domain, we used the database Flora do Brazil (List of Species of the Brazilian Flora, 2016, in http://floradobrasil.jbrj.gov.br) (see Magnago *et al*., 2015).

(6) Richness and abundance of threatened species: We classified threatened species as those listed on the IUCN Red List (IUCN, 2014) as vulnerable, endangered or critically endangered (see Magnago *et al*., 2015).

Phylogenetic and functional diversity

From our phylogenetic hypothesis we calculate two phylogenetic metrics weighted by abundance. (7) Phylogenetic diversity - the sum of evolutionary history in a community (Faith, 1992). This metric is given in millions of years. (8) Mean nearest taxon distance – mean phylogenetic distance between an individual and the most closely related (non-conspecific) individual (given in millions of years; Webb *et al*., 2000). Low levels suggest that closely related pairs of individuals (non-conspecific) co-occur and high values that they do not.

Since a functional dendrogram has the same structure as a phylogenetic tree (Pavoine & Bonsall 2010), we apply the same metrics used for phylogenetic diversity following Thuiller *et al*., (2014) to determine impacts on ecosystem functioning. (8) Functional diversity is defined as the total branch length of a functional dendrogram (Petchey & Gaston 2002). (9) Mean nearest taxon distance (Webb *et al*. 2000) – mean functional distance between an individual and the most closely related (non-conspecific) individual. Low levels suggest that pairs of individuals (non-conspecific) with similar functional traits co-occur and high values that they do not.

Measures of phylogenetic and functional diversity are sensitive to underlying species richness (Swenson 2014; Coronado et al., 2015). Hence we determine whether changes in phylogenetic and functional diversity resulting from habitat type were higher or lower than one would expect by chance, by calculating the standardized effect size (ses) of our two metrics of phylogenetic diversity (PD and MNTD-PD) and functional diversity (FD and MNTD-FD). The ses measures the number of standard deviations between the observed values and expected (see Text A3 for full details). Positive values of sesPD or sesFD indicate higher PD or FD than expected by chance for a given species richness, while negative values indicate lower PD or FD than expected by chance for a given species richness. High values of sesMNTD-PD and sesMNTD-FD indicate that the co-occurrence of related or functionally similar individuals is lower than expected by chance (*phylogenetic or functional overdispersion)* for a given species richness, and negative values indicate the co-occurrence of related or functionally similar individuals is higher than expected by chance (phylogenetic or functional clustering) for a given species richness. All analyzes of PD and FD were Performed in R version 3.2.1 (R Development Core Team 2015)

Statistical analysis

To investigate the effects of secondary forests on carbon storage and tree conservation value, we consider three habitat types (primary forest, secondary forest and cattle pasture), plus the length of secondary succession (years) and source distance (km). In addition, to assess co-benefits between carbon stock and biodiversity of trees, we used the total carbon storage in each of the 11 transect of sampled secondary forest. To evaluate these relationships, we used generalized linear models (GLMs; except 'similarity' see below), with Gaussian error and an identity link (normality was tested and confirmed by the Shapiro Wilk test), as implemented in the 'glm' function from *stats* package. For count data (e.g., the species abundance and abundance of categorical functional traits) we used GLMs, with a Poisson error distribution and a log link function, and negative binomial distributions with log link functions when the data showed significant overdispersion. These models were made using the 'glmmadmb' function from the package *glmmADMB*. We also performed pairwise comparisons (i.e., Tukey post hoc testing) between each habitat (primary forest, secondary forest and cattle pasture) using the function 'lsmeans' from *lsmeans* package. In terms of the effects of habitat type, length of secondary succession, source distance on community similarity to primary forest and co-benefits (i.e. between carbon and similarity to primary forest), we conducted Generalized Linear Mixed Model (GLMM), with site as a random variable (Bolker *et al*., 2009). The GLMM was built using the function "lmer" in the package *lme4*, with Gaussian error and an identity link, following pairwise comparisons only between each habitat (primary forest, secondary forest and cattle pasture) using the function 'difflsmeans' from *lmerTest* package.

In addition, we used the 'dredge' function from *MuMIn* package to test all possible combinations of secondary succession and source distance included in the global model. To select our best model we used an information theoretical approach based on the Akaike Information Criterion of Second Order (∆AICc), which is indicated for small sample sizes, and the best model was indicated by the lowest ∆AICc value (Burnham *et al*., 2011). Lastly, given that predictor (i.e., secondary forest age and source distance) variables may have multi-colinearity, we run a Pearson correlation. However, we find a low, non-significant correlation value (r = -0.370, *P* = 0.26; Fig. S2) and thus we did not remove any variable.

Results

Impacts of habitat type, forest age and source distance on carbon stock

Across all habitat types, we found a mean above-ground carbon stock of 228.9 ± 271.4, and within habitats types of 19.18 ± 32.4 Mg ha^{-1} in cattle pasture, 52.1 ± 17.33 Mg ha^{-1} in secondary forest and 386.3 ± 278.7 Mg ha^{-1} in primary forest. Carbon stocks differed significantly between habitats (Table S3), with pairwise comparisons revealing significant differences between all habitat pairs (Table S3; Fig. 1a). In terms of forest regeneration, considering only our best model (in which ∆AICc=0; Table S4), we found a significant positive effect of secondary forest age on carbon stock (Mg ha^{-1}, t = 3.765, *P* = 0.0044; Fig. 1b), while source distance (i.e., distance to large forest blocks) had no effect on carbon storage (see Table S4). Lastly, because we did not find a significant correlation between secondary forest age and source distance (Fig. S2), this suggests that these variables are impacting carbon stocks independently.

Impacts of habitat type, forest age and source distance on biodiversity

Forest community structure: Community structure differed significantly between all habitats (Fig. 2a and S3; Table S5), with pairwise comparisons revealing significant differences only between primary forest and secondary forest, and primary forest and cattle pasture for MDS axis 1 (Fig. 2b; Table S6) and all habitat pairs for MDS axis 2 (Table S6; Fig. S3a). In terms of forest regeneration and source distance, considering only our best model (in which ΔAICc=0; Table S7), the structure of communities was positively related with secondary forest age (MDS axis 1; t = 3.73, *P* = 0.0047; Fig. 1c; Table S8), not being affected by source distance (Table S7).

Similarity to primary forest: Similarity to overall primary forest community varied significantly between habitats (Fig. 2d; Table S5), with primary transects the most similar and pasture transects the least similar (all pairwise comparisons significantly different; Table S6). In terms of forest regeneration and source distance, considering only our best model (in which ΔAICc=0; Table S7), we found a positive impact of secondary forest age (t = 7.71, *P* = 0.0001; Fig. 2e; Table S8) and a negative impact of increasing source distance (t = -2.44, *P* = 0.0153; Fig. S3d; Table S8) on similarity to the primary forest community.

Species richness and abundance: Species richness was highest in primary forest and lowest in pasture (Fig. 2f; Table S5), with all pairwise comparisons significantly different (Table S6). Considering only our best model (in which ΔAICc=0; Table S7) of the effects of secondary forest and source distance, we found that species richness was positively related to secondary forest age (z = 3.52, *P* = 0.0004; Table S8; Fig. 2g). There was no significant impact of source distance (Table S7). For species abundance, we found a similar pattern between habitat types (Fig. S3b; Table S6), but considering only our best model (in which ΔAICc=0; Table S7), no effect of secondary forest (see Fig. S3c) or source distance (Table S8).

Richness and abundance of species endemic: Endemic species richness (Fig. 2h) and abundance (Fig. S3e) were highest in primary forest and lowest in pasture (Table S5), with all pairwise comparisons significantly different (Figs. 2h & S3e; Table S6). Considering only our best model (in which ΔAICc=0; Table S7) of the effects of secondary forest and source distance, secondary forest age impacted positively endemic species richness (z = 4.34, *P* = 0.00001; Fig. 2i; Table S8) and abundance (z = 4.32, *P* = 0.0001; Fig. S3f; Table S8). There was no impact of source distance (Table S7).

Richness and abundance of threatened species: There was a significant effect of habitat on threatened species richness and abundance (Table S5): pairwise comparisons revealed that richness was higher in primary than secondary forest, which were higher than in pasture (Fig. S3g; Table S6), while abundance was highest in primary forest, but did not differ between secondary forest and cattle pasture (Fig. S3i; Table S6). In terms of secondary forest age and source distance, considering only our best model (in which ΔAICc=0; Table S7), the richness of threatened species (t = 2.60, *P* = 0.0094; Fig. S3h; Table S8) and abundance (t = 2.56, *P* = 0.0100; Fig. S3j; Table S8) increased significantly with the secondary forest age. There was no impact of source distance (Table S7).

Impacts of habitat type, forest age and source distance on phylogenetic and functional diversity

Phylogenetic diversity (PD): PD differed significantly between habitats (Table S9), with PD in primary forest higher than in secondary forest, which were higher than in cattle pasture (Fig. 3a; Table S10). After controlling for species richness (sesPD), PD did not differ significantly between the three habitats (Tables S9 and S10), suggesting that variation in PD across habitats is largely driven by effects of species richness. Mean nearest taxon distance (MNTD-PD) differed significantly between habitats (Table S9), with pairwise comparisons again revealing significant differences between all habitats pairs (Fig. S4a; Table S10), but in this instance controlling for species richness (sesMNTD-PD) revealed larger sesMNTD-PD in primary forest than cattle pasture (Fig. S4c; Tables S9 and S10).

Considering only our best model (in which ΔAICc=0; Table S11) of the effects of secondary forest age and source distance, there was a positive impact of secondary forest age on PD (t = 2.75, *P* = 0.0227; Fig. 3b; Table S12). However, after controlling for species richness, sesPD was not significantly affected by secondary forest age (Table S12), indicating that the impact of secondary forest age on PD is largely driven by species richness. Finally, there was a negative relationship between secondary forest age and MNTD-PD, suggesting that older secondary forests have a greater number of closely related pairs of non-conspecific individuals, than that observed for younger secondary forests (t = -2.97, *P* = 0.0157; Fig. S4b; Table S12). There was no impact of source distance (Table S12).

Functional diversity (FD): FD differed significantly between habitats (Table S9), with FD in primary forest higher than in secondary forest, which were higher than in cattle pasture (Fig. 3c; Table S10). After controlling for species richness (sesFD), sesFD did not differ significantly between the three habitats (Tables S9 and S10), suggesting that variation in FD across habitats is largely driven by the effect of species richness. Mean nearest taxon distance (MNTD-FD) differed significantly between habitats (Table S9). However, pairwise comparisons showed that only cattle pasture was significantly different from primary forest and secondary forest (Fig. S4d; Table S10).

Considering only our best model (in which ΔAICc=0; Table S11) of the effects of secondary forest age and source distance on FD, there was a positive impact of secondary forest age on FD (t = 3.50, P = 0.006; Fig. 3d; Table S12). However, after controlling for species richness (sesFD), sesFD was not significantly affected by secondary forest age or source distance (Table S12), indicating that the impact of secondary forest age on PD is largely driven by species richness.

Are there co-benefits between carbon stock and conservation value?

We found a marginally significant positive impact of above-ground carbon stock on community structure (t = 2.22, P = 0.054; Fig. 4a; Table S13). For other biodiversity value metrics, we found a significant positive effect of above-ground carbon stock on similarity to primary forest community (t = 5.62, P = 0.0001; Fig. 4b; Table S13), species richness (z = 4.43, P = 0.0001; Fig. 4c; Table S13), endemic species richness (z = 4.76, P = 0.0001; Table S13; Fig. 4d) and abundance (z = 3.75, P = 0.0002; Table S13; Fig. S5a), and threatened species richness (t = 3.50, P = 0.0005; Fig. S5b; Table S13) and abundance (z = 4.15, P = 0.0001; Fig. S5c; Table S13).

In terms of phylogenetic diversity of trees, we found a strong positive co-benefit between above-ground carbon stock and PD (t = 4.16, P = 0.0025; Fig. 4e; Table S13). However, after controlling for species richness (sesPD), PD was not significantly affected by carbon storage (Table S13). Finally, we found a strong positive co-benefit between carbon stock and FD (F = 4.11, P = 0.0027; Table S13; Fig. 4f), which remained after controlling for species richness (sesFD; t = 2.37, P = 0.042; Table S13; Fig. S5d).

Discussion

Given the rapid conversion of rainforest and associated release of carbon dioxide (Fearnside & Laurance, 2004; Bonan, 2008; Van der Werf, 2009), and the massive shortfall in funding for biodiversity conservation (Miles & Kapos 2008; McCarthy *et al*., 2012), we urgently need to seek mechanisms that can simultaneously stem both carbon and biodiversity losses. One potential is for carbon-based payments for ecosystem services (e.g., REDD+) to protect biodiversity as a co-benefit for free (Gilroy *et al*., 2015; Magnago *et al*., 2015). Here, we investigated whether carbon enhancements via natural forest regeneration offer such co-benefits focusing for the first time in the highly fragmented Brazilian Atlantic forest and on tree diversity. We found a significant positive effect of secondary forest age on above-ground carbon storage of trees, with significant recovery of floristic similarity with primary forests, richness and abundance of endemic and IUCN red list species, and phylogenetic and functional diversity within secondary forest. Positive relationships between carbon stock and tree diversity recovery suggest there is potential for co-benefits of natural forest regeneration under REDD+.

Impacts of habitat type, forest age and source distance on carbon stock

Cattle pasture is the main land use in this region, but has very low above-ground carbon stocks (~18 Mg ha^{-1}). Forty-five years after pasture abandonment resulted in a nearly four-fold recovery of carbon stocks (~65 Mg ha^{-1}) representing about one sixth of the carbon stocks in a primary forest (~386 Mg ha^{-1}). However, relative to recent studies, our carbon recovery rates were low. In an analysis of 1,500 carbon plots across the lowland Neotropics (<1,000 m a.s.l.), Poorter *et al*., (2016) found an average recovery of 122 Mg ha^{-1} (range 20 to 225 Mg ha^{-1}) after 20 years of regeneration, with above-ground carbon stocks recovering 90% of old-growth values after 66 years. In the Tropical Andes of Colombia (>1,100 m a.s.l.), natural regeneration on cattle pasture resulted in ~130 Mg ha^{-1} of above-ground carbon stocks after 30 years, approximately half the stocks in a primary forest (Gilroy *et al*., 2014).

The likely reason for the lower rates of recovery in this study is that all secondary forest patches were isolated from primary forest fragments by the pasture and crop matrix, plus were >13 km from large forest blocks (≥1,000 hectares, with no effect of source distance on above-ground carbon stock recovery, see Results). By contrast, secondary forests in Gilroy *et al*., (2014) were adjacent to contiguous primary forest. Thus, increasing isolation likely limits seed dispersal from remaining forest fragments (Hubbell, 2001; Duque *et al.*, 2009) and the recovery of carbon stocks and carbon storage (Bello *et al.*, 2015). In support of this, in the Brazilian Atlantic there was significantly lower carbon stocks with higher levels of isolation by distance to large forest blocks in primary forest fragments (Magnago *et al.*, 2015) and isolation causes increased floristic differentiation between species in highly fragmented landscapes (Arroyo-Rodríguez *et al*., 2013; Sfair *et al*., 2016).

Impacts of habitat type, forest age and source distance on biodiversity

We showed a strong effect of secondary forest age on community structure and species richness (see also Barlow *et al*., 2007; Chazdon *et al*., 2007). This is likely related to the initial recovery of generalist species (i.e. pioneer and early secondary species) during the regeneration process, which leads to a rapid change in habitat structure, more suitable microhabitats for seed germination (Holl & Hoii, 1999), and increased occurrences of species that play important ecological dispersal services, such as birds, dung beetles, bats large mammals and small mammals (Barlow *et al*., 2007), followed by the replacement of generalist trees with intermediate secondary forest species (Finegan, 1996).

After four decades of secondary forest recovery, communities were much more similar to primary forest composition, harbouring many endemic and IUCN Red-listed tree species (Figs. 2 & S3). Indeed, the abundance of IUCN Red-listed species was similar in our ~40-year secondary forest patches to that observed for small fragments (~13 ha) of primary forest (Magnago *et al*., 2015). Even though recovery is occurring in locations that are very isolated from major sources of seeds, it appears that with time a diverse array of trees of high conservation value can recover. If secondary forest is recovered over much larger areas, perhaps via support from REDD+ (see below), then there is the potential for forest regeneration to improve landscape connectivity (Metzger *et al*., 2009) and reduce extinction risk.

Impacts of habitat type, forest age and source distance on phylogenetic and functional diversity

Phylogenetic diversity (PD) is vital for protecting evolutionary history (Veron, Pavoine & Cadotte, 2015), and we found that ~40-year secondary forest had recovered nearly two billion years of evolutionary history versus pasture, to contain ~60% of the PD found in a primary forest. Functional diversity (FD) is vital for protecting ecosystem services and functions (Cardinale *et al*., 2012; Hooper *et al*., 2005), with eight-fold higher FD in secondary forest than pasture, and with nearly half the FD in secondary than primary forest. Recovery of both PD and FD was due to species richness effects, with null models suggesting that on a per species basis there was no more PD or FD in secondary or primary forest than in cattle pasture.

Lower levels of mean nearest distance taxon (MNTD) suggest increasing co-occurrence of closely related pairs of (non-conspecific) individuals, which provides greater phylogenetic and functional redundancy, and thus increased resilience to disturbance within communities (Purschke *et al*., 2013). MNTD-PD and MNTD-FD were highest in cattle pasture, MNTD-PD was higher in secondary than primary forest (Fig. S4a,d), while MNTD-FD decreased with age of secondary forest (Fig. S4b; but see Lohbeck et al. 2012). Again, species richness explains most of these results (e.g., Fig. S4c): MNTD-PD and MNTD-FD tends to be negatively correlated with species richness (Coronado *et al*., 2015), because with more species there is an increased probability that the next individual sampled is a close relative of at least one kind of individual already sampled, reducing overall MNTD.

Are there co-benefits between carbon stock and conservation value

We found positive relationships between carbon stock and similarity to primary forest, species richness, endemic species richness and abundance, IUCN Red-listed species richness and abundance, phylogenetic diversity and functional diversity (FD & sesFD) (Figs 4 and S5). This suggests strong potential for co-benefits via carbon enhancements under natural forest regeneration in the Brazilian Atlantic, enabling biodiversity protection for free under well-directed REDD+ projects (see also Gilroy *et al*. 2014).

The majority of the carbon market is unlikely to offer enhanced payments to directly conserve biodiversity (possible under REDD+; Phelps et al., 2012a,b). Rather, market forces will likely seek the cheapest carbon, suggesting that REDD+ will not meet the opportunity costs of highly profitable plantation agriculture or selective logging (Fisher *et al*. 2011; except in peat swamps (Tata *et al*., 2014) and will instead focus on less profitable, more marginal systems. In the Tropical Andes, for example, economic returns from farming are very low while carbon recovery in pastures adjacent to contiguous forest is rapid, making it relatively cheap (~\$2 t^{-1} CO_2) to promote carbon enhancements (Gilroy et al. 2014). Although we have found significant recovery of carbon in isolated patches of secondary forest in the Brazilian Atlantic, the rates of recovery were relatively low (Gilroy et al. 2014; Poorter et al. 2016). This could result in higher carbon prices of secondary regrowth in locations isolated from primary forest patches blocks.

Policy recommendations and conclusions

Reducing anthropogenic climate change and tropical biodiversity loss are two of the greatest challenges facing humanity (Barnett & Adger, 2007; Turner, Oppenheimer & Wilcove, 2009; Cardinale *et al.,* 2012). One possibility is to tackle these challenges jointly (e.g. REDD+): our research underscores the importance of focusing more carbon sequestration and conservation efforts on enhancing the rate with which marginal land is abandoned. Of particular importance from a biodiversity conservation perspective is the potential for secondary forests to enlarge the area of existing fragments of primary forest (and to improve landscape connectivity (Metzger *et al*., 2008). Both are vital for arresting the arresting the declines in species, PD, and FD within more isolated primary forest fragments Matos *et al*., (in review).

Enhancing the rate of land abandonment may entail land purchase or renting (under long-term certified emissions reductions ICER schemes; Gilroy et al. 2014) to allow the regrowth of secondary forest, provided that programs ensure full prior and informed consent from land-owners. In much of the Tropical Andes, for example, it would be more profitable to grow carbon than cows (Gilroy et al. 2014). Because we found relatively low rates of carbon sequestration in our study secondary forest fragments, future studies are vital to evaluate the effect of landscape configuration and isolation from primary forest sources on co-benefits offered by natural forest regeneration, and in turn, how this affects carbon pricing. The best option may be to focus projects next to (or very near to) smaller patches with specific conservation-values and larger primary forest blocks, where they would buffer and enlarge these areas, likely reducing extinction risk, and likely offer higher rates of carbon recovery and lower carbon prices making them a more attractive win-win for conservation.

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Figures

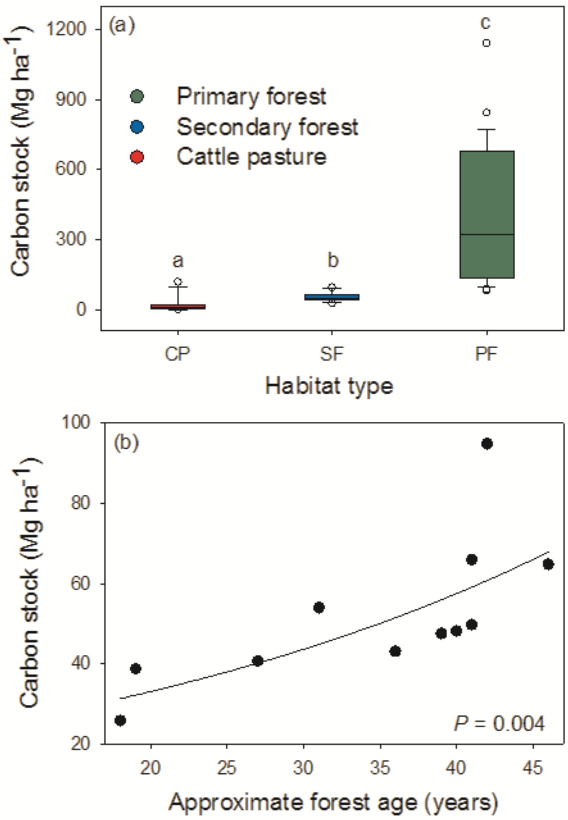

Fig. 1 – (a) Carbon stock between primary forest, secondary forest and cattle pasture; and (b) Carbon stock across secondary forest. Different letters in (a) indicate significance at $P \leq 0.05$. CP = Cattle pasture; SF = Secondary forest; and PF = Primary forest.

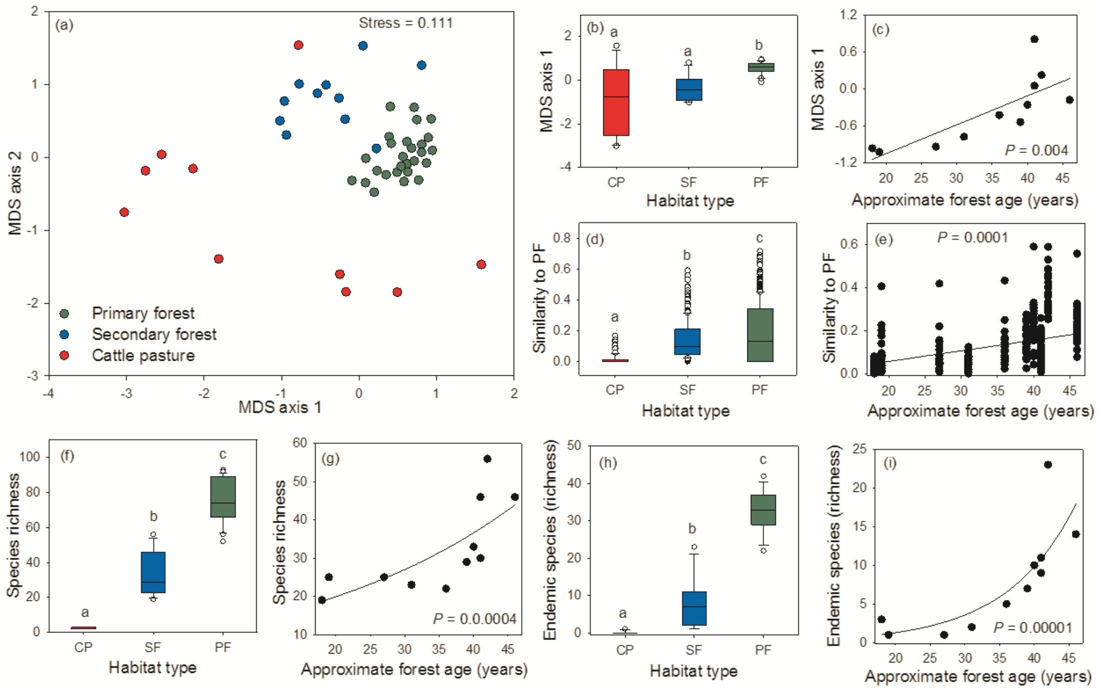

Fig. 2 – (a) Non-metric multidimensional scaling (MDS) ordination of community assemblages between primary forest, secondary forest and cattle pasture; (b) MDS axis 1 scores across habitat types; (c) MDS axis 1 scores across secondary forest; (d) Similarity to primary forest across habitat types; (e) Similarity to primary forest across secondary forest; (f) Species richness across habitat types; (g) Species richness across secondary forest; (h) Endemic species richness across habitat types; and (i) Endemic species richness across secondary forest. (b, d, f and h) different letters indicate significance at $P \leq 0.05$.

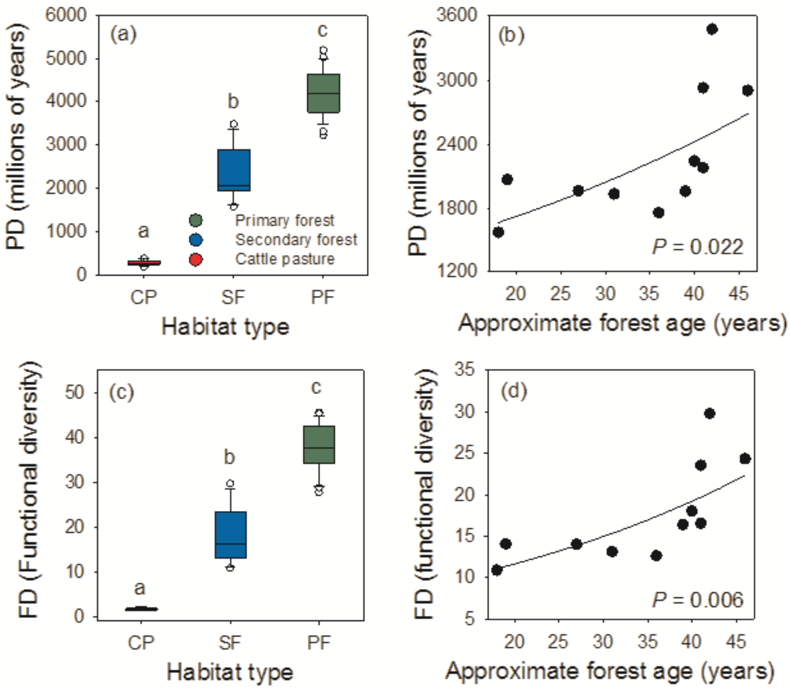

Fig. 3 – (a) Phylogenetic diversity - PD between primary forest, secondary forest and cattle pasture; (b) Phylogenetic diversity across secondary forest; (c) Functional diversity-FD across habitat types; and (d) Functional diversity across secondary forest. Different letters (a & c) indicate significance at $P \leq 0.05$.

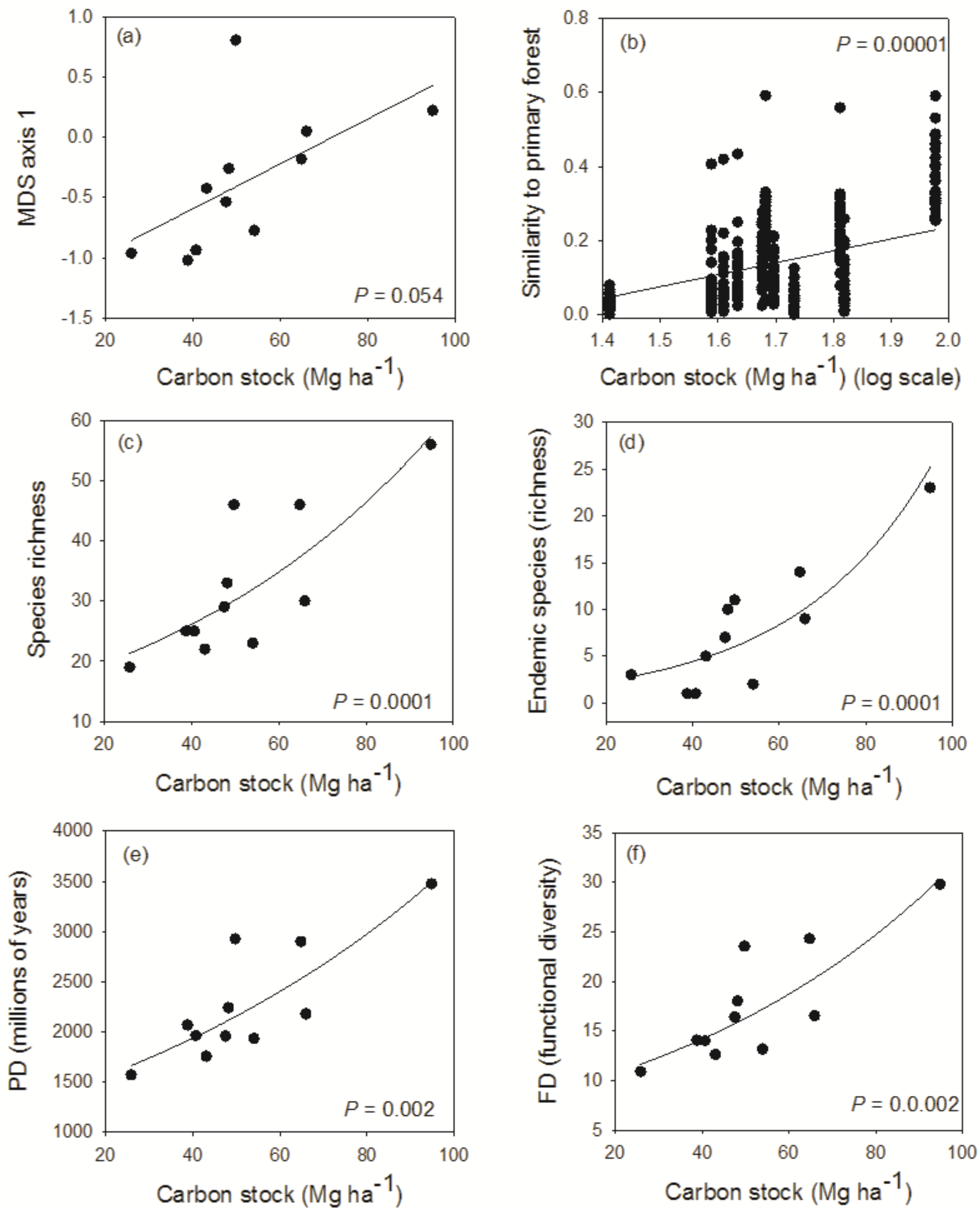

Fig. 4 – The impact of carbon stock on: (a) MDS axis 1 scores; (b) similarity to primary forest community; (c) species richness; (d) endemic species richness; (e) phylogenetic diversity (PD); and (f) functional diversity (FD).

VI - Conclusões Gerais

A partir dos resultados obtidos nos três capítulos pôde-se concluir que:

(i) Mudanças da composição das paisagens (i.e., porcentagem de cobertura florestal e densidade de fragmentos em 100 ha) e o efeito de borda, produzem alterações negativas na diversidade filogenética dentro dos fragmentos. Por outro lado, paisagens fragmentadas mantêm elevada história evolutiva dada a retenção de diversidade filogenética, através de uma gama de características de configuração das paisagens (i.e., isolamento, forma dos fragmentos e distância para fragmentos maiores que 1.000 hectares).

(ii) O isolamento entre fragmentos aumenta a diferenciação de nicho, através do incremento de espécies adaptadas ao distúrbio, seguido pela perda de espécies tardias. Porcentagem de cobertura florestal e tamanho do fragmento gera uma homogeinização de nicho, dada pelo aumento redundância funcional entre as espécies co-ocorrentes. Em adição, não encontramos evidências de que as alterações das características de composição e configuração das paisagens tenham levado a perda de espécies funcionalmente únicas.

(iii) Considerando as florestas em regeneração após distúrbio, encontramos que existem elevados co-benefícios entre carbono e biodiversidade de árvores. Isto indica, que mais ênfase deve ser colocada sobre as florestas tropicais em regeneração para iniciativas de conservação da biodiversidade, por meio do financiamento à base de carbono (REDD+), pois até mesmo manchas isoladas de floresta em regeneração pode contribuir para atenuar a crise de extinção da biodiversidade.

VII – SUPPLEMENTARY MATERIAL

III. CAPÍTULO I

Effects of landscape configuration, composition and edges on phylogenetic diversity of trees in a highly fragmented tropical forest

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This Supplementary Material includes:

Text S1 – Supplementary methods

Table S1 – Fragment details

Table S2 – Metrics of landscape configuration and composition

Table S3 – Values of landscape configuration and composition metrics in study fragments

Table S4 – Results of generalized linear models for landscape impacts

Table S5 – Results of generalized linear mixed models for fragment size and habitat impacts on phylogenetic diversity and structure

Figure S1 – Phylogenetic tree of tree species sampled

Figure S2 – Effect of forest cover on species richness

Figure S3 – Effect of fragment size and habitat on species richness

Supplemental references

Text S1 - Supplementary methods

Landscape structure

After the Amazon forest, the Brazilian Atlantic forest is the second largest area of tropical rainforest in South America (Oliveira-Filho & Fontes 2000). Currently it is estimated that 72% of the Brazilian population live in the potential distribution area of this biome and that of its original area of 148,194,638 ha only 16,377,472 ha (11.73%), remains, distributed in fragments of different successional stages, shapes, sizes and isolation levels (Ribeiro *et al*. 2009; Tabarelli *et al.* 2010; Magnago *et al*. 2014).

The first map of vegetation types of the Brazilian Atlantic forest was produced in 1985, and subsequently updated every five years up to 2005; further updates were generated for the 2005-2008, 2008-2010 periods and currently every year since 2010 (SOS Mata Atlântica/INPE 2015). The vegetation map used in this study is the update generated with remote sensing data from 2015 to produce the 2013-2014 update. Satellite data acquired by the Operational Land Imager (OLI) sensor onboard Landsat 8 were processed and used to generate the updated map with a minimum map unit of three hectares. The classification followed a visual interpretation and manual delineation approach to discriminate three forest formations (Atlantic forest, sandbank vegetation (*restinga*), and mangrove) and associated ecosystems which have a high distinction in their composition, vegetation type (Oliveira-Filho & Fontes 2000) and patterns of phylogenetic structure (Duarte *et al*. 2014); additionally, several non-forest classes were also identified and mapped: seasonally flooded vegetation (*várzea*), mountain systems, vegetation refuges, and dunes. Deforestation over forest classes were also mapped by comparison with data from previous periods.

Table S1 – Identification, habitats sampled, size and coordinates of studied fragments in Southeastern Brazil. Identification corresponds to fragment number in Figure 1.

Identification	Habitats	Size (ha)	Coordinates (Geographic WGS 84)	
1	edge and interior	428.94	19° 8'53.77"S	40° 7'20.24"W
2	edge and interior	61.38	19° 5'5.31"S	40°10'30.55"W
3	edge and interior	46.26	19° 7'59.17"S	40° 4'24.39"W
4	edge and interior	868.32	19° 5'18.06"S	40° 0'29.78"W
5	edge and interior	17716.14	19° 6'52.93"S	39°55'39.31"W
6	edge and interior	17716.14	19° 4'46.69"S	39°55'13.99"W
7	edge and interior	49.77	19° 4'10.94"S	39°58'59.18"W
8	edge and interior	13.05	19° 3'48.02"S	39°58'58.52"W
9	edge and interior	236.61	19° 3'9.60"S	40° 0'14.70"W
10	edge and interior	23480.37	19° 0'46.76"S	40° 7'17.80"W
11	edge and interior	1305.63	19° 2'17.18"S	39°55'2.14"W
12	edge and interior	119.79	19° 1'43.88"S	39°54'21.71"W
13	interior	153.54	18°25'35.55"S	40°22'10.01"W
14	interior	54.99	18°24'45.22"S	40°21'44.45"W
15	interior	56.16	18°23'37.27"S	40°20'47.32"W
16	interior	13.05	18°22'55.38"S	40°12'14.53"W
17	interior	2391.75	18°20'44.87"S	40° 8'28.39"W
18	interior	20.61	18°17'51.67"S	40°10'2.55"W
19	interior	188.55	18°26'50.72"S	39°55'26.16"W
20	interior	1048.05	18°22'13.76"S	39°51'27.51"W
21	interior	282.69	18°20'23.91"S	39°47'8.79"W
22	interior	153.9	18°19'29.07"S	39°46'35.41"W
23	interior	100.35	18°19'32.28"S	39°43'18.32"W
24	interior	1490.4	18°16'17.76"S	39°48'21.43"W
25	interior	620.64	17°45'40.80"S	39°30'45.30"W
26	interior	109.44	17°43'29.30"S	39°44'26.60"W
27	interior	45.81	17°34'40.40"S	39°33'29.85"W
28	interior	166.05	17°23'42.32"S	39°26'32.94"W

Table S2. Metrics used to describe the configuration and composition of the landscapes of globally threatened Brazilian Atlantic forest. All these metrics have been calculated individually for each of the 27 fragments sampled with search radius of 5 km from the edge. ρ = patchs characteristics; ¤ = characteristics that describe the forest class ‡ = and characteristics used to describe our landscapes.

Variable name (units)	Type	Description	Equation	Description equation
Configuration metrics				
Forest shape index (none)	ρ	Fragment forest perimeter divided by the minimum perimeter of the fragment forest area.	$\frac{.25_{p_{ij}}}{\sqrt{a_{ij}}}$	pij = perimeter (m) of patch ij; aij = area (m²) of patch ij.
Landscape shape index (none)	‡	Equals the sum of the fragment forest perimeter (m) in the landscape divided by the square root of minimum perimeter length for a maximally aggregated forest patch of the same total forest area.	$\frac{\sum_{j=1}^{n}\frac{0.25\,p_{ij}}{\sqrt{a_{ij}}}}{n_i}$	pij = perimeter (m) of fragment forest ij; aij = area (m²) of fragment forest ij; ni = number of land cover type I (forest).
Forest nearest neighbour (m)	ρ	The distance Euclidean to the nearest neighboring patch of the same type, based on shortest edge-to-edge distance.	h_{ij}	hij =distance (m) between patch ij and nearest neighbour patch of type i.
Mean forest nearest neighbour (m)	¤ ‡	Distance Euclidean mean to the nearest neighbour fragment for all fragments forest in the landscape.	$\frac{\sum_{j=1}^{n}}{n_i}h_{ij}$	hij =distance (m) between patch ij and nearest neighbour patch of type i, based on edge-to-edge distance; ni= number of patchs type i.
Source distance (Km)	ρ	Linear distance of the sampled fragment to the nearest fragment ≥ 1,000 hectares.	-	-
Composition metrics				
Forest patch size (ha)	ρ	Area equals the area (m²) of the fragment, divided by 10,000.	$a_{ij}\left(\frac{1}{10,000}\right)$	aij = area (m²) of fragment ij.
Forest cover (%)	¤ ‡	Percentage of the landscape covered by forest.	$\frac{\sum_{j=1}^{n}a_{ij}}{A}(100)$	aij = area (m²) of fragment ij; A = total landscape area (m²).
Forest patch density (fragments per 100 hectares)	‡	Amount of forest fragments divided by total landscape area.	$\frac{n_i}{A}(10,000)(100)$	ni = number of fragments in the landscape of patch type; A total landscape area (m²).

Table S3. Range, mean and standard deviation of the eight variables of landscape configuration and composition, sampled in 27 fragments of Atlantic rainforest. The description of each variable is given in table S2.

Landscape variable	**Minimum**	**Maximum**	**Mean**	**SD**
Configuration				
Forest shape index	1.15	9.84	2.63	1.77
Landscape shape index	3.15	21.59	10.26	4.19
Forest nearest neighbour (m)	60.00	792.02	183.73	174.91
Mean forest nearest neighbour (m)	166.30	1099.60	349.70	196.92
Source distance (km)	0.10	29.00	6.35	9.19
Composition				
Forest patch size (ha)	13.05	23480.37	2462.09	6151.44
Forest cover (%)	3.55	43.17	17.94	12.89
Forest patch density (in 100 ha)	0.13	0.68	0.31	0.13

Table S4 – Model selection for the impacts of landscape metrics on phylogenetic diversity and structure. Loglik = maximum likelihood; AICc = Akaike information criterion for small samples; ΔAICc = Difference between the AICc of a given model and that of the best model; and AICcWt = Akaike weights (based on AIC corrected for small sample sizes). See table S2 for more details on the metrics.

Global model = **PD**~Forest shape index+Landscape shape index+Forest nearest neighbour+Mean forest nearest neighbour+Source distance+Forest patch size+Forest cover+Forest patch density												
Intercept	For. shape index	Land. shape index	For. nearest neighbour	Mean for. nearest neighbour	Source distance	For. patch size	Forest cover	For. patch density	logLik	AICc	Δ AICc	AICcWt
3608.0	-	-	-	-	-	-	28.18	-	-208.45	423.90	0	0.15
3371.0	-	-	-	-	-	-	28.81	733.20	-207.70	425.10	1.25	0.08
3783.0	-	-	-	-0.35	-	-	25.28	-	-208.17	426.10	2.19	0.05
Global model = **SES.PD**~Forest shape index+Landscape shape index+Forest nearest neighbour+Mean forest nearest neighbour+Source distance+Forest patch size+Forest cover+Forest patch density												
Intercept	For. shape index	Land. shape index	For. nearest neighbour	Mean for. nearest neighbour	Source distance	For. patch size	Forest cover	For. patch density	logLik	AICc	Δ AICc	AICcWt
-0.09	-	-	-	-	-	-	-	-	-35.42	75.30	0	0.07
-0.42	-	-	-	-	-	-	0.02	-	-34.41	75.80	0.5	0.06
0.35	-	-	-	-	-	-	-	-1.44	-34.75	76.50	1.18	0.04
0.27	-	-	-	-	-0.17	-	-	-	-35.02	77.00	1.72	0.03
0.01	-	-	-	-	-	-	0.02	-1.30	-33.83	77.40	2.07	0.03
Global model = **MPD**~Forest shape index+Landscape shape index+Forest nearest neighbour+Mean forest nearest neighbour+Source distance+Forest patch size+Forest cover+Forest patch density												
Intercept	For. shape index	Land. shape index	For. nearest neighbour	Mean for. nearest neighbour	Source distance	For. patch size	Forest cover	For. patch density	logLik	AICc	Δ AICc	AICcWt
215.80	-	-	-	-	-	-	-	-17.56	-93.05	193.10	0	0.05
215.90	-	-	-	-	-2.57	-	-	-	-93.13	193.30	0.16	0.04
221.30	-	-	-	-0.01	-	-	-	-23.68	-91.90	193.50	0.45	0.04
210.30	-	-	-	-	-	-	-	-	-94.55	193.60	0.49	0.04
219.30	-	-	-	-	-2.09	-	-	-14.5	-92.06	193.90	0.77	0.03
213.00	-	-	-	-	-	-	0.13	-16.45	-92.14	194.00	0.93	0.03
207.70	-	-	-	-	-	-	0.15	-	-93.55	194.10	1.00	0.03
218.00	-	-	-0.08	-	-	-	-	-20.02	-92.51	194.70	1.66	0.02
207.90	6.76	-	-	-	-	-	-	-	-93.92	194.80	1.74	0.02
213.20	-	0.320	-	-	-2.85	-	-	-	-92.60	194.90	1.84	0.02
213.50	5.31	-	-	-	-2.35	-	-	-	-92.71	195.10	2.06	0.02
Global model = **SES.MPD**~Forest shape index+Landscape shape index+Forest nearest neighbour+Mean forest nearest neighbour+Source distance+Forest patch size+Forest cover+Forest patch density												
Intercept	For. shape index	Land. shape index	For. nearest neighbour	Mean for. nearest neighbour	Source distance	For. patch size	Forest cover	For. patch density	logLik	AICc	Δ AICc	AICcWt
-0.19	-2.42	-0.18	-	-	-	-	-	5.44	-36.47	85.70	0	0.07
0.10	-	-0.09	-	-	-	-	-	4.13	-38.10	85.90	0.27	0.06
-0.69	-	-	0.002	-	-0.45	-	-	5.62	-36.87	86.50	0.80	0.05
-0.54	-	-0.11	-	-	-	0.33	-	4.52	-37.01	86.70	1.07	0.04
-0.82	-	-	-	-	-	-	-	4.26	-39.92	86.80	1.18	0.04
-1.27	-	-	0.002	-	-	-	-	4.76	-38.91	87.60	1.89	0.03
-0.28	-	-	-	-	-0.31	-	-	4.72	-38.93	87.60	1.93	0.03
0.40	-	-0.08	-	-	-0.24	-	-	4.50	-37.48	87.70	2.01	0.03
Global model = **MNTD**~Forest shape index+Landscape shape index+Forest nearest neighbour+Mean forest nearest neighbour+Source distance+Forest patch size+Forest cover+Forest patch density												
Intercept	For. shape index	Land. shape index	For. nearest neighbour	Mean for. nearest neighbour	Source distance	For. patch size	Forest cover	For. patch density	logLik	AICc	Δ AICc	AICcWt
82.76	-	-	-	-	-	-	-	-	-96.05	196.60	0	0.09
79.73	8.50	-	-	-	-	-	-	-	-95.13	197.30	0.69	0.07
78.28	-	0.44	-	-	-	-	-	-	-95.21	197.40	0.84	0.06
83.62	-	-	-0.005	-	-	-	-	-	-95.89	198.80	2.20	0.03
Global model = **SES.MNTD**~Forest shape index+Landscape shape index+Forest nearest neighbour+Mean forest nearest neighbour+Source distance+Forest patch size+Forest cover+Forest patch density												
Intercept	For. shape index	Land. shape index	For. nearest neighbour	Mean for. nearest neighbour	Source distance	For. patch size	Forest cover	For. patch density	logLik	AICc	Δ AICc	AICcWt
0.01	-	-	-	-	-	-	-0.02	-	-34.25	75.50	0	0.06
-0.40	-	-	-	-	-	-	-	-	-35.88	76.20	0.74	0.04
-0.85	-	-	-	0.001	-	-	-	-	-34.67	76.30	0.84	0.04
0.65	-	-0.05	-	-	-	-	-0.03	-	-33.39	76.50	1.03	0.04
0.28	-0.75	-	-	-	-	-	-0.02	-	-33.67	77.10	1.58	0.03
0.44	-	-0.09	-	-	-	0.30	-0.04	-	-32.33	77.40	1.90	0.02
-0.60	-	-	0.001	-	-	-	-	-	-35.22	77.40	1.95	0.02
-0.87	-	-	-	-	0.22	-	-	-	-35.23	77.50	1.97	0.02
-0.34	-	-	-	0.001	-	-	-0.02	-	-33.98	77.70	2.21	0.02
Global model = **Species richness**~Forest shape index+Landscape shape index+Forest nearest neighbour+Mean forest nearest neighbour+Source distance+Forest patch size+Forest cover+Forest patch density												
Intercept	For. shape index	Land. shape index	For. nearest neighbour	Mean for. nearest neighbour	Source distance	For. patch size	Forest cover	For. patch density	logLik	AICc	Δ AICc	AICcWt
55.44	-	-	-	-	-	-	0.65	26.11	-101.91	213.50	0	0.14
63.89	-	-	-	-	-	-	0.63	-	-103.65	214.30	0.75	0.10
69.13	-	-	-	-0.01	-	-	0.54	-	-103.21	216.20	2.61	0.04

Table S5 – Model selection for the impacts of size and fragment location (edge vs. interior). Loglik = maximum likelihood; AICc = Akaike information criterion for small samples; ΔAICc = Difference between the AICc of a given model and that of the best model; and AICcWt = Akaike weights (based on AIC corrected for small sample sizes). SES.PD = standardized value of PD; MPD = mean phylogenetic distance (millions of years); MNTD = Mean nearest taxon phylogenetic distance (millions of years); SES.MPD = standardized value of MPD; SES.MNTD = standardized value of MNTD. Habitats = edge and interior.

Global model = **PD**~Forest patch size*Habitats							
Intercept	Forest patch size	Habitats	Forest patch size:Habitats	logLik	AICc	Δ AICc	AICcWt
3866.35	-	1240.75	-394.23	-172.98	362.91	0	0.39
4414.59	-	-	-	-177.99	363.18	0.28	0.34
4324.33	-	180.52	-	-177.37	364.85	1.94	0.15
Global model = **SES.PD**~Forest patch size*Habitats							
Intercept	Forest patch size	Habitats	Forest patch size:Habitats	logLik	AICc	Δ AICc	AICcWt
-0.13	-	-	-	-31.41	70.02	0	0.64
-0.13	-	0.01	-	-31.33	72.76	2.74	0.16
Global model = **MPD**~Forest patch size*Habitats							
Intercept	Forest patch size	Habitats	Forest patch size:Habitats	logLik	AICc	Δ AICc	AICcWt
208.88	-	-	-	-78.60	164.40	0	0.51
207.52	-	2.72	-	-77.87	165.85	1.46	0.25
200.90	-	-	-3.45	-78.45	167.01	2.61	0.14
Global model = **SES.MPD**~Forest patch size*Habitats							
Intercept	Forest patch size	Habitats	Forest patch size:Habitats	logLik	AICc	Δ AICc	AICcWt
1.28	-	-	-	-32.87	72.94	0	0.54
1.48	-	-0.39	-	-32.18	74.46	1.52	0.25
1.50	-0.08	-	-	-32.79	75.69	2.76	0.14
Global model = **MNTD**~Forest patch size*Habitats							
Intercept	Forest patch size	Habitats	Forest patch size:Habitats	logLik	AICc	Δ AICc	AICcWt
76.48	-	5.14	-	-78.89	171.12	0	0.24
85.50	-2.40	-	-	-80.64	171.39	0.27	0.21
82.93	-2.41	5.30	-	-80.65	171.40	0.28	0.21
79.05	-	-	-	-82.18	171.55	0.43	0.20
87.91	-4.25	4.82	3.70	-77.72	172.37	1.25	0.13
Global model = **SES.MNTD**~Forest patch size*Habitats							
Intercept	Forest patch size	Habitats	Forest patch size:Habitats	logLik	AICc	Δ AICc	AICcWt
0.16	-	-0.79	-	-22.95	59.23	0	0.70
-1.01	0.44	-0.38	-0.15	-22.75	62.43	3.20	0.14
Global model = **Species richness**~Forest patch size*Habitats							
Intercept	Forest patch size	Habitats	Forest patch size:Habitats	logLik	AICc	Δ AICc	AICcWt
69.40	4.22	28.64	-8.98	-89.40	185.99	0	0.46
80.75	-	4.50	-	-88.78	187.66	1.67	0.20
83.71	0.27	-	-	-85.45	187.85	1.86	0.18
83.00	-	-	-	-89.39	188.88	2.89	0.11

Fig. S1 – see attached pdf of Figure S1 for higher resolution

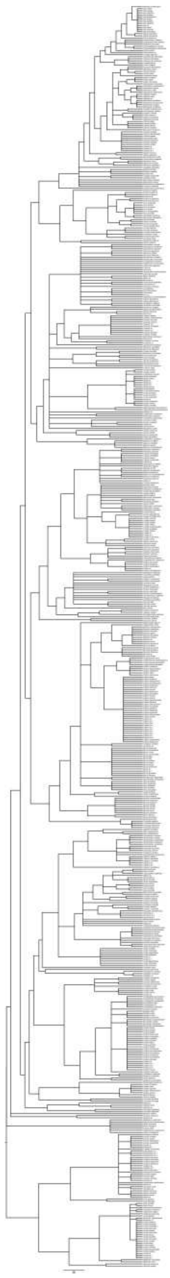

Fig. S1 - Phylogenetic tree of tree species sampled in study fragments (28 transects) in the Brazilian Atlantic forest. The phylogenetic relationships between families, genera and species were based on phylogenetic hypothesis (R20120829mod.new) modified by Gastauer and Meira-Neto (in press). The scale of this phylogenetic tree is in millions of years.

Fig. S2

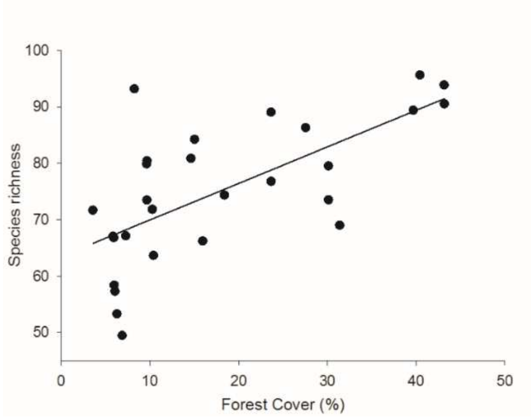

Fig. S2 - Effect of forest cover on species richness, analyzed in 28 transects sampled in the Brazilian Atlantic forest. Values were obtained after the summation of the raw residuals with the expected values for variable (y), assuming average value for the variable (partial residuals plots).

Fig. S3

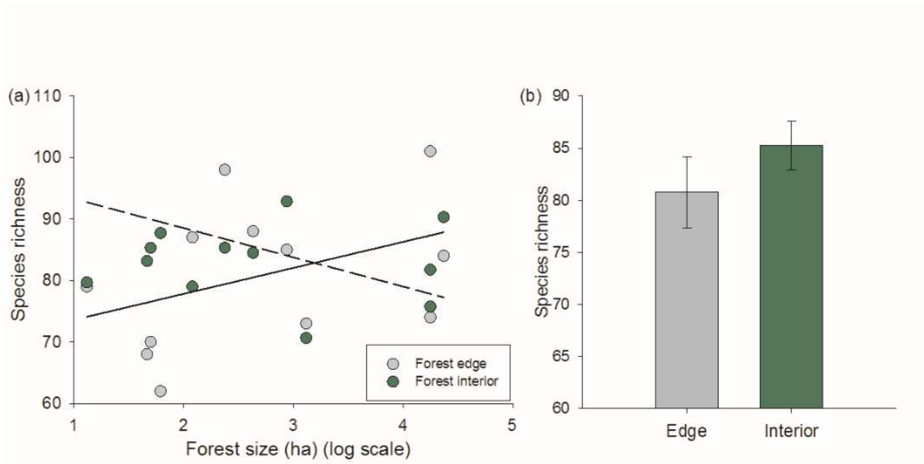

Fig. S3 - Relationship between fragment size and habitat (i.e., edge and interior) with species richness sampled in 24 transects of the Atlantic forest. (a) The effect of the interaction between fragments size and habitat on species richness; and (b) the effect of habitat on species richness. Continuous line (forest edge) and dashed line (forest interior) circles represent values obtained after summation of raw residuals with the expected values for each variable, assuming average values for other covariates. Errors bars represent standard errors.

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IV. CAPÍTULO II

Impacts of forest fragmentation on the functional diversity of trees: roles of landscape configuration and composition in the Brazilian Atlantic forest

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This Supplementary Information includes:

Text A1 – Supporting methods: Metrics of fragmentation

Text A2 – Supporting methods: Functional trait matrix

Table A1 – Fragment details

Table A2 – Values of landscape configuration and composition metrics in study fragments

Table A3 – Metrics of landscape configuration and composition

Table A4 – Results of generalized linear models for the impacts of landscape metrics on functional diversity and functional structure

Table A5 – Results of generalized linear models for the impacts of landscape metrics on the functionally unique species

Table A6 – Results of generalized linear models for the impacts of landscape metrics on the abundance of our six functional traits

Table A7 – Results of generalized linear models for the impacts of landscape metrics (i.e., configuration and composition) on the richness and abundance of our fruit dispersal syndrome traits

Table A8 – Results of generalized linear models for the impacts of landscape metrics (i.e., configuration and composition) on the richness and abundance of our forest structure traits

Table A9 – Results of generalized linear models for the impacts of landscape metrics (i.e., configuration and composition) on the functional trait of carbon storage (i.e. wood density)

Fig. A1 – Results of Generalized Linear Models results (only the best models according to AICc) for the effects of landscape configuration on richness per functional trait

Fig. A2 – Results of Generalized Linear Models results (only the best models according to AICc) for the effects of landscape configuration on abundance of species per functional trait

Fig. A3 - Results of Generalized Linear Models results (only the best models according to AICc) for the effects of landscape composition on richness of species per functional trait

Fig. A4 - Results of Generalized Linear Models results (only the best models according to AICc) for the effects of landscape composition on abundance of species per functional trait and wood density

Fig. A5 – Correlation between fragment size (x axis) and the level of irregularity of forest fragments (y axis)
Supporting references

Text A1 - Supporting methods: Metrics of fragmentation

After the Amazon forest, the Brazilian Atlantic forest is the second largest area of tropical rainforest in South America (Oliveira-Filho and Fontes, 2000). Currently it is estimated that 72% of the Brazilian population live in the potential distribution area of this biome and that of its original area of ~148Mha ha only ~16 Mha ha remains, distributed in fragments of different successional stages, shapes, sizes and isolation levels (Ribeiro et al., 2009; Tabarelli et al., 2010; Magnago et al., 2014).

The first map of vegetation types of the Brazilian Atlantic forest was produced in 1985, and subsequently updated every five years up to 2005; further updates were generated for the 2005-2008, 2008-2010 periods and currently every year since 2010 (SOS Mata Atlântica/INPE, 2015). The vegetation map used in this study is the update generated with remote sensing data from 2015 to produce the 2013-2014 update. Satellite data acquired by the Operational Land Imager (OLI) sensor onboard Landsat 8 were processed and used to generate the updated map with a minimum map unit of three hectares. The classification followed a visual interpretation and manual delineation approach to discriminate three forest formations (Atlantic forest, sandbank vegetation (*restinga*), and mangrove) and associated ecosystems which have a high distinction in their composition, vegetation type (Oliveira-Filho and Fontes, 2000) and patterns of phylogenetic structure (Duarte et al., 2014); additionally, several non-forest classes were also identified and mapped: seasonally flooded vegetation (*várzea*), mountain systems, vegetation refuges, and dunes. Deforestation over forest classes were also mapped by comparison with data from previous periods.

The original map of vegetation types of the Brazilian Altantic forest was first reclassified into a 2-class map of forest (i.e. only Tableland forest) and non-forest (i.e., all other types of natural and non-natural formations). Next, a buffer of 5 km around each one of the 27 sampled forest fragments was generated. Each fragment and its surroundings (defined by the 5 km buffer) delimited each analysis unit in this study (i.e., each landscape). A 5 km buffer was used to capture the high level of fragmentation and isolation of each forest patch considered in the analysis (see Magnago et al., 2014; Magnago et al., 2015 and Table A2). However, omission and commission errors were detected after comparison with available very-high optical spatial resolution satellite data from 2012 (World Imagery 2015). These were then manually corrected to obtain the most accurate spatial delineation of every forest fragment within each 5 km buffer. All forest fragments were then converted to raster format using the same spatial resolution (30 meters) used to generate the vegetation map of this biome. Additionally, deforestated areas were mapped by comparing the spatial distribution of forest classes across maps of two consecutive periods.

Text A2 - Supporting methods: Functional trait matrix

We used six functional traits, which are associated with: (i) Quantity and type of food resource; (ii) Fruit dispersal syndrome; (iii) Forest structure; and (iv) Carbon storage (see Magnago et al., 2014 for more details).

(i) Food resource: (1) fruit diameter (mm); (2) seed diameter (mm); and (3) fruit type - categorized into fleshy fruit, when the pericarp can accumulate water and many organic compounds (see Coombe, 1976 and Magnago et al. 2014), and non-fleshy fruits. These metrics were obtained from specimens in Herbarium of the Vale (CVRD) and literature, supported the database of SpeciesLink (for more details see: http://splink.cria.org.br/).

(ii) Fruit dispersal syndrome: (4) dispersion type – categorized into zoochoric and non-zoochoric according to Van der Pijl, (1982). A zoochoric tree produces diaspores surrounded by fleshy pulp, an aryl or other features that are typically associated with dispersal by animals, and a non-zoochoric tree has characteristics that indicate dispersal by abiotic means, such as winged seeds, feathers or a lack of features that indicate dispersal via methods other than downfall or explosive indehiscence (Magnago et al., 2014). The dispersion type of each species was again obtained from specimens in CVRD and through the data available in SpeciesLink (for more details see: http://splink.cria.org.br/), and Magnago et al., (2014).

(iii) Forest structure: (5) successional groups – categorized as pioneer, initial secondary and later secondary according to Bongers et al., (2009). We considered as pioneers those trees that develop in conditions of high light and generally do not occur in the understory, initial secondary those trees that develop in intermediate shading conditions and as later secondary those trees that develop exclusively and permanently in the understory (see Magnago et al., 2014). The study species were classified using the databases of Jesus and Rolim, (2005) and Magnago et al., (2014).

(iv) Carbon storage: (6) wood density in dry weight (g cm^{-3}) - obtained from Global Wood Density database (GWD) (available in: http://goo.gl/Upv8Ry, Chave et al., 2009; Zanne et al., 2009). When a species was identified at the genus level or was not present in the GWD database, we used the average density of wood for all species of the same genus in the database (for more details see Flores and Coomes, 2011; Hawes et al., 2012; Magnago et al., 2014).

Table A1. Identification, size and coordinates of each transect in the studied fragments in the Brazilian Atlantic forest. Identification corresponds to the fragment identification number in Figure 1. * = transect sampled in the same fragment, separated by 4 km.

Identification	Size (ha)	Coordinates (Geographic WGS 84)	
1	428.94	19° 8'53.77"S	40° 7'20.24"W
2	61.38	19° 5'5.31"S	40°10'30.55"W
3	46.26	19° 7'59.17"S	40° 4'24.39"W
4	868.32	19° 5'18.06"S	40° 0'29.78"W
5	17716.14 *	19° 6'52.93"S	39°55'39.31"W
6	17716.14 *	19° 4'46.69"S	39°55'13.99"W
7	49.77	19° 4'10.94"S	39°58'59.18"W
8	13.05	19° 3'48.02"S	39°58'58.52"W
9	236.61	19° 3'9.60"S	40° 0'14.70"W
10	23480.37	19° 0'46.76"S	40° 7'17.80"W
11	1305.63	19° 2'17.18"S	39°55'2.14"W
12	119.79	19° 1'43.88"S	39°54'21.71"W
13	153.54	18°25'35.55"S	40°22'10.01"W
14	54.99	18°24'45.22"S	40°21'44.45"W
15	56.16	18°23'37.27"S	40°20'47.32"W
16	13.05	18°22'55.38"S	40°12'14.53"W
17	2391.75	18°20'44.87"S	40° 8'28.39"W
18	20.61	18°17'51.67"S	40°10'2.55"W
19	188.55	18°26'50.72"S	39°55'26.16"W
20	1048.05	18°22'13.76"S	39°51'27.51"W
21	282.69	18°20'23.91"S	39°47'8.79"W
22	153.9	18°19'29.07"S	39°46'35.41"W
23	100.35	18°19'32.28"S	39°43'18.32"W
24	1490.4	18°16'17.76"S	39°48'21.43"W
25	620.64	17°45'40.80"S	39°30'45.30"W
26	109.44	17°43'29.30"S	39°44'26.60"W
27	45.81	17°34'40.40"S	39°33'29.85"W
28	166.05	17°23'42.32"S	39°26'32.94"W

Table A2. Range, mean and standard deviation (SD) of the eight metrics describing landscape configuration and composition in 27 fragments sampled in the Atlantic rainforest. Information about each metric can be obtained in Table A3.

Landscape variable	Minimum	Maximum	Mean	SD
Configuration				
Forest shape index	1.15	9.84	2.63	1.77
Forest nearest neighbour (m)	60.00	792.02	183.73	174.91
Mean forest nearest neighbour (m)	166.30	1099.60	349.70	196.92
Source distance (km)	0.10	29.00	6.35	9.19
Composition				
Forest patch size (ha)	13.05	23480.37	2462.09	6151.44
Forest cover (%)	3.55	43.17	17.94	12.89
Forest patch density (in 100 ha)	0.13	0.68	0.31	0.13

Table A3. Metrics used to describe landscape configuration and composition in the globally threatened Brazilian Atlantic forest. All these metrics were calculated individually for an area encompassing each sampled forest fragment and a 5 km buffer. ρ = patchs characteristics; ¤ = characteristics that describe the forest class ‡ = and characteristics used to describe our landscapes.

Variable name (units)	Type	Description	Equation	Description equation
Configuration metrics				
Forest shape index (none)	ρ	Fragment forest perimeter divided by the minimum perimeter of the fragment forest area.	$\frac{.25p_{ij}}{\sqrt{a_{ij}}}$	pij = perimeter (m) of patch ij; aij = area (m²) of patch ij.
Forest nearest neighbour (m)	ρ	The distance Euclidean to the nearest neighboring patch of the same type, based on shortest edge-to-edge distance.	h_{ij}	hij =distance (m) between patch ij and nearest neighbour patch of type i.
Mean forest nearest neighbour (m)	¤ ‡	Distance Euclidean mean to the nearest neighbour fragment for all fragments forest in the landscape.	$\frac{\sum_{j=1}^{n}}{n_i}h_{ij}$	hij =distance (m) between patch ij and nearest neighbour patch of type i, based on edge-to-edge distance; ni= number of patchs type i.
Source distance (Km)	ρ	Linear distance of the sampled fragment to the nearest fragment ≥ 1,000 hectares.	-	-
Composition metrics				
Forest patch size (ha)	ρ	Area equals the area (m²) of the fragment, divided by 10,000.	$a_{ij}\left(\frac{1}{10,000}\right)$	a_{ij} = area (m²) of fragment ij.
Forest cover (%)	¤ ‡	Percentage of the landscape covered by forest.	$\frac{\sum_{j=1}^{n}a_{ij}}{A}(100)$	a_{ij} = area (m²) of fragment ij; A = total landscape area (m²).
Forest patch density (fragments per 100 hectares)	‡	Amount of forest fragments divided by total landscape area.	$\frac{n_i}{A}(10,000)(100)$	n_i = number of fragments in the landscape of patch type; A total landscape area (m²).

Table A4. Model selection for the impacts of landscape metrics on functional diversity and functional structure of tree communities. Log-likelihood = maximum likelihood; AICc = Akaike information criterion for small samples; ΔAICc = Difference between the AICc of a given model and that of the best model; and AICcWt = Akaike weights (based on AIC corrected for small sample sizes). See table S3 for more details on the metrics.

Global model = **FRic**~Forest shape index+Forest nearest neighbour+Mean forest nearest neighbour+Source distance+Forest patch size+Forest cover+Forest patch density, family = gaussian											
Intercept	For. shape index	For. nearest neighbour	Mean for. nearest neighbour	Source distance	For. patch size	Forest cover	For. patch density	logLik	AICc	Δ AICc	AICcWt
2.45	-	-	-	-	-	-	-	-32.55	69.60	0	0.15
2.67	-	-	-	-	-	-	-0.01	-31.99	71.00	1.41	0.07
2.14	-	-	-	0.14	-	-	-	-32.19	71.40	1.81	0.06
2.58	-0.36	-	-	-	-	-	-	-32.40	71.80	2.22	0.05
Global model = **sesFRic**~Forest shape index+Forest nearest neighbour+Mean forest nearest neighbour+Source distance+Forest patch size+Forest cover+Forest patch density, family = gaussian											
Intercept	For. shape index	For. nearest neighbour	Mean for. nearest neighbour	Source distance	For. patch size	Forest cover	For. patch density	logLik	AICc	Δ AICc	AICcWt
-0.29	-1.38	-	-	0.27	-	-	-	-25.63	61.00	0	0.11
0.68	-1.55	-	-	-	-	-0.02	-	-25.90	61.50	0.52	0.08
0.37	-1.54	-	-	-	-	-	-	-27.56	62.10	1.12	0.06
0.01	-1.55	-	-	0.30	-	-	-0.93	-25.15	63.00	2.03	0.04
Global model = **FEve**~Forest shape index+Forest nearest neighbour+Mean forest nearest neighbour+Source distance+Forest patch size+Forest cover+Forest patch density, family = gaussian											
Intercept	For. shape index	For. nearest neighbour	Mean for. nearest neighbour	Source distance	For. patch size	Forest cover	For. patch density	logLik	AICc	Δ AICc	AICcWt
0.72	-	-0.00011	-	-	-0.02	-	-	56.01	-102.30	0	0.17
0.72	0.03	-0.00010	-	-	-0.02	-	-	56.53	-100.30	1.96	0.06
0.84	-	-0.00014	-	-0.03	-0.03	-0.002	-	58.08	-100.20	2.14	0.06
Global model = **sesFEve**~Forest shape index+Forest nearest neighbour+Mean forest nearest neighbour+Source distance+Forest patch size+Forest cover+Forest patch density, family = gaussian											
Intercept	For. shape index	For. nearest neighbour	Mean for. nearest neighbour	Source distance	For. patch size	Forest cover	For. patch density	logLik	AICc	Δ AICc	AICcWt
1.57	-	-0.0028	-	-	-0.49	-	-	-32.09	73.90	0	0.18
4.55	-	-0.0035	-	-0.66	-0.79	-0.04	-	-29.78	75.60	1.65	0.08
1.48	0.65	-0.0026	-	-	-0.56	-	-	-31.74	76.20	2.28	0.06
Global model = **FDiv**~Forest shape index+Forest nearest neighbour+Mean forest nearest neighbour+Source distance+Forest patch size+Forest cover+Forest patch density, family = gaussian											
Intercept	For. shape index	For. nearest neighbour	Mean for. nearest neighbour	Source distance	For. patch size	Forest cover	For. patch density	logLik	AICc	Δ AICc	AICcWt
0.81	-0.05	0.00007	-	-	-	-	-	63.58	-117.40	0	0.11
0.81	-0.06	-	0.00005	-	-	-	-	63.19	-116.60	0.79	0.07
0.79	-	0.00009	-	-	-	-	-	61.25	-115.50	1.93	0.04
0.82	-0.05	0.00006	-	-	-	-0.0004	-	64.06	-115.40	2.03	0.04
Global model = **sesFDiv**~Forest shape index+Forest nearest neighbour+Mean forest nearest neighbour+Source distance+Forest patch size+Forest cover+Forest patch density, family = gaussian											
Intercept	For. shape index	For. nearest neighbour	Mean for. nearest neighbour	Source distance	For. patch size	Forest cover	For. patch density	logLik	AICc	Δ AICc	AICcWt
-0.20	-1.24	-	0.001	-	-	-	-	-26.18	62.10	0	0.08
-0.06	-1.09	0.002	-	-	-	-	-	-26.28	62.30	0.20	0.07
-0.54	-	0.002	-	-	-	-	-	-28.01	63.00	0.92	0.05
1.43	-1.92	-	-	-	-	-0.02	-1.84	-25.35	63.40	1.33	0.04
0.70	-1.55	-	-	-	-	-0.02	-	-27.14	64.00	1.91	0.03
0.40	-1.54	-	-	-	-	-	-	-28.53	64.10	1.96	0.03
0.22	-1.17	0.001	-	-	-	-0.01	-	-25.69	64.10	2.00	0.03
Global model = **FDis**~Forest shape index+Forest nearest neighbour+Mean forest nearest neighbour+Source distance+Forest patch size+Forest cover+Forest patch density, family = gaussian											
Intercept	For. shape index	For. nearest neighbour	Mean for. nearest neighbour	Source distance	For. patch size	Forest cover	For. patch density	logLik	AICc	Δ AICc	AICcWt
2.53	-0.53	-	-	-	-	-0.01	-	12.52	-15.30	0	0.15
2.65	-0.59	-	-	-	-	-0.01	-0.30	13.28	-13.80	1.46	0.07
2.60	-0.43	-	-	-	-0.05	-0.01	-	13.22	-13.70	1.59	0.07
2.13	-0.46	-	-	0.11	-	-	-	11.51	-13.30	2.02	0.05
Global model = **sesFDis**~Forest shape index+Forest nearest neighbour+Mean forest nearest neighbour+Source distance+Forest patch size+Forest cover+Forest patch density, family = gaussian											
Intercept	For. shape index	For. nearest neighbour	Mean for. nearest neighbour	Source distance	For. patch size	Forest cover	For. patch density	logLik	AICc	Δ AICc	AICcWt
1.20	-2.39	-	-	-	-	-0.04	-	-28.02	65.80	0.00	0.15
1.84	-2.72	-	-	-	-	-0.04	-1.62	-26.74	66.20	0.42	0.12
3.49	-3.43	-	-0.002	-	-	-0.06	-3.21	-25.27	66.50	0.75	0.10
1.49	-1.95	-	-	-	-0.21	-0.04	-	-27.24	67.20	1.42	0.07
2.13	-2.29	-	-	-	-0.21	-0.04	-1.61	-25.90	67.80	2.02	0.05

Table A5. Model selection for the impacts of landscape metrics (i.e., configuration and composition) on the functionally unique species. Log-likelihood = maximum likelihood; AICc = Akaike information criterion for small samples; ΔAICc = Difference between the AICc of a given model and that of the best model; and AICcWt = Akaike weights (based on AIC corrected for small sample sizes). See table S3 for more details on the metrics.

Global model = **Functional uniquenes**~Forest shape index+Forest nearest neighbour+Mean forest nearest neighbour+Source distance+Forest patch size+Forest cover+Forest patch density, family = gaussian											
Intercept	For. shape index	For. nearest neighbour	Mean for. nearest neighbour	Source distance	For. patch size	Forest cover	For. patch density	logLik	AICc	Δ AICc	AICcWt
2.45	-	-	-	-	-	-	-	-32.55	69.60	0	0.15
2.67	-	-	-	-	-	-0.01	-	-31.99	71.00	1.41	0.07
2.14	-	-	-	0.14	-	-	-	-32.19	71.40	1.81	0.06
2.58	-0.36	-	-	-	-	-	-	-32.40	71.80	2.22	0.05

Table A6. Model selection for the impacts of landscape metrics (i.e., configuration and composition) on the fruit diameter, seed diameter, richness and abundance of our food resource traits. Log-likelihood = maximum likelihood; AICc = Akaike information criterion for small samples; ΔAICc = Difference between the AICc of a given model and that of the best model; and AICcWt = Akaike weights (based on AIC corrected for small sample sizes). See table S3 and S4 for more details on the metrics.

Global model = **Fruit diameter**~Forest shape index+Forest nearest neighbour+Mean forest nearest neighbour+Source distance+Forest patch size+Forest cover+Forest patch density, family = gaussian											
Intercept	For. shape index	For. nearest neighbour	Mean for. nearest neighbour	Source distance	For. patch size	Forest cover	For. patch density	logLik	AICc	Δ AICc	AICcWt
21.66	-	-	-	-	-	-	-	-72.13	148.70	0	0.16
22.39	-2.07	-	-	-	-	-	-	-71.83	150.70	1.93	0.06
22.84	-	-	-	-	-0.49	-	-	-71.87	150.70	2.00	0.06
Global model = **Seed diameter**~Forest shape index+Forest nearest neighbour+Mean forest nearest neighbour+Source distance+Forest patch size+Forest cover+Forest patch density, family = gaussian											
Intercept	For. shape index	For. nearest neighbour	Mean for. nearest neighbour	Source distance	For. patch size	Forest cover	For. patch density	logLik	AICc	Δ AICc	AICcWt
10.34	-	-	-	-	-	-	-	-42.05	88.60	0	0.10
10.65	-	-0.0017	-	-	-	-	-	-41.03	89.10	0.48	0.07
11.62	-	-0.0023	-	-	-0.35	-	-	-39.94	89.60	1.04	0.06
10.06	0.81	-	-	-	-	-	-	-41.66	90.30	1.74	0.04
10.65	-	-	-0.0009	-	-	-	-	-41.71	90.40	1.83	0.04
10.79	-	-	-	-	-0.19	-	-	-41.73	90.50	1.88	0.04
10.72	1.62	-	-	-	-0.40	-	-	-40.54	90.80	2.22	0.03
Species richnnes											
Global model = **Fleshy fruits**~Forest shape index+Forest nearest neighbour+Mean forest nearest neighbour+Source distance+Forest patch size+Forest cover+Forest patch density, family = negative.binomial											
Intercept	For. shape index	For. nearest neighbour	Mean for. nearest neighbour	Source distance	For. patch size	Forest cover	For. patch density	logLik	AICc	Δ AICc	AICcWt
3.49	-	-	-	-	-	0.0128	-	-100.21	207.40	0	0.13
3.40	0.23	-	-	-	-	0.0130	-	-99.39	208.50	1.09	0.07
3.72	-	-	-	-0.08	-	0.0090	-	-99.59	208.90	1.49	0.06
3.39	-	-	-	-	0.05	0.0122	-	-99.68	209.10	1.68	0.06
3.54	-	-0.00020	-	-	-	0.0120	-	-99.93	209.60	2.18	0.04
Global model = **Non-fleshy fruits**~Forest shape index+Forest nearest neighbour+Mean forest nearest neighbour+Source distance+Forest patch size+Forest cover+Forest patch density, family = negative.binomial											
Intercept	For. shape index	For. nearest neighbour	Mean for. nearest neighbour	Source distance	For. patch size	Forest cover	For. patch density	logLik	AICc	Δ AICc	AICcWt
0.41	-	-	-	-	-	-	-	-33.01	70.50	0	0.19
0.47	-0.17	-	-	-	-	-	-	-32.99	73.00	2.46	0.06
Species abundance											
Global model = **Fleshy fruits**~Forest shape index+Forest nearest neighbour+Mean forest nearest neighbour+Source distance+Forest patch size+Forest cover+Forest patch density, family = negative.binomial											
Intercept	For. shape index	For. nearest neighbour	Mean for. nearest neighbour	Source distance	For. patch size	Forest cover	For. patch density	logLik	AICc	Δ AICc	AICcWt
4.57	0.47	-	-	-0.16	-	-	-	-125.05	259.80	0	0.07
3.99	0.62	-	-	-	-	0.01	-	-125.25	260.20	0.39	0.05
4.84	-	-0.00064	-	-0.16	-	-	-	-125.26	260.30	0.43	0.05
4.65	0.35	-0.00047	-	-0.14	-	-	-	-124.07	260.90	1.02	0.04
4.80	-	-	-	-0.19	-	-	-	-127.18	261.40	1.51	0.03
3.91	-	-	-	-	0.14	0.01	-	-125.86	261.50	1.62	0.03
3.88	0.44	-	-	-	0.08	0.01	-	-124.45	261.60	1.79	0.03
4.17	-	-0.00058	-	-	0.13	-	-	-126.10	261.90	2.10	0.02
Global model = **Non-fleshy fruits**~Forest shape index+Forest nearest neighbour+Mean forest nearest neighbour+Source distance+Forest patch size+Forest cover+Forest patch density, family = negative.binomial											
Intercept	For. shape index	For. nearest neighbour	Mean for. nearest neighbour	Source distance	For. patch size	Forest cover	For. patch density	logLik	AICc	Δ AICc	AICcWt
4.69	-0.53	-	-	-	-	-	-	-125.29	257.60	0	0.18
4.74	-0.53	-	-	-	-	-0.0030	-	-124.92	259.60	2.00	0.07

Table A7. Model selection for the impacts of landscape metrics (i.e., configuration and composition) on the richness and abundance of our fruit dispersal syndrome traits. Log-likelihood = maximum likelihood; AICc = Akaike information criterion for small samples; ΔAICc = Difference between the AICc of a given model and that of the best model; and AICcWt = Akaike weights (based on AIC corrected for small sample sizes). See table S3 and S4 for more details on the metrics.

Species richnnes											
Global model = **Zoochoric dispersion**~Forest shape index+Forest nearest neighbour+Mean forest nearest neighbour+Source distance+Forest patch size+Forest cover+Forest patch density, family = negative.binomial											
Intercept	For. shape index	For. nearest neighbour	Mean for. nearest neighbour	Source distance	For. patch size	Forest cover	For. patch density	logLik	AICc	Δ AICc	AICcWt
3.83	-	-	-	-	-	0.01	-	-105.45	217.90	0	0.12
3.90	-	-0.00028	-	-	-	0.01	-	-104.71	219.20	1.25	0.06
3.77	0.16	-	-	-	-	0.01	-	-104.93	219.60	1.69	0.05
4.47	-	-	-0.00045	-0.13	-	-	-	-105.00	219.70	1.83	0.05
3.75	-	-	-	-	0.04	0.01	-	-105.01	219.80	1.85	0.05
3.74	-	-	-	-	-	0.01	0.26	-105.01	219.80	1.85	0.05
4.00	-	-	-	-0.06	-	0.01	-	-105.01	219.80	1.86	0.05
3.93	-	-	-0.00021	-	-	0.01	-	-105.04	219.80	1.91	0.05
3.60	0.25	-	-	-	-	0.01	0.42	-103.89	220.50	2.61	0.03
Global model = **Non-zoochoric dispersion**~Forest shape index+Forest nearest neighbour+Mean forest nearest neighbour+Source distance+Forest patch size+Forest cover+Forest patch density, family = negative.binomial											
Intercept	For. shape index	For. nearest neighbour	Mean for. nearest neighbour	Source distance	For. patch size	Forest cover	For. patch density	logLik	AICc	Δ AICc	AICcWt
3.19	-1.09	-	-	-	-	-	-	-81.13	169.30	0	0.19
3.31	-1.16	-	-0.0003	-	-	-	-	-80.61	171.00	1.70	0.08
3.30	-1.08	0.0007	-0.0007	-	-	-	-	-79.18	171.10	1.82	0.08
3.07	-1.03	-	-	-	-	-	0.32	-80.77	171.30	2.02	0.07
Species abundance											
Global model = **Zoochoric dispersion**~Forest shape index+Forest nearest neighbour+Mean forest nearest neighbour+Source distance+Forest patch size+Forest cover+Forest patch density, family = negative.binomial											
Intercept	For. shape index	For. nearest neighbour	Mean for. nearest neighbour	Source distance	For. patch size	Forest cover	For. patch density	logLik	AICc	Δ AICc	AICcWt
5.23	-	-0.00069	-	-0.12	-	-	-	-132.76	275.30	0	0.09
5.11	0.23	-0.00058	-	-0.11	-	-	-	-132.01	276.70	1.48	0.04
4.70	-	-0.00064	-	-	0.11	-	-	-133.55	276.80	1.58	0.04
5.32	-	-0.00076	-	-0.10	-	-	-0.37	-132.19	277.10	1.84	0.04
5.03	-	-0.00063	-	-0.09	0.05	-	-	-132.38	277.50	2.23	0.03
Global model = **Non-zoochoric dispersion**~Forest shape index+Forest nearest neighbour+Mean forest nearest neighbour+Source distance+Forest patch size+Forest cover+Forest patch density, family = negative.binomial											
Intercept	For. shape index	For. nearest neighbour	Mean for. nearest neighbour	Source distance	For. patch size	Forest cover	For. patch density	logLik	AICc	Δ AICc	AICcWt
4.49	-1.44	-	-	-	-	-0.01	-	-111.76	233.30	0	0.17
3.79	-1.39	-	-	0.20	-	-	-	-112.23	234.20	0.94	0.11
3.69	-1.27	0.00043	-	0.18	-	-	-	-111.32	235.40	2.12	0.06

Table A8. Model selection for the impacts of landscape metrics (i.e., configuration and composition) on the richness and abundance of our forest structure traits. Log-likelihood = maximum likelihood; AICc = Akaike information criterion for small samples; ΔAICc = Difference between the AICc of a given model and that of the best model; and AICcWt = Akaike weights (based on AIC corrected for small sample sizes). See table S3 and S4 for more details on the metrics.

Species richnnes											
Global model = **Pioneers**~Forest shape index+Forest nearest neighbour+Mean forest nearest neighbour+Source distance+Forest patch size+Forest cover+Forest patch density, family = negative.binomial											
Intercept	For. shape index	For. nearest neighbour	Mean for. nearest neighbour	Source distance	For. patch size	Forest cover	For. patch density	logLik	AICc	Δ AICc	AICcWt
2.25	-	-	-	-	-0.31	-	-	-60.57	128.10	0	0.11
2.50	-	-	-	-	-0.32	-	-0.75	-60.03	129.80	1.66	0.05
1.73	-1.01	-	-	0.25	-	-	-1.42	-58.57	129.90	1.73	0.05
1.84	-	-	-	0.12	-0.25	-	-	-60.16	130.10	1.92	0.04
0.95	-	-	-	0.25	-	-	-	-61.58	130.20	2.04	0.04
Global model = **Initial secondary**~Forest shape index+Forest nearest neighbour+Mean forest nearest neighbour+Source distance+Forest patch size+Forest cover+Forest patch density, family = negative.binomial											
Intercept	For. shape index	For. nearest neighbour	Mean for. nearest neighbour	Source distance	For. patch size	Forest cover	For. patch density	logLik	AICc	Δ AICc	AICcWt
2.79	-	-	-	0.11	-	-	-	-78.66	164.30	0	0.08
2.93	-0.31	-	-	0.10	-	-	-	-77.33	164.40	0.09	0.08
3.28	-	-	-	-	-0.10	-	-	-79.19	165.40	1.06	0.05
2.54	-	-	-	0.18	-	0.01	-	-77.95	165.60	1.33	0.04
3.17	-0.38	-	-	-	-	-	-	-79.45	165.90	1.59	0.04
2.77	-	0.00023	-	0.10	-	-	-	-78.20	166.10	1.82	0.03
2.99	-	-	-	0.08	-0.06	-	-	-78.24	166.20	1.90	0.03
2.72	-0.28	-	-	0.15	-	0.00470	-	-76.91	166.50	2.23	0.03
Global model = **Later secondary**~Forest shape index+Forest nearest neighbour+Mean forest nearest neighbour+Source distance+Forest patch size+Forest cover+Forest patch density, family = negative.binomial											
Intercept	For. shape index	For. nearest neighbour	Mean for. nearest neighbour	Source distance	For. patch size	Forest cover	For. patch density	logLik	AICc	Δ AICc	AICcWt
3.84	-	-	-	-0.17	-	0.01	0.79	-97.56	207.80	0	0.19
4.17	-	-	-	-0.26	-	-	0.84	-99.74	209.20	1.38	0.10
4.29	-	-	-0.00035	-0.24	-	-	0.64	-98.58	209.90	2.04	0.07
Species abundance											
Global model = **Pioneers**~Forest shape index+Forest nearest neighbour+Mean forest nearest neighbour+Source distance+Forest patch size+Forest cover+Forest patch density, family = negative.binomial											
Intercept	For. shape index	For. nearest neighbour	Mean for. nearest neighbour	Source distance	For. patch size	Forest cover	For. patch density	logLik	AICc	Δ AICc	AICcWt
1.18	-	0.0013	-	0.48	-	-	-	-93.44	196.60	0	0.11
1.35	-	-	-	0.53	-	-	-	-95.37	197.70	1.12	0.07
2.25	-1.20	-	-	0.54	-	-	-1.81	-92.79	198.30	1.69	0.05
1.05	-	-	0.0009	0.50	-	-	-	-94.35	198.40	1.81	0.05
1.70	-0.82	-	-	0.49	-	-	-	-94.42	198.60	1.95	0.04
1.42	-0.57	0.0011	-	0.47	-	-	-	-93.01	198.70	2.12	0.04
Global model = **Initial secondary**~Forest shape index+Forest nearest neighbour+Mean forest nearest neighbour+Source distance+Forest patch size+Forest cover+Forest patch density, family = negative.binomial											
Intercept	For. shape index	For. nearest neighbour	Mean for. nearest neighbour	Source distance	For. patch size	Forest cover	For. patch density	logLik	AICc	Δ AICc	AICcWt
3.55	-0.59	-	-	0.33	-	-	-0.98	-107.96	228.60	0	0.16
3.06	-	-	-	0.33	-	-	-	-111.75	230.50	1.85	0.06
3.70	-0.73	-0.00035	-	0.35	-	-	-1.23	-107.35	230.70	2.06	0.06
Global model = **Later secondary**~Forest shape index+Forest nearest neighbour+Mean forest nearest neighbour+Source distance+Forest patch size+Forest cover+Forest patch density, family = negative.binomial											
Intercept	For. shape index	For. nearest neighbour	Mean for. nearest neighbour	Source distance	For. patch size	Forest cover	For. patch density	logLik	AICc	Δ AICc	AICcWt
5.32	-	-0.00057	-	-0.24	-	-	-	-132.41	274.60	0	0.08
5.38	-	-	-0.00051	-0.23	-	-	-	-132.51	274.80	0.19	0.07
5.27	-	-	-	-0.26	-	-	-	-134.13	275.30	0.70	0.06
4.11	-	-	-	-	0.16	0.01	-	-133.01	275.80	1.21	0.04
4.90	0.40	-	-	-0.27	-	-	0.77	-131.53	275.80	1.22	0.04
5.15	-	-	-	-0.28	-	-	0.55	-133.17	276.10	1.53	0.04
5.10	-	-	-0.00052	-0.18	0.08	-	-	-131.78	276.30	1.74	0.03
5.15	0.26	-	-	-0.25	-	-	-	-133.38	276.50	1.94	0.03
4.96	-	-	-	-0.21	0.08	-	-	-133.38	276.50	1.94	0.03
5.22	-	-0.00049	-	-0.25	-	-	0.38	-131.95	276.60	2.07	0.03

Table A9. Model selection for the impacts of landscape metrics (i.e., configuration and composition) on the functional trait of carbon stock (i.e. wood density). Log-likelihood = maximum likelihood; AICc = Akaike information criterion for small samples; ΔAICc = Difference between the AICc of a given model and that of the best model; and AICcWt = Akaike weights (based on AIC corrected for small sample sizes). See table S3 and S4 for more details on the metrics.

Global model = Wood density~Forest shape index+Forest nearest neighbour+Mean forest nearest neighbour+Source distance+Forest patch size+Forest cover+Forest patch density, family = gaussian											
Intercept	For. shape index	For. nearest neighbour	Mean for. nearest neighbour	Source distance	For. patch size	Forest cover	For. patch density	logLik	AICc	Δ AICc	AICcWt
0.63	-	-	-	-0.02	-	-	0.14	54.79	-99.80	0	0.10
0.60	0.05	-	-	-0.02	-	-	0.17	55.89	-99.10	0.79	0.06
0.60	-	-	-	-	-	-	0.12	52.79	-98.60	1.27	0.05
0.58	-	-	-	-	-	0.00	0.13	54.07	-98.40	1.46	0.05
0.55	0.05	-	-	-	-	0.00	0.16	55.52	-98.30	1.53	0.04
0.57	0.05	-	-	-	-	-	0.15	54.00	-98.30	1.59	0.04
0.57	-	-	-	-	0.01	-	0.13	53.85	-98.00	1.89	0.04
0.66	-	-	-0.00007	-	-	-	-	52.18	-97.4	2.49	0.03

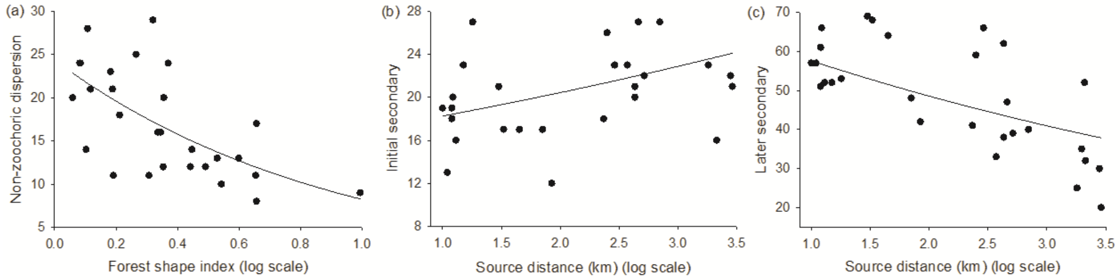

Fig. A1. Results of the Generalized Linear Models analysis (only the best models according to AICc) in terms of the effects of landscape configuration metrics on richness of species by functional trait. (a) Effect of forest shape index on non-zoochoric dispersion; (b) effect of source distance on initial secondary species; and (c) effect of source distance on later secondary species.

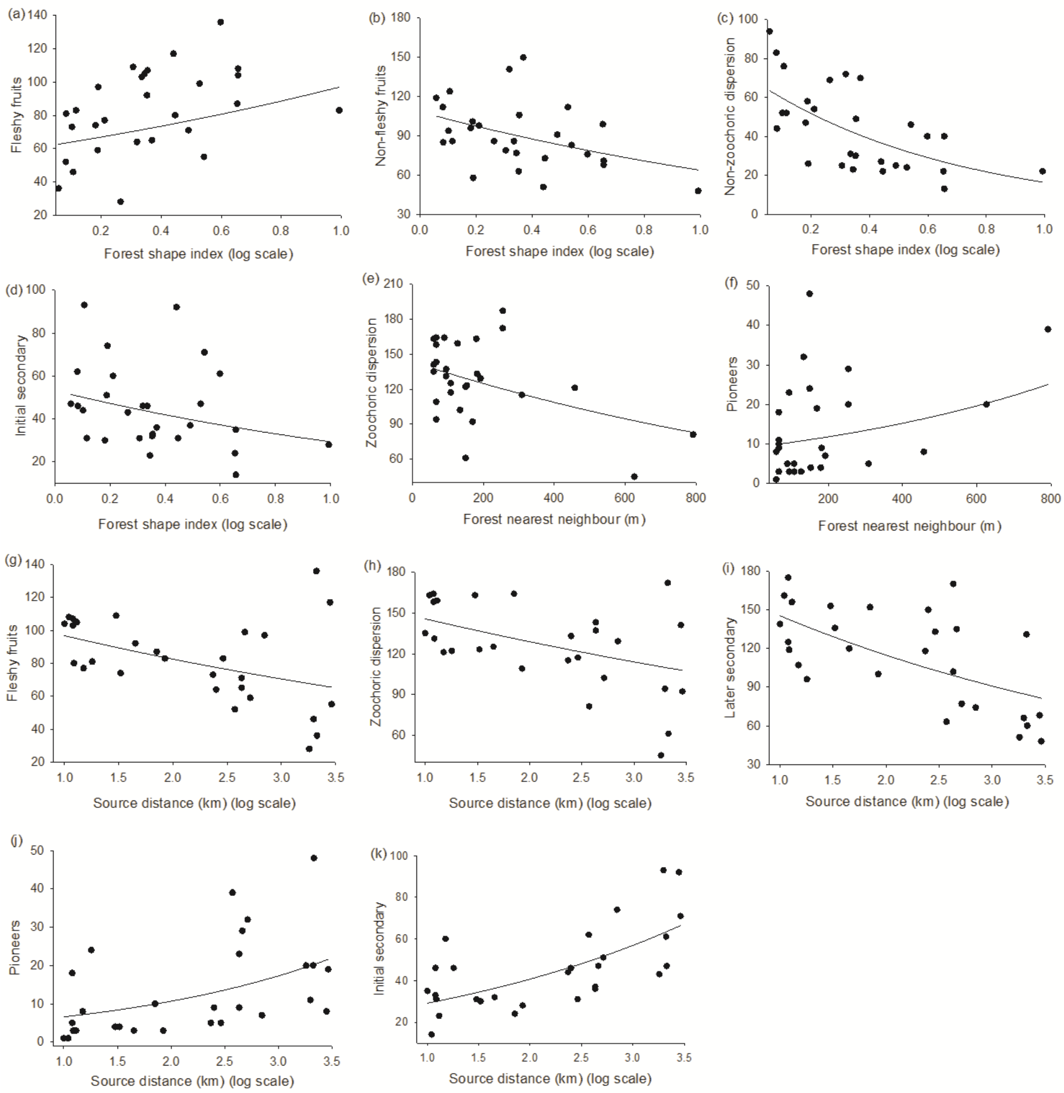

Fig. A2. Results of the Generalized Linear Models analysis (only the best models according to AICc) in terms of the effects of landscape configuration on abundance of species by functional trait. (a) Effect of forest shape index on fleshy fruits; (b) effect of forest shape index on non-fleshy fruits; (c) effect of forest shape index on non-zoochoric dispersion; (d) effect of forest shape index on initial secondary species; (e) effect of forest nearest neighbor on zoochoric dispersion; (f) effect of forest nearest neighbor on pioneers; (g) effect of source distance on fleshy fruits; (h) the effect of source distance on zoochoric dispersion; (i) the effect of source distance on later secondary; (j) effect of Source distance on pioneers species; and (k) effect of source distance on initial secondary species.

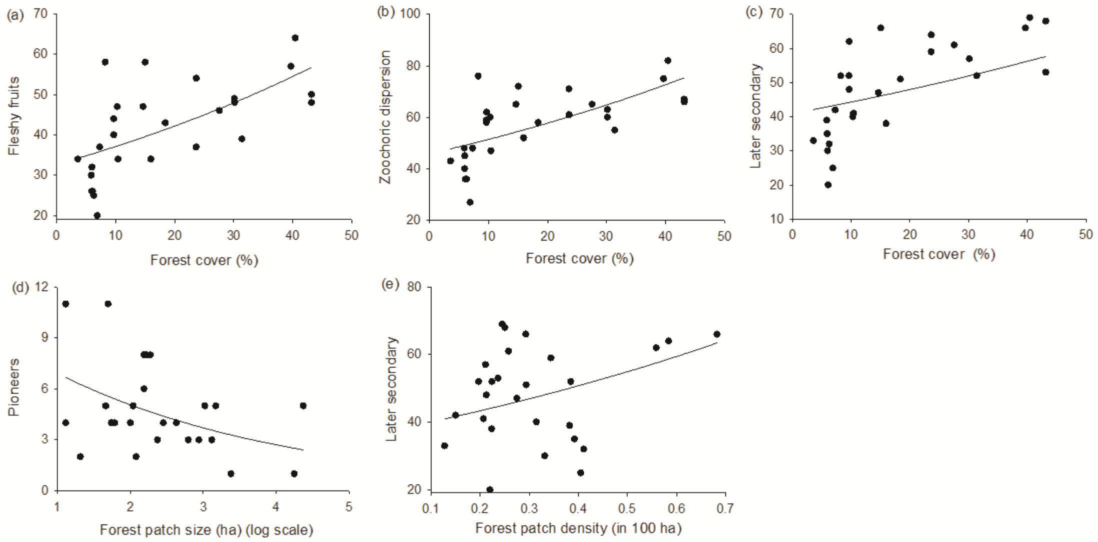

Fig. A3. Results of the Generalized Linear Models analysis (only the best models according to AICc) in terms of the effects of landscape composition on richness of species per functional trait. (a) Effect of forest cover on fleshy fruits; (b) effect of forest cover on zoochoric dispersion; (c) effect of forest cover on later secondary species; (d) effect of forest patch size on pioneers; and (e) effect of forest patch density on later secondary species.

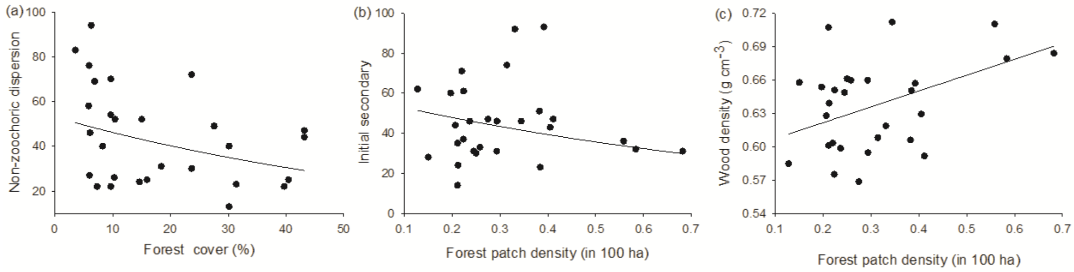

Fig. A4. Results of the Generalized Linear Models analysis (only the best models according to AICc) in terms of the effects of landscape composition on abundance of species by functional trait and wood density. (a) Effect of forest cover on non-zoochoric dispersion; (b) effect of forest patch density on initial secondary species; and (c) effect of forest patch size on wood density.

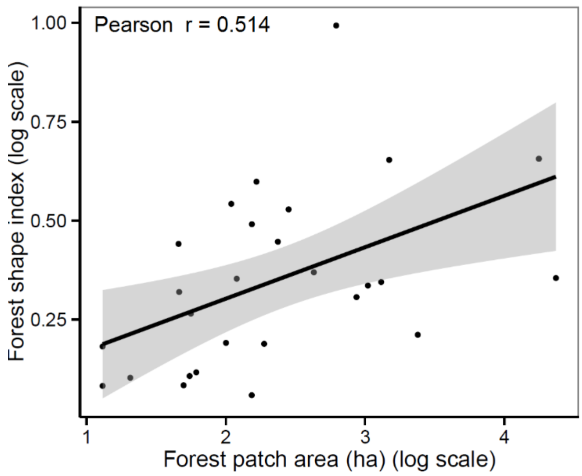

Fig. A5. Correlation between fragment size (x axis) and the level of irregularity of forest fragments (y axis). Fitted values (black line) and 95% confidence limits in gray above and below the fitted lines (*P* = 0.0054).

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IV. CAPÍTULO III

Does secondary forest offer important carbon-biodiversity co-benefits in a highly fragmented landscape?

Text A1 - Supporting methods: Secondary forest age and source distance

The linear distance of secondary forest patches (km) from large forest blocks (≥1,000 hectares; herein 'source distance'), was computed with ArcGis (v 10.1) using as a base the vegetation map of Brazilian Atlantic forest (SOS Mata Atlântica/INPE 2015). This linear distance is only between fragments belonging to the same type of forest (i.e., Tableland forest).

The map of vegetation used to create "source distance" was produced in 1985, and subsequently updated every five years up to 2005; further updates were generated for the 2005-2008, 2008-2010 periods and currently every year since 2010 (SOS Mata Atlântica/INPE, 2015). The vegetation map used in this study is the 2013-2014 update generated with remote-sensing data from 2015. Satellite data were acquired by the Operational Land Imager (OLI) sensor onboard Landsat 8 were processed and used to generate the updated map with a minimum map unit of three hectares. This dataset depicts the spatial distribution of the main forest formations within this biome, and has been used to describe landscape structure via forest loss and fragmentation (Ribeiro *et al*., 2009) and to generate estimates of carbon loss due to habitat fragmentation (Pütz *et al*., 2014).

Text A2 - Supporting methods: Functional trait matrix

We used 6 functional traits, under described, which are associated with: (i) Quantity and type of food resource; (ii) Fruit dispersal syndrome; (iii) Forest structure; and (iv) Carbon storage (see Magnago *et al*., 2014 for more details).

(i) Food resource: (1) fruit diameter (mm); (2) seed diameter (mm); and (3) fruit type - categorized into fleshy fruit, when the pericarp can accumulate water and many organic compounds (see Coombe, 1976 and Magnago *et al*. 2014), and non-fleshy fruits. These metrics were obtained from specimens in Herbarium

CVRD and literature, supported the database of SpeciesLink (for more details see: http://splink.cria.org.br/).

(ii) Fruit dispersal syndrome: (4) dispersion type – categorized into zoochoric and non-zoochoric according to Van der Pijl, (1982). A zoochoric tree produces diaspores surrounded by fleshy pulp, an aryl or other features that are typically associated with dispersal by animals, and a non-zoochoric tree has characteristics that indicate dispersal by abiotic means, such as winged seeds, feathers or a lack of features that indicate dispersal via methods other than downfall or explosive indehiscence (Magnago *et al*., 2014). These dispersion type of each species was again obtained from specimens in Herbarium of the Vale - CVRD and trought the data available in SpeciesLink (for more details see: http://splink.cria.org.br/), and Magnago *et al*., (2014).

(iii) Forest structure: (5) successional groups – categorized as pioneer, initial secondary and later secondary according to Bongers *et al*., (2009). We considered as pioneers those trees that develop in conditions of high light and generally do not occur in the understory, initial secondary those trees that develop in intermediate shading conditions and as later secondary those trees that develop exclusively and permanently in the understory (see Magnago *et al*., 2014). The study species were classified using the databases of Jesus and Rolim, (2005) and Magnago *et al*., (2014).

(iv) Carbon storage: (6) wood density in dry weight (g cm^{-3}) - obtained from Global Wood Density database (GWD) (available in: http://goo.gl/Upv8Ry, Chave et al., 2009; Zanne et al., 2009). When a species was identified at the genus level or was not present in the GWD database, we used the average density of wood for all species of the same genus in the database (for more details see Flores and Coomes, 2011; Hawes *et al*., 2012; Magnago *et al*., 2014).

Text A3 - Supporting methods: Null model

Ses takes the following form: *[(observed – mean expected) / standard deviation of expected]*, where *observed* values are obtained from the sampled data, *expected mean* is the average of 999 randomizations and *standard deviation of expected* is the standard deviation of the 999 simulated communities.

We calculated these metrics of phylogenetic and functional diversity using "picante" package (Kembel *et al*. 2010) in R, version 3.2.1 (R Development Core

Team. 2015). For the standard effect size (ses) calculations, our tree was compared with 10,000 null model randomizations using the algorithm "phylogeny pool" (Swenson 2014). The applied null model randomizes the identity of species occurring in each sample, however maintains constant species richness and abundance within each transect. Assuming therefore, that all species are equally likely to occur in any fragment the habitat type (Arroyo-Rodríguez *et al*., 2012).

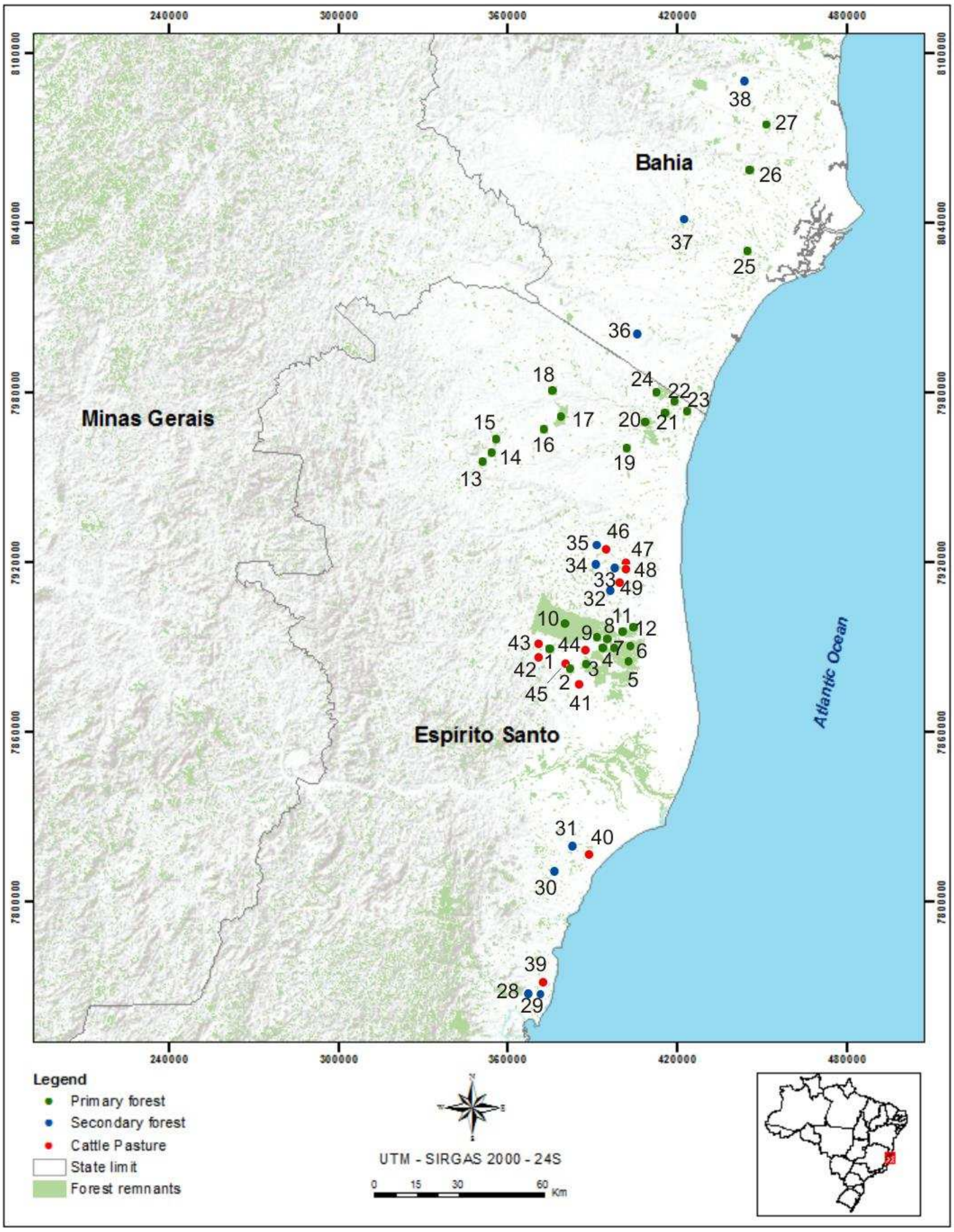

Fig S1 - Study area sampled in the Brazilian Atlantic Forest. Additional information about each habitat type can be seen in the Table S1.

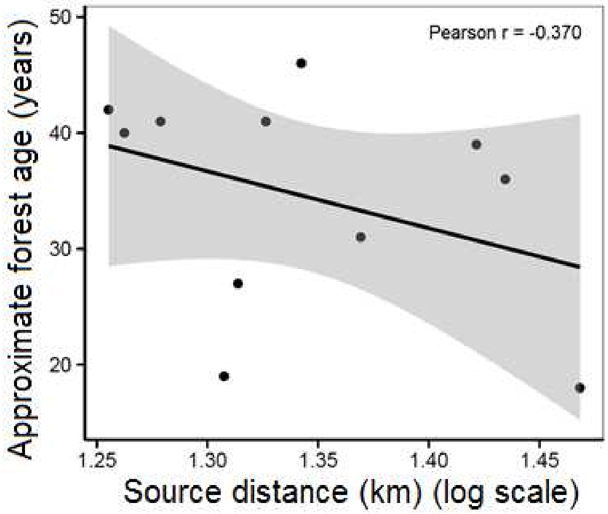

Fig. S2. Lack of correlation between source distance and secondary forest age. Fitted values (black line) and ±95% confidence limits in gray around the fitted lin e (P = 0.0262).

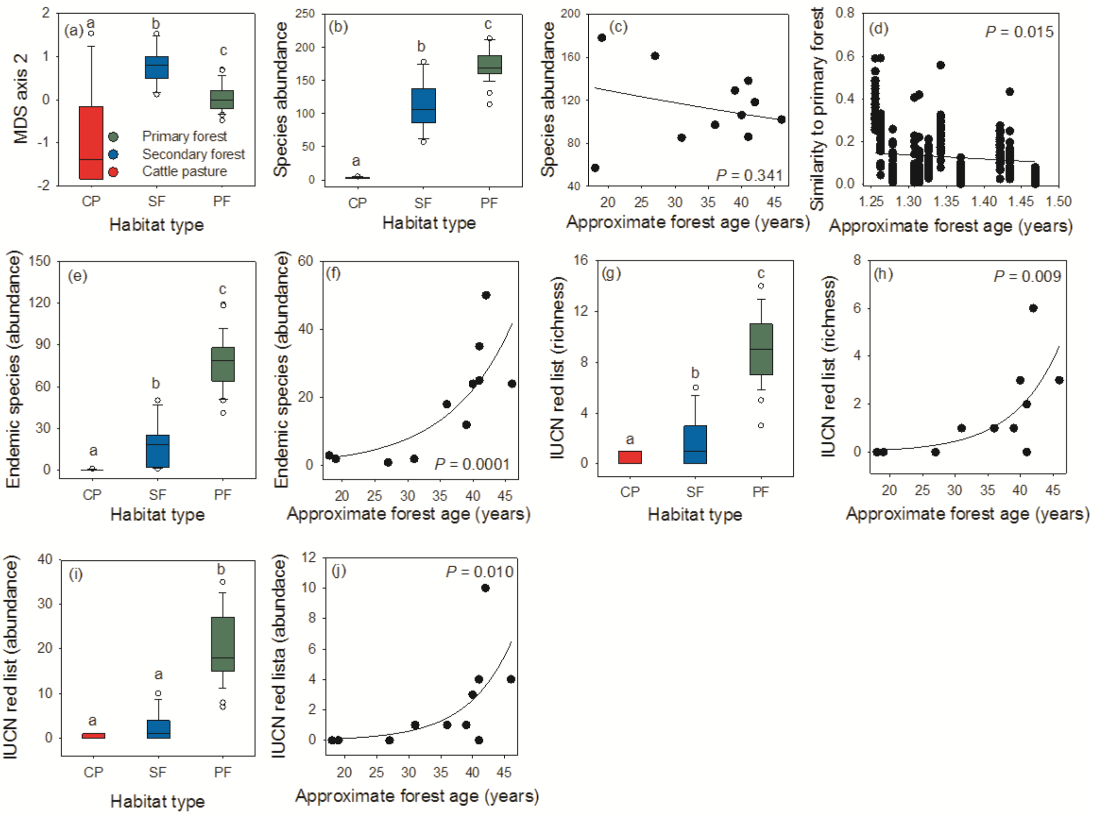

Fig. S3 – (a) MDS axis 2 scores across habitat types; (b) Species abundance across habitat types; (c) Species abundance with secondary forest age; (d) Similarity to primary forest with source distance (x-axis is on a log scale); (e) Endemic species abundance across habitat types; (f) Endemic species abundance with secondary forest age; (g) IUCN red list richness across habitat types; (h) IUCN red list richness with secondary forest age; (i) IUCN red list abundance across habitat types; and (j) IUCN red list with secondary forest age. (a, b, e, g and i) different letters indicate significance at $P \leq 0.05$.

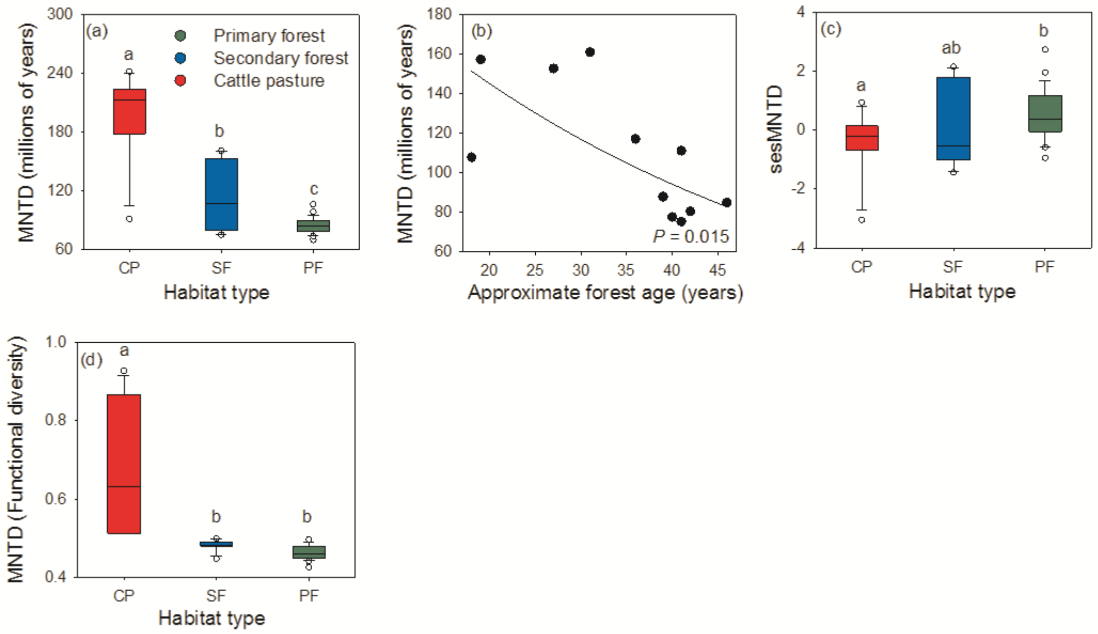

Fig. S4 - (a) Mean nearest taxon distance (MNTD) of phylogenetic diversity between cattle pasture (CP), secondary forest (SF) and primary forest (PF); (b) MNTD-PD across secondary forest; (c) Standardized effect size (ses) of phylogenetic diversity - MNTD (sesMNTD-PD) across habitat types; (d) MNTD of functional diversity across habitat types. (a, c, and d) different letters indicate significance at $P \leq 0.05$.

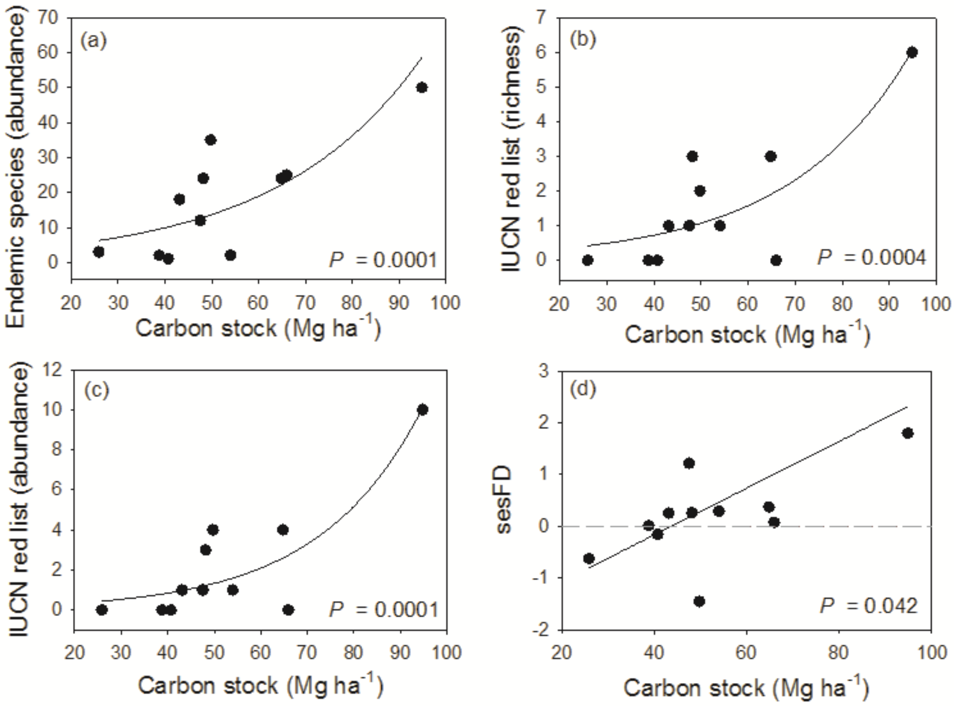

Fig. S5 – The impact of carbon stock recovery in secondary forest on: (a) Endemic species abundance; (b) IUCN red list richness; (c) IUCN red list abundance; and (d) Standardized effect size of functional diversity (sesFD).

Table S1- Identification, habitat type, size, secondary forest age, source distance (i.e., distance of secondary forest to primary fragments ≥1,000 ha) and coordinates of each transect studied in the Brazilian Atlantic forest. Identification corresponds to the fragment identification number in Figure S1. * = transect sampled in the same fragment, separated by 4 km.

Local identification	Habitat type	Size (ha)	Regeneration (years)	Source distance (km)	Coordinates (WGS 84)	
1	primary forest	428.94	-	-	19° 8'53.77"S	40° 7'20.24"W
2	primary forest	61.38	-	-	19° 5'5.31"S	40°10'30.55"W
3	primary forest	46.26	-	-	19° 7'59.17"S	40° 4'24.39"W
4	primary forest	868.32	-	-	19° 5'18.06"S	40° 0'29.78"W
5	primary forest	17716.14*	-	-	19° 6'52.93"S	39°55'39.31"W
6	primary forest	17716.14*	-	-	19° 4'46.69"S	39°55'13.99"W
7	primary forest	49.77	-	-	19° 4'10.94"S	39°58'59.18"W
8	primary forest	13.05	-	-	19° 3'48.02"S	39°58'58.52"W
9	primary forest	236.61	-	-	19° 3'9.60"S	40° 0'14.70"W
10	primary forest	23480.37	-	-	19° 0'46.76"S	40° 7'17.80"W
11	primary forest	1305.63	-	-	19° 2'17.18"S	39°55'2.14"W
12	primary forest	119.79	-	-	19° 1'43.88"S	39°54'21.71"W
13	primary forest	153.54	-	-	1 8°25'35.55"S	40°22'10.01"W
14	primary forest	54.99	-	-	18°24'45.22"S	40°21'44.45"W
15	primary forest	56.16	-	-	18°23'37.27"S	40°20'47.32"W
16	primary forest	13.05	-	-	1 8°22'55.38"S	40°12'14.53"W
17	primary forest	2391.75	-	-	18°20'44.87"S	40° 8'28.39"W
18	primary forest	20.61	-	-	1 8°17'51.67"S	40°10'2.55"W
19	primary forest	188.55	-	-	1 8°26'50.72"S	39°55'26.16"W
20	primary forest	1048.05	-	-	18°22'13.76"S	39°51'27.51"W
21	primary forest	282.69	-	-	1 8°20'23.91"S	39°47'8.79"W
22	primary forest	153.9	-	-	1 8°19'29.07"S	39°46'35.41"W
23	primary forest	100.35	-	-	18°19'32.28"S	39°43'18.32"W
24	primary forest	1490.4	-	-	1 8°16'17.76"S	39°48'21.43"W
25	primary forest	620.64	-	-	1 7°45'40.80"S	39°30'45.30"W
26	primary forest	45.81	-	-	1 7°34'40.40"S	39°33'29.85"W

27	primary forest	166.05	-	-	1 7°23'42.32"S	39°26'32.94"W
28	secondary forest	22.86	27	20.6	20° 9'25.88"S	40°12'29.17"W
29	secondary forest	20.14	19	20.3	20° 9'40.96"S	40°13'4.13"W
30	secondary forest	89.1	31	23.4	9°48'22.46"S	40°10'57.17"W
31	secondary forest	10	18	29.4	19°45'8.57"S	40° 4'40.36"W
32	secondary forest	133.23	36	27.2	18°45'5.26"S	39°57'47.65"W
33	secondary forest	97.11	40	18.3	18°42'10.61"S	39°56'42.30"W
34	secondary forest	54.9	46	22	18°44'33.72"S	39°51'44.47"W
35	secondary forest	18.16	39	26.4	18°47'20.33"S	39°52'19.47"W
36	secondary forest	749.1	42	18	18° 4'54.20"S	39°54'58.50"W
37	secondary forest	178.89	41	21.2	1 7°43'29.30"S	39°44'26.60"W
38	secondary forest	346.94	41	19	17°15'41.00"S	39°29'43.00"W
39	cattle pasture	-	-	-	1 9°45'52.00"S	40° 3'22.10"W
40	cattle pasture	-	-	-	1 9°44'22.50"S	40° 6'22.50"W
41	cattle pasture	-	-	-	19° 4'46.09"S	40° 2'42.40"W
42	cattle pasture	-	-	-	19° 4'30.40"S	40°13'6.30"W
43	cattle pasture	-	-	-	19° 7'0.30"S	40°13'32.40"W
44	cattle pasture	-	-	-	19° 7'45.90"S	40° 8'16.00"W
45	cattle pasture	-	-	-	19°10'16.60"S	40° 5'5.40"W
46	cattle pasture	-	-	-	18°41'47.32"S	39°56'53.63"W
47	cattle pasture	-	-	-	1 8°44'33.72"S	39°51'44.47"W
48	cattle pasture	-	-	-	18°45'6.99"S	39°51'27.08"W
49	cattle pasture	-	-	-	18°47'19.18"S	39°51'57.83"W

Table S2 – Patterns of land use in the 13 cities that have sampled transects in the Brazilian Atlantic forest. The area of primary land uses is listed (× 1,000 km^2), and as a percentage of total area. Permanent crops = those not subject to replanting after harvest (e.g., *Coffee*); Temporary crops = those subject to replanting after harvest (e.g., sugar cane); and Planted forest = includes the planting of tree species with commercial interests (e.g., *Eucalyptus* spp.). Information on land use were obtained to the census carried out in 2006 by Instituto Brasileiro de Geografia e Estatística (see: http://goo.gl/dUPLnD, for full details). The information for the tableland forest remnants were obtained from the report developed by the SOS Mata Atlântica/INPE, with reference to the year 2005-2008 (see: https://www.sosma.org.br/, for full details).

Cities	States	Total area (x 1,000 km^2)	Area (x 1,000 km^2) of: Cattle pasture		Permanent crops		Temporary crops		Planted forests		Tableland forests	
			Area	(%)	Area	(%)	Area	(%)	Area	(%)	Area	(%)
Linhares	ES	3.50	1.090	31.106	0.366	10.454	0.107	3.067	0.042	1.199	0.550	15.686
Sooretama	ES	0.59	0.092	15.648	0.106	18.009	0.002	0.317	0.030	5.112	0.246	41.999
Serra	ES	0.55	0.089	16.062	0.019	3.430	0.001	0.114	0.028	5.138	0.048	8.684
Aracruz	ES	1.42	0.153	10.719	0.078	5.488	0.014	1.010	0.340	23.907	0.074	5.201
São Mateus	ES	2.34	0.454	19.412	0.203	8.691	0.118	5.052	0.367	15.711	0.094	4.027
Conceição da Barra	ES	1.18	0.095	8.017	0.048	4.047	0.110	9.283	0.411	34.644	0.087	7.345
Pedro Canário	ES	0.43	0.161	37.191	0.043	9.984	0.136	31.287	0.011	2.438	0.008	1.914
Pinheiros	ES	0.97	0.315	32.370	0.083	8.565	0.109	11.155	0.003	0.342	0.039	4.008
Mucuri	BA	1.79	0.31	17.42	0.044	2.440	0.130	7.283	0.573	32.063	0.060	3.340
Teixeiras de Freitas	BA	1.17	0.62	53.57	0.079	6.746	0.016	1.411	0.081	6.954	0.033	2.799
Caravelas	BA	2.40	0.35	14.46	0.046	1.904	0.147	6.154	0.477	19.919	0.069	2.889
Alcobaça	BA	1.48	0.13	8.63	0.028	1.896	0.018	1.230	0.083	5.591	0.081	5.451
Prado	BA	1.69	0.39	23.22	0.092	5.431	0.036	2.161	0.012	0.701	0.399	23.661
All	-	**19.51**	**4.25**	**21.78**	**1.23**	**6.33**	**0.95**	**4.84**	**2.46**	**12.60**	**1.79**	**9.16**

Table S3 – Generalized Linear Model (*GLMs*) results for the impact of habitat type and pairwise comparison between habitat types (*Tukey post hoc testing*) on above-ground carbon stock of trees.

Model	Parameter	Estimate	SE	*t* value	P(>t)
GLMs					
Carbon storage	Intercept	1.52	0.36	4.26	0.0001
	Primary forest	4.16	0.42	9.86	0.0001
	Secondary forest	2.39	0.50	4.74	0.0001
	Cattle pasture	-	-	-	-
Model	**Parameter**	**Estimate**	**SE**	***z* ratio**	**P value**
Tukey post hoc testing					
Carbon storage	Prymary forest x Cattle pasture	-4.16	0.42	-9.86	0.0001
	Prymary forest x secondary forest	1.77	0.42	4.20	0.0001
	Secondary forest x Cattle pasture	-2.39	0.50	-4.74	0.0001

Table S4 - Model selection of the Generalized Linear Models for the relation between above-ground carbon stock, and secondary forest age and source distance. Showing models with the AICc ≤ 2, plus the first model after this value. Log-likelihood = maximum likelihood; AICc = Akaike information criterion for small samples; ΔAICc = Difference between the AICc of a given model and that of the best model; and AICcWt = Akaike weights (based on AIC corrected for small sample sizes).

Global model = Carbon stock~Secondary forest age (years) + Source distance (log), family = gaussian						
Intercept	Secondary forest	Source distance	logLik	AICc	Δ AICc	AICcWt
2.95	0.03		2.12	5.20	0	0.50
5.67	0.02	-1.89	4.61	5.40	0.25	0.44
7.91	-	-2.99	-0.19	9.80	4.63	0.05

Table S5 - Generalized Linear Model results for the impact of habitat type on biodiversity.

Model	Parameter	Estimate	SE	*t* value	P(>t)
MDS axis 1	Intercept	-0.99	0.24	-4.13	0.00010
	Primary forest	1.55	0.28	5.43	0.00100
	Secondary forest	0.63	0.34	1.85	0.07110
	Cattle pasture	-	-	-	-
MDS axis 2	Intercept	-0.87	0.18	-4.88	0.00001
	Primary forest	0.90	0.21	4.26	0.00001
	Secondary forest	1.66	0.25	6.59	0.00001
	Cattle pasture	-	-	-	-
Similarity to primary forest	Intercept	0.01	0.02	0.31	0.00010
	Primary forest	0.20	0.02	8.27	0.00010
	Secondary forest	0.12	0.03	3.81	0.00020
	Cattle pasture	-	-	-	-
Model	**Parameter**	**Estimate**	**SE**	**z value**	**P(>z)**
Species richness	Intercept	2.27	3.30	0.69	0.49500
	Primary forest	72.65	3.92	18.54	0.00010
	Secondary forest	29.91	4.67	6.40	0.00010
	Cattle pasture	-	-	-	-
Species abundance	Intercept	2.82	7.38	0.38	0.70400
	Primary forest	170.55	8.76	19.47	0.00010
	Secondary forest	111.46	10.44	10.67	0.00010
	Cattle pasture	-	-	-	-
Endemic species (richness)	Intercept	-2.00	1.01	-1.99	0.00010
	Primary forest	5.50	1.01	5.45	0.00010
	Secondary forest	3.96	1.02	3.87	0.00010
	Cattle pasture	-	-	-	-
Endemic species (abundance)	Intercept	-1.19	1.01	-1.18	0.23700
	Primary forest	5.57	1.01	5.50	0.00010
	Secondary forest	3.86	1.03	3.75	0.00010
	Cattle pasture	-	-	-	-
IUCN red list (richness)	Intercept	-1.00	0.51	-1.96	0.00010
	Primary forest	3.21	0.51	6.23	0.00010
	Secondary forest	1.43	0.58	2.45	0.01400
	Cattle pasture	-	-	-	-
IUCN red list (abundance)	Intercept	-0.41	0.52	-0.80	0.42700
	Primary forest	3.44	0.52	6.59	0.00001
	Secondary forest	1.09	0.61	1.79	0.07400
	Cattle pasture	-	-	-	-

Table S6 - Pairwise comparison between habitat types (*Tukey post hoc testing*) on biodiversity.

Model	Parameter	Estimate	SE	*z* ratio	P value
MDS axis 1	Primary forest x Cattle pasture	-1.55	0.28	-5.43	0.0001
	Primary forest x Secondary forest	0.92	0.28	3.22	0.0036
	Secondary forest x Cattle pasture	-0.63	0.34	-1.85	0.1543
MDS axis 2	Primary forest x Cattle pasture	-0.90	0.21	-4.26	0.0001
	Primary forest x Secondary forest	-0.76	0.21	-3.60	0.0009
	Secondary forest x Cattle pasture	-1.66	0.25	-6.59	0.0001
Model	**Parameter**	**Estimate**	**SE**	***t* value**	**P value**
Similarity to primary forest	Primary forest x Cattle pasture	-0.20	0.02	-8.27	0.0001
	Primary forest x Secondary forest	0.10	0.03	3.11	0.003
	Secondary forest x Cattle pasture	-0.10	0.03	-3.81	0.0001
Model	**Parameter**	**Estimate**	**SE**	***z* ratio**	**P value**
Species richness	Primary forest x Cattle pasture	-72.65	3.92	-18.54	0.0001
	Primary forest x Secondary forest	42.74	3.92	10.91	0.0001
	Secondary forest x Cattle pasture	-29.91	4.67	-6.40	0.0001
Species abundance	Primary forest x Cattle pasture	-170.55	8.76	-19.47	0.0001
	Primary forest x Secondary forest	59.10	8.76	6.75	0.0001
	Secondary forest x Cattle pasture	-111.45	10.44	-10.67	0.0001
Endemic species (richness)	Primary forest x Cattle pasture	-5.50	1.01	-5.45	0.0001
	Primary forest x Secondary forest	1.54	0.34	4.47	0.0001
	Secondary forest x Cattle pasture	-3.96	1.02	-3.87	0.0003
Endemic species (abundance)	Primary forest x Cattle pasture	-5.57	1.01	-5.50	0.0001
	Primary forest x Secondary forest	1.71	0.43	3.98	0.0002
	Secondary forest x Cattle pasture	-3.86	1.03	-3.75	0.0005
IUCN red list (richness)	Primary forest x Cattle pasture	-3.21	0.51	-6.23	0.0001
	Primary forest x Secondary forest	1.78	0.51	3.52	0.0013
	Secondary forest x Cattle pasture	-1.43	0.58	-2.45	0.0379
IUCN red list (abundance)	Primary forest x Cattle pasture	-3.44	0.52	-6.59	0.0001
	Primary forest x Secondary forest	2.35	0.63	3.71	0.0006
	Secondary forest x Cattle pasture	-1.09	0.61	-1.79	0.1739

Table S7 - Model selection of Generalized Linear Models for the relation between biodiversity, and secondary forest age and source distance. Models with AICc ≤ 2, plus the first model after this value are shown. Log-likelihood = maximum likelihood; AICc = Akaike information criterion for small samples; ΔAICc = Difference between the AICc of a given model and that of the best model; and AICcWt = Akaike weights (based on AIC corrected for small sample sizes).

Global model = MDS axis 1~Secondary forest age (years) + Source distance (log), family = gaussian						
Intercept	Secondary forest	Source distance	logLik	AICc	Δ AICc	AICcWt
-1.98	0.05	-	-3.75	16.90	0	0.87
-0.27	0.04	-1.18	-3.48	21.60	4.69	0.08
Global model = MDS axis 2~Secondary forest age (years) + Source distance (log), family = gaussian						
Intercept	Secondary forest	Source distance	logLik	AICc	Δ AICc	AICcWt
0.79	-	-	-5.35	16.20	0	0.73
0.47	0.01	-	-5.10	19.60	3.43	0.13
Global model = Similarity to primary forest~Secondary forest age (years) + Source distance (log), family = gaussian						
Intercept	Secondary forest	Source distance	logLik	AICc	Δ AICc	AICcWt
0.22	0.00	-0.19	342.45	-674.70	0	0.87
32.00	-	-	339.51	-670.90	3.82	0.13
Global model = Species richness~Secondary forest age (years) + Source distance (log), family = negative binomial						
Intercept	Secondary forest	Source distance	logLik	AICc	Δ AICc	AICcWt
2.39	0.03	-	-37.06	83.60	0	0.62
5.15	0.03	-1.93	-35.31	85.30	1.7	0.26
7.40	-	-2.94	-39.22	87.90	4.31	0.07
Global model = Species abundance~Secondary forest age (years) + Source distance (log), family = negative binomial						
Intercept	Secondary forest	Source distance	logLik	AICc	Δ AICc	AICcWt
8.26	-	-	-54.13	113.80	0	0.62
7.13	-	-1.78	-53.00	115.40	1.66	0.27
4.71	0.001	-	-54.13	117.00	3.92	0.09
Global model = Endemic species (richness)~Secondary forest age (years) + Source distance (log), family = negative binomial						
Intercept	Secondary forest	Source distance	logLik	AICc	Δ AICc	AICcWt
-1.74	0.10	-	-26.42	62.30	0	0.83
2.59	0.09	-3.09	-25.43	65.50	3.24	0.16
Global model = Endemic species (abundance)~Secondary forest age (years) + Source distance (log), family = negative binomial						
Intercept	Secondary forest	Source distance	logLik	AICc	Δ AICc	AICcWt
-1.03	0.10	-	-36.15	81.70	0	0.83
3.86	0.10	-3.63	-35.18	85.00	3.29	0.16
Global model = IUCN red list (richness)~Secondary forest age (years) + Source distance (log), family = negative binomial						
Intercept	Secondary forest	Source distance	logLik	AICc	Δ AICc	AICcWt
-5.05	0.14	-	-14.38	38.20	0	0.77
3.06	0.13	-5.80	-13.56	41.80	3.60	0.13
Global model = IUCN red list (abundance)~Secondary forest age (years) + Source distance (log), family = negative binomial						
Intercept	Secondary forest	Source distance	logLik	AICc	Δ AICc	AICcWt
-4.91	0.15	-	-17.41	44.30	0	0.78
5.02	0.15	-7.63	-16.67	48.00	3.75	0.12

Table S8 - Results of fitting Generalized Linear Models to assess the impact of secondary forest age and source distance on biodiversity. We present only the best models according to Akaike information criterion corrected for small samples (ΔAICc=0).

Model	**Parameter**	**Estimate**	**SE**	***t* value**	**P(>t)**
MDS axis 1	Intercept	-1.98	0.45	-4.43	0.0017
	Secondary forest (years)	0.05	0.01	3.73	0.0047
MDS axis 2	Intercept	-2.05	2.99	-0.69	0.5120
Similarity to primary forest	Intercept	0.22	0.11	1.96	0.0513
	Secondary forest (years)	0.005	0.001	7.71	0.0001
	Source distance (km)	-0.19	0.08	-2.44	0.0153
Model	**Parameter**	**Estimate**	**SE**	**z value**	**P(>z)**
Species richness	Intercept	2.39	0.32	7.35	0.00010
	Secondary forest (years)	0.03	0.01	3.52	0.00043
Species abundance	Intercept	8.26	1.89	4.36	0.00010
Endemic species (richness)	Intercept	-1.74	0.94	-1.86	0.06300
	Secondary forest (years)	0.10	0.02	4.34	0.00001
Endemic species (abundance)	Intercept	-1.02	0.97	-1.06	0.29000
	Secondary forest (years)	0.10	0.02	4.32	0.00010
IUCN red list (richness)	Intercept	-5.05	2.26	-2.23	0.02560
	Secondary forest (years)	0.14	0.05	2.60	0.00940
IUCN red list (abundance)	Intercept	-4.91	2.38	-2.06	0.03900
	Secondary forest (years)	0.15	0.06	2.56	0.01000

Table S9 - Generalized Linear Model results for the impact of habitat type on phylogenetic and functional diversity metrics.

Model	Parameter	Estimate	SE	*t* value	P(>t)
Phylogenetic diversity (PD)	Intercept	258.90	148.60	1.74	0.0883
	Primary forest	3927.20	176.30	22.27	0.0001
	Secondary forest	2010.30	210.20	9.56	0.0001
	Cattle pasture	-	-	-	-
sesPD	Intercept	0.17	0.23	0.74	0.4640
	Primary forest	-0.05	0.28	-0.18	0.8550
	Secondary forest	0.00	0.33	-0.01	0.9920
	Cattle pasture	-	-	-	-
MNTD (phylogenetic diversity)	Intercept	5.26	0.06	87.42	0.0001
	Primary forest	-0.82	0.07	-11.48	0.0001
	Secondary forest	-0.60	0.09	-7.00	0.0001
	Cattle pasture	-	-	-	-
sesMNTD	Intercept	-0.45	0.30	-1.47	0.1473
	Primary forest	1.01	0.36	2.81	0.0073
	Secondary forest	0.52	0.43	1.20	0.2357
	Cattle pasture	-	-	-	-
Functional diversity (FD)	Intercept	1.81	1.49	1.22	0.2290
	Primary forest	35.89	1.76	20.35	0.0001
	Secondary forest	15.76	2.10	7.50	0.0010
	Cattle pasture	-	-	-	-
sesFD	Intercept	0.22	0.31	0.70	0.4850
	Primary forest	0.08	0.37	0.21	0.8350
	Secondary forest	-0.03	0.44	-0.07	0.9410
	Cattle pasture	-	-	-	-
MNTD (Functional diversity)	Intercept	0.70	0.03	27.69	0.0001
	Primary forest	-0.24	0.03	-7.90	0.0001
	Secondary forest	-0.22	0.04	-6.09	0.0001
	Cattle pasture	-	-	-	-
sesMNTD	Intercept	-0.28	0.30	-0.96	0.3419
	Primary forest	0.64	0.35	1.82	0.0748
	Secondary forest	0.14	0.42	0.33	0.7455
	Cattle pasture	-	-	-	-

Table S10 - Pairwise comparison between habitat types (*Tukey post hoc testing*) on phylogenetic and functional diversity metrics.

Model	Parameter	Estimate	SE	*z* ratio	P value
Phylogenetic diversity (PD)	Primary forest x Cattle pasture	-3927.20	176.34	-22.27	0.0001
	Primary forest x Secondary forest	1916.91	176.34	10.87	0.0001
	Secondary forest x Cattle pasture	-2010.30	210.21	-9.56	0.0001
sesPD	Primary forest x Cattle pasture	0.05	0.28	0.18	0.9815
	Primary forest x Secondary forest	-0.05	0.28	-0.17	0.984
	Secondary forest x Cattle pasture	0.004	0.33	0.01	0.9999
MNTD (Phylogenetic diversity)	Primary forest x Cattle pasture	0.82	0.07	11.48	0.0001
	Primary forest x Secondary forest	-0.22	0.07	-3.13	0.0050
	Secondary forest x Cattle pasture	0.60	0.09	7.00	0.0001
sesMNTD	Primary forest x Cattle pasture	-1.01	0.36	-2.81	0.0138
	Primary forest x Secondary forest	0.50	0.36	1.38	0.3539
	Secondary forest x Cattle pasture	-0.52	0.43	-1.20	0.4522
Functional diversity (FD)	Primary forest x Cattle pasture	-35.89	1.76	-20.35	0.0001
	Primary forest x Secondary forest	20.12	1.76	11.41	0.0001
	Secondary forest x Cattle pasture	-15.76	2.10	-7.50	0.0001
sesFD	Primary forest x Cattle pasture	-0.08	0.37	-0.21	0.9761
	Primary forest x Secondary forest	0.11	0.37	0.30	0.9522
	Secondary forest x Cattle pasture	0.03	0.44	0.07	0.997
MNTD (Functional diversity)	Primary forest x Cattle pasture	0.24	0.03	7.90	0.0001
	Primary forest x Secondary forest	-0.02	0.03	-0.64	0.7981
	Secondary forest x Cattle pasture	0.22	0.04	6.09	0.047
sesMNTD	Primary forest x Cattle pasture	-0.64	0.35	-1.82	0.162
	Primary forest x Secondary forest	0.50	0.35	1.43	0.3235
	Secondary forest x Cattle pasture	-0.14	0.42	-0.33	0.9429

Table S11 - Model selection of Generalized Linear Models for the relation between phylogenetic and functional diversity metrics, and secondary forest age and source distance. Showing models with the AICc ≤ 2, plus the first model after this value. Log-likelihood = maximum likelihood; AICc = Akaike information criterion for small samples; ΔAICc = Difference between the AICc of a given model and that of the best model; and AICcWt = Akaike weights (based on AIC corrected for small sample sizes).

Global model = Phylogennetic diversity (PD)~Secondary forest age (years) + Source distance (log), family = gaussian						
Intercept	Secondary forest	Source distance	logLik	AICc	Δ AICc	AICcWt
7.11	0.02	-	3.92	1.60	0	0.32
9.46	0.01	-1.63	6.50	1.70	0.07	0.31
10.72	-	-2.24	3.85	1.70	0.15	0.30
7.70	-	-	0.57	4.40	2.76	0.08
Global model = sesPD~Secondary forest age (years) + Source distance (log), family = gaussian						
Intercept	Secondary forest	Source distance	logLik	AICc	Δ AICc	AICcWt
1.71	-0.04	-	-9.56	28.50	0	0.45
0.17	-	-	-11.75	29.00	0.46	0.36
7.84	-0.06	-4.26	-8.18	31.00	2.49	0.13
Global model = MNTD (phylogenetic diversity)~Secondary forest age (years) + Source distance (log), family = gaussian						
Intercept	Secondary forest	Source distance	logLik	AICc	Δ AICc	AICcWt
5.41	-0.02	-	2.24	5.00	0	0.78
4.66	-	-	-1.53	8.60	3.59	0.13
Global model = sesMNTD~Secondary forest age (years) + Source distance (log), family = gaussian						
Intercept	Secondary forest	Source distance	logLik	AICc	Δ AICc	AICcWt
2.72	-0.08	-	-16.15	41.70	0	0.45
0.07	-	-	-18.15	41.80	0.09	0.43
11.04	-0.09	-5.77	-15.43	45.50	3.80	0.07
Global model = Functional diversity (FD)~Secondary forest age (years) + Source distance (log), family = gaussian						
Intercept	Secondary forest	Source distance	logLik	AICc	Δ AICc	AICcWt
1.96	0.02	-	2.43	4.60	0	0.59
4.37	0.02	-1.67	4.41	5.80	1.29	0.31
6.40	-	-2.67	0.30	8.80	4.28	0.07
Global model = sesFD~Secondary forest age (years) + Source distance (log), family = gaussian						
Intercept	Secondary forest	Source distance	logLik	AICc	Δ AICc	AICcWt
0.19	-	-	-13.29	32.10	0	0.69
-0.81	0.03	-	-12.67	34.80	2.70	0.18
Global model = MNTD (functional diversity)~Secondary forest age (years) + Source distance (log), family = gaussian						
Intercept	Secondary forest	Source distance	logLik	AICc	Δ AICc	AICcWt
-0.73	-	-	23.89	-42.30	0	0.72
-0.70	0.00	-	24.42	-39.40	2.87	0.17
Global model = sesMNTD~Secondary forest age (years) + Source distance (log), family = gaussian						
Intercept	Secondary forest	Source distance	logLik	AICc	Δ AICc	AICcWt
-0.15	-	-	-13.35	32.20	0	0.62
6.42	-	-4.89	-12.33	34.10	1.89	0.24
-0.93	0.02	-	-12.99	35.40	3.20	0.12

Table S12 - Results of fitting Generalized Linear Models to assess the impact of secondary forest age and source distance on phylogenetic and functional diversity metrics. We present only the best models according to Akaike information criterion corrected for small samples (ΔAICc=0).

Model	Parameter	Estimate	SE	*t* value	P(>t)
Phylogenetic diversity (PD)	Intercept	7.11	0.22	32.00	0.00010
	Secondary forest (years)	0.02	0.01	2.75	0.02270
sesPD	Intercept	1.70	0.76	2.25	0.05070
	Secondary forest (years)	-0.04	0.02	-2.10	0.06510
MNTD (phylogenetic diversity)	Intercept	5.41	0.26	20.89	0.00001
	Secondary forest (years)	-0.02	0.01	-2.97	0.01570
sesMNTD	Intercept	2.72	1.38	1.98	0.07960
	Secondary forest (years)	-0.08	0.04	-1.99	0.07760
Functional diversity (FD)	Intercept	1.96	0.25	7.70	0.00001
	Secondary forest (years)	0.02	0.01	3.50	0.00669
sesFD	Intercept	0.33	6.20	0.05	0.00001
MNTD (functional diversity)	Intercept	-0.64	0.21	-3.02	0.00001
sesMNTD	Intercept	5.37	5.98	0.90	0.39600

Table S13 - Generalized Linear Models to assess the co-benefits between carbon stock and tree conservation value (including biodiversity, phylogenetic and functional diversity).

Model	Parameter	Estimate	SE	*t* value	P(>t)
MDS axis 1	Intercept	-1.34	0.46	-2.89	0.0178
	Carbono (Mg ha^{-1})	0.02	0.01	2.22	0.054
MDS axis 2	Intercept	1.02	0.41	2.51	0.0332
	Carbono (Mg ha^{-1})	-0.004	0.01	-0.61	0.5603
Similarity to primary forest	Intercept	-0.41	0.10	-4.18	0.0001
	Carbono (Mg ha^{-1})	0.32	0.06	5.62	0.0001
Model	**Parameter**	**Estimate**	**SE**	**z value**	**P(>z)**
Species richness	Intercept	2.69	0.20	13.74	0.0001
	Carbono (Mg ha^{-1})	0.01	0.00	4.43	0.0001
Species abundance	Intercept	4.68	0.27	17.29	0.0001
	Carbono (Mg ha^{-1})	0.001	0.005	0.21	0.83
Endemic species (richness)	Intercept	0.23	0.45	0.50	0.610
	Carbono (Mg ha^{-1})	0.03	0.01	4.76	0.0001
Endemic species (abundance)	Intercept	1.00	0.60	1.68	0.0930
	Carbono (Mg ha^{-1})	0.03	0.01	3.75	0.0002
IUCN red list (richness)	Intercept	-1.85	0.79	-2.36	0.0185
	Carbono (Mg ha^{-1})	0.04	0.01	3.50	0.0005
IUCN red list (abundance)	Intercept	-1.96	0.81	-2.43	0.0150
	Carbono (Mg ha^{-1})	0.05	0.01	4.15	0.0001
Model	**Parameter**	**Estimate**	**SE**	***t* value**	**P(>t)**
Phylogenetic diversity (PD)	Intercept	7.14	0.14	50.29	0.0001
	Carbono (Mg ha^{-1})	0.01	0.003	4.16	0.0025
sesPD	Intercept	0.21	0.74	0.29	0.0001
	Carbono (Mg ha^{-1})	-0.001	0.01	-0.07	0.9500
MNTD (phylogenetic diversity)	Intercept	5.00	0.27	18.54	0.00001
	Carbono (Mg ha^{-1})	-0.01	0.005	-1.30	0.22800
sesMNTD	Intercept	0.69	1.31	0.52	0.6140
	Carbono (Mg ha^{-1})	-0.01	0.02	-0.50	0.6320
Functional diversity (FD)	Intercept	2.10	0.19	11.28	0.00001
	Carbono (Mg ha^{-1})	0.01	0.003	4.11	0.0027
sesFD	Intercept	-1.32	0.67	-1.97	0.0805
	Carbono (Mg ha^{-1})	0.03	0.01	2.37	0.0421
MNTD (functional diversity)	Intercept	-0.73	0.03	-25.00	0.00001
	Carbono (Mg ha^{-1})	0.05	0.05	0.001	0.9990
sesMNTD	Intercept	-1.62	0.69	-2.35	0.0433
	Carbono (Mg ha^{-1})	0.03	0.01	2.25	0.0509

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