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Dinâmica de nutrientes em florestas alteradas do sul da Bahia

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Tese apresentada para a obtenção de título de Doutor em Ecologia e Conservação da Biodiversidade. Área de concentração: Ecologia de Ecossistemas.

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RESUMO

A dinâmica do carbono (C) e do nitrogênio (N) geralmente é afetada por distúrbios no microclima e na composição das espécies, os quais são substancialmente influenciados pelo desmatamento. Embora alterações consideráveis nos processos ecológicos (e.g. dispersão de sementes) tenham sido atribuídas à perda de florestaperda de cobertura florestal, pouco se sabe sobre sua relação com a dinâmica de nutrientes.

Nesta tese, serão discutidos os impactos da perda de cobertura floresta na paisagem sobre os processos ecossistêmicos, especificamente sobre a dinâmica de C e N. Além disso, será discutida a influência da perda de cobertura florestal sobre a biomassa de árvores. O presente estudo foi conduzido em florestas inseridas em 18 paisagens com diferentes porcentagens de cobertura florestal na Mata Atlântica do sul da Bahia. Foram utilizados indicadores específicos para avaliar as variações de C e N em folhas de árvores, serapilheira e nos primeiros 30 centímetros abaixo da superfície do solo: i.e., conteúdos totais e razão de C e N, bem como valores isotópicos de C e N. Primeiro, foi observado que a perda de cobertura florestal na paisagem afetou a maioria desses indicadores linearmente. As florestas dentro de paisagens menos cobertas mostraram menor biomassa de árvores. O conteúdo total de de C e N não no solo não mudou com a redução da cobertura florestal na paisagem, entretanto, na serapilheira e nas folhas, o conteúdo de C diminuiu enquanto o conteúdo de N aumentou. A relação C:N presente no solo, folhas e serapilheira diminuiu com a perda de cobertura florestal na paisagem. Por outro lado, o valor de $\delta^{15}N$ não variou no solo, folhas e serapilheira sob tais condições, mas o valor de $\delta^{13}C$ aumentou em todos os materiais analisados com a perda de floresta.

Por último, a partir dos valores de $\delta^{13}C$, pôde-se inferir que as influências da perda de cobertura florestal sobre os valores de C e N do solo, serapilheira e folhas foram mediadas pela elevação da temperatura nos remanescentes florestais inseridos nas paisagens com menores coberturas vegetais. Esses resultados sugerem que as dinâmicas de C e N variam gradualmente com a perda de cobertura florestal, a qual consiste numa métrica importante a ser considerada nos programas de conservação na Mata Atlântica.

Palavras-chave – perda de cobertura florestal, escale de paisagem, nitrogênio, carbono, isótopos, estrutura da floresta, composição de espécies

ABSTRACT

The dynamics of carbon (C) and nitrogen (N) commonly change with forest disturbances, and deforestation substantially influences them through disturbances in microclimate and species composition. Although considerable changes in ecological processes have been ascribed to forest loss, little is known about its relationship with nutrient dynamics. Forest loss usually triggers shifts in ecosystem functioning. However, yet uncertainty remains regarding its real consequence to C and N dynamics.

In this thesis, I studied the impacts of forest loss at the landscape scale on ecosystem processes, specifically on C and N dynamics. Furthermore, I investigate the influence of forest loss on tree biomass storage. I conducted my study in forests of 18 landscapes with different percentages of forest cover placed in the Atlantic forest in southern Bahia. I utilized specific indicators of C and N dynamics in leaves, leaf litter, and soil: i.e., total C and N, C:N ratio, C and N isotopes, and aboveground tree biomass. First, I found that forest loss affected most of these indicators linearly. Forests within less-covered landscapes showed a decreasing aboveground tree biomass, but an unchanged soil total C and N. However, the C:N ratio decreased with forest loss. The $\delta^{15}N$ did not vary, while $\delta^{13}C$ increased according to deforestation. I found the same isotope patterns for leaves and litter. Furthermore, total C of leaves and leaf litter decreased, while N content increased with deforestation. The C:N ratio declined in leaves and litter. The influences of forest loss on C and N were mediated by disturbances in the structure of forests placed in deforested landscapes.

These results suggest that C and N dynamics shift gradually with forest loss, being an important metric to be considered in future conservation planning in the Atlantic forest. This biome lost approximately 90% of its forest cover, remaining a high number of small fragments and few large tracts of forest. Here, I show the importance of considering the remaining forest cover at the landscape to predict better the dynamics of C and N.

Key-words: forest loss, landscape scale, nitrogen, carbon, isotopes, forest structure, species composition

1. INTRODUÇÃO

A compreensão da ciclagem de nutrientes nos ecossistemas florestais consiste numa questão de grande interesse para os ecólogos (Schimel & Bennett, 2004), pois alguns nutrientes, em condições limitantes, podem reduzir a capacidade das florestas de se desenvolver e estocar carbono (Pellegrini *et al.*, 2014). Alguns estudos sugerem que tanto o carbono (C) quanto o nitrogênio (N) podem ser afetados por mudanças na estrutura e composição das florestas, com ambos decrescendo em disponibilidade quando a floresta é levada a condições de degradação semelhantes a estágios sucessionais iniciais (Knops & Tilman, 2000; Hooker & Compton, 2003). Embora tais estudos reportem os efeitos das perturbações locais (*i.e.* em escala de fragmento), pouco se sabe como as ciclagens de C e N respondem à perda de floresta em escala de paisagem. Recentemente, vários estudos têm analisado os impactos das alterações na paisagem sobre o funcionamento das florestas, estabelecendo duas vias de discussão, isto é, aquela que considera a perda de floresta na paisagem o principal agente de mudanças dos processos ecossistêmicos e ecológicos nos fragmentos florestais (Andrade *et al.*, 2015; Menezes *et al.*, 2016; Rocha-Santos *et al.*, 2016; Santos *et al.*, 2015), e a outra que atribui tais mudanças a variações na estrutura da paisagem (configuração e composição) (Haddad *et al.*, 2017). Até o presente momento, estudos conduzidos na Mata Atlântica indicam que a perda de floresta na paisagem promove mudanças consideráveis nos processos ecológicos (Pessoa *et al.*, 2016; Rocha-Santos *et al.*, 2016; Santos *et al.*, 2016).

As florestas tropicais têm sido reconhecidas como um dos principais ecossistemas com ação mitigadora das mudanças climáticas causadas pelo acúmulo de dióxido de carbono na atmosfera (Trumbore *et al.*, 2015). Considerando as projeções para o clima nas próximas décadas (IPCC, 2014), torna-se cada vez mais importante o manejo adequado de florestas considerando seus processos ecológicos e ecossistêmicos (Melo *et al.*, 2013).

Provavelmente, os principais impactos nas ciclagens de N e C desencadeados pela perda de floresta na paisagem estão relacionados ao aumento dos processos ligados ao efeito de borda. O efeito de borda influencia particularmente o microclima da floresta através da dessecação e mudanças na disponibilidade de luz solar e no regime de vento (Nascimento & Laurance, 2004, Ewers & Banks-Leite, 2013). Tais mudanças também podem resultar em alterações da composição das espécies, promovendo a substituição das espécies adaptadas ao interior da floresta por aquelas adaptadas a áreas perturbadas (Nascimento & Laurance, 2004). Com a perda de floresta na paisagem, os remanescentes florestais tendem a ser colonizados por árvores de rápido crescimento e menor razão C:N (Laurance *et al.*, 2006). Assim, as florestas perturbadas podem apresentar uma composição peculiar de espécies adaptadas a áreas degradadas (Santos *et al.*, 2008), e uma eventual recolonização de tais florestas por espécies tardias poderá afetar a razão entre C e N do sistema (Amazonas *et al.*, 2011).

Alguns estudos utilizaram cronosequências de florestas secundárias para demonstrar como as dinâmicas de C e N podem alterar com a estrutura e composição da floresta (Davidson *et al.*, 2007). Neste caso, algumas espécies de estágios sucessionais iniciais facilitam o progresso da floresta para estágios avançados fixando N, o que possibilita a superação da limitação inicial de N (Crews, 2016). No entanto, tais estudos não consideram a possível influência da paisagem. Algumas florestas em paisagens com grande perda de floresta, por exemplo, aparentemente não apresentam qualquer habilidade para atingir estágios sucessionais avançados devido a outros fatores além da limitação de N (Bello *et al.*, 2015; Magnago *et al.*, 2015; Peres *et al.*, 2016; Santos *et al.*, 2008). Alguns estudos atribuem essa condição à ruptura de processos ecológicos, como a dispersão de sementes devido à defaunação local (Silva & Tabarelli, 2000a; Bello *et al.*, 2015), prejudicando a colonização de árvores características de florestas mais conservadas (Costa *et al.*, 2012).

Outros estudos têm documentado a homogeneização florística em paisagens com alto índice de perda de floresta (Gámez-Virués *et al.*, 2015; Thier & Wesenberg, 2016) com os fragmentos sendo dominados por espécies pioneiras (Lôbo *et al.*, 2011). Nesse contexto, considerando que as espécies pioneiras investem menos em tecidos estruturais lignificados e concentram mais N por área foliar (Aidar *et al.*, 2003), a razão entre C e N da matéria orgânica que chega ao solo pode ser diferente entre paisagens com predominância de diferentes grupos funcionais: i.e. paisagens dominadas por espécies de estágios sucessionais iniciais ou avançados (Aidar *et al.*, 2003).

Paisagens cujas florestas possuem comunidades mais diversas podem superar o domínio das espécies pioneiras através do crescimento de espécies tardias, as quais passam a limitar a entrada de luz no subosque (Nascimento & Laurance, 2004). No entanto, algumas florestas degradadas parecem experimentar uma sucessão retrogressiva, indicando que não possuem habilidade para crescer sem intervenção humana (Santos *et al.*, 2008; Rocha-Santos *et al.*, 2016). O resultado é a baixa produtividade da floresta, bem como capacidade limitada para sequestrar e estocar carbono (Magnago *et al.*, 2015; Paula *et al.*, 2011).

Este tipo de degradação é uma ameaça para o desenvolvimento do sistema, especialmente em paisagens onde o pastoreio, a herbivoria e a exploração madeireira impedem o desenvolvimento de leguminosas que exercem papel considerável na entrada de N no sistema (Vitousek & Howarth, 1991). Neste caso crítico, a sucessão retrogressiva seria intensificada pela falta de leguminosas capazes de reverter a limitação inicial de N (Vitousek & Howarth, 1991). Com isso, a ciclagem de N pode ser bastante diferente entre florestas relativamente degradadas e não-degradadas devido à sua composição típica de espécies. Portanto, é necessário entender a resposta tanto do C quanto do N, entre outros nutrientes, a eventuais mudanças na quantidade de floresta da paisagem.

Nesse sentido, as técnicas isotópicas têm auxiliado na análise das dinâmicas de C e N em vários ecossistemas, em complemento às técnicas mais tradicionais (Dawson *et al.*, 2002). A análise isotópica pode integrar fatores que influenciam a ciclagem de nutrientes em momentos distintos (Robinson, 2001). Por exemplo, os sinais de $\delta^{15}N$ da planta indicam processos bióticos que controlam a disponibilidade de N a curto prazo, enquanto que $\delta^{15}N$ do solo pode descrever o processo que controla a estabilização do N nos solos a longo prazo (Craine *et al.*, 2015). A diferença entre os dois pode ser usada para indicar a fração de N total do solo disponível para as plantas (Craine *et al.*, 2015).

1.1 Perda de cobertura florestal

A perda de floresta e a fragmentação em alguns casos são confundidas como o mesmo processo porque são dependentes um do outro (Fahrig, 1999). Mas uma determinada floresta pode experimentar algum nível de perda de cobertura florestal e permanecer contínua (Fahrig, 1999). A fragmentação ocorre quando a floresta é separada em fragmentos após a redução constante da cobertura original. Assim, a redução do tamanho do fragmento, refere-se à perda de floresta propriamente dita.

Embora ainda não sejam observados estudos que abordam os efeitos da perda de floresta em escala de paisagem sobre a ciclagem de nutrientes, alguns estudos têm buscado compreender a influência de outras métricas da paisagem sobre a ciclagem de nutrientes. Analisando pequenos fragmentos com a mesma composição florística, Billings & Gaydess (2008) utilizaram a escala de fragmento para examinar a dinâmica de N. Eles encontraram uma influência positiva e significativa do tamanho do fragmento sobre a disponibilidade de N. Isto sugere que fragmentos maiores têm a capacidade de manter um aporte de N característico de sistemas menos perturbados. Em outro estudo, Haddad *et al.* (2015) abordaram a fragmentação para avaliar a disponibilidade de nutrientes. Eles consideraram métricas de fragmentação para analisar diferentes processos ecossistêmicos. Eles observaram que a disponibilidade de N diminui com a redução do tamanho do fragmento, onde foi observado maior isolamento e área de borda. Neste caso, a perda de floresta favoreceu as espécies pioneiras, o que sugere que tanto a perda de floresta quanto a mudança nos estágios sucessionais promoveram a redução do N.

1.2 Raciocínio da pesquisa

De acordo com o que foi mencionado, a perda de cobertura florestal na paisagem desencadeia uma série de mudanças na composição e estrutura da floresta capazes de influenciar a dinâmica de C e N. Entretanto, estudos que investigam os impactos da perda de floresta nas ciclagens de C e N, consideram apenas o desmatamento em escala local sem considerar a quantidade de floresta no contexto da paisagem. À medida em que a quantidade de floresta diminui na paisagem, os processos de degradação florestal tendem a aumentar, como efeitos de borda provocados pela fragmentação. Portanto, para compreender a dinâmica de C e N nas florestas tropicais é de extrema importância considerar os impactos causados pela perda de cobertura florestal na paisagem. Com isso, faz-se necessário compreender as relações causais entre essas duas variáveis, o que justifica o presente trabalho, uma vez que a perda de cobertura florestal, até certo ponto, pode ser utilizada em detrimento de outras métricas de paisagem (e.g. isolamento dos fragmentos), facilitando planos de conservação que visam compreender os impactos do desmatamento sobre a dinâmica de C e N. Desta forma, as investigações objetos dessa tese irão auxiliar os programas de manejos florestais que requerem especial atenção para as ciclagens de C e N.

1.3 Objetivos

Essa tese tem como objetivo investigar como as dinâmicas de C e N respondem à perda de floresta em escala de paisagem, abordando este objetivo em dois capítulos, além deste primeiro e introdutório. No segundo capítulo, eu investigo os efeitos da perda de floresta em escala de paisagem sobre biomassa de árvores. Essa investigação tem como foco analisar as consequências da perda de cobertura florestal para os grupos funcionais considerando a densidade da madeira. O terceiro capítulo, investiga a influência da perda de cobertura florestal na dinâmica de C e N, levando em conta as vias que medeiam a relação da redução da cobertura florestal com as ciclagens de C e N.

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2. THE UNACCOUNTED LOSS*:* LANDSCAPE-SCALE DEFORESTATION AND THE DECAYING OF TREE BIOMASS AND BELOW GROUND CARBON CONTENT IN TROPICAL FOREST FRAGMENTS.

ABSTRACT

The influence of deforestation on forest carbon (C) can be perceived even today in tropical landscapes. Deforestation leaves the remaining forests more susceptible to degradation, which in turn strongly reduces the forest ability to retain C. We analyzed the impact of deforestation on the aboveground tree biomass and soil C content along a gradient of forest cover from adjacent areas to understand the extent to which species interplays with deforestation to affect C. We quantified both tree biomass and soil C and N content. In addition, we measured $\delta^{13}C$ and $\delta^{15}N$ values to detect mechanisms that might explain changes in aboveground tree biomass. Aboveground tree biomass decreased with the loss of forest cover at the landscape owing to gradual disappearance of most hardwood trees. Deforestation did not affect softwood trees, showing the distinct contribution of the hardwood guild to maintain the forest reservoirs of carbon. Our results demonstrate that softwood and hardwood trees responded differently to deforestation, creating a peculiar forest structure capable of alter the $\delta^{13}C$ values, but not $\delta^{15}N$. Furthermore, deforestation seems to lower the soil C content following the floristic and structural changes, suggesting that deforestation indirectly disturbs the ecosystem processes through both of them.

Keywords: landscape deforestation, biomass, wood density, soil carbon, C/N ratio, carbon and nitrogen isotope ratios.

2.1 INTRODUCTION

Tropical forests harbor the largest carbon stocks among forest ecosystems (Pan *et al.*, 2011), with outstanding importance for primary production and climate regulation (Houghton, 2013). A recent attempt to provide a benchmark for world´s forest carbon stocks has shown the staggering importance of the aboveground biomass, contributing to ~78% of the total estimated carbon stock of 247 Gt (Saatchi *et al.*, 2011). Despite its overwhelming importance, the fraction represented by the aboveground biomass is highly vulnerable. During the last decades, government efforts successfully led tropical nations to reduce to 13 million ha year^{-1} the rate of deforestation compared to 16 million ha year^{-1} in the 1990s (FAO, 2010). Nevertheless, the debate about tree biomass loss goes beyond the protection of forests against deforestation and must include adverse outcomes of forest degradation.

Forest degradation changes structural and functional aspects of the ecosystem, altering its capacity to store carbon in aboveground biomass (Parrotta *et al.*, 2012). Although forest degradation is an intrinsic and important part of the dynamics of most ecosystems (Turner, 2010), such process has increased in both frequency and intensity due to the widespread and chronic anthropogenic actions. Harvest for timber and fuel, selective logging (Villela *et al.*, 2006), fires (Michalski *et al.*, 2007), pest outbreaks (Turner 2010), hunting (Bello *et al.*, 2015) and forest fragmentation (Magnago *et al.*, 2015a) are important human-associated drivers of forest degradation, encompassing mechanisms capable of depressing the existing tree biomass (Houghton, 2007). Moreover, these drivers of forest degradation act synergistically with other anthropogenic pressures determining the forest ability to store carbon and recover biomass. For instance, whereas some land-use practices, such as slash-and-burn, cause high rates of nutrient loss limiting biomass recovery potential (Piccolo *et al.*, 1994), the loss of large seed dispersers due to the widespread defaunation further constrains the re-establishment of large hardwood trees on such nutrient-limited areas, decreasing their ability to store carbon (Bello *et al.*, 2015; Peres *et al.*, 2016).

It is estimated that around 100 million hectares' are annually affected by forest degradation (Nabuurs *et al.*, 2007), but when it comes to quantifying its actual contribution to carbon emission, the task becomes more difficult (Houghton, 2012). It is because the loss of carbon via degradation is more subtle and variable than the evident demise of forest cover revealed by deforestation. Forest degradation includes the changes of structural vegetation characteristics (e.g. canopy cover, tree density and composition) (Clark & Clark, 2000).

Despite these idiosyncratic changes, theoretical and empirical studies have shown the link between forest carbon stocks and landscape configuration, with decreasing aboveground tree biomass stored in smaller and more isolated remnants (Magnago *et al.*, 2015a; Melito *et al.*, 2018). Not surprisingly, part of the vast carbon reservoir in tropical forests remains within edge-affected forests, therefore under constant anthropogenic pressure (Haddad *et al.*, 2015). Among the best documented modification in edge-altered areas, is the shift in species composition with a selective demise of shade-tolerant trees and the concomitant proliferation of light-demanding species (Silva & Tabarelli, 2000b), modifications likely to change the capacity of a giving forest to store carbon in tree biomass (Laurance *et al.*, 2006b; Paula *et al.*, 2011). This is because most light-demanding species have low wood density (softwood) (Laurance *et al.,* 2006b; Parolin, 2002; Slik *et al.*, 2008; Henry *et al.*, 2010). Their traits are related to rapid height growth, which require less investment in wood per unit of volume (wood density) that is a low-cost strategy (King *et al.*, 2006).

In addition, the more open vegetation from edge-affected areas often translates in a higher variation of microclimatic local conditions, such as temperature and humidity (Radler *et al.*, 2010; Ewers & Banks-Leite, 2013), which in turn are likely to influence both above and below ground carbon. For instance, shifts in microclimatic regime, i.e. increasing local temperatures, can alter the ability of soils to retain carbon (Don *et al.*, 2011), with an increasing in decomposition rates in more degraded, edge-affected areas (Davidson *et al.*, 2006), thus leaking more soil C to the atmosphere.

Furthermore, the level and intensity of human disturbance can slow or even arrest forest succession (see Tabarelli *et al.*, 2008), and such pattern can further increasing the possibility of carbon losses (Quested *et al.*, 2007). Among the factors limiting local productivity, thus carbon storage, the amount of available N in forest soil is likely to exert a strong influence in most degraded forests (Laurance *et al.*, 1999).

More recently, the remaining habitat at landscape scale has been proposed as a better single predictor for local changes (Fahrig, 2013). Following this approach, the amount of forest cover remaining at landscape-scale of Neotropical forest fragments has been used as a reliable predictor of the diversity (Rocha-Santos et al., 2017), resilience

(Pardini *et al.*, 2010) and several aspects of functionality (Muñiz-Castro *et al.*, 2006). Forest cover is usually correlated with other metrics of forest fragmentation that affects aboveground carbon stocks (see Magnago *et al.*, 2015), but we still lack information about stocks *per se* in general, and particularly below ground carbon stocks.

Here, we investigate the extent to which landscape-scale forest cover influences the local aboveground tree biomass (AGB), and the soil carbon and nitrogen contents in forest remnants. We further assessed whether AGB changes according to specific shifts on tree functional characteristics related to wood density. In addition, we attempted to verify changes in forest conditions measuring $\delta^{13}C$ that describes changes in forest structure and composition (Martinelli *et al.*, 1991), and $\delta^{15}N$, commonly used as a descriptor of forest N availability (Martinelli *et al.*, 1999).

We expect that landscape-scale deforestation cause a decrease in AGB and soil C. We also predict that the decaying AGB are mostly explained by changes in tree species functional groups, thus triggered by the selective loss of those hard-wooded trees in those fragments within more deforested landscapes, which are not compensated by an eventual increasing of those softwood counterparts. We also expect that the N content of the forest soil decreases according to deforestation. Although the impacts of deforestation may affect both soil C and N negatively, such nutrients tend to increase during the forest recovery (Knops & Tilman, 2000). However, their accumulation rates can be quite different with the forest development, accumulating more C in proportion to accrual of N (Knops & Tilman, 2000). Thus, we expect an increasing C:N ratio along the forest cover gradient. We finally hypothesize that $\delta^{13}C$ value increases with the forest cover reduction in the landscape. This is because the forest degradation can induce a wider openness of the canopy, increasing solar radiation and increasing evapotranspiration. In turn, to avoid damaging water losses, leaves reduced their stomatal conductance, leading to an increase of $\delta^{13}C$ values (Farqhuar *et al.*, 1982). On the other hand, we expect lower $\delta^{15}N$ with increasing landscape deforestation, because N availability will be lower due to decreases in above and below ground nitrogen stocks.

2.2 METHODS

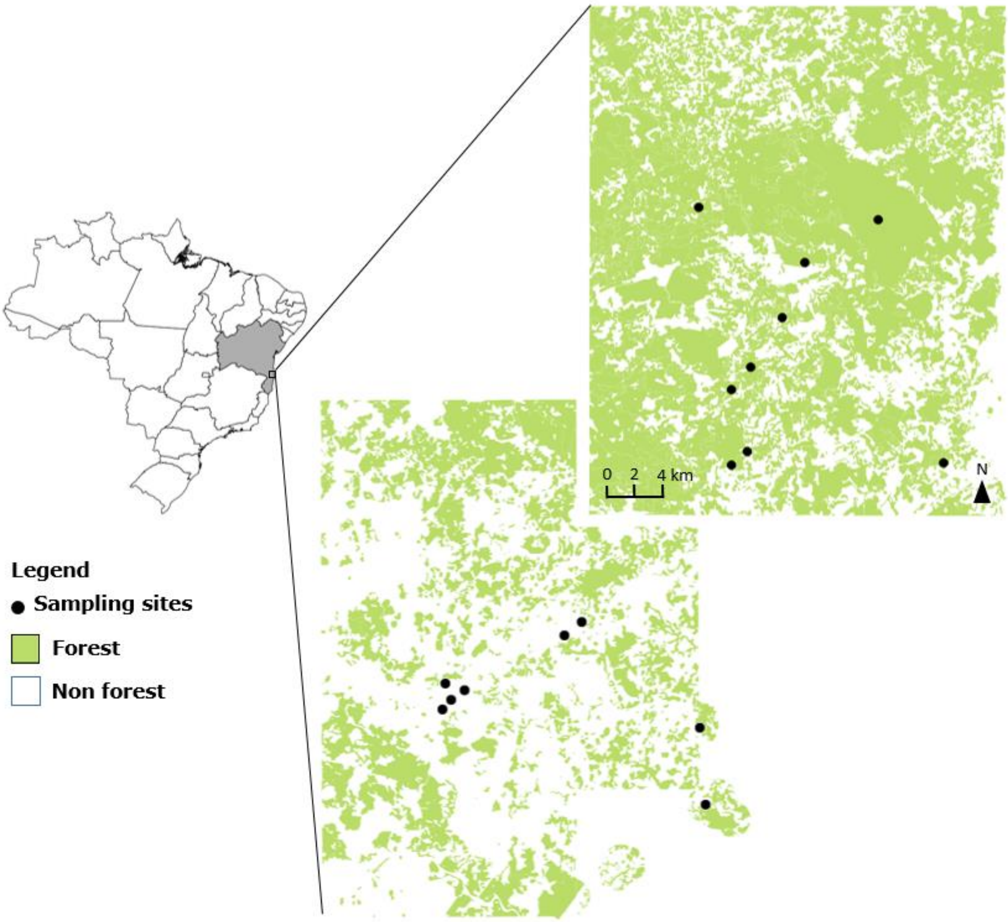
2.2.1 Sites description

We conduced our study in the Atlantic forest of three municipalities of southern Bahia, i.e. Una, Belmonte and Mascote (Fig. 1a). Herein we undertook our sampling in the Lowland Wet Forest type, that according to Thomas (2003), is a physiognomy that naturally exhibits a classical structure of rainforest with four layers, i.e. emergent trees, canopy, sub-canopy and herbaceous. This forest type has high species diversity, including a large number of epiphyte species, and a typical caulescent canopy palm – *Euterpe edulis* Mart. (Arecaceae). The total anual precipitation in this region is between 1800-2200 mm year^{-1} (Santos & França, 2011), with no pronounced dry season, and the predominant soil types are podzol and latosol (Thomas, 2003).

2.2.2 Landscape selection and forest cover measurement

Historically, the last period of higher deforestation in southern Bahia dates from the 70's, when the opening of BR-101 road intensified the forest loss promoting high-intensity wood removal and human expansion. It is estimated that 80% of 11,000 km² of forest were cleared in only ten years (Mesquita, 1997). Currently, most Atlantic forest landscapes are highly fragmented and predominantly composed of small fragments embedded in a human-modified matrix (e.g. pasture, agriculture) (Ribeiro *et al.*, 2009). To identify areas with remaining large tracts of forest, we used Landsat images (MSS/TM/ETM+) (INPE) from the region between the rivers Jequitinhonha and das Contas. First, we classified the vegetation types from satellite images (Rapid Eye, from 2009-2010; QuikBird and WorldView, from 2011) using ArcGIS. Then, we identified forest patches from high-resolution maps (scale 1:10,000) based on the following patch features: color, texture, shape, position and context. We classified and delimited the forest patches by using tools available at the ArcGIS environment (Esri 2007). In total, we selected 17 sample sites within forest patches with a minimum distance of one kilometer. Finally, we used a 2 km buffer around each of our 17 sample sites to calculate their forest cover (Fig. 1). The 17 selected landscapes (buffered sites) had different percentages of forest cover, ranging from 6% to 100%.

Fig. 1. Map showing the distribution of the landscapes across the South of Bahia, Brazil. Filled points represent the sample sites within a 2 km landscape surrounding each site, in the Atlantic Rainforest of southern Bahia, Brazil.



2.2.3 Botanical material

Within each of the 17 sampling sites, we located five subplots of 4 × 25 m (100 m^2) equidistant at least 25 m, in which we recorded and measured all trees with DBH (diameter at breast height) ≥ 10 cm. We maintained a minimum of 50 m distance between subplots and the edge of the fragment. We collected botanical samples from all recorded trees. Botanical samples were identified at the herbarium of the Centro de Pesquisa do Cacau (CEPEC/CEPLAC) and the herbarium of the Universidade Estadual de Santa Cruz (HUESC). When available, reproductive material (flowers and/or fruits) was included in the botanical collection of the mentioned herbaria. Our 17 sample sites belong to the same vegetation type (Lowland Wet Forest). We recorded a total of 886 trees with DBH > 10 cm, of which 88.4% (783 trees, 263 species) were identified at the species level whereas the identification of the remaining individuals was limited to the genus (56 trees) and family level (28 trees). It was not possible to identify 19 trees.

2.2.4 Aboveground biomass and functional classification of tree species

We estimated the AGB of the recorded trees through a pantropical allometric model (Chave *et al.*, 2014) with three parameters: DBH, height (H) and wood density (WD). We measured total height of 227 trees randomly chosen. To do so, we climbed the trees and measured total height by using a metric tape. Two people always took this procedure. We grouped the trees into three DBH classes (10-15 cm, 15-20 cm and >20 cm) and sampled at least one tree of each class distributed in three equidistant points along the plots. We further used these data to fit a site-specific model to predict tree height from DBH:H relationship for those trees we did not total height in the field. We fit our model (H = 3.74 × DBH0.4837) using a non-linear approach in which we modeled the heteroscedastic variance of the dataset (Marra *et al.*, 2015). For details, see the Supporting information of this study. We compiled wood density from the Global Wood Density Database (Chave *et al.*, 2009; Zanne *et al.*, 2009). For species where wood density data was not available, or the identification was carried out to the genus level (59 genera), we applied the mean value for all species from the same genus occurring in the Lowland Wet Atlantic forest. For trees identified up to the family level (25 families), we used the mean value of genera from that family. For 19 unidentified trees, we used the mean wood density value of all recorded trees in that particular site. We divided the tree species into three classes considering their wood densities as follow: Hardwood > 0.7 g/cm3, Semi-hardwood 0.5-0.6 g/cm3 and Softwood < 0.5 g/cm3 (adapted from Michalski *et al.*, 2007).

2.2.5 Soil samples and analyses

We collected soil samples located in the middle and in two opposite sides of each subplot, totaling three samples per subplot. We used a soil auger to sample at three depths, 0-10, 10-20 and 20-30 cm. All samples were dried at ambient temperature and passed through a sieve (2.0 mm mesh) to remove undesirable roots and other debris. In a second moment, we took representative subsamples, grinded handly and passed through another sieve (50 µm diameter) to remove smaller particles. For analyses of organic C and N, we again grinded the subsamples until produce a finer powder. We then weighed 250 mg of soil in a ceramic cup and added 450 mg of tungsten trioxide (WO_3) to improve the combustion. Finally, we carried out it on VarioMax CN-analyzer (Elementar Analysensysteme GmbH, Hanau, Germany) to determine both C and N content. We also measured both $\delta^{13}C$ and $\delta^{15}N$ using a Combustion Elementary Analyzer Carlo Erba (Milan, Italy) aligned with a Mass Spectrometer (IRMS Delta Plus, Finnigan Mat, San José, CA, USA).

2.2.6 Statistics

We performed generalized linear mixed effect models (GLMMs) to examine the effects of forest cover at the landscape scale on tree diversity (abundance and richness), basal area and biomass of hardwood, semi-hardwood and softwood species, as all species together. For the analysis, we accounted for the data assessed in each subplot, as this was the basic sampling unit. We used Poisson errors to model the effects of forest cover on both abundance and richness data, and due to overdispersion and correlation of variance and the mean we used negative binomial errors to model the effects of forest cover over the basal area, biomass, soil total C and N, and $\delta^{15}N$. We also used

Gaussian errors to run δ^{13}C. In all models, the data from the subplots were included in the error terms of mixed effects models (Crawley, 2007). We also regressed total soil C and N and their respective isotopes against forest cover using linear mixed effect models. All analyses were run in R environment (R development core team 2016) using lmer, glmer and glmer.nb functions of the lme4 package (Bates *et al.*, 2015).

2.3 RESULTS

We reported that landscape-scale deforestation decreases the local abundance and richness of hardwood species (Fig. 2). The overall decrease in local species abundance (54%) and richness (46%) in deforested landscapes is attributed to the selective loss of hardwood species (F = 12.667, $p < 0.05$ and F = 23.501, $p < 0.05$), with the diversity of soft and semi-hardwood being maintained regardless changes in landscape-scale deforestation. However, the loss of forest cover led to a reduction of local basal area and AGB in both semi (F = 9.416, $p < 0.05$ and F = 9.270, $p < 0.05$, respectively, Fig. 2) and hardwood species (F = 11.174, $p < 0.05$ and F = 13.509, $p < 0.05$, respectively, Fig. 2). For example, the AGB decreased from 117 Mg ha^{-1} in forest present in the least disturbed forested landscape to only 18 Mg ha^{-1} in fragments present in the heavily deforested landscape (6% of forest cover).

By contrast, deforestation did not affect soil stocks of C and N (F = 2.349, $p > 0.005$ and F = 0.006, $p > 0.05$, respectively, Fig. 3a-b). However, the C:N ratio sharply decreased as deforestation increased at landscape level (F = 9.359 and $p < 0.005$, Fig. 3c). We observed a linear decreasing in the soil δ^{13}C with increase forest cover at landscape level, but no variations in the soil δ^{15}N (F = 10.396, $p < 0.05$ and F = 0.148, $p < 0.05$, respectively, Fig. 4).

Fig. 2. Tree abundance, species richness, basal area and aboveground biomass in subplots of forest fragments as a function of the percentage of forest cover remaining within a 2km landscape surrounding each forest fragment, in the Atlantic Rainforest of southern Bahia, Brazil. The solid lines represent the relationship that was significant (p < 0.5).

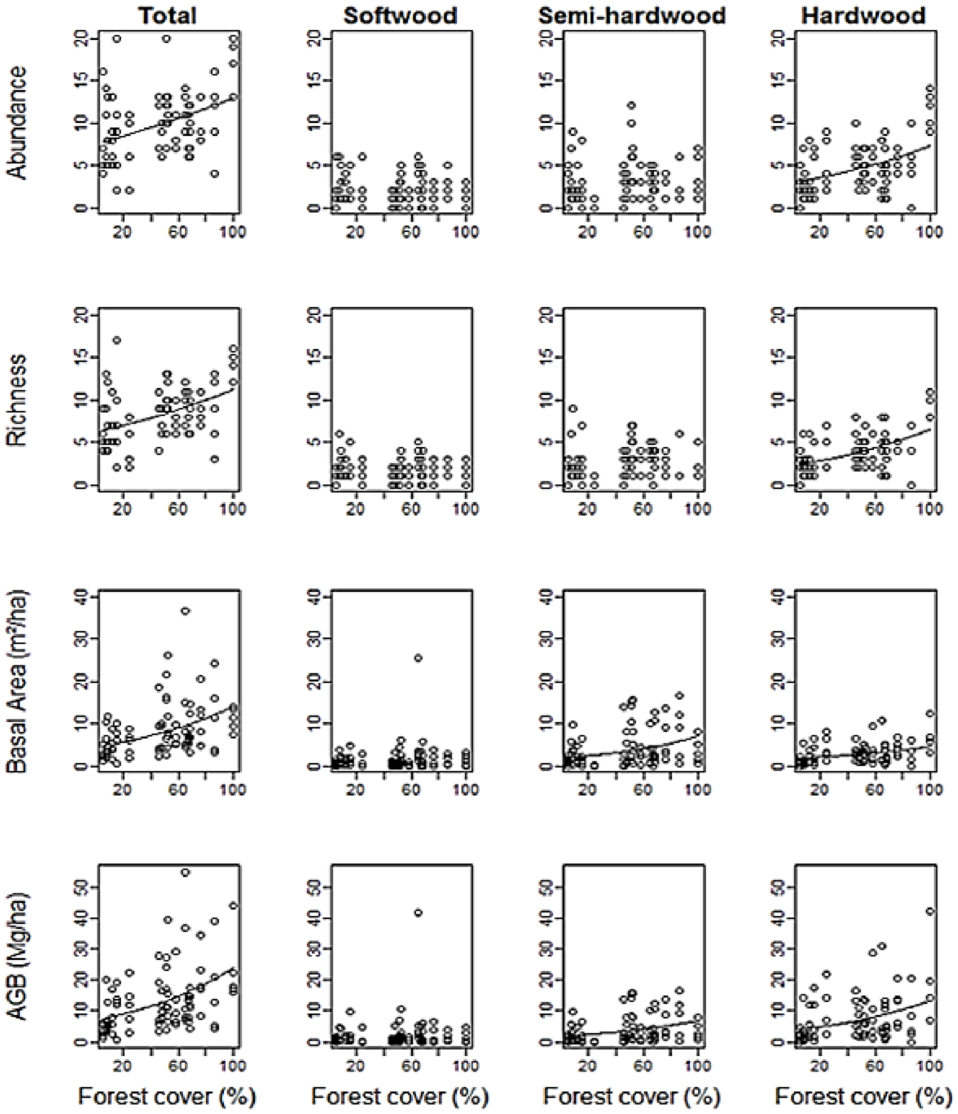


Fig. 3. Soil N (a), organic C (b) and C:N ratio (c) in subplots of forest fragments as a function of the percentage of forest cover remaining within a 2km landscape surrounding each forest fragment, in the Atlantic Rainforest of southern Bahia, Brazil. The solid lines represent the relationship that was significant ($p < 0.5$).

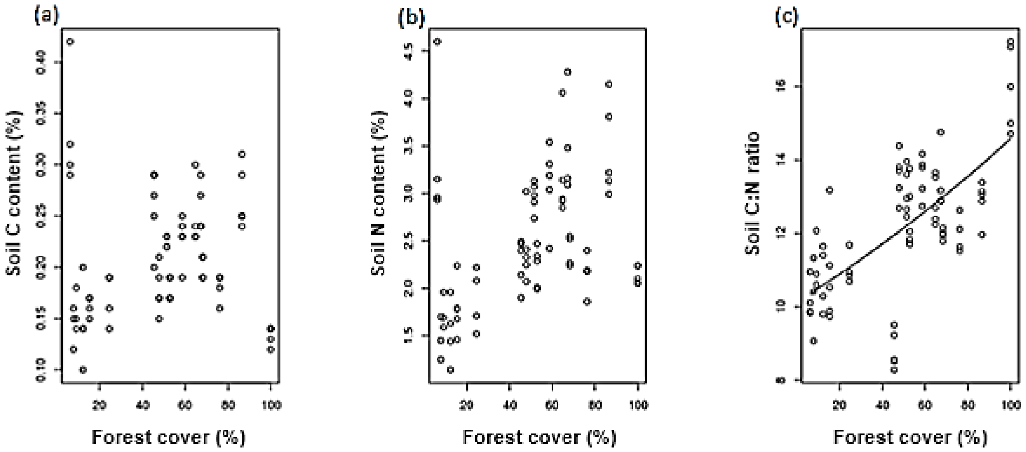
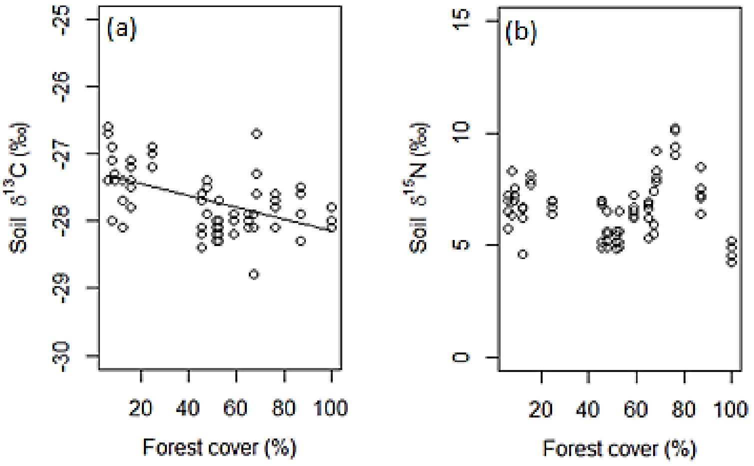


Fig. 4. Soil $\delta^{13}C$ (a) and $\delta^{15}N$ (b) in subplots of forest fragments as a function of the percentage of forest cover remaining within a 2km landscape surrounding each forest fragment, in the Atlantic Rainforest of southern Bahia, Brazil. The solid lines represent the relationship that was significant ($p < 0.5$).



2.4 DISCUSSION

2.4.1 Aboveground biomass and deforestation

The existing investigations on changes in tree biomass in response to landscape-level disturbances provide non-conflicting results (Pütz *et al.*, 2014; Magnago *et al.*, 2015a; Melito *et al.*, 2018). Studies that incorporate fragmentation report that biomass decreases considerable following the reduction of the fragment sizes in Atlantic forest (Magnago *et al.*, 2015a). Most of these small fragments have been affected by extensive degradation, including selective logging and tree mortality as the main causes of biomass loss (Villela *et al.*, 2006; Groeneveld *et al.*, 2009). Congruently, our study has shown a clear decrease in biomass related to the pervasive reduction of forest cover at landscape scale. The more deforested landscape has ~100 Mg ha^{-1} less than the most covered landscape. In addition, such decrease is linearly related to forest loss.

An overall decreasing in tree diversity influences such expressive decreasing in local aboveground tree biomass. We verified an important loss of tree species in more deforested landscapes, which is in line with a previous work conducted in the same area that we investigated (Rocha-Santos *et al.*, 2016). More specifically, the progressive loss of biomass is directly related to a selective loss of hardwood trees. This result is in agreement with previous studies (Oliveira *et al.*, 2008; Santos *et al.*, 2008), suggesting the importance of hardwood species to carbon sequestration and storage in the Atlantic forest fragments (Thier & Wesenberg, 2016).

Although, contrary to what we expected, we did not find a proliferation of softwood species with increase of deforestation at landscape level; softwood dominance increased, limiting the ability of our degraded forests to store carbon (Michalski *et al.*, 2007). Several tropical fragments in areas with predominance of high rates of deforestation have been shown a similar local dominance of softwood species (Santos *et al.*, 2008; Paula *et al.*, 2011; Magnago *et al.*, 2015a; Santo-Silva *et al.*, 2016; Thier & Wesenberg, 2016). Although, such species present high rates of carbon gaining, their life-history traits indicate lower biomass storage potential, which impairs larger biomass accumulation across deforested landscapes (Swaine & Whitmore, 1988).

Most of our hardwood trees are large-seeded species (Pessoa *et al.*, 2016), and the disappearance of some forest-specialist dispersers (Morante-Filho *et al.*, 2015), apparently has been reducing the proliferation of them in deforested landscapes. We note that the better preserved landscapes has more hardwood species in our study area (Menezes *et al.*, 2016; Pessoa *et al.*, 2016; Santos *et al.*, 2016). However, the proliferation of hardwood species will depend, in part, on the particular landscape abilities to support the dispersion of seeds (Costa *et al.*, 2012).

Given the substantial changes in the forest structure across the landscapes, the light-demanding genera were favored by the degraded forest structure (i.e., lower tree density and higher canopy openness) (see Rocha-Santos *et al.*, 2016). For instance, *Poincianella* and *Albizia* characterized by softwood, faster growth and abiotic dispersion germinated and grew successfully in our sites within less covered landscapes.

On the other hand, the maintenance of hardwood trees is a consequence associated with forest-interior conditions (Faria *et al.*, 2009). For example, the hardwood genera *Manilkara* and *Pouteria* require suitable habitat conditions for germination and growth (Pennington, 1990), which favored their development in our most preserved sites. These genera increased in abundance according to the landscape-forest cover. Similar increasing were found by Lima & Mariano-Neto (2014), suggesting that more covered landscapes continue successfully maintaining conditions to store significant amounts of carbon.

By comparing the biomass found here with lowland forests of the most preserved continuous area in the Atlantic Forest biome (Alves *et al.*, 2010), we observe that our least disturbed landscapes still have a considerable lower biomass than these more pristine areas.

2.4.2 The soil compartment

Forest degradation remains as the major constraint to an adequate quantification of changes in carbon stock, since it is more difficult to quantify than clear-cut deforestation (Houghton, 2012). However, the use of carbon isotope may improve the detection of forest degradation. Foliar $\delta^{13}C$ values led to insights about the relative discrepancies of C fixation in open versus closed forests following variation in light penetration

(Farquhar *et al.*, 1989; Martinelli *et al.*, 1991). $\delta^{13}C$ values tend to increase from closed to opened forests common in degraded areas. In addition, other studies have showed that soil $\delta^{13}C$ values can also change in response to timber harvest (i.e., $\delta^{13}C$ values increase after loss of tree biomass) (Diochon & Kellman, 2008; Huang *et al.*, 2012; Achat *et al.*, 2015). These results add insights into the influence of forest degradation on tree biomass. Although we did not measure degradation directly, our soil $\delta^{13}C$ values increased with the loss of forest cover, suggesting that degradation may strongly impair biomass accumulation in more deforested landscapes.

Contrary to what was observed for aboveground tree biomass, we did not find a significant decreasing in soil carbon nor soil nitrogen stocks with decreasing forest cover at landscape level. The belowground C is physically and chemically more stable than aboveground (Davidson & Janssens, 2006), although it has been shown that some remnants within the Atlantic forest have lower soil C stocks in more degraded landscapes (Robinson *et al.*, 2015). However, we did report a linear decreasing trend of carbon relative to nitrogen availability on the soil (lower C:N). This result suggests that our degraded sites appear to delay their soil C loss, which comprises some level of ecosystem-function debt (Haddad *et al.*, 2015a).

The decreasing of C:N ratio on the soil can be attributed to different processes, such as biological fixation and changes in the rate of decomposition (Xu *et al.*, 2016). Biological N fixation by leguminous species, a very common group of species often associated with disturbed forests (Vitousek & Howarth, 1991), can decrease the soil C:N ratio. This is likely to be the case in our study because the richness and abundance of leguminous species has increased in our deforested landscapes (Rocha-Santos *et al.*, 2017). Furthermore, the C:N pattern seems to be in accordance with the isotope results. Leguminous species that fix atmospheric nitrogen usually have $\delta^{15}N$ value near zero (Martinelli *et al.*, 1992), and the average soil $\delta^{15}N$ value reported for our deforested landscapes was +2.9‰, suggesting the influence of N-fixing trees.

Most of the Atlantic forest fragments present critical conditions of degradation, which drastically reduces their ability to store carbon (Ribeiro *et al.*, 2009; Pütz *et al.*, 2014). Among the factors limiting local productivity, N is likely to exert a strong influence in most degraded forests (Laurance *et al.*, 1999). However, we found no variation in soil N stock along a deforestation gradient, indicating an important availability of N to the biomass accumulation along our sample sites. Similarly, $\delta^{15}N$ value did not varied showing that our landscapes have similar N availability (Craine *et al.*, 2015). Although detailed analysis of soil fertility is needed to infer the N limitation accurately, this pattern suggests that even for the less covered landscapes, tree biomass storage seems not be limited by soil N.

2.5 CONCLUSION

This study pursues relevant evidences on the role of hardwood trees in increasing forest biomass along the gradient of forest cover. Softwood trees dominate deforested landscapes, whereas they are relatively lower in more covered landscapes. In addition, the loss of hardwood trees in deforested landscapes is associated with a distinct forest degradation capable of change the dynamic of C in the forest soil. Thus, our results highlight that the disappearance of hardwood trees is the main driver constraining the biomass accumulation. Our findings still indicate that the degraded forests decrease the C:N ratio that may be attributed to the presence of leguminous species. The landscapes maintain similar N stock, suggesting that the forest loss did not decrease the N availability. Our results support considerations on C and N accumulation along the landscapes (Knops & Tilman, 2000). Furthermore, landscapes with high forest cover harbor less degraded forests, which apparently have a higher ability of soil C retention. Finally, these findings indicate that hardwood trees are more common when landscape forest cover increases, and that the landscape approach may be a reasonable descriptor of biomass and nutrient cycling, being central to support carbon conservation programs.

SUPPORTING INFORMATION

Height estimation model

We fit our *H* estimation model using three variance modeling approaches: non-linear least square, ordinary least square with log-linear regression and a non-linear approach in which we modeled the heteroscedastic variance of the dataset (Marra *et al.*, 2015). In the last approach, we modeled variance as a function of *DBH* with a normally distributed residual error:

$$\varepsilon_i = N(\hat{y}_i, \sigma_i),$$

where *i* is the subscript for individuals (*i* = 1, …, n) and σ_i is modeled with a heteroscedastic variance according to:

$$\sigma_i = c_i * DBH_i^{c_2}.$$

We fit our *H* estimation model with non-informative uniform priors using WinBUGS 1.4.1 (Lunn *et al.*, 2000; Spiegelhalter *et al.*, 2002). Three chains were run in parallel, and convergence of the posterior distribution for each parameter was assessed by convergence to one of the ratio of pooled to mean within-chain central 80% intervals or by the stability of both intervals (Brooks & Gelman, 1998; Brooks & Roberts, 1998). To select the best approach we calculated the *DIC* Deviance Information Criterion, a generalization of *AIC* Akaike's Information Criterion, which is a cross-validatory term that expresses the goodness of the fit and the model's complexity. The lower the value the better the predictive ability and parsimony (Spiegelhalter *et al.*, 2002). We also checked whether the 95% credible intervals of the coefficient's posterior distributions excluded zero. However, we did not attempt to test the null hypothesis that a particular parameter is zero (Bolker, 2008; Bolker *et al.*, 2013). Contrasts were evaluated by monitoring differences between parameters or predictions based on their posterior distribution. To support the selection of the best modeling approach, we also calculated the R^2adj adjusted coefficient of determination and the *Syx%* relative standard error as a percentage. The *Syx%* was calculated as follows:

$$Syx\% = \left(\frac{2s}{\hat{y}\sqrt{N}}\right) \text{ (3)},$$

where *s*, $\hat{y}$ and *N* are the standard deviation of the regression, the mean of the focal independent variable and the number of observations, respectively. For the *OLS* approach including log-transformed variables, we calculated the *Syx%* using untransformed data. To correct for the bias introduced by the log-transformed data, a *CF* correction factor was calculated as follows:

$$CF = \exp\left(\frac{SSE^2}{2}\right) \text{ (4),}$$

where *SSE* is the standard error of the estimate (Sprugel, 1983). We selected the best modeling approach based on quality of the height predictions of those trees for which we had measured height values, namely lower root square mean error), higher DIC and lower *Syx*%.

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3. CHANGES IN FOREST STRUCTURE ARE THE MAIN DRIVERS ALTERING CARBON AND NITROGEN CYCLING IN DEFORESTED LANDSCAPES IN THE ATLANTIC FOREST, BRAZIL.

ABSTRACT

Understanding the dominant controls on carbon and nitrogen dynamics is key to separate the influence of multiple factors disturbing ecosystem processes in natural forests. We investigated changes in carbon (C) and nitrogen (N) dynamics influenced by forest loss. We analyzed multiple indicators of C and N dynamics (total C and N, C:N ratio, $\delta^{13}C$ and $\delta^{15}N$) along a gradient of forest cover at the landscape scale. We also performed a path analysis to test the potential for forest structure and species composition to play a central role in mediating C and N variation with forest loss. The measured indicators changed with forest loss, and forest structure was the dominant factor mediating their alterations. Total C and C:N ratio decreased with forest loss while total N and $\delta^{13}C$ increased. The $\delta^{15}N$ did not vary with forest loss. These same patterns were observed considering forest structure as a predictor variable, confirming forest structure as the main path for explaining C and N changes with forest loss. Probably because changes in forest structure trigger microclimate disturbances, which comprise a powerful mechanism of nutrient variation. Here, we report preliminary findings indicating mechanisms leading tropical landscapes to distinct changes in ecosystem processes. Although it still requires complementary studies, especially considering direct measurements of microclimate changes, it is imperative to consider forest loss as a detrimental factor for continued ecosystem functioning.

Keywords: path analysis, isotopes, forest structure, landscape scale, forest cover.

3.1 INTRODUCTION

Deforestation is a major driver of biodiversity loss in tropical regions (Sala *et al.*, 2000). As these realms are the largest global biodiversity reservoirs, shifts in biodiversity patterns have major implications for our human life-support system. In addition to the evident disappearance of trees after deforestation, degradation of the remaining forests further alters the ability of such systems to deliver key services (Thomas *et al.*, 2004). Along the last decades, major advances in ecological research provided us with a reliable picture on how deforestation and degradation affect species diversity patterns (Joly *et al.*, 2014), but larger gaps remain when it comes to understand these effects on key ecosystem services (Trumbore *et al.*, 2015). Yet, it is estimated that nearly 60 percent of the ecosystem services are being degraded at a global scale (Millenium Ecosystem Assessment, 2005).

Biogeochemical cycles occurring in different compartments of forest strata, such as carbon (C) and nitrogen (N) cycling, are pivotal to ecosystem functioning of tropical forests. The availability of both elements is known to be affected by deforestation and degradation. For instance, while deforestation readily accounts for massive losses in carbon, degradation due to an increased proportion of edge-affect forests in fragmented, anthropogenic landscapes is estimated to further decrease the carbon stored within the remaining fragments (Laurance *et al.*, 2007; Haddad *et al.*, 2015b). Degradation creates unstable environments for carbon (C) and nitrogen (N) dynamics, ultimately decreasing the retention of both elements in forest remnants (Haddad *et al.*, 2015b).

Despite the importance of such cycling for forest maintenance, we still lack a reliable understanding on how these elements are regulated by more proximal drivers related with deforestation and fragmentation. These anthropogenic processes alter a variety of local features that are closely linked with C and N cycling, including forest structure, microclimatic conditions and floristic composition (Martinelli *et al.*, 2000), all attributes directly affected by deforestation and fragmentation. For instance, edge-affected forests show specific alterations in forest structure that include an increasing in the canopy openness, loss of basal area and height, which are important to modulate both C and N through sunlight availability, temperature and moisture variations (Schmidt *et al.*, 2017). The elevation of average temperatures on forest edges (Ewers & Banks-

Leite, 2013; Melo *et al.*, 2013b; Magnago *et al.*, 2015b) increases the rates of mineralization (Melillo *et al.*, 2002; Szukics *et al.*, 2010; Tian *et al.*, 2010). While more C is eliminated from the system by heterotrophic respiration, part of the N remains available for uptake by plants or microbes. This process elevates the soil N in the absence of leaching and volatilization, reinforcing the C:N ratio decreasing of the system as degradation increases (Yang & Luo, 2011; Xu *et al.*, 2016).

Degradation also triggers significant shifts in floristics (Santos *et al.*, 2008; Rocha-Santos *et al.*, 2016), and this reassembly of tree species in edges-affected forests results in carbon losses, through the loss of high density wood trees which is not compensated by the proliferation of light-demanding species. These alteration in species composition and stand structure also affect the distribution of nutrients in an ecosystem (Naeem *et al.*, 1994; Hooper & Vitousek, 1997) via changes in the decomposition process of the plant material that reaches the soil (Gessner *et al.*, 2010). On the other hand, variations in the nutritional composition of plants, caused by changes in species composition, may also alter the process of plant decomposition (Hattenschwiler & Gasser, 2005; Hattenschwiler *et al.*, 2011), similarly affecting the distribution of nutrients within the system (Lodge *et al.*, 1994). Floristic shifts influence forest nutrients by their particular stoichiometry (Tanaka-Oda *et al.*, 2016). In particular, light-demanding species usually show high rates of carbon fixation by photosynthesis, but a relative low ability to retain it compared with those shade-tolerant species (Nascimento & Laurance, 2004; Barros & Fearnside, 2016), as these early-successional species invest less in recalcitrant carbon such as lignin, maintaining lower C:N ratios (Knops & Tilman, 2000). This ratio is typical of plants adapted to degraded areas (Reich *et al.*, 1995; Quested *et al.*, 2007), while forest-adapted species tend to retain more C, producing more lignified and slow-growing tissues (Quested *et al.*, 2007). Tissue traits comprise the first driver of decomposition following eventual changes in vegetation community (Quested *et al.*, 2007). In this case, the early-successional species' stoichiometry (e.g. low C:N ratio) will favor the activity of microbial decomposers with a significant increase in soil CO_2 efflux (Gessner *et al.*, 2010). In addition, average higher temperatures tend to accelerate the rates of mineralization (Melillo *et al.*, 2002, Szukics *et al.*, 2010, Tian *et al.*, 2010).

Considering the above-mentioned rationale, links between forest degradation and C and N dynamics are complex and probably comprising alternative and interrelated pathways (Martinelli *et al.*, 2000; Laurance *et al.*, 2011; Houghton, 2012; Chaplin-Kramer *et al.*, 2015). In this context, here we investigated whether local content of C, N and the ratio of C:N in tree leaves and leaf litter (hereafter litter) of forest remnants are affected by the forest remaining at landscape-scale. We hypothesized that landscape-scale forest loss decreases, in both assessed forest strata, the local C content while N tends to increase, thus reflecting in lower C:N ratios. To understand qualitative differences in C and N more adequately, we also assessed whether deforestation changes the $\delta^{13}C$ and $\delta^{15}N$ of the samples. The stable isotopes comprise an essential integrator of ecological processes that change both spatially and temporally (Robinson, 2001). The stable C isotope is commonly used to asses forest quality, while ^{15}N can help address important questions on N loss from the system (Dawson *et al.*, 2002b). Finally, we used path analyses to identify proximal drivers by which deforestation operates local changes in nutrient dynamic. Based on previous observations from our study sites (see Rocha *et al.*, 2016) we hypothesized that the increasing canopy openness in more deforested landscapes triggers changes in forest structure, which may affect the litter C and N contents via perturbations in temperature, and changes the species composition. We draw our diagram considering that both of them increase the rates of heterotrophic respiration and mineralization. Thus, we hypothesize that the observed variation in litter C and N results from the modification of both forest structure and species composition. In this setting, degraded forests into less-covered landscapes (i.e. warmer forests) will present a relative loss of C and an accumulation of N in the litter compartment.

3.2 METHODS

3.2.1 Site Description

The present study was conducted in the municipalities of Una: Belmonte and Mascote located in the Atlantic Forest of southern Bahia (Figure 1a). This study was carried out in the Lowland Wet Forests that are characterized by a well-defined stratification encompassing the emergent trees, canopy, understory and herbaceous strata (Thomas, 2003). Although severely reduced by deforestation and degradation, these forests are considered among the richest forest in the world in terms of tree species and endemics (Myers *et al.*, 2000). The region's rainfall is 1800-2200 mm per year (Santos & França, 2011) with no pronounced dry season, and the predominant soil types are Podzol and Latosol (Thomas, 2003).

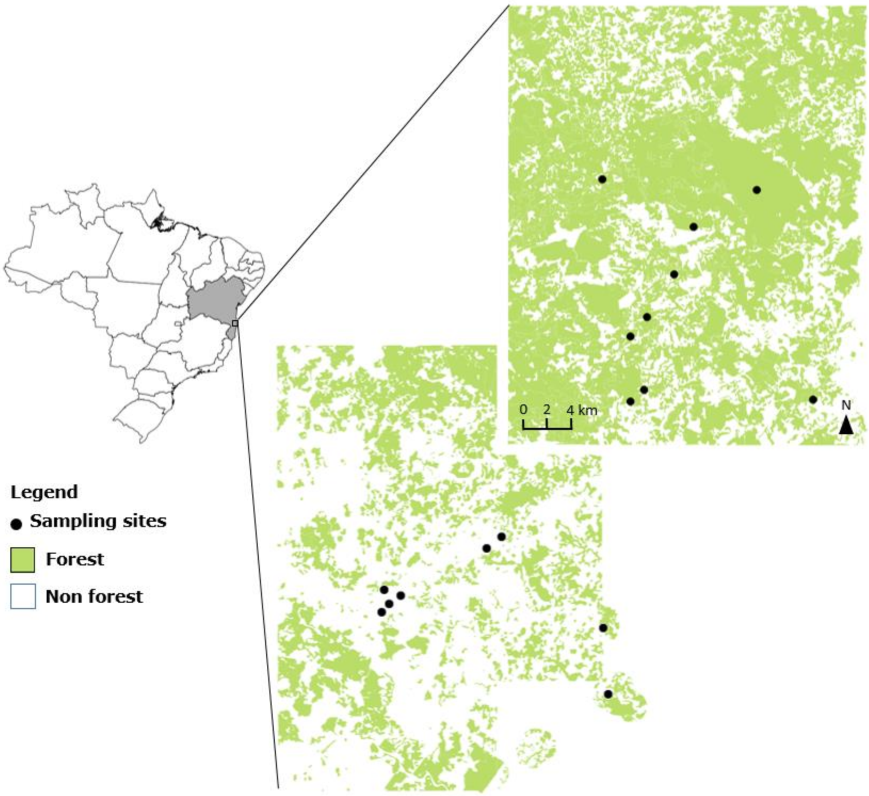
3.2.2 Landscape selection and forest cover measurement

Historically, the last period of significant deforestation in southern Bahia dates back to the 1970s, when the opening of the BR-101 highway intensified deforestation, promoted an unprecedented logging activity that triggered a vast loss of wood stocks in the region. It is estimated that 80% of 11,000 km² of forest were lost in just ten years (Mesquita, 1997), although the effect of logging activities is still unknown. Currently, most of the Atlantic Forest landscapes are highly fragmented and composed of small and isolated fragments (Ribeiro *et al.*, 2009), despite the fact that these forests represent the largest continuous forest remaining in the Northeastern Atlantic Forest biome.

We mapped the distribution of forest remnants in the region using satelite images (Rapid Eye, from 2009-2010, QuikBird and WorldView, as of 2011) available between the Jequitinhonha and Contas rivers. Vegetation types were visually interpreted using the aforementioned high-resolution maps (1: 10,000 scale), and we identified forest patches based on the following patch features: color, texture, shape, position, and context. The forest areas were delimited using the tools available in the ArcGIS (Esri 2007). From the total area (qual a área mapeada em km2??) we selected 18 forest fragments sampling sites within forest areas with a minimum distance of one kilometer.

Finally, we used a 2 km radius buffer from each of the 18 sample sites to calculate their forest cover (Fig. 1b, 1c).

Fig. 1. Map showing the distribution of the landscapes across the South of Bahia, Brazil. Filled points represent the sample sites within a 2 km landscape surrounding each site, in the Atlantic Rainforest of southern Bahia, Brazil.



3.2.3 Sampling of botanical material

In each sampling site we located five subplots of 4 × 25 m (100 m2) equidistant at least 25 m. They were placed >30 m from the forest edge to minimize the interference of surrounding areas. In each plot we collected leaves of at least three individuals of the most common species. We followed the sample methods proposed by Cornelissen *et al.* (2003) that exclude leaves affected by pathogens, herbivores, and shading. We sampled 358 trees of which 84.6% was identified to the species level (303 trees).

Furthermore, 87.4% (313 trees) were identified to the genus level and the majority to the family level, 90.7% (325 trees). The botanical samples were identified at the herbaria of The Center for Cocoa Research (CEPEC) and The State University of Santa Cruz (HUESC). When available, the reproductive material (flowers and fruits) was included in the botanical collection of the referred herbaria. The sampling of leaf litter was conducted in only 17 landscapes during twelve months, beginning in April 2013. For that, we installed three collectors of 0,237 m^2 in each subplot.

3.2.4 Laboratory analysis

The litter from each litter trap was screened to obtain only leaf material, which was oven-dried at 60 ° C for 48 h. The samples were ground to a finer powder for extract a subsample of 1.5 to 2 mg. The subsamples were encapsulated and loaded onto a ThermoQuest-Finnigan Delta Plus mass spectrometer (Finnigan-MAT; CA, USA) interfaced with an Elemental Analyzer (Carlo Erba model 1110; Milan, Italy). We applied the same procedures for leaves. Finally, we determined the contents of C and N, and the composition of ^{13}C and ^{15}N for both leaf litter and leaves. We presented the isotopes using the ‘delta’ notation (δ) expressed in parts per mil (‰).

3.2.5 Density of wood

We assessed the Wood density values (WD) from the Global Wood Density Database (Chave *et al.*, 2009). When WD values were not available for some species, or for those which the identification was limited to the genus level (12 individuals), we applied the average value of WD from all species of the same genus that occur in the Atlantic Forest. For the trees identified up to the family level (10 individuals), we used the mean value of genera from this family, and for the 33 unidentified trees we considered the mean WD value of all recorded trees in that particular sampling site.

3.2.6 Forest structure

We placed a 4 x 20 m plot within surveyed sampling sites to estimate the vertical foliage profile, which is the foliage density measured along the forest height, at three sampling points established 10 m apart along each parcel. We estimated canopy foliage density using a 5 m high pole to allow for a vertical sighting and estimated the intervals filled with foliage, i.e. any foliage touching this imaginary vertical line extending from the ground up to the top of the forest height. We estimated foliage density along eight distinct strata: 0–1 m, 1–5 m, 5–10 m, 10–15 m, 15–20 m, 20–25 m, 25–30 m and 30–35 m high, and considered the mean interval of points (m) filled by vegetation in each stratum.

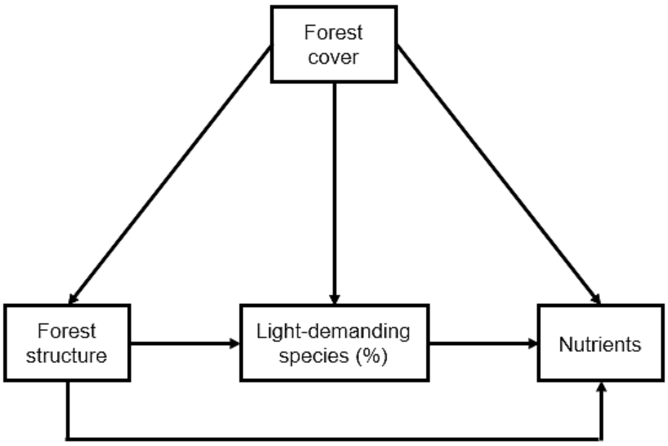
We used forest structure as a compound variable, considering the mean foliage density measured along the forest strata. This variable has been successfully used to describe the vertical profile of a forest (Faria *et al.*, 2009, method modified from Malcom 1995), indicating, for instance, the presence and quantity of the forest canopy (Rocha-Santos *et al.*, 2016). This variable is also highly correlated with the local diversity of several biological groups in tropical forests (Pardini *et al.*, 2010; Morante-Filho *et al.*, 2015; Rocha-Santos *et al.*, 2017). We ran a PCA with this data and used the first axis (explaining 64.6% of the total variation) that represents a gradient of forest disturbance, i.e. with a decreasing density of canopy vegetation (> 10-25 m) and an increasing of the density of forest understory (< 5 m) following the forest loss at the landscape-scale.

3.2.7 Statistical analysis

We used Generalized Linear Mixed Effects Models (GLMM) to examine the effects of forest loss at the landscape scale on the following parameters: total C and N, C:N ratio, $\delta^{15}N$ and $\delta^{13}C$ of leaves and leaf litter. We used Gaussian errors to analyze the data. In all models, the subplot data were included in the error terms of the mixed effect models (Crawley, 2007). All analyses were performed in the R (Development Core Team 2016) environment using the lmer, glmer and glmer.nb functions of the lme4 package (Bates *et al.*, 2015).

We applied path analysis, using Maximum Likelihood estimation, to identify explore the potential influences of forest loss on C and N alteration mediated by forest structure and species composition. Because pioneering species usually exhibit softwood traits, we used the proportion of softwood to the hardwood as representative of the dominance of pioneering species. We built a path model to examine the causal relationship among forest loss and nitrogen and carbon in litter (Fig. 2). We thus tested this conceptual model predicting that the loss of forest cover causes local changes in C, N and C:N ratio through changes in forest structure and species composition. The model also includes a direct effect of forest loss on the nutrients, a pathway accounting for any other more proximal driver triggered by deforestation but not explicitly included in our model.

Fig. 2. Hypothesized relatioship between the reamining forest cover at the landscape and the C and N contents. The straight sigle-headed arrows indicate the unidirecional causal between variables.



3.3 RESULTS

The GLMM showed that the landscape-scale deforestation affected the local availability of C, N and C:N ratio in both forest strata. As deforestation progressed, we reported a linear decreasing of the local carbon and an increasing of nitrogen content in leaves ($F = 13.721$, $p < 0.05$ and $F = 3.940$, $p < 0.05$, respectively, Fig. 3a-b). The litter had the same pattern: i.e. decreasing C and increasing N ($F = 6.544$, $p < 0.05$ and $F = 5.239$, $p < 0.05$, respectively, Fig. 3c-d). Considering the reduction on the forest cover of ~90%, i.e. from the lowest (100%) to the highest (~6%) deforested landscapes, we observed a reduction of 2% in both foliar and litter carbon, while nitrogen increased 1.2% in leaf and 0.6% in litter.

On average, both leaves and litter had 45% of carbon. The leaves presented minimum and maximum values of 44 and 48% of C, while litter varied from 39 to 48%. Due to this contrasting variation observed of local C and N along the deforestation gradient assessed, both foliar and litter C:N ratio linearly decayed according to the reduction of forest cover at landscape-scale ($F = 9.688$, $p < 0.05$ and $F = 4.404$, $p < 0.05$, respectively, Fig. 3e-f). The leaves presented on average C:N of 22, varying from 13 to 35, from highest to lowest forested landscapes. Considering this same gradient, the proportional increase of C:N ratio in litter ranged from 20 to 46 with a mean of 35.

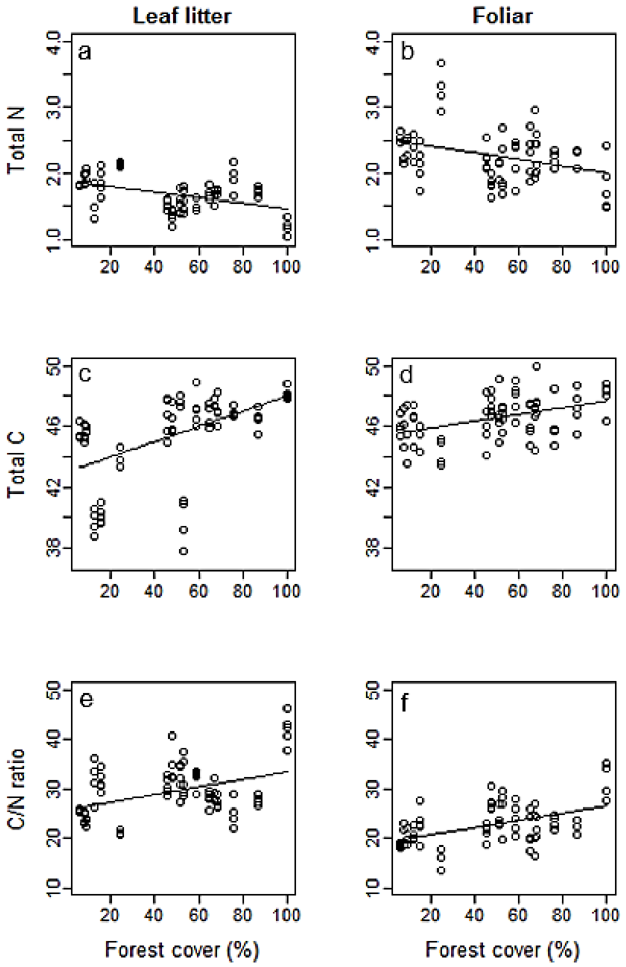
Furthermore, the isotopic fractions of ^{15}N in leaves and litter did not show significant variation according to a deforestation gradient ($F = 0.000$, $p > 0.05$ and $F = 0.085$, $p > 0.05$, respectively, Fig. 4a-b). By contrast, concentration foliar and litter $\delta^{13}C$ increased significantly according to the forest loss ($F = 7.956$, $p < 0.05$ and $F = 8.290$, $p < 0.05$, respectively, Fig. 4c-d). On average, forest litter showed higher average concentrations of $\delta^{13}C$ than the living foliage ($F = 41.59$, $p < 0.001$, Fig. 5). Furthermore, comparison of the $\delta^{15}N$ of legumes and non-leguminous trees did not show significant difference ($F = 2.38$, $p > 0.05$, Fig. 6).

All of our conceptual models significantly explained the local variation of C, N and C:N of tree leaves and leaf litter, and indicated that forest structure is the sole pathway through which landscape forest loss influences the observed variations, but not through changes in species dominance.

3.4 DISCUSSION

The significant decrease of carbon in deforested landscapes comparable to that measured from conserved landscapes suggests that the forest cover is a distinct driver of carbon loss in the Atlantic forest fragments. On average, the C content of leaves and litter were significantly lower in deforested landscapes (~45%) than in more covered landscapes (48%). Such differences have been observed across chronosequences of different biomes, suggesting that C tends to accumulate in aboveground vegetation and litter from degraded to conserved forests (Yang *et al.*, 2011; Robinson *et al.*, 2015). By contrast, nitrogen tended to decrease with the increase of forest cover. The N content, on average, decreased from 2.6% to 1.8% in leaves and from 1.8% to 1.2% in litter according to forest loss. This unusual tendency to decrease N diverge from the global pattern that exhibits a gain of N during stand development (Yang et al., 2011). At first, these variations are consistent with our first hypothesis, in which forest loss promotes changes in the plant community favoring species harboring lower C and more N, leaf traits often observed in early-successional species thriving in degraded forests (Reich *et al.*, 1995; Knops & Tilman, 2000). Early-successional trees harboring more foliar N have been observed in anthropogenic landscapes (Aidar *et al.*, 2003b).

Fig. 3. Carbon and nitrogen contents of leaves and litter in subplots of forest fragments as a function of the percentage of forest cover remaining within a 2km landscape surrounding each forest fragment, in the Atlantic Rainforest of southern Bahia, Brazil. The solid lines represent the relationship that was significant ($p < 0.5$).

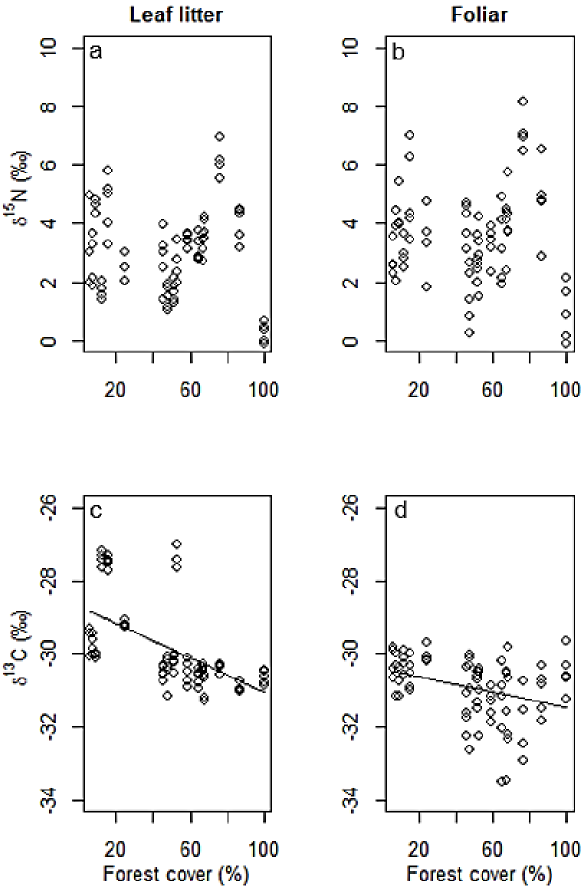


Considering the litter compartment, another explanation may originate from the fact that these forests probably support warmer conditions becoming the litter C losses more rapid, insofar as high temperature favors mineralization (Melillo *et al.*, 2002; Szukics *et al.*, 2010; Tian *et al.*, 2010).

Although we do not have measured microclimate directly, prior studies in our sites report that canopy openness changed in proportion to forest loss, suggesting the elevation of temperature due to gradual sunlight incidence (Andrade *et al.*, 2015). Indirectly, the foliar $\delta^{13}C$ corroborates this microclimate variation showing lower discrimination against ^{13}C during photosynthesis in deforested landscapes (Fig. 2a-b).

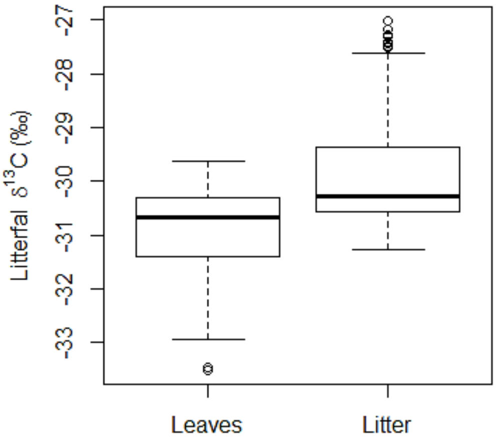
Less discrimination means more ^{13}C fixed by Rubisco in response to stomatal closure in warmer conditions of high-deforested landscapes (Farquhar & Sharkey, 1982).

Fig. 4. δ^{13}C and δ^{15}N of leaves and litter in subplots of forest fragments as a function of the percentage of forest cover remaining within a 2km landscape surrounding each forest fragment, in the Atlantic Rainforest of southern Bahia, Brazil. The solid lines represent the relationship that was significant ($p < 0.5$).



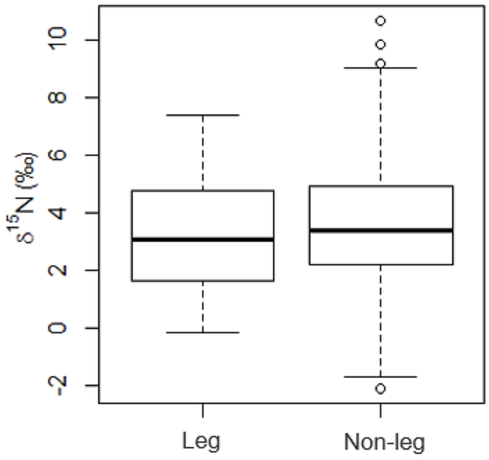
This analysis can be complemented by comparing the averages of foliar δ^{13}C (-30.9) and litter δ^{13}C (-29.8) which reveal an isotope enrichment with high fractionation against ^{13}C (Fig. 3). The primary explanation relies on the loss of $^{12}CO_2$ during respiration promoted by the warmer forests placed in deforested landscapes (Farquhar *et al.*, 1989).

Fig. 5 – Box-whisker plots of δ^{13}C values for leaves and leaf litter in subplots of forest fragments within a 2km landscape surrounding each forest fragment, in the Atlantic Rainforest of southern Bahia, Brazil.



Forest loss did not changed both litter and foliar δ^{15}N according to the forest cover gradient (Fig. 2a-b), which can be explained by little influence of N-fixing legumes (Hietz *et al.*, 2011). On average, the δ^{15}N of leaves from legumes does not differ from the non-leguminous species suggesting that legumes were not fixing nitrogen (Fig. 6). Thus, the increased N content observed in our deforested landscapes cannot be ascribed to N fixation. Previously, studies have shown that most tree families from another tropical forest tend to maintain the same foliar δ^{15}N values from degraded forest edges to forest interior (Crowley *et al.*, 2012).

Fig. 6 – Box-whisker plots of δ^{15}N values for leaves and leaf litter in subplots of forest fragments within a 2km landscape surrounding each forest fragment, in the Atlantic Rainforest of southern Bahia, Brazil.

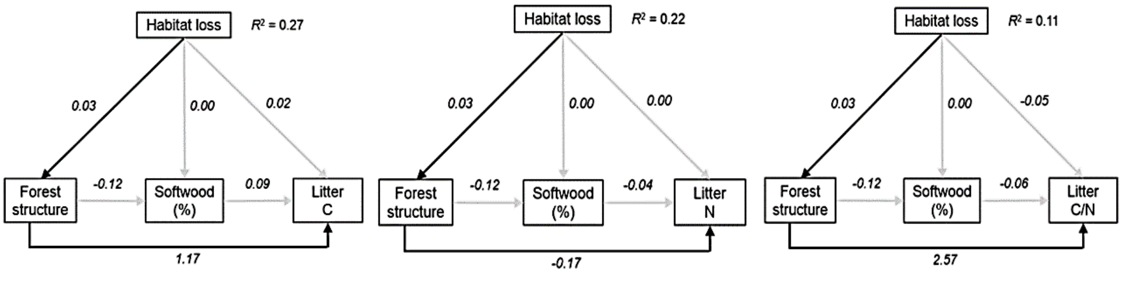


Because the ^{15}N composition can also reflect the difference in plant preference for N forms (*e.g.* organic N, NH_4^+, NO_3^-) (Högberg, 1997), the δ^{15}N derived from analysis of leaves suggests that the forms of N used by the species appear to be little different throughout the landscapes. Such pattern has been observed in other sites showing the coexistence of trees that share the same N forms (Houlton *et al.*, 2007).

However, they differed in their leaf N content; i.e., forest loss has induced compositional shifts favoring species with more foliar N. Although the effects of forest loss changed the forest structure and species composition in our sample sites (Rocha-Santos *et al.*, 2016, 2017), it was not enough to promote any N limitation, as observed in other studies (Davidson *et al.*, 2007). As mentioned above, this condition cannot be caused by the presence of nitrogen-fixing leguminous trees (Gehring *et al.*, 2005), since we did not find any δ^{15}N reduction, as observed by Gehring *et al.* (2005) for leaf and litter from sites dominated by N_2-fixing plants.

Our study indicates that forest loss at the landscape scale influences the dynamics of C and N of remnant forests. However, we highlight that this influence is mediated by local modifications of forest structure (Fig. 4). Our path model demonstrates that C and N of litter are not governed by species, against our expectation. Instead, forest loss exerted a powerful influence on forest structure, which in turn affected all indicators of C and N dynamics in the litter. This is in line with δ^{13}C results, which is widely used to indicate modifications of canopy structure (Medina & Minchin, 1980; Ometto *et al.*, 2006). As aforementioned, the assumed increase in sunlight availability and temperature as a result of modifications of forest structure plays a major role in explaining variability in indicators of litter C and N dynamics.

Fig. 7 – Path models with significant paths (bold arrows) for predicting indicators of C and N dynamics in the leaf litter.



Our path model considers that forest loss can degrade remnant forests by exposing vegetation to wood extraction and additional edge effects (Broadbent *et al.*, 2008). Much of these degradation agents cause a cascade of compositional and microclimatic alterations, often generating two important mechanisms of C and N variation – early-successional species dominance and temperature elevation (Santos *et al.*, 2008; Schmidt *et al.*, 2017). Such events have been found in tropical forests, especially in small forest fragments and contribute to low foliar C:N ratio and decomposition (Quested *et al.*, 2007; Mitchell *et al.*, 2014).

Thus, the second important message from our study is that modifications of forest structure play a significant role in changing C and N dynamics in deforested landscapes. This hypothesis described in our path model can be corroborated by regression analysis considering forest structure as a predictor (Axis 1), in which C and N varied similarly to forest loss.

In conclusion, the C and N patterns described here leave no doubt about the importance of considering forest loss as a detrimental factor for continued ecosystem functioning. These results have implications for conservation of tropical forests because potential biotic or abiotic factors contributing to additional modifications of forest structure are expected to intensify C and N variations. Nevertheless, it is important to consider that we report preliminary findings about processes with complex causes and consequences. Therefore, for a better understanding of C and N dynamics, it is needed complementary studies, especially considering direct measurements of microclimate disturbances and decomposition.

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