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Research Article

Carbon storage in a fragmented landscape of Atlantic forest: the role played by edge-affected habitats and emergent trees

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Abstract

Patterns of carbon retention and distribution across human-modified landscapes have been poorly investigated. In this paper carbon distribution across three forest habitats of a fragmented Atlantic forest landscape in northeast Brazil is examined. Data on tree assemblages (DBH ≥10 cm) inhabiting forest interior stands, forest edges and fragments (2.05-365 ha) were obtained via information from 59 0.1-ha plots (a total of 4,845 stems and 198 tree species), and it was further incorporated in four allometric equations for estimation of above-ground biomass and carbon. Stocks of carbon were highly variable within habitats of Serra Grande, but forest interior plots retained almost three times more carbon (202.8 ± 23.7 TonC/ha) than edge and fragment plots, while these edge-affected habitats exhibited similar scores. Moreover, emergent tree species accounted for the majority of the carbon retained (59.13%) in interior plots with understorey species playing a minor role. However, carbon retained by emergent species decreased by a half across forest edges and forest fragment since large stems (> 70 cm DBH) and very tall trees (> 31 m height) were very rare in these habitats. Finally, a forest cover mapping revealed the occurrence of 213.19 km^2 of forest interior habitat in the whole Atlantic forest of northeast Brazil. This figure means that only 8% of total remaining forest habitat has a full potential for carbon storage, with the other 92% (edge-affected habitats) storing just a half of that. Our results suggest that habitat fragmentation and the consequent establishment of edge-affected habitats (forest edges and fragments) drastically limit forest capacity for carbon storage across human-modified landscapes since the loss of carbon due to reduced abundance of large trees is not compensated by either canopy or understorey species.

Keywords: ecological services; habitat fragmentation; human-modified landscapes; tropical forests.

Resumo

Padrões de retenção e distribuição de carbono em paisagens antrópicas têm sido pouco investigados. Neste artigo nós examinamos a distribuição de carbono em três habitats de uma paisagem de floresta Atlântica fragmentada. Dados sobre a assembleia de árvores (DAP ≥10 cm) em trechos de floresta madura, bordas e pequenos fragmentos florestais (2,05-365 ha) foram obtidos com base em 59 parcelas de 0,1 ha (4845 indivíduos de 198 espécies de árvores). Estes dados foram utilizados em quatro equações alométricas para estimar a biomassa vegetal e o carbono da floresta acima do nível do solo. Os estoques de carbono foram altamente variáveis, mas as parcelas da floresta madura retiveram três vezes mais carbono (202,8 ± 23,7 TonC/ha) do que aquelas nas bordas e fragmentos, enquanto que estes habitats afetados pelos efeitos de borda apresentam escores similares de carbono. Além disso, as espécies de árvores emergentes responderam pela maioria do carbono retido (59,13%) na floresta madura, tendo as espécies de sub-bosque uma importância pequena. Todavia, o carbono retido pelas espécies emergentes diminuiu pela metade nas bordas e fragmentos, uma vez que grandes troncos (> 70 cm DAP) e árvores muita altas (> 31 m de altura) foram raras nestes habitats. Finalmente, o mapeamento dos remanescentes de floresta Atlântica nordestina revelou a ocorrência de 213,19 km^2 de floresta madura/interior, o que representa apenas 8% da floresta remanescente com potencial de reter o máximo de carbono. Os 92% restantes devem reter apenas a metade do carbono retido na floresta madura, conforme dados obtidos em Serra Grande. Nossos resultados indicam que a fragmentação de habitats e o estabelecimento de bordas e pequenos fragmentos limitam a capacidade da floresta de armazenar carbono nas paisagens antrópicas, uma vez que a perda de carbono devido à redução na abundância de grandes árvores não é compensada pelas espécies de dossel e de sub-bosque.

Palavras-chave: serviços ecológicos, fragmentação de habitats, paisagens antrópicas, florestas tropicais.

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Introduction

Sixty percent of the world's total forest carbon in living biomass (298 billion tons of Carbon) is stored in tropical forests [1] but every year from 2000 to 2010 over 90.000 km² of this forest type was cleared, representing 70% of global forest loss [1]. This figure represents 1.5 billion tons of carbon emitted annually (2000 to 2010), although increments are not expected in the near future [2]. It is not a surprise that deforestation has been identified as a key driver of the current climate change [3], raising the need for research on the drivers of carbon cycling and cross-forest differences in terms of carbon storage. In this context, evergreen forests store much more living carbon per unit of area than seasonal ones, most of it stored in the aboveground biomass [4], but human disturbances are likely to alter forest potential for carbon storage in ways that are not completely understood yet [5].

In addition to deforestation, other human-related disturbances may disrupt the carbon-storage services provided by tropical forests, such as biomass collapse due to edge effects [6], when human disturbances convert intact forest landscapes into archipelagos of small fragments and regenerating forest patches [7, 8] embedded in harsh matrixes dominated by pastures, croplands, and urban areas [9]. In such human-modified landscapes, remaining forest cover consists preferentially of edge-affected habitats, which become progressively impoverished in terms of large-seeded [10], understorey and shade-tolerant [11], vertebrate-dispersed and vertebrate-pollinated species [12, 13], heavy-wooded [14], outbreeding species [12], supra-annual [15] and large-tree species [16].

Large-tree species (most of them emergent species) usually represent only about 10% of the total tropical tree species richness, but can have a disproportional influence on forest structure and ecosystem functioning [17, 18]. Emergent trees store a large portion of above-ground biomass, contributing decisively to other ecological services such as nutrient cycling [18], water catchment, soil erosion control [20], biodiversity retention [16, 21], and provision of forest products [22]. Unfortunately, emergent species are susceptible to wind turbulence and physiological stress in edge-affected habitats, which may result in increased mortality [23, 24] and reduced recruitment of large stems [16]. In addition, selective logging can also reduce populations of emergent tree species in fragmented landscapes [25]. Conversion of tropical forests into human-modified landscapes can thus reduce the abundance of large trees, profoundly affecting the ecological services provided by the tropical forest ecosystem. This is particularly true if canopy and understorey tree species prove unable to benefit from the loss of large tree populations to compensate for edge-related carbon loss.

Here we investigate spatial patterns of carbon distribution in an aging and highly fragmented Atlantic forest landscape in order to assess potential services provided by human-modified landscapes. We offer estimates of stored carbon in pristine (forest interior) and edge-affected habitats (edge forest and forest fragments), and in three tree functional groups relative to forest stratification: emergent, canopy and understorey tree species. We used carbon volume obtained at landscape level to address the current potential for carbon retention/storage exhibited by the Atlantic forest in northeast Brazil, a distinct biogeographic unit of the Atlantic Forest region [26]. Finally, we examine some mechanisms leading to the reduction of carbon storage in edge-affected habitats and potential consequences for ecological services provided by modified landscapes, which are the dominant scenario in many tropical regions.

Methods

Study area

Forest carbon distribution was examined at Usina Serra Grande— a 667-km^2 privately held sugarcane plantation in the state of Alagoas, northeastern Brazil (8º 30' S, 35º 50' W). Soils include yellow–red latosols and podzols. Annual rainfall is approximately 2000 mm, and the dry season (<60 mm rainfall/month) extends from November to February [27].The Serra Grande landscape still retains nearly 9000 ha of evergreen and semi-deciduous lowland forests (< 400 m a.s.l.), which are dominated by Fabaceae, Lauraceae, Sapotaceae, Euphorbiaceae, Chrysobalanaceae, and Lecythidaceae species. This landscape preserves over 100 forest fragments (range: 1.67–3500 ha in size), all of them completely surrounded by a monoculture of sugarcane. Sugarcane cultivation started in the early 18th century and was associated with the clearing of large tracts of old-growth forest for agricultural purposes. Remaining forest has been protected against fire and logging to guarantee the water supply for sugarcane irrigation [10], including the 3,500-ha Coimbra Forest—the best preserved private forest patch in northeast Brazil [27].

Tree assemblages and carbon estimates

To estimate above-ground biomass and carbon storage in forest habitats of the Serra Grande landscape, we used data on tree species assemblages and stem size distribution compiled from two previous studies carried out by our research team [10, 16]. Tree assemblages (DBH ≥10 cm) were surveyed in 59 0.1-ha plots (10 × 100 m) throughout three types of forest configurations as follows: (a) 10 forest-edge plots positioned randomly along the 39.9-km perimeter of the Coimbra Forest (a 3500-ha forest fragment), starting at the edge and penetrating perpendicularly 100 m into the forest; (b) 20 randomly located core-forest plots in Coimbra (forest interior); and (c) 29 0.1-ha plots in 29 small forest fragments (2.05-365 ha in size); one plot per fragment at the geometric center of each fragment. The distance between plots and the nearest forest edge was 0 m for edge plots, 200–1012.7 m for forest interior plots, and 60.4–502.7 m for plots in forest fragments. The average distance between all 59 plots exceeded 1000 m [15]. Previous studies with this data set have demonstrated that plot taxonomic composition is not correlated with soil type, but exhibits a small effect from vegetation type and a stronger effect from habitat type (i.e. forest interior, forest edge, forest fragments). Finally, a Mantel test carried out previously [16] failed to uncover any large-scale spatial effect on the taxonomic similarity of the 59 plots we examined here. All plant vouchers were deposited at the Federal University of Pernambuco (UFP) Herbarium, Brazil (Serra Grande vouchers No. 34,445– 36,120), and a detailed map of the Serra Grande plot setup has been provided elsewhere [10].

Data on stem distribution and woody density at genus/species level [28] were incorporated in four allometric equations for above ground biomass estimations as adopted elsewhere [29]. The final value of biomass was determined by the average of these four equations, and the stored above-ground carbon was estimated to be half of the calculated biomass as recommended by the Intergovernmental Panel of Climate Change [30]. We examined total above-ground carbon per forest habitat (forest interior, forest edges and fragments), and in three functional groups; i.e. emergent, canopy and understorey species according to group definitions adopted previously [10] and considering all stems with DBH ≥10 cm. Cross-habitat and cross-group differences in terms of retained carbon were examined via a Two-Way ANOVA followed by Tukey post-hoc tests.

Configuration of remaining forest habitat

To estimate the amount of forest interior habitat still persisting in the Atlantic forest of northeast Brazil (56,000 km^2 of original cover), we produced a digital map of remaining forest habitat through supervised classification of LANDSAT 7 images dated from 2001 to 2005, and we combined this map with a vegetation type map produced by IBGE [31]. Fragments smaller than 5 hectares were eliminated from a final forest cover map, based on which we examined the size distribution of forest fragments and the amount of interior habitat by applying a buffer of 300 m length oriented from the forest edge toward the central area of all fragments. These procedures were carried out in Arcgis 9.2. [32].

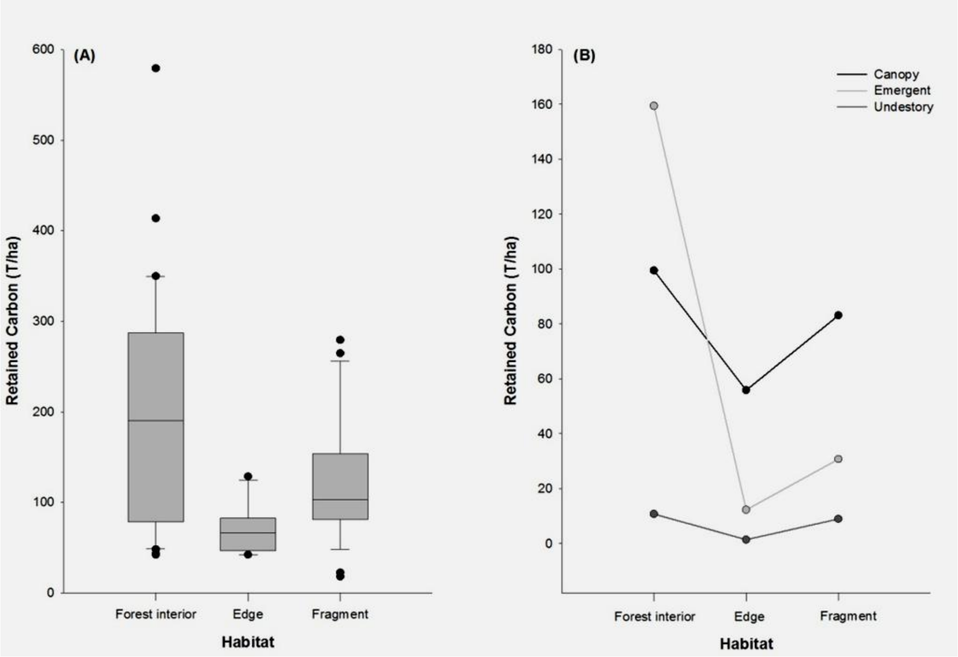
Results

In the three habitats 4,845 stems (DBH ≥ 10 cm) classified into 198 species were recorded; 820 were assigned as belonging to emergent species, 3612 as canopy, and 413 as understorey species. Stocks of carbon were highly variable within habitats of the Serra Grande landscape, with scores ranging from 42.1 TonC/ha (forest edge) up to 579.01 TonC/ha (forest interior). Despite such variation, forest interior plots retained almost three times more carbon (202.8 ± 23.7 TonC/ha, mean ± SE) than edge and fragment plots (Fig. 1a), while these edge-affected habitats exhibited similar scores (Table 1).

Table 1. Parameters of a Two-Way Anova fitted to retained carbon (TonC/ha) in three habitats (forest interior, forest edge, forest fragments) and three ecological groups of tree species at Serra Grande landscape, northeast Brazil (a total of 4,845 stems from 198 species).

Source of Variation	d.f.	SS	MS	F	P
Habitat	2	120535.7	60267.8	33.8	<0.001
Ecological group	2	147034.6	73517.3	41.2	<0.001
Interaction	4	130643.2	32660.8	18.3	<0.001
Residual	168	299256.7	1781.2		

Relative to tree ecological groups, emergent tree species accounted for the majority of the carbon retained by forest interior plots achieving, on average, 159.93 ± 9.4 TonC/ha per ha, with understorey species exhibiting a minor role regardless of habitat (Fig. 1b). However, carbon retained by emergent species decreased by one-half in edge-affected habitats, as it dropped from 30.7 ± 7.8 TonC/ha (forest fragments) to 12.2 ± 13.2 TonC/ha in forest edge plots. Carbon retained by canopy species exhibited a slight decrease, particularly in forest edge plots, while carbon stocks from understorey species remained unaltered in all habitats. In sum, 59.1% of total above-ground carbon present in forest interior plots was stored by the emergent tree species, but this group accounted for 25.02% and 17.63% in forest fragments and forest edges respectively (Fig. 2). Stem distribution of emergent tree species in the habitats of the Serra Grande landscape was marked by the rarity of large stems (> 70 cm DBH) and very tall trees (> 31 m height) in edge-affected habitats (Appendix 1); note that forest edges lacked any stem bigger than 26 m, but small stems and short trees remained present in all habitats.



Fg. 1. Average retained carbon in (A) core areas of forest interior (n = 20), forest edges (n = 10), and forest fragments (n = 29); and in (B) forest habitats and within tree ecological groups at Serra Grande landscape, Brazil (a total of 4,845 stems from 198 species).

Finally, we identified 6,170 forest fragments bigger than 5 hectares in the Atlantic forest of northeast Brazil (via a digital map), which added up to 2,696.68 km^2 of remaining forest habitat. However, only 374 forest fragments (6.06%) exhibited interior areas farther than the 300 meters from forest edges, which resulted in 213.19 km^2 of forest interior habitat— 0.38% of the original area once covered by this biota (56,000 km^2). Thus, only 8% of total remaining forest habitat has a full potential for carbon storage (i.e. 202.8 ± 23.7 TonC/ha as documented in forest interior plots), with the other 92% (edge-affected habitats) storing only half of that, as indicated by the scores obtained from forest edges and forest fragments in the Serra Grande landscape.

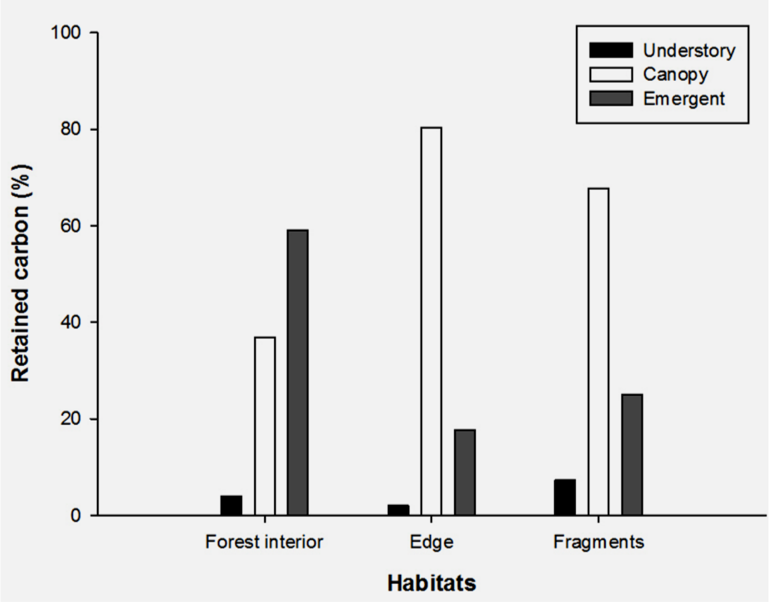


Fig. 2. Percentage of retained carbon in three habitats of the Serra Grande landscape: core areas of forest interior (n = 20), forest edges (n = 10), and small forest fragments (n = 29) at Serra Grande landscape, Brazil. A total of 4,845 stems from 198 tree species.

Discussion

Our results suggest that aboveground biomass/carbon storage in hyper-fragmented landscapes may be highly variable in forest habitats. However, habitat fragmentation and the consequent establishment of permanent forest edges reduce forest capacity for carbon retention, because forest edges and fragments (edge-affected habitats) retain only one-third as much carbon as forest interior habitat. Moreover, carbon retention is largely dependent on the emergent tree species, but the relative abundance of this ecological group decreases toward forest edges. Finally, our results suggest that carbon reduction in edge-affected habitats results (partially) from a reduced abundance of large trees (particularly very tall trees) as well as from lack of carbon compensation by remaining canopy and understorey tree species. As forest interior and forest edge plots were immersed in the same large Atlantic forest fragments (the Coimbra forest), baseline variables affecting forest biomass and species composition (e.g., soil, climate, plot spatial location) can not explain the patterns that emerged despite our relatively reduced sample effort. In fact, baseline variables have not been able to explain any cross-habitat variation on the structure of tree assemblages in the Serra Grande landscape [see 10, 12, 15, 16].

Patterns of carbon and biomass retention and distribution in human-modified landscapes still deserve documentation, although shifts of aboveground biomass and forest structure in response to habitat fragmentation have already been examined [6, 33, 44]. Biomass of forest edges in the Amazonian forest was reduced by one third in just 10-17 years after habitat fragmentation [6]. Such reduction, with tangible effects on carbon retention, has been primarily associated with increased mortality of large trees up to 300 m from forest edges [23, 33]. Here we offer evidence for a biomass reduction that is not restricted to the proximity of forest edges, but also occurs in forest stands in the central area of forest fragments located up to 500 m from forest edges. We also offer a comparative picture of the role played by tree ecological groups in terms of carbon storage and response to habitat fragmentation (i.e. creation of artificial forest edges), a picture that confirms the irreplaceability of emergent species [see also 18, 19, 33]. Such findings reinforce the notion that the reduction of the above-ground biomass represents a spatially pervasive and persistent, rather than ephemeral, edge-related effect, since tree assemblages in aging fragments and forest edges of the Serra Grande landscape are likely to have achieved near-equilibrium conditions, i.e. self-perpetuating pioneer populations [10].

In tropical forests, the large tree stand is expected to collapse in the aftermath of habitat fragmentation, because large trees may experience increased mortality due to physiological stress [23, 33] and uprooting along forest edges [24]. Although emergent tree species persist in the aging edge-affected habitats of Serra Grande as either small/middle-sized or short stems (see Fig. 3), recruitment of large trees is limited, as remaining stems exhibit depressed height/diameter ratio in this landscape [16], suggesting acclimation to chronic wind stress that inhibits the recruitment of large trees. Additionally, droughts [34], delayed mortality induced by surface fires [35, 36], and logging can depress large tree populations (extinction filters) in intensively human exploited landscapes [37], but this is not the case in the Serra Grande landscape, where such disturbances have been controlled [16].

In this study we documented again the relative rarity of large trees in the aging edge-affected habitats of Serra Grande, which, in part, explains the biomass reduction and reduced scores of retained carbon in this type of habitat. However, we also reveal that carbon and biomass loss associated with the reduced abundance of large trees is not compensated by canopy or understorey species, which is surprising considering that in the absence of large trees extra resources (e.g. light, water, soil nutrients) become available for remaining ecological groups. In fact, increased mortality and reduced recruitment of large trees parallel or facilitate proliferation of pioneers [38] with their low scores of wood density and per capita retained carbon relative to old-growth flora [39]. Pioneers can account for over 80% of tree species and stems (DBH ≥ 10 cm) in edge-affected habitats of hyper-fragmented Atlantic forest landscapes, including Serra Grande [27]. Such replacement of hard (many emergent species) by softwood stems, already documented in the Amazonian forest [14, 40, 41], represents not just an additional force leading to biomass reduction and carbon loss, but a key mechanism that limits the forest ability to recover its biomass in the absence of original large tree stands in edge-affected habitats.

Implications for conservation

Finally, we must call attention to the potential collapse of Atlantic forest ability to store carbon due to the current configuration of the remaining forest, which is largely dominated by edge-affected habitats (8% of forest interior) in addition to massive habitat loss at regional scale (13.4% of original forest cover). Such a scenario of reduced retained carbon and above-ground biomass is expected to persist, while edge-affected habitats dominate human-modified landscapes of the Atlantic forest [39]. Probably it is becoming worse as this biota is currently experiencing a regional-scale homogenization due to the proliferation of pioneer trees [42]: since 1980 many short-lived pioneers have already tripled their abundance. Assuming that human-modified landscapes (most hyper fragmented) may represent the future of most tropical forests [43], further studies should verify patterns and mechanisms examined here for the sake of tropical forest ecological services. Unfortunately, the evidence accumulated so far suggests a permanent collapse of large tree stands along with proliferation of pioneer species in edge-affected habitats (forest edges but small fragments as well), greatly reducing the potential of human-modified landscapes for ecological services.

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Appendix 1. Average percentage (± SD) of stems (≥ 10 cm in DBH) from emergent tree species within classes of DBH, and height in 59 0.1-ha plots in core areas of forest interior (n = 20), forest edges (n = 10), and forest fragments (n = 29) at Serra Grande landscape, Brazil. A total of 820 stems.