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Original Paper

Non-negligible role of dead organic matter in a rainforest remnant in Northeast Brazil

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Abstract
Dead organic matter represents an essential reservoir of carbon, especially that allocated in standing dead trees, coarse woody debris, and fine litter, playing a pivotal role in nutrient cycling and habitat provisioning. However, necromass is frequently disregarded in forest assessments. Here, we aimed to perform the first assessment of multiple necromass compartments in the Atlantic Forest of Northeast Brazil, providing a basis for future integrative studies related to necromass in this region. We registered 17 standing dead trees in 0.5 hectare and 239 logs of coarse woody debris. Necromass had 3.9 $Mg.ha^{-1}$ of standing dead trees, 54.24 $Mg.ha^{-1}$ of coarse woody debris and 7.2 $Mg.ha^{-1}$ of litter. We indicate that standing dead trees and coarse debris were mostly in the intermediate and final stages of decomposition. Leaves were the dominant component of litter, and drier months had more litterfall. Finally, we highlight that assessing standing dead trees and coarse woody debris adds 25.6% on top of aboveground tree mass, improving information about organic matter storage in rainforest ecosystems. Our findings emphasize that the necromass compartment must be considered in forest assessments, also including small pieces of coarse woody debris, which could inform better practices of forest management.
Key words: decay stage, DOM, line-intercept method, litter, urban forest.

Resumo
A matéria orgânica morta representa uma reserva essencial de carbono, especialmente aquela alocada na necromassa arbórea (árvores mortas em pé, serapilheira grossa e serapilheira fina), desempenhando um papel fundamental na ciclagem de nutrientes e na provisão de habitat. Entretanto, a necromassa é frequentemente desconsiderada em inventários florestais. Aqui, objetivamos realizar o primeiro levantamento de vários componentes da necromassa na Floresta Atlântica do Nordeste do Brasil, fornecendo uma base para futuros estudos integrativos relacionados à necromassa nessa região. Registramos 17 árvores mortas em pé em 0,5 hectare e 239 tocos de serapilheira grossa. As estimativas de necromassa foram 3,9 $Mg.ha^{-1}$ para árvores mortas em pé, 54,24 $Mg.ha^{-1}$ para serapilheira grossa e 7,2 $Mg.ha^{-1}$ para serapilheira fina. Indicamos que a maior parte das árvores mortas em pé e serapilheira grossa estavam em estágios intermediários e finais de decomposição. A fração folhas foi o componente dominante da serapilheira fina e meses secos tiveram maior queda deste componente. Finalmente, destacamos que inventariar árvores mortas em pé e serapilheira grossa representa um incremento de 25,6% na biomassa arbórea acima do solo, aprimorando as informações sobre estoques de matéria orgânica em florestas úmidas. Destacamos que o compartimento de necromassa deve ser considerado em inventários florestais, também incluindo pedaços pequenos de serapilheira grossa, o que pode informar melhores práticas de manejo florestal.
Palavras-chave: estágio de decomposição, MOM, linha interceptadora, serapilheira, floresta urbana.

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Introduction

Dead organic matter (DOM) derived from trees in natural or anthropic ecosystems is stored in different compartments (*e.g.*, standing or fallen dead trees, dead trunks, and branches, woody bark, and litter (Keller *et al.* 2004; Barbosa *et al.* 2009; Palace *et al.* 2012). These dead plant components represent a remarkable contribution to long-term ecosystem functioning and balance, especially in forest ecosystems (Sanchez *et al.* 2009; Gove *et al.* 2012; Bassett *et al.* 2015). In such systems, forest necromass helps to ensure energy and habitat for a wide range of living organisms, acting as an essential nutrient pool on the forest floor (Barbosa *et al.* 2017). Also, it stores impressive amounts of carbon in tropical forests (Palace *et al.* 2008; Sefidi & Mohadjer 2010), with further benefits for water absorption and storage (Zaninovich *et al.* 2016).

Forest plant necromass is commonly divided into two groups: fine litter/ litter (elements with diameter < 2 cm) and coarse litter (diameter > 2 cm). The coarse litter includes two important compartments, standing dead trees (SDT) and coarse woody debris (CWD) (Barbosa *et al.* 2009; Palace *et al.* 2012). The fine litter is composed of plant debris accumulated on the forest floor, corresponding to ~20% of the total aboveground necromass (Palace *et al.* 2007). Fine litter composition (hereafter, litter) consists of leaves, flowers, fruits, seeds, barks, and thin branches, as well as miscellaneous, non-identifiable material (Schessl *et al.* 2008; Espig *et al.* 2009).

In mature forests, total necromass (fine and coarse litter) contributes between 5 to 25% of total plant stock and can range from 5–40% (Brown 1997), 10–20% (Houghton *et al.* 2001), or 20–40% (Palace *et al.* 2012) of aboveground carbon. The forest necromass component has been frequently studied to understand its role in ecosystem functioning, such as rates of accumulation and decomposition involved in nutrient cycling and respiration. Furthermore, applied questions are also assessed, such as its role on forest management and conservation, carbon storage in restored areas (Longhi *et al.* 2011), and its changes along forest successional stages (Delaney *et al.* 1998; Chambers *et al.* 2000; Scheer 2008; Vendrami *et al.* 2012).

Previous studies in Brazil did not take into account all necromass compartments and were performed predominantly in the Amazon rainforest (Chambers *et al.* 2000; Keller *et al.* 2004; Rice *et al.* 2004; Palace *et al.* 2007; Baker *et al.* 2007; Palace *et al.* 2008; Chao *et al.* 2009; Cruz Filho & Silva 2009; Silva *et al.* 2016). In some regions of the Atlantic Forest, on the contrary, the study of necromass is in its early stages. Particularly concerning the coarse compartments of necromass (CWD and SDT), there are even fewer studies in the Atlantic forest, with more information in the southern regions of Brazil (Vieira *et al.* 2011; Ribeiro *et al.* 2012; Sanquetta *et al.* 2014; Deus *et al.* 2018; Fonsêca *et al.* 2019; Moreira *et al.* 2019b; Villanova *et al.* 2019).

The complete characterization of necromass compartments in forest inventories is critical to understand ecosystem dynamics and health, because it allows a better comprehension of ecosystem services provided by forest remnants, and contributes to forest planning, conservation, and management (Stinson *et al.* 2011; Fonsêca *et al.* 2019). Considering that few studies accurately assess necromass compartments, our question was related to how much necromass is stored in coarse and fine compartments. All forest compartments are dynamic, but the values reach certain stability in mature systems. Data collected in a single moment represents this dynamic stability, which happens in various paces, from swift to seasonal or supra-annual rates. In this study, we performed a thorough inventory of plant dead organic matter (DOM) comprehensively including its two major components: coarse litter (fallen trees and standing dead trees) and aboveground fine litter, in a fragment of Atlantic Forest in the Northeast of Brazil. Since litter is the component with the fastest dynamics, we evaluated litter stock and seasonal production. Thus, we portrayed not only the relationship between compartments but also the intense dynamics necessary to maintain them, as exemplified by the litter.

Material and Methods

Study site

The study was conducted in a remnant of Atlantic rainforest located in the Dois Irmãos State Park (PEDI). The PEDI is a protected area in the state of Pernambuco, Northeast Brazil, comprising 1,157.72 ha and divided into two parts, with very distinct characteristics: mature forest (MF) with 384.7 ha (7°57'S; 34°56'W) and Regenerating forest (RF) with 773.02 ha (Fig. 1). The necromass inventory was conducted in the mature forest, which hosts the most conserved forest patch.

The climate is classified as As' according to Köppen classification, which represents a warm and humid climate, with an average annual precipitation of 2,417 mm. Rainfall is concentrated in autumn-winter, while monthly mean temperatures are always higher than 23 ºC (data available in the repository of the National Institute of Meteorology: <www.inmet.gov.br>). According to the Brazilian Soil Database, in the region where PEDI is located, ferralsols, acrisols, and arenosols are the predominant soil types. Soil acidity varies from medium to high, which is as expected for regions with high rainfall (Caldas 2007). The vegetation is composed of typical botanical families found in the Atlantic Forest, including Moraceae, Fabaceae and Melastomataceae, comprising 265 species of plants with average density of stems as 1025.75 $ind.ha^{-1}$ (PPBio Program/ Atlantic Forest Network/ PEDI site in the study area - Cunha *et al*. 2021). Diameter at the breast height varies from 5 to 114 cm (mean = 15.65 ± standard deviation = 13.82), and the height of living trees varies from 2 to 27 m (10.73 ± 5.87) (Fonsêca *et al.* 2020). Furthermore, the average tree biomass is 255.67 $Mg.ha^{-1}$, with average wood density registered of 0.6413 $g.cm^3$ (Fonsêca *et al.* 2020).

Standing Dead Trees (SDT)

To assess the standing dead tree compartment (also known as 'snags'), we used 50 plots (10 m × 10 m), which were 10 m apart from each other. We considered SDT as (i) dead individuals without leaves, (ii) with dead tissue under the bark (Veiga 2010), and (iii) DBH (diameter at breast height) ≥ 5 cm. We recorded DBH for each dead tree and additionally the diameter at soil level and height. Additionally, we classified all SDT according to their decomposition stage, using a tactile-visual categorization, following the PPBio protocol for necromass assessment (Barbosa *et al.* 2009) (Tab. 1). Decomposition stage is essential to estimate tree density since we did not use stem specific density as a parameter.

We classified SDT in four classes of diameter, based on DBH: class A (5 to 9.9 cm), class B (10 to

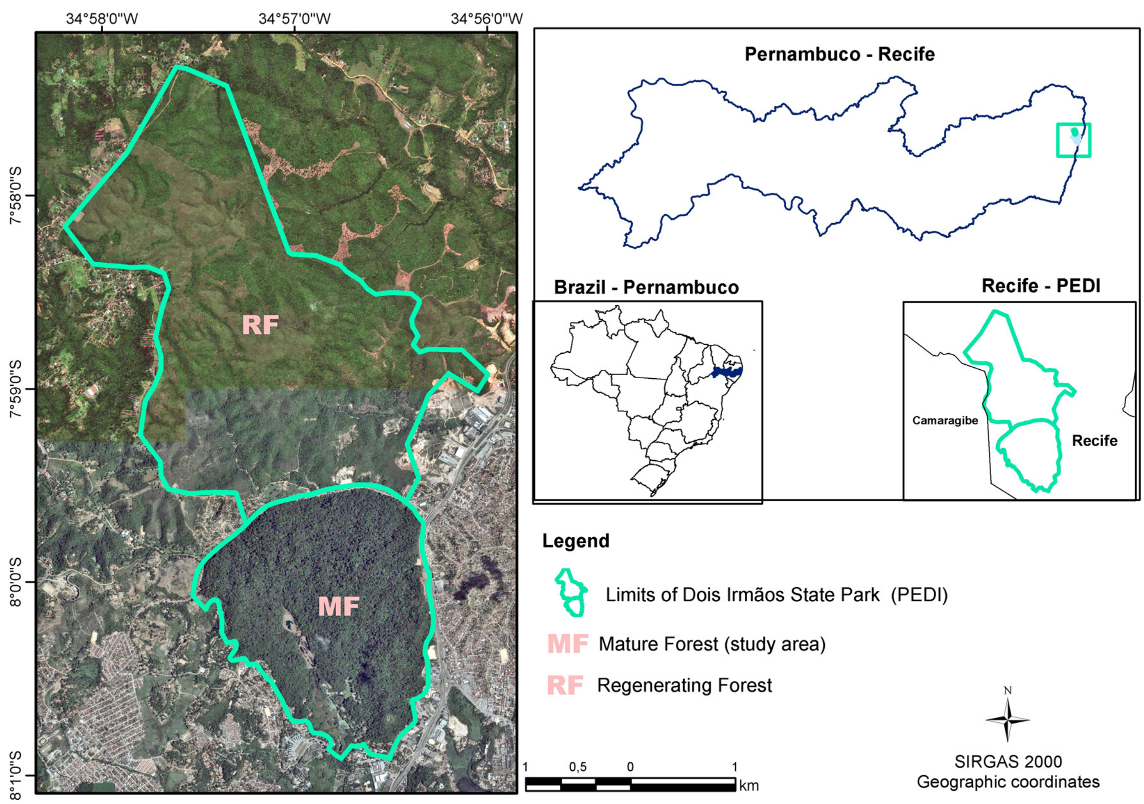

Figure 1 – Representation of the study site, Dois Irmãos State Park, Northeast, Brazil. This study was carried out in the MF area, representing a mature and well-conserved forest surrounded by a peri-urban matrix.

Table 1 – Decomposition stages used to classify standing dead trees (SDT) (based on Barbosa *et al.* 2009) and stages of coarse woody debris (CWD) (based on Harmon *et al.* 1995).

Decomposition stage	Description of decomposition stage categories
Standing dead trees (SDT)	
Stage 1	Trees recently dead with no sign of insect or fungal damage, showing no apparent decomposition (< 10% mass loss)
Stage 2	Trees with minor signs of insect and fungal damage, usually with small hollows but still showing high mechanical resistance to touch (10-30% mass loss)
Stage 3	Trees on advanced decomposition stage, with few signs of rotting and that often crumbled at touch (> 30% mass loss).
Coarse woody debris (CWD)	
Stage 1	Logs with the most extensive bark cover, showing remaining leaves and twigs, and least decayed
Stage 2	Solid wood with intact bark (recently started to fall) but no leaves or branches
Stage 3	Logs with no bark, but the heartwood (inner part of the CWD) was relatively undecayed
Stage 4	Logs with no branches or bark cover, already rotten and fragile wood that can be broken if kicked
Stage 5	Rotten, fragile wood that could be disintegrated or easily break if clamped by hand

29.9 cm), class C (30 to 49.9 cm), and class D (≥ 50 cm). These classes were adopted to categorize SDT information of density (ind.ha^{-1}), necromass (Mg.ha^{-1}) and basal area (m².ha^{-1}). Then, we calculated volume by using the method indicated by Harmon & Sexton (1996) and adapted for this study, using the following equation:

$$\boldsymbol{V} = \frac{H\ (A_b + 4A_m + A_s)}{6} \qquad (1)$$

where V = estimated volume (m³.ha^{-1}), H = height, A_b = basal area (using diameter at soil level), A_m = mean area (calculated using DBH), A_s = upper area (using the taper function indicated by Chambers *et al.* (2000) to determine D_h, the upper diameter).

Coarse woody debris (CWD)

We adopted the Line Intersect Sampling (LIS) method (Warren & Olsen 1964; van Wagner 1968) to sample logs on the forest floor. The LIS method comprises lines on the forest floor to sample logs that were intercepted by the line in its central axis (Deus *et al.* 2018; Fonsêca *et al.* 2019). In this study, we installed ten straight lines of 100 m, 20 m apart from each other, systematically positioned on the left side of the plots used to assess SDT, comprising 1 km of assessed length.

Log diameters were recorded at the point intersected by the line, considering pieces with ≥ 2 cm diameter, measured with a tape. In samples damaged by decomposition, we registered two perpendicular measures to avoid bias in the measure (Barbosa *et al.* 2009). We used diameters to calculate the estimated volume (V_{Est}) of coarse woody debris in the field, following van Wagner's equation:

$$\boldsymbol{V_{Est}} = \frac{\pi^2 \times d^2}{8 \times L} \qquad (2)$$

where V_{Est} = estimated volume (m³.ha^{-1}), d = diameter of each piece included in the sampling line, L = length of the sampling line (100 m).

We adopted diameter classes indicated by Keller *et al.* (2004) to adjust the solid volume obtained for each of the pieces of wood assessed. Thus, we considered (i) small pieces (S) = between 2 and 4.9 cm, (ii) intermediate pieces (I) = between 5 and 9.9 cm, (iii) and large pieces (L) = diameter ≥ 10 cm. We adopted the same rationale used to classify decomposition stage of SDT, but with small adjustments. A tactile-visual categorization was performed regarding the decomposition stage (Tab. 1) of all pieces measured in the transects, following the recommendations of Harmon *et al.* (1995).

Necromass estimation for SDT and CWD

The necromass for both SDT and CWD was obtained based on the volume of each piece of wood and tree measured in the field, and the basic density ($g.cm^3$) indicated by Veiga (2010), by diameter category and degree of decomposition of the pieces (Tab. S1, available on supplementary material <https://doi.org/10.6084/m9.figshare.19379882.v1>). We choose the values reported by Veiga (2010) because they were standardized in the same decomposition class that we adopted here. Moreover, Veiga (2010) reported wood density values from the Atlantic Forest that can also be considered in our study site (in the lack of an adequate assessment of wood density). The necromass of wood and tree pieces was obtained by multiplying the volume of each category by its basic density ($g.cm^3$) (3):

$$\boldsymbol{Necr} = V_{Est} * D_b \qquad (3)$$

where Necr = necromass ($Mg.ha^{-1}$), V_{Est} = estimated volume ($m^3.ha^{-1}$); D_b = basic density ($g.cm^3$).

Production and storage of fine litter (Lt)

The fine litter was assessed from August 2012 to July 2014, comprising two years of monthly sampling. We placed squared litter traps with 0.25 m² (0.5 × 0.5 m), ~1 mm mesh size, in 1.0 m above the forest floor (Schessl *et al.* 2008). Litter traps were randomly placed within a subset of 10 plots from the 50 plots used to assess SDT. We used plastic bags to collect Lt every month and later weighed them on a 0.1 g precision scale to obtain the wet weight. Then, we separated samples into four categories (leaves, branches < 2 cm in diameter, reproductive parts and unidentifiable parts - miscellaneous) and finally dried at 60 °C for 72 h to measure the dry weight, our primary Lt variable (Schessl *et al.* 2008).

The litter-layer was estimated at the end of the study period, from the random arrangement of 10 squares with the same dimensions as the litter traps (0.5 × 0.5 m), in the same plots used to access the production. In those squares, we collected all litter above forest soil (stopping the sampling when we reached the fine root mat, which was not considered (Sampaio *et al.* 1988). Then, we stored in plastic bags, oven-dried and weighed using the same methods for litter production. We highlight that, even though the standard protocol suggests a time-replicated sampling of the litter-layer, our study site is a forest with evergreen vegetation which do not presents extreme values of leaf fall across the year. Therefore, we argue that potential gains of information from litter-layer would be greater than a possible bias from a single-time sampling.

Data analysis

We estimated the values of SDT, CWD and Lt to hectares. To describe the compartments, we calculated the mean, standard deviation, and confidence intervals. Correlation analysis was also performed with the historical record of rainfall averages (30 years) from the climatological series provided by INMET from 1961–1990. We further applied analysis of variance (ANOVA), considering blocks (two years of records) and replicates (10 litter traps), using the Assistat software (Silva & Azevedo 2002). We considered years as blocks in the ANOVA test because there is little evidence to expect significant differences between one year and the other. By doing this, we could understand if the same months from different years presented divergent patterns of litterfall. In both analyses, data were normalized by a logarithmic transformation to base 10.

Results

Standing dead trees (SDT)

The standing dead trees (SDT) compartment presented 17 trees, with an estimated density of 34 $ind.ha^{-1}$. The estimated volume was 10.31 $m^3.ha^{-1}$, with a stored necromass of 3.9 $Mg.ha^{-1}$ (Fig. 2). The classification of SDT in three decomposition stages resulted in more individuals belonging to the intermediate stage of decomposition (stage 2 = 52.9%) than in initial and final stages (stages 1 = 11.7% and stage 3 = 35.2%). Regarding the diameters, we identified a predominance of individuals with intermediate diameters (class B = 52.9%,). Classes A and C presented the same proportion, with 17.6% of the individuals (Tab. 2). When the basal area values were analyzed, we found that despite classes C and D only adding up to 10 individuals, they had higher values than the other classes: 73.2% of the necromass and 72.5% of the total basal area.

Coarse woody debris (CWD)

Our study registered 239 pieces of trunks and fallen trees on the ground (CWD), which comprised a volume of 284.74 $m^3.ha^{-1}$ and a necromass of 54.24 $Mg.ha^{-1}$ (Fig. 2). Most logs were in intermediate to high decomposition stage, with 41.4% (n = 99) considered in DS4 and 28.4% in DS5 (n = 68). Other degrees of decomposition made up 30.13% of the log frequency.

However, when we considered not only the frequency but the necromass stored per each decomposition stage, we found that DS4 summed up to 50% (27 $Mg.ha^{-1}$) and DS3 28.48% (15.45 $Mg.ha^{-1}$) of total necromass. DS5, DS2 and DS1 had altogether 21.7% of the remaining necromass (Tab. 3). Regarding the adopted diameter classes, larger diameter CWD pieces (class G) predominated in the necromass stock, with 42 $Mg.ha^{-1}$ (79.5% of the fallen necromass, with 37 pieces). This value is higher than for M and P classes, which stored 15% and 8.1% of the necromass, respectively.

Fine litterfall and litter-layer

The monthly average of litterfall was 0.95 $Mg.ha^{-1}$ (Standard deviation ±0.33), with an annual fall of 11.36 $Mg.ha^{-1}.year^{-1}$ (SD ± 3.98). The wet mass of the fine litter was 1.55 $Mg.ha^{-1}.month^{-1}$ (SD ± 0.55) and 18.65 $Mg.ha^{-1}.year^{-1}$ (SD ± 6.56), with 37% of water loss after drying, which indicate a higher water accumulation in litter. Litterfall was mostly composed of leaves, which accounted for 58% (6.58 $Mg.ha^{-1}.year^{-1}$) of the total litterfall. Branches, reproductive parts and miscellaneous fractions accounted for 22.2% (2.52 $Mg.ha^{-1}.year^{-1}$), 13.7% (1.56 $Mg.ha^{-1}.year^{-1}$) and 6.2% (0.70 $Mg.ha^{-1}.year^{-1}$), respectively. Interestingly, the major fall of branches (0.4 $Mg.ha^{-1}$) occurred in July 2013, when the second-highest precipitation value (415.6 mm) was recorded. The total stock of fine litter on the forest soil summed 7.2 $Mg.ha^{-1}$ (SD ± 1.78) (Fig. 2), which is much lower than the annual fall of plant material.

Precipitation during the study period ranged from 8.2 mm (November 2012) to 481.5 mm (June 2013), with a monthly average of 183.5 mm (SD ± 128.4 mm), registering higher values between May and July and having an annual sum of 1,968 mm and 2,435 mm for the first and second year, respectively (average 2,201.5 mm). Data from the historical series ranged from 35.7 mm (November) to 388.1 mm (July), summing up to 2417.6 mm. The monthly temperature varied 4 °C during the study period, with a minimum of 23.8 °C (August/2012) and a maximum of 27.8 °C (February/2013).

The correlation between historical data of precipitation and present monthly litterfall revealed

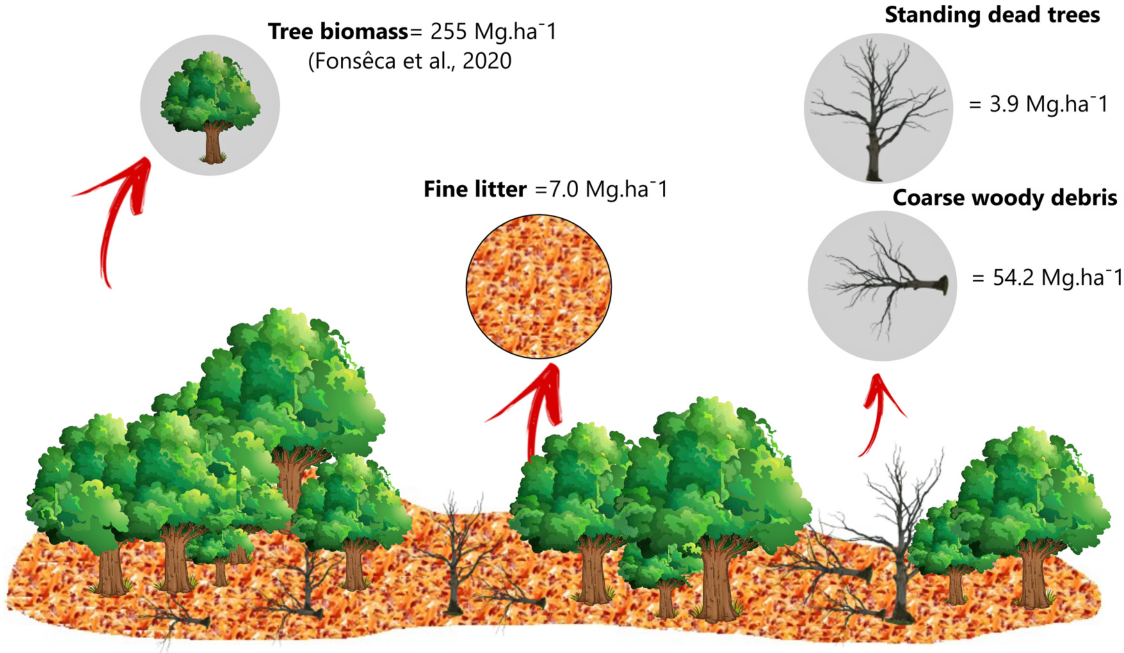

Figure 2 – Distribution of necromass components, sampled in a forest of the Dois Irmãos State Park, Northeast, Brazil.

Table 2 – Distribution by diameter classes of standing dead tree density (ind.ha^{-1}), necromass (Mg.ha^{-1}) and basal area (m².ha^{-1}), with values between parenthesis indicating the range for each class at Dois Irmãos State Park, Pernambuco, Brazil.

	A (5–9.9 cm)	B (10–29.9 cm)	C (30–49.9 cm)	D (≥ 50 cm)	Total
Density (ind.ha^{-1})	6 (17.6%)	18 (52.9%)	6 (17.6%)	4 (11.8%)	34 (100%)
Necromass (Mg.ha^{-1})	0.04 (1.1%)	1.01 (25.7%)	1.52 (39%)	1.34 (34.2%)	3.9 (100%)
Basal area (m².ha^{-1})	0.02 (1.65%)	0.27 (25.83%)	0.30 (28.91%)	0.45 (43.61%)	1.03 (100%)

a significant negative relationship ($r = -0.68$, $p < 0.05$) (Fig. 3). We found a negative correlation between litterfall and mean current precipitation ($r = -0.78$, $p < 0.01$). Regarding temporal changes in litterfall during the study, as expected, there was a clear difference within each year (between months), with a sharp distinction between the low litterfall in wetter months (March, April and July) and high litterfall in drier months (October, December and January) (Fig. 3).

Discussion

We found that necromass is a crucial compartment in mass storage, comprising ~58 Mg.ha^{-1} of fallen and standing dead trees, plus ~7 Mg.ha^{-1} of fine litter accumulated on the forest floor (Fig. 2). Furthermore, as a temporary component, fine litter summed ~11 Mg.ha^{-1} per year. Our data suggest that necromass stocks add 25.6% on top of estimated aboveground tree biomass (previously measured for the same forest, Fonsêca *et al.* 2019). Necromass from late-stage succession forests are usually 5–25% aboveground biomass (FAO 2020), indicating that the study site still stores an impressive amount of necromass, even though such compartment is often neglected in forest ecosystem assessments.

Coarse woody debris represented the most significant part of necromass when standing dead trees and fine litter were compared. The pattern CWD > SDT > Lt is expected because coarse pieces of necromass are more frequent in the forest floor, usually have more volume and require more time to decompose due to woody compounds, such as lignin (Gessner *et al.* 2010). The literature indicates large values with a high variation of CWD in the Amazon rainforest, ranging from 31 to 62.3 Mg.ha^{-1} (Palace *et al.* 2012; Keller *et al.* 2004; Nascimento & Laurance 2002; Rice *et al.* 2004). The few studies available in the Atlantic Forest were performed in very contrasting ecosystems, such as seasonal semi-deciduous forests, *Araucaria angustifolia*-dominated forests, and lowland rainforests. Their reports were lower than the Amazon and ranged from ~4 to 30 Mg.ha^{-1} for CWD (Deus *et al.* 2018; Moreira *et al.* 2019a; Villanova *et al.* 2019; Fonsêca *et al.* 2019; Maas *et al.* 2020), which indicates an extensive variation even within Atlantic Forest systems. Accordingly, standing dead trees (SDT) follow the same pattern, but with less variation reported in the Amazon (from 4 to 10 Mg.ha^{-1}; Nascimento & Laurance 2006; Baker *et al.* 2007; Chao *et al.* 2008a) and with a remarkable divergence in the Atlantic Forest (0.6 Mg.ha^{-1} to 19.6 Mg.ha^{-1}; Veiga 2010; Luccas 2011; Maas *et al.* 2020). Our sampling indicated a significant amount of necromass stored in CWD (54.24 Mg.ha^{-1}), which is even higher than previous estimates (the first in the North of Atlantic Forest) on the same study site using different methods (fixed-plots, Fonsêca *et al.* 2019).

In contrast to the CWD pool, SDT stored ~4 Mg.ha^{-1}, but most necromass was stored in few snags with high diameter, even though most dead trees had intermediate diameter. When putting our data in an integrated perspective, impressive high values of CWD and low values of SDT could suggest that dead trees do not remain standing, which increases CWD component. In the same forest, Fonsêca *et al.* (2020) found 37 recently fallen trees along 4 km of line intercepts, which might indicate that the forest floor is a major repository of dead trees and would explain the reason why SDT component had so few individuals and necromass. Moreover, standing dead trees are usually a result of physiological stress, such as light competition (Chao *et al.* 2008b). However, broken or uprooted dead trees are more likely an outcome of mortality events derived from the surrounding environment (Esquivel-Muelbert *et al.* 2020), such as windstorms and edge-effects (Magnago *et al.* 2015). Such predictions are in accordance with the fact that our study site is a small peri-urban forest, often under multiple disturbances derived from

Table 3 – Coarse woody debris (CWD) abundance and necromass per decomposition stage (DS), with percentage values between parenthesis, at the Dois Irmãos State Park, Pernambuco, Brazil.

	DS1	DS2	DS3	DS4	DS5	Total
Log abundance	1 (0.4%)	11 (4.6)	60 (25.1%)	99 (41.4%)	68 (28.45)	**239 (100%)**
Necromass ($Mg.ha^{-1}$)	0.02 (0.05%)	3.08 (5.7%)	15.45 (28.48%)	27.0 (49.8%)	8.69 (16.0%)	**100%**

external factors (*i.e.*, wind and edge-effects). Future investigations can elucidate whether mortality type (standing dead, uprooted, or broken trees) respond to wind, temperature, and light competition.

The decomposition stage of coarse necromass is a crucial parameter to characterize dead organic matter but also provides insights about ecosystem functioning because decomposition is the main process related to nutrient cycling in forest ecosystems. Coarse woody debris was often in intermediate to advanced stages of decomposition (Fonsêca *et al.* 2019; Moreira *et al.* 2019a), likely because of more time in contact with the forest floor, which contains most microbial activity (Gora & Lucas 2019). In contrast, late-decomposition CWD stores less carbon (Harmon *et al.* 2013) and is likely not as effective as live biomass to remove carbon from the atmosphere. Even though larger pieces of necromass are harder to decompose due to higher area to volume ratio (Harmon *et al.* 2020), we found that most CWD registered were in advanced stages of decomposition and had larger pieces of deadwood, storing more necromass (and potentially more carbon). The higher abundance of late-stage decomposition pieces of CWD is likely a function of accumulation through time. Such discrepancy was not found in the SDT compartment. Standing dead trees were in earlier stages of decomposition and mostly in intermediate sizes. This pattern likely exists because of two factors. First, decomposition is slower when the organic matter is far from the soil (Gora & Lucas 2019), due to reduced moisture which decreases microorganism activity (Gessner *et al.* 2010). Second, SDT in advanced stages of decomposition are highly susceptible to fall on the forest floor in episodes of forest disturbance (Anderegg *et al.* 2016), transferring more necromass to the CWD compartment.

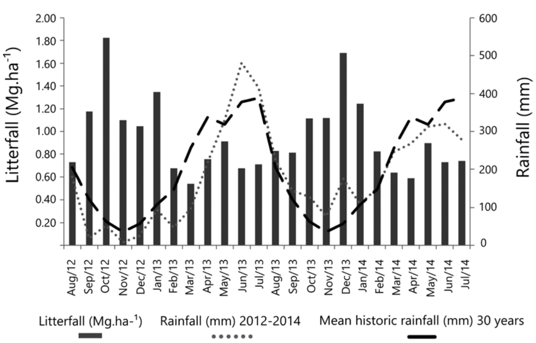

Figure 3 – Values of fine litterfall ($Mg.ha^{-1}$) per each month studied, compared with historical and current precipitation (mm). The data were collected from August 2012 to July 2014, in the Dois Irmãos State Park, Northeast, Brazil.

The fine litter compartment embodied 11% of all necromass, with a litterfall of 11.36 $Mg.ha^{-1}$ per year and a stock of 7.2 $Mg.ha^{-1}$. Values of fine litter production that we reported in this study follow previous reports from forests located in similar areas of Atlantic Forest (10.07–14.74 $Mg.ha^{-1}$; Espig *et al.* (2009); Schessl *et al.* (2008)). As expected, most parts of litter were leaves (58%), which is similarly reported by several studies (Espig *et al.* 2009; Schessl *et al.* 2008; Longhi *et al.* 2011), with proportions varying from 48.5–74.7%. In contrast, litter stock seems to be lower than other sites. Maas *et al.* (2020) performed two samples of litter stock and indicated that such compartment represented 33% of all necromass in an Araucaria-dominated forest in the South of Brazil, while our values of litter stock represented 10% of total necromass. Sampaio *et al.* (1993) registered 13 $Mg.ha^{-1}$ of litter stock for the same forest studied here more than 30 years ago. However, we draw attention to caveats of comparing litter stocks due to non-standardized sampling. Still, Litter-layer stock values in our system must be interpreted carefully because this compartment typically needs seasonal sampling due to litterfall seasonality and correlation to abiotic conditions (Schessl *et al.* 2008). We emphasize that our study was performed in a region where the vegetation is evergreen and not seasonally deciduous, as shown by Lima *et al.*

(2008). When compared to other Atlantic rainforest sites, whether this recorded low value is explained by a geographic pattern (response to climate) or is a consequence of the forest conservation status (size, age, disturbances) is still a question to be answered when more data are gathered. Furthermore, our aim was not to follow litter stocks through time but to account for as many necromass compartments as possible.

Our results from different compartments allow us to discuss the implications of coarse and fine necromass to the functioning of our study site. First, coarse necromass has a non-negligible role in carbon storage. Due to the correlation between biomass/necromass and carbon storage in tropical rain forests, we inferred that ~45% of the total stored mass is carbon (Veiga 2010; Moreira *et al.* 2019b). Thus, CWD and SDT are estimated to store 26 MgC.ha^{-1}, which is equivalent to ~20% of the total carbon stored in aboveground tree biomass for our study site (Fonsêca *et al.* 2019) and represents an important ecosystem service of regulation. This potential role of carbon storage is very relevant, especially to larger CWD pieces. Second, the litterfall deposition increased over time and is likely returning more nutrients to the forest floor. We found a massive increase in litterfall from the 1980s (Sampaio *et al.* 1988) to present values, with 3 Mg.ha^{-1}.year^{-1} more litter at the present time. Considering the high decomposition rates (Sena *et al.* 2018) coupled with more litter falling aboveground, we could suggest that nutrients are cycling faster, and there is more primary production in the forest. That is especially true for leaves in the fine litter compartment. Strong evidence suggests that leaves decompose seven times faster than other fractions, adding inputs of particularly Fe, Mn, and N (Caldeira *et al.* 2008; Vital *et al.* 2004; Barbosa *et al.* 2017) that are absorbed by thin and superficial roots (Sampaio *et al.* 1988).

Information derived from coarse and fine compartments of necromass can be fundamental to forest management and monitoring, providing insights about ecosystem dynamics and stocks. For example, forest management initiatives should keep larger pieces of CWD in the forest because they store more carbon (Nascimento & Laurance 2002). However, our results indicate that if necromass with less than 10 cm is not considered, managers should be careful that necromass estimations can still be potentially 20% lower. We suggest that CWD from all sizes and decomposition stages should be considered in the line intercept method, mainly because this method is not as costly and time-consuming as the fixed-plots approach (Fonsêca *et al.* 2019). However, our results indicate that the SDT compartment stored a small portion of necromass compared to CWD. Therefore, we strongly suggest that forest inventories should prioritize CWD component over SDT when time and financial resources are limited.

After depicting necromass compartments, we found that long-term and transient compartments were differently distributed in the forest, with distinct characteristics. We firstly registered a high amount of necromass storage for the Northeast Atlantic forest, with higher values than other areas in the same ecosystem. Moreover, our results highlight that coarse woody debris were from intermediate to late-stage decomposition and were mostly composed of intermediate diameter, storing high amounts of necromass (and consequently carbon). Transient compartments, such as fine litterfall, are mostly comprised of leaves and present higher values in drier months. We indicate that necromass compartments must be included in forest inventories and ecological research, especially coarse woody debris compartment, which represented an impressive pool of necromass.

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