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After trees die: quantities and determinants of necromass across Amazonia

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Abstract

The Amazon basin, one of the most substantial biomass carbon pools on earth, is characterised by strong macroecological gradients in biomass, mortality rates, and wood density from the west to the east. These gradients could affect necromass stocks, but this has not yet been tested. This study aims to assess the stocks and determinants of necromass patterns across Amazonian forests. Field-based and literature data were used to find relationships between necromass and possible determinants. The final regression result was used to estimate and extrapolate the necromass stocks across *terra firma* Amazonian forests. In eight northwestern and three northeastern Amazonian permanent plots, volumes of coarse woody debris (≥10 cm diameter) were measured in the field and density of each decay class was estimated. Forest structure and historical mortality data were used to determine controlling factors of necromass. Necromass is greater in forests with low stem mortality rates (northeast) rather than forest with high stem mortality rates (northwest) (58.5 ± 10.6 and 27.3 ± 3.2 Mg ha^{-1}, respectively). After integrating all published necromass values, we find that necromass across *terra firma* forests in Amazonia is positively related to stand biomass, mortality mass input, and average wood density of live trees ($\rho_{BA\,j}$). We applied these relationships to estimate necromass for plots where necromass has not been measured. The estimates, together with other actual measurements of necromass, were scaled-up to project a total Amazonian necromass of 9.6 ± 1.0 Pg C. The ratio of necromass (on average weighted by forest region) to coarse aboveground biomass is 0.127. Overall, we find (1) a strong spatial trend in necromass in parallel with other macroecological gradients and (2) that necromass is a substantial component of the carbon pool in the Amazon.

1 Introduction

Coarse woody debris (CWD) is a crucial component of forest function, as it constitutes a substantial aboveground pool of carbon and nutrients (Harmon et al., 1986). Research has shown that CWD can account for 6 to 25% of total aboveground vegetative mass (biomass plus necromass) in the neotropics (Nascimento and Laurance, 2002; Delaney et al., 1998; Rice et al., 2004), but these studies are limited in their spatial extent. In Amazonia, the world's largest tropical forest which is responsible for ~50% of the biome's productivity and respiration, necromass reports have been biased to forests in eastern Amazonia, which are known to be atypical of Amazon forests in both structure and function (Malhi et al., 2006; Phillips et al., 2004). There are only two studies of CWD stocks (necromass) (Chao et al., 2008a; Baker et al., 2007) and one of CWD volume (Gale, 2000) from western forests, and there has been little pan-Amazon evaluation of necromass stocks (e.g., Saatchi et al., 2007). In the absence of direct measurements, necromass is often estimated as a fixed percentage of biomass (e.g. Houghton et al., 2001; Malhi et al., 2006; Saatchi et al., 2007), assuming that higher biomass forests should also accrue more necromass. However, the relationship between necromass and biomass has not yet been adequately demonstrated in Amazonia, nor have other potential determinants (e.g. mortality mass, decomposition rate) been properly considered. A comparison of CWD stocks in regions of contrasting biomass and dynamics in the Amazon would help reveal their determinants.

Factors that potentially can control necromass include forest type, structure, and successional stage (Harmon et al., 1986), but must ultimately be related to the balance of mortality inputs and decomposition outputs (forest dynamics) (Olson, 1963). Quantitative studies of mortality input in mass and CWD decay rates in the tropics are few (e.g. Chambers et al., 2000; Carey et al., 1994). However, some other strong macroecological gradients across Amazonia have been shown. There is a two-fold increase in tree mortality rates from east to west (Phillips et al., 2004), with smaller concomitant decreases in biomass and wood densities (Baker et al., 2004; Malhi et al., 2006). It may be expected that these differences are reflected in necromass, too.

The questions we asked in this study are: (1) is there a variation in quantities of necromass across Amazonia? (2) Can necromass be predicted from forest structural parameters (biomass) or dynamic parameters (mortality measures and decomposition estimates) of a stand? We hypothesised that forest dynamics, rather than forest structure, determine necromass stocks. First, we predicted ($P_{1.1}$) that there is no relationship between stocks of biomass and necromass, contrary to a basic assumption made in many carbon budget studies. Our second prediction ($P_{2.1}$) is that forests with high mass-mortality rates and slow decomposition rates have higher stocks of necromass. As decomposition rate is negatively correlated with wood density (Chambers et al., 2000), we also expected ($P_{2.2}$) that forest stands with higher wood density also have lower estimated decay rate, and thus higher necromass stocks.

We explore these ideas using our field measurements, published data, and a tree-by-tree census dataset (the RAINFOR project; Malhi et al., 2002; Peacock et al., 2007). Firstly, for the field data, volumes of CWD were measured using the plot-based method (Harmon and Sexton, 1996) for two regions of Amazonia, densities of CWD were estimated using equations developed by Chao et al. (2008a). Secondly we examined the relationships between necromass and forest structures and dynamics (i.e., mortality) using our field results and published data. Finally, the relationships were applied to predict CWD stocks for places where necromass has not been measured, assuming a steady state (Olson, 1963). A fully pan-Amazonian perspective on necromass was developed by combining existing measurements with those predicted values.

2 Methods

2.1 CWD stocks: data sources

There are three types of data: measured necromass based on our field work (hereafter termed as field-based), measured necromass based on literature (literature), and estimated necromass based on census data (estimated).

Field-based necromass measurements were conducted in two regions of mature *terra firma* Amazonian forests: one in the northwestern region (NW, eight ca. 1-ha plots), and the other in the northeastern region (NE, three 0.5-ha plots). NW Amazonia plots (ALP-A, ALP-B, SUC-01, SUC-02, SUC-04, SUC-05, YAN-01 and YAN-02) were located in northern Peru (Allpahuayo, 3°57′ S, 73°26′ W; Sucusari, 3°26′ S, 72°54′ W; Yanamono 3°26′ S, 72°51′ W) (Vásquez Martínez and Phillips, 2000; Vásquez Martínez, 1997). The NE Amazonian plots are located at El Dorado (ELD-01/02 and -03/04, 6°05–06′ N, 61°24′ W) and Rio Grande (RIO-01/02, 8°06′ N, 61°41′ W), Venezuela (Veillon, 1985). Since the establishment of these plots, living trees with a diameter ≥10 cm have been tagged, identified, and measured at approximately four to five year intervals (Malhi et al., 2002).

Literature necromass values were published results from across humid, lowland Amazonian forests. We used both the literature and our field-based necromass to explore pan-Amazonian patterns in forest structure and dynamic parameters to necromass.

Estimated necromass values were obtained for plots in the RAINFOR database (Peacock et al., 2007) where stocks of necromass have not been measured. The RAINFOR plots are restricted to those located in *terra firma* Amazonian forests, which have been recently recensused (between 2000 and 2006) (Appendix A). The estimating method was based on the regression relationships (between forest structure and dynamic parameters to necromass) found in this study. The estimated necromass values, together with measured CWD values (field-based and literature), were used to extrapolate necromass stocks across Amazonia in the discussion section.

2.2 CWD stocks: field-based measurement

CWD stock (necromass, $\mathrm{Mg\,ha^{-1}}$) for decay class d (d=1 to 3) is the product of volume (v) and density (ρ_d), and then standardised by the size of the plot. In our field work, we measured volume and classified decay classes for all dead woody material, including trees, lianas, and palms, with a diameter ≥10 cm.

CWD volume within a plot was measured by the plot-based method (Harmon and Sexton, 1996) in 2004 for the NE plots and 2005 for the NW plots. Both CWD lying on the ground (fallen CWD) and standing and broken stumps (standing CWD) were included. Diameter 1 (D_1) and 2 (D_2) at each end of a CWD piece were measured to the nearest centimeter. For logs tapering to less than 10 cm diameter, diameters and lengths were taken up to that point. When wood was partially buried in litter and therefore hard to measure, diameters were taken at two perpendicular cross-sections, one horizontal and one vertical to the ground. Diameters of standing CWD were measured at the lowest part of the trunk above buttress root. The diameter of the narrower end of a stump was taken from the fallen log on the ground, and where this was not possible it was visually estimated. Major attached branches of standing trees were visually estimated. Where CWD was hollow, the thickness of the solid section was recorded and used to adjust the volume of CWD. The volume (v, m^3) of each CWD piece was calculated using Smalian's formula (Phillip, 1994):

$$v = L_{\mathrm{CWD}} \left[\frac{\pi (D_1/2)^2 + \pi (D_2/2)^2}{2} \right] \qquad (1)$$

where L_{CWD} (m) is the length of a CWD piece, and D is the diameter (m) at either end. If two measurements (horizontal and vertical to the ground) were taken, the geometric mean of that end was used. For hollowed CWD pieces, volume was calculated by subtracting the inner void volume from the outer volume.

Decay classes (d) of CWD were classified in the field, including intact (class 1, d=1), partially decayed (class 2, d=2), and rotten (class 3, d=3) as described in Chao et al. (2008a). Where the decay classes of bark and heartwood were very different, classes were assigned separately. In humid, lowland neotropical forests, density of each CWD decay class (ρ_d, g cm^{-3}) is closely related to the plot-level living wood density (Chao et al., 2008a). Thus, ρ_d was estimated as a function of the plot-average wood density of live trees.

$$\rho_{d=1} = 1.17[\rho_{BA\,j}] - 0.21 \qquad (2)$$

and

$$\rho_{d=2} = 1.17[\rho_{BA\,j}] - 0.31 \qquad (3)$$

where $\rho_{d=1}$ and $\rho_{d=2}$ represent the CWD densities in decay class (d) one and two, respectively, and $\rho_{BA\,j}$ (g cm^{-3}) is the wood density of living trees of plot j, weighted by their basal area. For CWD in decay class three, the average value of density for debris in "decay class three" from published studies of humid, lowland neotropical forests (0.29 g cm^{-3}) was used, as suggested by Chao et al. (2008a). The living wood density ($\rho_{BA\,j}$) of plot j were obtained from the RAINFOR database (Peacock et al., 2007) and a species wood density database (Chave et al., 2006; Lopez-Gonzalez et al., 2006; Baker et al., 2004). Wood density data were matched to plot data on a tree-by-tree basis. In cases where species-level wood densities were unavailable, the average for the genus (34% of 5401 individuals) or family (5%) was used. For unidentified trees and individuals where family-level data were lacking (2%), the average wood density of all stems in the plot was used.

2.3 CWD determinants: CWD input and decay rate

CWD input (annual mortality mass input, I, Mg ha^{-1} year^{-1}) for each plot is the sum of dead tree biomass (AGB$_{\text{coarse}}$, see next section), calculated using prior-to-death diameter measures and the allometric models (Chambers et al., 2001; Chave et al., 2005), divided by the census interval. We used short interval (about 4-year) census data to represent recent mortality events ($I_{\text{short-term}}$, Mg ha^{-1} year^{-1}).

Decay rates of CWD was estimated using a simple model from Olson (1963).

$$k_{ss} = I/N \qquad (4)$$

where k_{ss} is the decomposition rate at steady state (year^{-1}), I is the mortality mass input (Mg ha^{-1} year^{-1}) of that plot, and N is necromass (Mg ha^{-1}). This is based on the following equation,

$$dN/dt = I - k_{ss}N \tag{5}$$

Assuming forests are close to dynamic equilibrium (steady state), the change of necromass (dN/dt) would be equal to zero.

2.4 CWD determinants: coarse aboveground biomass

Aboveground biomass in dry weight (AGB, kg) of each plot was estimated. A locally-derived AGB allometric model is currently unavailable for our studied regions, so we applied two models developed from other tropical forests. The first model is the Chambers model (Chambers et al., 2001), based on harvesting at one site near Manus, Brazil (Higuchi et al., 1998), derived from trees larger than 5 cm in diameter at 1.3 m or above the buttresses (n=315). This model is adjusted to account for species-level wood density as suggested by Baker et al.(2004):

$$\text{AGB} = \left[\frac{\rho_i}{0.67}\exp\left(0.333\,[\ln D_i] + 0.933\,[\ln D_i]^2 - 0.122\,[\ln D_i]^3 - 0.370\right)\right] \tag{6}$$

where ρ_i (g cm^{-3}) is the species-level wood density of tree i, and D_i (cm) is the diameter at 1.3 m of the same tree.

The second model is the Chave model, a pan-tropical, multi-site (n=15) study of “moist forests” with allometric models derived from trees larger than 5 cm (Chave et al., 2005). The Chave model has accounted for species-level wood density and the equation is:

$$\text{AGB} = \rho_i \exp\left(2.148\,[\ln D_i] + 0.207\,[\ln D_i]^2 - 0.0281\,[\ln D_i]^3 - 1.499\right) \tag{7}$$

Our preliminary comparisons showed that estimates using the Chave model were generally greater than those based on the Chambers models, especially for trees larger than 80 cm. We report estimates using both models to represent a possible range of AGB for plots.

Coarse aboveground biomass (AGB_{coarse}, Mg) was estimated by multiplying AGB with a correction factor (0.85) to account for the proportion of biomass in branches ≥10 cm diameter only (Higuchi, unpublished data, cited in Chambers et al., 2000)

3 Results

3.1 Stocks of measured CWD

In our field study, necromass of CWD was greater in northeastern than in northwestern plots (Mann-Whitney U test, $p=0.025$) (Table 1). In both regions, most CWD was partially decayed (Table 1). The ratio of standing to fallen CWD is 0.34 in the NW and 0.43 in the NE plots (Table 1). Taking CWD into account increased coarse aboveground vegetative mass by up to 11% in NW Amazonia and 19% in NE Amazonia, compared with aboveground live biomass alone (N/AGB_{coarse}, Table 1).

The average (±1 SE) necromass of other Amazonian studies is 31.7±2.8 (Mg ha^{-1}) in *terra firma*, 27.4±7.7 in white sand forests, and 10.4±2.5 in floodplain forests (Table 2). The necromass measures of *terra firma* Amazonia will be referred as literature necromass values hereafter.

3.2 Determinants of measured CWD across *terra firma* Amazonian forests

We found positive relationships between biomass (AGB_{coarse}) and necromass measures (from field-based and literature, Table 2) (Fig. 1a):

$$N = 0.133[AGB_{coarse}] - 1.678 \quad (r^2 = 0.124, p = 0.038) \tag{8}$$

Also, necromass is positively related to recent mortality mass input ($I_{\text{short-term}}$) (Fig. 1b):

$$N = 5.945[I_{\text{short-term}}] + 0.077 \quad (r^2 = 0.277, p = 0.003) \tag{9}$$

Across Amazonia, necromass was also positively related to plot-level average living wood density (Fig. 1c):

$$N = 187.179[\rho_{BA\,j}] - 85.685 \quad (r^2 = 0.418, p < 0.001) \tag{10}$$

4 Discussion

This study showed new measurements of CWD quantities from two regions with two-fold differences in mortality rates, and also the patterns of CWD with other parameters across Amazonia.

4.1 Stocks and determinants of measured CWD across *terra firma* Amazonian forests

Based on our field data, we showed that stocks of CWD within regions are higher in the low-mortality NE Amazonia than in the high-mortality NW Amazonia. In other Amazonian studies, coarse necromass ranges from 2.5 Mg ha^{-1} in a dry and poor-nutrient white sand forest in Venezuela (Kauffman et al., 1988) to 86.6 Mg ha^{-1} in an old-growth Brazilian *terra firma* forest that was recovering from a period of high mortality (Rice et al., 2004). The NE Amazonian forests in our study are towards the higher end of the range, whereas the NW forests are close to the average for *terra firma* forests. Although the number of dead stems in NE Amazonia was low (low-mortality), there was high mortality mass (Table 2). This suggests big trees died in the NE forests (see also Chao et al., 2008b) and necromass is closely related to mass-mortality rates.

When using a larger sample of published *terra firma* studies, we find positive relationships between necromass and biomass ($\text{AGB}_{\text{coarse}}$), mortality mass input ($I_{\text{short-term}}$), and plot-level average living wood density ($\rho_{BA\,j}$). These findings suggest that across Amazonian forests there is a gradient in necromass that relates to these macroecological gradients in Amazonian forests (see Baker et al., 2004; Malhi et al., 2006). These results do not support the prediction ($P_{1.1}$) that there is no relationship between stocks of necromass and biomass, but support the predictions ($P_{2.1}$ and $P_{2.2}$) that necromass is positively related to mass-mortality rates and plot-level wood density. Based on the r^2 values in Fig. 1, we can propose a new hypothesis (modified from our original hypotheses) that necromass is better explained by forest dynamics than forest structure.

4.2 Improving necromass estimation method

To account for the carbon store in coarse woody debris across Amazonia, current research (e.g. Houghton et al., 2001; Malhi et al., 2006; Saatchi et al., 2007) typically uses a simplified necromass/biomass ratio (0.091, reviewed in Houghton et al., 2001). However, the Houghton et al. (2001) result was not specifically applicable for humid forests and included a wide selection of forest types (e.g. abandoned pastures in Uhl et al., 1988; tropical dry forest in Delaney et al., 1997). Moreover, some eastern Amazonian studies, based on a small region, showed an even higher ratio (e.g., 0.33 in Rice et al., 2004) that may result from past disturbances. Because necromass is a function of mortality and decomposition, and the link between necromass and biomass is indirect and tenuous, methods for estimating necromass stocks in Amazonia can be improved using a larger dataset based on dynamic measures.

Here, we apply new understanding from this study to generate an updated estimate of necromass across Amazonia. This is achieved by firstly obtaining a necromass regression model based on the assumption of steady state. Secondly by estimating necromass for plots presently without field-based measurement of necromass. Thirdly by scaling up both the estimated and measured results of necromass regionally and then to the entire Amazonian forests.

Assuming forests are close to dynamic equilibrium, the decomposition rate (k_{ss}) of available data from Table 2 can be generated as a function of necromass and mortality input. As decomposition rate is negatively correlated with wood density (Chambers et al., 2000), the estimated decomposition rates across Amazonian forests are related to average living wood density ($\rho_{BA\,j}$, g cm^{-3}):

$$k_{ss} = 0.879[\rho_{BA\,j}]^2 - 2.134[\rho_{BA\,j}] + 1.202 \;(r^2 = 0.329, p = 0.007) \tag{11}$$

where k_{ss} (year^{-1}) is the estimated decomposition rate in steady state, derived from the ratio of recent mortality input rate and necromass, and $\rho_{BA\,j}$ is the average living wood density, weighted by basal area, of plot j. This regression function would help to estimate the decomposition rate of a region.

As a result, for a plot where necromass has not been measured, necromass can be predicted by known mortality inputs and decomposition rate (Olson, 1963). Therefore, we can apply Eq. (11) to estimate necromass for Amazonian plots as:

$$N = I_{\text{short-term}}/k_{ss} = I_{\text{short-term}}/(0.879[\rho_{BA\,j}]^2 - 2.134[\rho_{BAj}] + 1.202), \tag{12}$$

where $I_{\text{short-term}}$ is recent mortality mass input (Mg ha^{-1} year^{-1}), and $\rho_{BA\,j}$ is the average living wood density, weighted by basal area, of plot j.

4.3 Estimating necromass based on RAINFOR data

We applied Eq. (12) (based on mortality mass input and wood density) to estimate necromass stocks for all Amazonian *terra firma* permanent plots (n=27) in a long-term research project (RAINFOR) (Appendix A) that met four criteria: currently without necromass measurement, censused between 2000 and 2006, have short-term (3.5 to 6 years) mortality mass input data, and are captured by a tree-by-tree database (Peacock et al., 2007). These estimated necromass values (Appendix A) together with measured necromass (n=42, in Table 2) showed a decreasing necromass gradient from the north-eastern to the south-western of Amazonia (Fig. 2).

4.4 Extrapolating necromass across Amazonia

To extrapolate necromass across Amazonia, we averaged both the estimated and measured results of necromass for each broadly-defined Amazonian regions (Table 3). Then, we multiplied the averaged values of necromass by the “tropical rainforest” area (reported by FAO, 2000) in the same region (Table 3), to estimate total necromass for each region (same method was applied for biomass). Finally, we assumed that coarse woody debris and living trees are 50% carbon by dry weight (Elias and Potvin, 2003). Thus, across Amazonia, the estimated carbon stock (±1 SE) in coarse necromass is 9.6±1.0 Pg C and in coarse biomass 80.4±3.3 Pg C (Table 3). Together, total coarse aboveground dead and alive coarse woody mass accounts for 90.0±4.3 Pg C (Table 3).

The quantity of coarse biomass estimated here is very similar to a result estimated by a kriging-based method (79.1±19.6 Pg C (85% of the original reported value to account only for coarse wood) (Malhi et al., 2006)), but much higher than a remote-sensing-based result (56.3±9.6 Pg C, Saatchi et al., 2007, adjusted by the 85% coarse wood factor). This may be partially explained by different methods for calculating forest cover. The other uncertainty is the definition of forest types: Saatchi et al. (2007) classified forest type into *terra firma*, floodplain, and other vegetation types, whereas Malhi et al. (2006) and our study both used a broader definition of “tropical rainforest” defined by FAO (2000). Based on data from Table 2, the ratio of necromass to coarse biomass is different among forest types. It is on average (±1 SE) 0.129±0.012 in *terra firma*, 0.131±0.026 in white sand forests, and 0.061±0.013 in floodplain forests, suggesting that forest type can influence the quantity of CWD. Therefore, discounting the variation of aboveground dead and living mass in different forest types could lead to either over- or underestimating stocks across Amazonia.

This study has shown that necromass is not an invariant fraction of biomass, even within *terra firma* forests, nor is it invariant across regions (Kruskal-Wallis test, $p=0.021$, Table 3). Moreover, the average ratio weighted by area of each region (0.127) is greater than the commonly used value (0.091) reported in Houghton et al. (2001). Future studies can either apply Eq. (12) for a plot-level necromass estimation, or apply the updated necromass/biomass ratios reported in Table 3 for regional estimations. To accurately account for the aboveground carbon pools across Amazonia, further research should consider both the forest cover and quantities of necromass on different forest types.

4.5 Uncertainties of results

It is arguable that in the cross site comparisons the field-based necromass (N) measurements are not independent of plot-level living wood density ($\rho_{BA\,j}$) for Fig. 1c. These arguments may come from (1) N was calculated as a function of CWD wood density (ρ_d); (2) ρ_d was derived from stand-average of wood density ($\rho_{BA\,j}$); (3) $\rho_{BA\,j}$, and AGB were both derived from individual wood density (ρ_i). It seems that correlations between these parameters are inevitable as they are founded on the same measures. However, parts of findings are based on other published, independently measured, *terra firma* data (Fig. 1). Also, when examining the relationship between $\rho_{BA\,j}$ and *volume* of CWD (independent of $\rho_{BA\,j}$) across *terra firma* plots, the relationship persists (linear regression, $p<0.001$, $r^2=0.389$, only slightly lower than that of Eq. 10). Together, these results confirm the strong gradient of decreasing CWD stocks from east to west parallel to a decrease in plot-level living wood density (Fig. 1c).

A further source of uncertainty is possible due to temporal variation in mortality rates and equilibrium status of necromass stocks. The calculations were based on the assumption that the studied forests are in steady state (*dynamic equilibrium*). The studied plots are located in forests free of cyclones, but wind-storms or droughts affect most forests. However, the extreme value of CWD reported from Tapajos (Rice et al., 2004), for example, may partly reflect an earlier large disturbance. Chronosequences of CWD decomposition and dynamics, in conjunction with abiotic variation, would provide a valuable extension to this study.

5 Conclusions

Other studies have demonstrated several macroecological gradients from east to west across Amazonia: increasing mortality rates (Phillips et al., 2004), and decreasing biomass (Baker et al., 2004; Malhi et al., 2006) and average wood density (Baker et al., 2004). This study reveals an additional gradient, such that necromass decreases from east to west. Across a large sample of *terra firma* forests in Amazonia, necromass stocks are related to biomass, and especially the mortality mass input and living wood density of the same plot. Necromass is better explained by forest dynamics than forest biomass, partially supporting the hypothesis of this study. Coarse woody debris is a more significant component, relative to aboveground biomass, than most studies of large-scale carbon budgets have assumed, but conversely is substantially less important than ecological reports based in eastern Amazonia had suggested. Future research should focus on the long-term dynamics and controlling factors of decomposition of coarse woody debris, and explanations of the observed macroecological gradient.

Appendix A

Estimated necromass of other RAINFOR plots

Necromass of the RAINFOR plots (n=27) estimated by applying the necromass Eq. (12). All plots are *terra firma* forests located in Amazonia, have been recensused between 2000 and 2006 (similar range with our measured NE and NW forests), and have short-term (3.5 to 6 years) mortality mass input data. All values are for trees $\geq$10 cm diameter – see Table A1.

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Table 1. Necromass and coarse aboveground biomass in the northwestern (NW) and northeastern (NE) Amazonia (average ±1 SE).

(a) Necromass

Region	Year	Necromass (N) (Mg ha^{-1})				S/F[a]
		Intact	Partially decayed	Rotten	Total	
NW	2005	10.1±1.5	15.2±2.6	2.0±0.5	27.3±3.2	0.34±0.07
NE	2004	18.4±7.1	39.0±8.7	1.1±0.6	58.5±10.6	0.43±0.22

(b) Biomass

Region	Year	Biomass (AGB_{coarse}) (Mg ha^{-1})[b]		N/AGB^{c}_{coarse}	
		Chambers	Chave	Chambers	Chave
NW	2001	247.9±1.9	266.7±2.5	10.3±1.3	11.1±1.3
NW	2005	253.6±3.1	274.6±4.8	10.1±1.3	10.9±1.4
NE	2000	344.5±58.4	376.4±76.5	16.8±4.5	18.0±4.4
NE	2004	337.3±59.4	368.6±75.9	17.3±4.8	18.5±4.8

[a] S/F: the ratio of standing to fallen CWD. [b] AGB_{coarse} was estimated by two allometric models (Chave et al., 2005; Chambers et al., 2001) ∼4 years prior to the CWD census and in the year of CWD census itself. [c] N/AGB_{coarse} (%): the ratio of total necromass to coarse biomass.

Table 2. Coarse woody debris across humid, lowland Amazonian forests, including *terra firma*, floodplain, and white sand. Results from this study and other publications. D., minimum diameter criteria of coarse woody debris (cm); Volume (V, $\mathrm{m}^3\,\mathrm{ha}^{-1}$); Necromass ($N$, $\mathrm{Mg\,ha}^{-1}$, ±1 SE); S/F, ratio of standing to fallen CWD; $\mathrm{AGB}_{\mathrm{coarse}}$, coarse aboveground biomass ($\mathrm{Mg\,ha}^{-1}$); $I_{\text{short-term}}$, recent mortality mass input ($\mathrm{Mg\,ha}^{-1}\,\mathrm{year}^{-1}$); $\rho_{BA\,j}$, average living wood density of plot j, weighted by basal area ($\mathrm{g\,cm}^{-3}$).

Forest type[a]	Region[b]	Plot Name	D.	Volume	Necromass[c]	S/F	$\mathrm{AGB}^{d}_{\mathrm{coarse}}$	$I_{\text{short-term}}$	$\rho^{g}_{BA\,j}$	Reference
terra firma	NE	ELD-01/02	10	118.31	74.5 (± –, a)	0.27	434.5	6.7	0.769	This study
terra firma	NE	ELD-03/04	10	137.36	62.8 (± –, a)	0.16	229.7	8.6	0.648	This study
terra firma	NE	RIO-01/02	10	72.62	38.4 (± –, a)	0.87	347.8	6.3	0.708	This study
terra firma	NE	ELD-01/02 and RIO-01/02	2.5	–	33.3 (±7.5, a)	0.80	303.7	2.6^{g}	0.740	Delaney et al. (1998)
terra firma	NE	San Carlos de Rio Negro	7.6	–	23.1 (± 10.3, b)	–	–	–	–	Kauffman et al. (1988)
terra firma	NE	San Carlos de Rio Negro	7.6	–	7.6 (± 4.9, b)	–	–	–	–	Kauffman et al. (1988)
terra firma	NW	Upper Rio Negro	5	–	26.3 (± 9.1, a)	–	187.9	–	–	Saldarriaga et al. (1988)
terra firma	NW	ALP-A	10	71.62	31.4 (± –, a)	0.16	254.7	2.5	0.649	This study
terra firma	NW	ALP-B	10	94.55	41.1 (± –, a)	0.71	235.3	7.9	0.617	This study
terra firma	NW	SUC-01	10	54.70	21.5 (± –, a)	0.20	251.0	5.9	0.593	This study
terra firma	NW	SUC-02	10	62.57	27.4 (± –, a)	0.10	251.1	4.4	0.614	This study
terra firma	NW	SUC-04	10	55.81	25.5 (± –, a)	0.43	260.0	5.5	0.623	This study
terra firma	NW	SUC-05	10	92.92	37.9 (± –, a)	0.35	253.3	4.8	0.607	This study
terra firma	NW	YAN-01	10	42.05	15.4 (± –, a)	0.24	263.0	4.8	0.560	This study
terra firma	NW	YAN-02	10	44.87	18.6 (± –, a)	0.52	260.4	4.1	0.593	This study
terra firma	NW	JEN-11	10	46.60	20.3 (± –, a)	0.41	254.8	4.6	0.669	Chao et al. (2008a)
terra firma	SW	CUZ-01	10	49.52	19.8 (± –, a)	-	226.0^{g}	4.9^{g}	0.581	Baker et al. (2007, raw data)
terra firma	SW	CUZ-02	10	60.58	23.9 (± –, a)	-	193.6^{g}	5.2^{g}	0.513	Baker et al. (2007, raw data)

[a] *terra firma* is defined as humid, lowland forest, presumed not to have experienced fluvial flooding in at least 250 years (Phillips et al., 2004), and not on white sand soils. [b] NE: north-eastern (Venezuela, Guyana, Suriname, and French Guiana); NW: north-western (Columbia, Ecuador, and northern Peru); SW: south-western (Acre state of Brazil and southern Peru); E: eastern (Brazil, excluding Acre). [c] Types of CWD, a: includes both fallen and standing CWD; b: only fallen CWD; c: unclear. [d] $\mathrm{AGB}_{\mathrm{coarse}}$: aboveground biomass (AGB, estimated by the Chambers model – Eq. 6) multiplied by coarse correction factor, 0.85. [e] Palace et al. (2007). [f] estimated from decomposition rate, assuming in steady state. [g] calculated in this study, using adjacent plots from the RAINFOR database (Baker et al., 2004; Lopez-Gonzalez et al., 2006; Chave et al., 2006; Peacock et al., 2007). [h] Average of 13 most dominant trees, weighted by volume.

Table 2. Continued.

Forest type[a]	Region[b]	Plot Name	D.	Volume	Necromass[c]	S/F	AGB$^{d}_{coarse}$	$I_{short-term}$	$\rho^{g}_{BA\,j}$	Reference
terra firma	SW	CUZ-03	10	41.66	16.6 (± –, a)	–	199.4^{g}	4.6^{g}	0.566	Baker et al. (2007, raw data)
terra firma	SW	CUZ-04	10	52.76	21.0 (± –, a)	–	240.8^{g}	7.4^{g}	0.586	Baker et al. (2007, raw data)
terra firma	SW	TAM-01	10	35.04	13.5 (± –, a)	–	201.9^{g}	3.7^{g}	0.527	Baker et al. (2007, raw data)
terra firma	SW	TAM-02	10	81.20	33.1 (± –, a)	–	210.6^{g}	4.8^{g}	0.539	Baker et al. (2007, raw data)
terra firma	SW	TAM-04	10	22.76	9.8 (± –, a)	–	249.5^{g}	5.3^{g}	0.618	Baker et al. (2007, raw data)
terra firma	SW	TAM-05	10	35.63	14.3 (± –, a)	–	215.2^{g}	4.7^{g}	0.606	Baker et al. (2007, raw data)
terra firma	SW	TAM-06	10	15.76	6.3 (± –, a)	–	219.9^{g}	3.5^{g}	0.506	Baker et al. (2007, raw data)
terra firma	SW	TAM-07	10	37.76	14.9 (± –, a)	–	223.6^{g}	3.9^{g}	0.579	Baker et al. (2007, raw data)
terra firma	SW	TAM-08	10	51.84	21.6 (± –, a)	–	188.8^{g}	3.0^{g}	0.598	Baker et al. (2007, raw data)
terra firma	E	Rondônia	?10	–	30.0 (± -, b)	–	242.3	–	0.760^{h}	Brown et al. (1995)
terra firma	E	Rondônia	2.5	–	30.5 (± 6.9, b)	–	260.8	–	–	Cummings et al. (2002)
terra firma	E	Juruena, Mato Grosso,	10	-	43.2 (± 1.6, a)	0.14	223.6	7.9^{f}	–	Palace et al. (2007)
terra firma	E	TUF1, Tapajós UF, Pará	10	94.60	52.8 (± 14.9, c)	0.17^{e}	239.7	7.9^{f}	0.691	Keller et al. (2004)
terra firma	E	TUF2 , Tapajós UF, Pará	10	94.20	51.8 (± 10.1, c)	0.17^{e}	239.7	7.9^{f}	0.691	Keller et al. (2004)
terra firma	E	CUF1, Cauaxi UF, Pará	10	86.60	43.8 (± 12.0, b)	–	–	–	0.691	Keller et al. (2004)
terra firma	E	CUF2, Cauaxi UF, Pará	10	97.10	52.8 (± 14.3, b)	–	–	–	0.691	Keller et al. (2004)
terra firma	E	Tapajós UF, Pará	10	–	52.4 (± 2.4, a)	0.17	239.7	8.5^{f}	–	Palace et al. (2007)
? terra firma	E	Paragominas, Pará	10	–	55.0 (± 7.5, a)	0.67	219.3	–	–	Gerwing (2002)
? terra firma	E	Vitoria Ranch, Pará	7.61	–	42.3 (± 19.7, b)	–	–	–	–	Uhl and Kauffman (1990)
terra firma	E	Tapajós, Pará	10	166.70	86.6 (± 13.4 (95 % CI), a)	–	250.6	4.8	0.691	Rice et al. (2004)
terra firma	E	Manaus	10	–	21.0 (± -, c)	–	310.2^{g}	3.6	0.703	Chambers et al. (2000)
terra firma	E	BIONTE, Manaus	?	–	29.7 (± 12.2 (? SD), c)	–	310.2^{g}	2.3^{g}	0.703	Summers (1998, cited in Chambers et al., 2000)
terra firma	E	Reserva Florestal Adolfo Ducke, Manaus	3	–	9.5 (± –, b)	–	–	–	–	Martius and Bandeira (1998)
terra firma	E	Manaus	10	–	31.0 (± 2.5, a)	0.25	276.7	–	–	Nascimento and Laurance (2002)
Average				68.5 (± 6.6)	31.7 (± 2.8)	0.36 (± 0.06)	249.1 (± 7.9)	5.2 (± 0.3)	0.63 (± 0.01)	
White sand	NE	SCR-04D	10	32.18	16.2 (± –, a)	0.43	290.8	–	0.701	Chao et al. (unpublished data)
White sand	NE	SCR-05D	10	75.87	39.8 (± –, a)	0.52	295.1	–	0.721	Chao et al. (unpublished data)
White sand	NE	San Carlos de Rio Negro	7.6	–	2.5 (± 1.6, b)	–	–	–	–	Kauffman et al. (1988)

Table 2. Continued.

Forest type[a]	Region[b]	Plot Name	D.	Volume	Necromass[c]	S/F	AGB^{d}_{coarse}	$I_{short-term}$	$\rho^{g}_{BA\,j}$	Reference
White sand	NW	ALP-30	10	76.93	37.1 (± –, a)	0.91	233.9	3.3	0.660	Chao et al. (unpublished data)
White sand	NW	JEN-12	10	86.00	41.1 (± –, a)	0.47	236.6	0.6	0.699	Chao et al. (2008a)
Average				67.7 (± 12.1)	27.4 (± 7.7)	0.58 (± 0.11)	264.1 (± 16.7)	2.0 (± 1.4)	0.70 (± 0.01)	
Floodplain	NW	floodplain plot, Jenaro Herrera	10	42.30	10.3 (± –, b)	–	214.8	–	0.510	Chao et al. (2008a)
Floodplain	NW	SUC-03	10	37.29	21.0 (± –, a)	0.27	284.9	3.4	0.718	Chao et al. (unpublished data)
Floodplain	E	Lago Cobra 23–25 m a.s.l., Manaus	?	–	3.6 (± –, c)	–	–	6.0	–	Martius (1997)
Floodplain	E	Lago Cobra 25–26 m a.s.l., Manaus	?	–	10.4 (± –, c)	–	–	–	–	Martius (1997)
Floodplain	E	Lago Cobra 26–27 m a.s.l., Manaus	?	–	5.9 (± –, c)	–	–	–	–	Martius (1997)
Floodplain	E	Lago Central 23–25 m a.s.l., Manaus	?	–	11.4 (± -, c)	–	–	–	–	Martius (1997)
Average				39.8 (± 2.5)	10.4 (± 2.5)	–	249.9 (± 35.1)	4.7 (± 1.3)	0.61 (± 0.10)	

Table 3. Stocks of coarse necromass and coarse aboveground biomass of tropical rainforest[a] across Amazonian regions. *N*, necromass, the average (±1 SE) of measured (n=42, Table 2) and estimated (n=27, using Eq. 12) necromass; $\mathrm{AGB}_{\mathrm{coarse}}$, coarse aboveground biomass.

Region[b]	Area	Average (Mg ha^{-1})			Carbon stock (Pg C)[c]		
	(10^6 km^2)[d]	N	$\mathrm{AGB}_{\mathrm{coarse}}$	$N/\mathrm{AGB}_{\mathrm{coarse}}$	N	$\mathrm{AGB}_{\mathrm{coarse}}$	Total
NE	0.53	39.9±10.1	328.9±42.8	0.166±0.039	1.1±0.3	8.8±1.1	9.8±1.4
E	3.95	36.0±2.7	284.7±7.8	0.132±0.013	7.1±0.5	56.3±1.5	63.4±2.1
NW	0.76	24.5±2.6	238.2±8.5	0.103±0.011	0.9±0.1	9.0±0.3	9.9±0.4
SW	0.42	17.5±1.8	216.5±5.8	0.082±0.009	0.4±0.0	4.6±0.1	4.9±0.2
S	0.17	17.4±3.0	206.7±17.4	0.090±0.020	0.1±0.0	1.8±0.1	1.9±0.2
Total	5.83				9.6±1.0	80.4±3.3	90.0±4.3
Average[e]		33.0±3.0	275.5±14.9	0.127±0.010			

[a] defined as all monthly mean temperature ≥18°C and ≤3 dry months in FAO (2000).

[b] NE: north-eastern (Venezuela, Guyana, Suriname, and French Guiana); NW: north-western (Columbia, Ecuador, and northern Peru); SW: south-western (Acre state of Brazil and southern Peru); S: southern (Bolivia); E: eastern (Brazil, excluding Acre). [c] C stock is estimated as 50% of mass (Elias and Potvin, 2003). [d] area of tropical rainforest (FAO, 2000). [e] weighted by the area of forest cover in each region.

Table A1. See Appendix A.

Region[a]	Plot name	Census date	Latitude	Longitude	*Necromass**	$\mathrm{AGB}^{\mathrm{b}}_{\mathrm{coarse}}$	$I^*_{\mathrm{short-term}}$	$\rho^*_{BA\,j}$
NW	SUM-01	2002.50	−1.8	−77.6	14.31	205.33	4.79	0.516
NW	TIP-02	2002.09	−0.6	−76.2	14.17	181.06	3.77	0.574
SW	ALM-01	2004.50	−11.8	−71.5	19.92	252.48	6.00	0.544
SW	MNU-03	2001.70	−11.9	−71.4	16.06	184.51	5.61	0.505
SW	MNU-04	2001.62	−11.9	−71.4	14.08	224.34	4.18	0.548
S	CHO-01	2001.45	−14.4	−61.1	20.47	124.10	4.20	0.631
S	CRP-01	2001.45	−14.5	−61.5	19.17	239.46	3.02	0.680
S	CRP-02	2001.45	−14.5	−61.5	14.46	209.16	3.76	0.580
S	HCC-21	2001.42	−14.6	−60.7	28.80	215.82	6.99	0.596
S	HCC-22	2001.42	−14.6	−60.7	14.41	239.06	3.33	0.606
S	LFB-01	2001.40	−14.6	−60.9	6.93	212.45	1.71	0.592
E	BDF-03	2003.71	−2.4	−59.9	25.27	308.33	4.07	0.676
E	BDF-04	2003.71	−2.4	−59.9	27.46	238.33	3.62	0.708
E	BDF-05	2003.71	−2.4	−59.9	27.01	276.92	3.45	0.713
E	BDF-06	2003.71	−2.4	−59.9	40.21	262.98	5.34	0.707
E	BDF-07	2004.04	−2.4	−59.9	26.59	328.85	2.99	0.730
E	BDF-08	2004.13	−2.4	−59.9	28.03	289.93	3.96	0.697
E	BDF-09	2002.50	−2.4	−59.9	31.91	348.46	3.49	0.734
E	BDF-10	2002.54	−2.4	−59.9	31.56	282.21	4.19	0.707
E	BDF-11	2002.54	−2.4	−59.9	15.24	339.29	1.98	0.710
E	BDF-12	2002.54	−2.4	−59.9	54.00	327.21	7.75	0.695
E	BDF-13	2003.29	−2.4	−59.9	39.19	314.42	4.54	0.726
E	BDF-14	2003.13	−2.4	−59.9	20.70	350.78	2.42	0.725
E	CAX-01	2004.59	−1.7	−51.5	23.21	338.91	2.73	0.724
E	CAX-02	2003.20	−1.7	−51.5	36.28	323.57	4.79	0.708
E	JAC-01	2002.50	−2.6	−60.2	28.10	275.75	4.09	0.693
E	JAC-02	2002.50	−2.6	−60.2	27.43	268.75	3.88	0.697

[a] NE: north-eastern Amazonia (Venezuela, Guyana, Suriname, and French Guiana); NW: north-western Amazonia (Columbia, Ecuador, and northern Peru); SW: south-western Amazonia (Acre state of Brazil and southern Peru); S: southern Amazonia (Bolivia); E: eastern Amazonia (Brazil, excluding Acre). [b] coarse aboveground biomass (Mg ha^{-1}), which is calculated by multiplying aboveground biomass (AGB, kg) with a correction factor (0.85) to account for the proportion of biomass in branches ≥10 cm diameter only (Higuchi, unpublished data, cited in Chambers et al., 2000). AGB is calculated by the equation in Chambers et al. (2001) and adjusted by species wood density (Baker et al., 2004).

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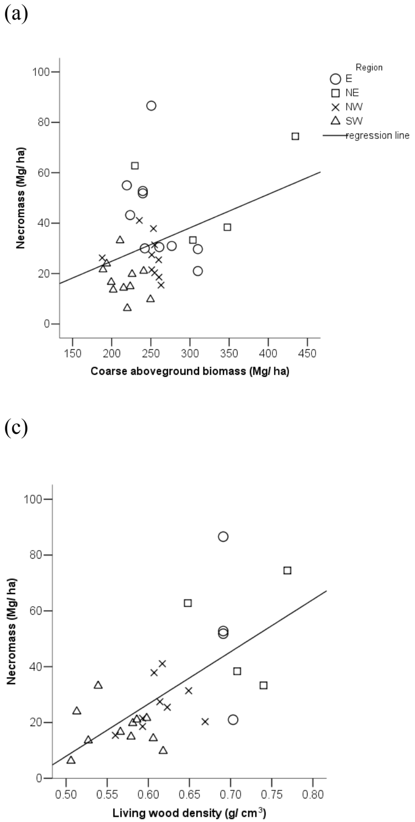

Fig. 1. Relationships between necromass and **(a)** coarse aboveground biomass, **(b)** mortality mass input, and **(c)** plot-average living wood density across *terra firma* Amazonian forests. Relationships between necromass and coarse aboveground biomass ($\text{AGB}_{\text{coarse}}$) ($r^2$=0.124, p=0.038), mortality mass input ($I_{\text{short-term}}$) (r^2=0.277, p=0.003), and plot-average living wood density ($\rho_{BA\,j}$) (r^2=0.418, p<0.001) are all significant. All sites in Table 2 with appropriate data are plotted.

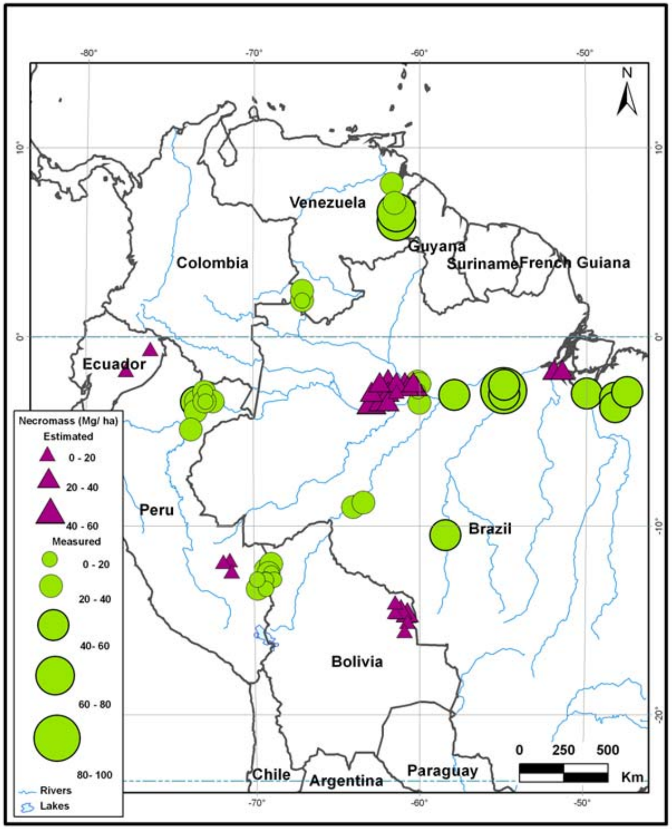

Fig. 2. Necromass in *terra firma* Amazonian forests. Estimated necromass (using Eq. (12), n=27), on the basis of known mortality rate and stand-level wood density ($\rho_{BA\,j}$). Measured necromass (Table 2, n=42), on the basis of field measurement from this study and other published literature.