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Propriedades físicas do solo e seus efeitos sobre a estrutura da floresta determinam os estoques de necromassa na Amazônia Central

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Sinopse: Analisamos a distribuição dos estoques de necromassa e a densidade da madeira morta em 79 parcelas na Amazônia central. Foram consideradas propriedades físicas do solo, estrutura da vegetação, características topográficas e climáticas para investigar a influência de tais variáveis nos estoques de necromassa ao longo de diferentes paisagens

Palavras-chave: Propriedades físicas do solo, estrutura da vegetação, índice topográfico, amostragem de intercepção linear, anoxia

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Resumo

A necromassa é um componente essencial nos ecossistemas tropicais e seus estoques apresentam grande variação nas diferentes paisagens. No presente estudo, relações entre necromassa, fatores edáficos e climáticos foram analisados para compreender as causas da variação da necromassa nos diferentes tipos de solo da Amazônia Central. Foram avaliadas 79 parcelas de 0.5 ha em florestas próximas a Manaus e ao longo da rodovia BR-319 para estimar estoques de necromassa e densidade da madeira morta. Propriedades físicas do solo foram avaliadas usando trincheiras de 2m de profundidade e amostras de trado. Dados de vegetação foram obtidos de parcelas permanentes. Propriedades físicas do solo foram os melhores preditores de necromassa. Anoxia no solo e profundidade do solo explicaram maior variação na necromassa (35% e 30%, respectivamente em duas regressões simples). Estoques de necromassa em solos sem propriedades físicas restritivas, profundos e não saturados (33,1 Mg ha^{-1}) foram duas vezes maiores do que em solos com propriedades físicas restritivas (16,0 Mg ha^{-1}). Um índice topográfico, que descreve a distribuição espacial da umidade do solo, também explicou variação significativa nos estoques necromassa. Parâmetros da vegetação, principalmente biomassa média por árvore, foram controladas pelas condições do solo que tiveram forte influência sobre os estoques de necromassa locais. Biomassa média por árvore sozinha explica cerca de 20% da variação na necromassa. No entanto, quando anoxia no solo foi incluído em modelos de regressão, os parâmetros de vegetação já não eram significativos sugerindo que, apesar de ser apenas um efeito indireto, há uma forte ligação entre as propriedades físicas do solo e estoques necromassa. Anoxia sazonal no solo e restrição ao enraizamento profundo em algumas regiões provavelmente influenciam a estrutura e a dinâmica das florestas, que por sua vez diminuem a produção dos estoques de necromassa. Variação substancial na necromassa pode ser estimada em grandes escalas através de propriedades físicas do solo, índice topográfico e estrutura da floresta.

Abstract

Soil-induced impacts on forest structure drive necromass stocks across Central Amazonia

Necromass is an essential component in tropical forest ecosystems and presents great variation in different forest landscapes. Relationships between necromass, soil, forest structure, and other environmental factors were analyzed to understand the drivers of necromass variation in different soil types across Central Amazonia. To estimate necromass stocks and density of dead wood, 79 plots of 0.5 ha were assessed along a transect spanning ~700 km in undisturbed forests from north of the Rio Negro to south of the Rio Amazonas. Soil physical properties were evaluated by digging 2 m deep pits and taking auger samples. Vegetation data were obtained from permanent plots. Soil physical properties were the best predictors of necromass. Soil anoxia and soil depth explained the most variation in necromass (35% and 30%, respectively). Necromass stocks on physically non-restrictive, deep, unsaturated soils (33.1 Mg ha^{-1}) were twice those on soils with restrictive physical properties (16.0 Mg ha^{-1}). A topographic index, which describes the spatial distribution of soil moisture, also explained significant variation in necromass stocks. Vegetation parameters, notably average biomass per tree, were modulated to soil conditions which had strong influence on local necromass stocks. Average biomass per tree alone explains about 20% of the variation in necromass. However, when soil anoxia was included in regression models, vegetation parameters were no longer significant, with this suggesting that, despite of only an indirect effect, there is a strong link between soil physical properties and necromass stocks. Seasonal soil anoxia and restrictive rooting depth in some regions are likely to influence forest structure and dynamics which in turn decreases necromass production and stocks. Substantial variation in necromass may be estimated over large scales through soil physical properties, topographic index, and forest structure.

Sumário

Introdução

O crescente aumento de CO_2 na atmosfera nos últimos anos tem sido o grande responsável pelo aquecimento global e as mudanças climáticas (Hansen et al. 2008). Esses efeitos tiveram ampla repercussão e, por isso, têm sido vastamente discutidos. Como resultado, houve um aumento nos investimentos para a conservação de zonas ricas em carbono, como por exemplo, as florestas tropicais que representam 40% do carbono estocado na biomassa terrestre (Dixon et al. 1994). Estudos sobre a dinâmica florestal da Amazônia, uma região rica em carbono, são essenciais para a resolução de questões científicas que envolvem "o funcionamento de ecossistemas, o papel da biosfera nos ciclos biogeoquímicos e na resposta dos ecossistemas a perturbações locais e globais" (Malhi et al. 2004).

A literatura recente tem indicado alterações na dinâmica das florestas tropicais no decorrer dos últimos anos. Há evidências de que houve um aumento nas taxas de recrutamento de indivíduos arbóreos (Phillips and Gentry 1994; Phillips et al. 2004) e um aumento da dominância de lianas (Phillips et al. 2002) nas florestas tropicais, indicando uma aceleração na dinâmica florestal. Estas mudanças ocorrem não apenas na estrutura das florestas, mas também em suas taxas de assimilação de carbono. Nas florestas tropicais, o acúmulo de biomassa vegetal em parcelas permanentes tem excedido a perda por morte de árvores nas últimas décadas (Phillips et al. 1998, Lewis et al. 2009). Além disso, muitas das árvores dessas florestas conseguem manter o carbono fixado em suas estruturas durante aproximadamente 800 anos (Chambers et al. 1998). Todas essas mudanças anteriormente citadas na dinâmica das florestas podem ter ocorrido como uma resposta desses ecossistemas florestais ao aumento de CO_2 na atmosfera. No entanto, as alterações climáticas resultantes do contínuo aumento de CO_2 atmosférico podem ainda vir a modificar as relações florestais previamente citadas.

Eventos intensificados do El Niño podem diminuir a produtividade das árvores (Condit et al. 1995) e aumentar a mortalidade (Nepstad et al. 2002) em determinadas áreas das florestas tropicais. As mudanças climáticas também podem ser responsáveis por alterações nos regimes pluviométricos resultando em secas, e estas podem intensificar a mortalidade de árvores nas florestas, revertendo o padrão vigente de acúmulo de biomassa (Phillips et al. 2009). Em um cenário mais drástico, os eventos acima citados poderiam levar a uma reversão do funcionamento de sumidouro das florestas tropicais, transformando-as em fontes de CO_2

para a atmosfera, uma vez que seria esperado um grande aumento nas taxas de acréscimo de matéria morta das árvores na camada de liteira[1].

A liteira possui uma importante participação nos sistemas ecológicos (Nascimento e Laurance 2002). Ela é constituída por detritos orgânicos, em sua maioria vegetais (folhas, flores, frutos, galhos e troncos), produzidos pelas florestas. A liteira pode ser classificada como serapilheira fina (folhas, flores e frutos) e liteira grossa (material lenhoso com diametro> 2 cm); esta última será denominada como necromassa a partir deste ponto.

A necromassa é uma componente essencial dos ecossistemas, uma vez que a mesma tem participação importante nos ciclos biogeoquímicos. Ela pode incrementar substancialmente a fertilidade do solo ao ser decomposta, chegando a exceder a liberação de nutrientes da liteira fina (Schowalter 1992). A necromassa também é fundamental no ciclo do carbono. Ela é uma fonte considerável de CO_2, pois é mais lábil quando comparada à madeira viva (Chambers et al. 2000, Clark et al. 2002), e pode ter um estoque de carbono variando de 7 a 25 % da massa vegetal total acima do solo (Nascimento e Laurance 2002, Rice et al. 2004). A quantidade de CO_2 liberada pela necromassa pode ser influenciada principalmente por fatores abióticos como temperatura, pluviosidade e umidade do ar (Chambers et al. 2000), porém a produção dessa matéria morta pode ser influenciada por diversos fatores nas florestas tropicais.

Nas florestas da bacia amazônica, a produção de necromassa pode apresentar grandes variações. Florestas impactadas por madeireiras que realizam extração mecanizada convencional apresentam maior produção e estoque de necromassa em relação às florestas primárias (Feldpausch et al. 2005; Palace et al. 2007). Essa diferença ocorre devido à ação direta do corte, e suas implicações como alteração da paisagem para extração e manuseio da madeira. Logo, as estimativas de necromassa podem ser importantes para compreender o histórico de perturbações da floresta.

Não obstante, as diferenças de produção de necromassa podem ser intrínsecas das florestas. Nas florestas primárias da Amazônia, a necromassa varia entre 17,5 $Mg.ha^{-1}$ e 86,6

[1] Liteira: Conjunto de resíduos orgânicos, predominantemente de origem vegetal (folhas, flores, frutos, gravetos e galhos finos, etc) que se depositam sobre o solo da floresta (Vieira, 1988 – Manual de Ciência do Solo, p.121).

Vieira, L.S. 1988. Manual de Ciência do Solo, com ênfase em solos tropicais. 2ª. ed., Editora Agronômica Ceres, Piracicaba, SP. 464p.

$Mg.ha^{-1}$ (Rice et al. 2004; Baker et al. 2007; Chao et al. 2009a) No sudoeste e oeste da Amazônia as árvores possuem a madeira menos densa e morrem duas vezes mais rápido em relação às árvores da Amazônia central e oriental (Phillips et al. 2004). Contudo, o estoque de necromassa no nordeste amazônico é maior do que no noroeste e sudoeste (Chao et al. 2009a). Isso ocorre devido à produção de necromassa estar relacionada à mortalidade de biomassa (quantidade de massa que morre em um espaço de tempo) e não apenas à mortalidade de indivíduos arbóreos (número de indivíduos que morrem em um determinado tempo). Tais estudos mostram que as variações das características das florestas e do ambiente podem influenciar a dinâmica das florestas. Isto é muito importante, uma vez que existem diferentes gradientes ambientais atuando na bacia amazônica (Baker et al. 2004; Malhi et al. 2006; Chao et al. 2009a).

A Amazônia é caracterizada como um ecossistema heterogêneo, pois apresenta variações ambientais como diferentes formações florestais, índices pluviométricos e cotas de relevo. Os solos da região amazônica, por exemplo, variam quanto às suas características físicas e químicas, formando gradientes de fertilidade do solo e também ampla variação em seus atributos físicos (Quesada et al. 2010, 2011). Alguns estudos mostram a relação de gradientes de fertilidade do solo com a produtividade primária de florestas (Malhi et al. 2004; Quesada et al. 2012), taxas de recrutamento e mortalidade de árvores (Phillips et al. 2004; Quesada et al. 2012) e densidade da madeira (Baker et al. 2004; Quesada et al. 2012).

Porém, estudos que consideram as características físicas dos solos de florestas amazônicas são raros. Diferentes atributos do solo como drenagem, densidade do solo e impedimentos ao crescimento de raízes, somados a diferentes condições climáticas (como pluviosidade e duração da estação seca), podem ser importantes para a produção e o estoque de necromassa. Por exemplo, Quesada et al. (2012) relatam que as taxas de reposição das árvores em 59 parcelas nas florestas da Amazônia (média entre as taxas de recrutamento e mortalidade) foram amplamente controladas pela qualidade dos atributos físicos dos solos (profundidade efetiva, estrutura, capacidade de drenagem e topografia) e não por fatores vinculados à fertilidade dos solos. Ainda de acordo com Chao et al. (2008), ambientes constantemente perturbados por inundações seriam dominados por árvores com menor densidade da madeira, o que acarreta em um menor estoque de necromassa. Assim, solos mal drenados podem causar estresse hídrico e um ambiente anóxico para as raízes das árvores em épocas mais chuvosas ocasionando um baixo estoque de necromassa. Em contrapartida, solos com melhor drenagem e melhores condições físicas poderiam levar a uma densidade de madeira maior, e, por conseguinte, a maiores estoques de necromassa.

Os fatores que influenciam a dinâmica do carbono na Amazônia ainda são pouco conhecidos, tornando-se necessária a determinação de fatores que auxiliem a formulação de estimativas mais precisas sobre o balanço total de carbono. O objetivo geral deste estudo é ampliar a compreensão da dinâmica do carbono, levando em conta as interações da necromassa com características estruturais da vegetação e do ambiente. Essas características podem influenciar a densidade da madeira das árvores e o armazenamento de carbono nas diferentes florestas da bacia amazônica, além de influenciar diretamente a taxa de mortalidade das árvores. Pensando nos fatores previamente discutidos, pretendemos investigar como parâmetros estruturais da vegetação (biomassa, densidade de indivíduos por hectare, área basal dos indivíduos arbóreos e densidade da madeira das árvores vivas) e ambientais (propriedades físicas do solo, topografia e pluviosidade afetam: i) os estoques; ii) a variação de necromassa de diferentes florestas; e iii) a densidade da madeira morta nas diferentes florestas.

A hipótese investigada é:

os estoques de necromassa são maiores em solos com propriedades físicas favoráveis e menores em solos com condições físicas mais restritivas.

Objetivo

Avaliar a distribuição e causas da variação dos estoques de necromassa em diferentes solos na região centro Amazônica. Com este trabalho pretendemos entender quais mecanismos ambientais controlam os estoques de necromassa nas diferentes paisagens da Amazônia.

Objetivo específicos

Responder as seguintes questões: como parâmetros estruturais da vegetação (biomassa, densidade de indivíduos por hectare, área basal dos indivíduos arbóreos e densidade da madeira das árvores vivas) e ambientais (propriedades físicas do solo, topografia e pluviosidade afetam: i) os estoques; ii) a variação de necromassa de diferentes florestas; e iii) a densidade da madeira morta nas diferentes florestas.

Capítulo 1

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Abstract

Background: Necromass is an essential component in tropical forest ecosystems and varies widely in different forest landscapes.

Aims: Relationships between necromass, soil, forest structure, and other environmental factors were analysed to understand the drivers of necromass variation in different soil types across Central Amazonia.

Methods: To estimate necromass stocks and density of dead wood debris, 79 plots of 0.5 ha were assessed along a transect spanning ~700 km in undisturbed forests from north of the Rio Negro to south of the Rio Amazonas. Soil physical properties were evaluated by digging 2 m deep pits and taking auger samples. Vegetation data were obtained from permanent plots.

Results: Soil physical properties were the best predictors of necromass. Soil anoxia explained the most variation in necromass. Necromass stocks on physically non-restrictive soils were twice those on physically restrictive soils. A topographic index describing spatial distribution of soil moisture also explained significant variation in necromass stocks. Vegetation parameters (biomass per tree) were modulated by soil conditions which in turn had a strong influence on local necromass stocks.

Conclusion: Soil physical properties are likely to influence forest structure and dynamics which in turn decreases necromass production and stocks.

Key words

Soil physical properties, woody debris, vegetation structure, topographic index, line intercept sampling, tropical forest, anoxia, carbon, forest dynamics

1 Introduction

Necromass is an essential component in tropical forest ecosystems, and plays a large role in biogeochemical cycles (Chambers et al. 2000; Clark et al. 2002; Wilcke et al. 2005). Within tropical forests necromass accounts for 6 to 25% of total aboveground carbon stocks (Nascimento and Laurance 2002; Rice et al. 2004; Baker et al. 2007), implying a total pan-Amazon necromass carbon stock of ~10 Pg (Chao et al. 2009a). The rate of carbon dioxide release from necromass decomposition responds to climatic factors such as temperature and moisture (Chambers et al. 2000); however, coarse woody debris stocks may be modulated by additional factors in tropical forests.

Amazonia holds a great diversity of trees (ter Steege et al. 2000), and varies substantially in both vegetation dynamics (Quesada et al. 2012, Phillips et al. 2004), and structure (Baker et al. 2004, Malhi et al. 2006 Feldpausch et al. 2011, Nogueira et al. 2008). Such singularities in this great ecosystem may affect necromass stocks in several ways. Necromass appears to generally decrease from north-eastern to south-western Amazonia (Baker et al. 2007, Chao et al. 2009a). Spatial variation in necromass stocks across the landscape may respond both to short-term climatic disturbances (e.g., Phillips et al. 2009, Negrón-Juárez et al. 2010) and to long-term differences in forest dynamics in response to environmental characteristics (Malhi et al. 2006; Chao et al. 2009a). Soils represent an important environmental gradient in Amazonia, with a wide variety of soil types across the Basin and with diverse chemical and physical conditions (Quesada et al. 2010, 2011). Variations in soil physical properties across the basin have been shown to account for a large proportion of the variation in tree turnover rates and mean forest wood density, with soils influencing forest disturbance level and vegetation structure of Amazonian forests (Quesada et al. 2012).

Very few studies have attempted to understand landscape-scale drivers of necromass stocks. Kissing and Powers (2010), working in secondary forests in Costa Rica, showed strong correlations between stand age and the amount of coarse wood debris (CWD). Chao et al. (2009a) working in mature forests in Amazonia showed that there is a relationship between forest structure and necromass, in particular with regard to biomass, wood density of living trees and mortality mass input. Although these studies successfuly associated necromass stocks with forest structure and dynamics, there has been no analysis of a potential effect of edaphic properties on necromass stocks. Since edaphic factors such as effective soil depth and structure are important factors controling forest structure and dynamics (Jirka et al 2007, Quesada et al. 2012), they can be expected to influence vegetation characteristics and through that affect both the production and the stocks of CWD. We hypothesise that because physically poor soils impose constraining conditions for plant establishment, they result in increased stem turnover rates, in turn limiting the maximun size that trees can attain, so that ultimately the impact of soil physical constraints on vegetation structure negatively affects CWD stocks.

If this general hypothesis is correct, we may expect landscape-scale variation in soils to drive substantial variation in necromass stocks. The forests south of the Rio Amazonas represent a huge but extremely poorly studied region in central Amazonia in terms of both vegetation and soil. The region is broadly defined as containing hydromophic soils (RADAMBRASIL, 1978; Quesada et al., 2011), in contrast to soils north of the Rio Negro which are dominated by well-drained deep soils. The region is also expected to have large variation in above-ground biomass (AGB) (IBGE 1997). Central Amazonia, therefore, represents an ideal testing ground of edaphic and vegetation drivers of necromass stocks, while controlling for climatic variation.

Our study, therefore, examines the causes of necromass variation across Central Amazonia. We tested the specific hypothesis: that necromass stocks are greatest in soils without tree growth restrictions and least in more constrained soils.

2 Methods

2.1 Study sites

Fieldwork was conducted across a ~700 km transect in Central Amazonia over a one-year period (2010–2011) (Figure 1). Data were collected in permanent plots located north and south of the Rio Amazonas in the state of Amazonas, Brazil. The northern-most sites are in the *Reserva Florestal Adolfo Ducke* (hereafter Ducke Reserve) in plots monitored by the Program of Biodiversity Research (*Programa de Pesquisa em Biodiversadade – PPBio*), and in the Conservation Unit of the Biological Dynamics of Forest Fragments Project (BDFFP) in permanent plots monitored by BDFFP and the Tropical Ecology Assessment and Monitoring Network (TEAM). The southern sites are located in the Purus – Madeira interfluvial zone on a ~600 km transect established along the Manaus – Porto Velho road (BR-319, modules M1–M11). The permanent plots at these sites are also monitored by PPBio.

The Ducke Reserve is managed by the National Institute for Amazonian Research (*Instituto Nacional de Pesquisas da Amazonia* – INPA), spanning 10,000 ha of mature *terra firme* tropical moist forest at the periphery of the city of Manaus (02° 95' S, 59° 95' W). The vegetation has a closed canopy of 30-37 m height, with emergent trees reaching 45 m (Ribeiro et al., 1999). Mean annual precipitation is 2524 mm (*Coordenação de Pesquisas em Clima e Recursos Hídricos* – CPCRH – INPA, unpublished data). The Reserve has a grid covering a 64 km² area. Soils are Ferralsols and Acrisols along the slopes and plateaus, which are highly weathered and thus have favorable physical conditions (Chauvel et al. 1987; Quesada et al. 2010). In general soils are deep, well drained, and have low bulk density. The Ducke Reserve also has wet, sandy soils (Podzols) near streams and valley bottoms, but these were not included in this study. A total of 18 plots were sampled on Acrisols and Ferralsols at the Ducke Reserve. All plots were at least 1 km apart and are 250 m long and 20 m wide (0.5 ha), following the topographic contour.

The BDFFP study site is located 80 km north of Manaus (2º30´S, 60ºW). Data were collected in mature *terra firme* tropical moist forest, at least 1000 m away from borders and in forest fragments greater than 500 ha (Laurance et al. 1998). The forest canopy is 30-37 m tall with emergent trees reaching up to 55 m. Precipitation ranges from 1900–2500 mm (Nascimento and Laurance 2002). Necromass and soil were sampled from forests over Ferralsols and Acrisols. The plots located in the BDFFP Conservation Unit (*n*=12) have a different plot design from PPBio plots as they were installed by another research group. Plots are 100 x 100 m and are positioned independently of topographic features.

The plots located south of the Rio Amazonas are spaced at points along the BR-319 Highway on the interfluvial area between the Purus and Madeira rivers. Along the road, plots located closer to Manaus have a somewhat denser tropical moist forest (IBGE 1997), while plots located closer to Porto Velho have a more open lowland evergreen forest. The region is characterized by a very flat topography varying between 30 and 50 m in altitude over large distances. Mean annual precipitation of the area varies from 2155–2624 mm (WorldClim; Hijmans et al. 2005). The soils along the BR-319 are predominantly Plinthosols and Gleysols (Sombroek 2000), with these generally having varying degrees of soil water saturation and anoxic conditions. Soil physical structure is generally restrictive to root growth, with very high bulk density in the subsoil, and thus these soils have varying degrees of hardness and effective soil depth. Subsoil layers that limit root penetration are often found and vary from 50 to 100 cm deep in these plots (RADAMBRASIL, 1978).

All plots located along the BR-319 Highway (*n*=49) are distributed into 10 modules, which are installed at intervals of between 40 and 60 km. Each module is composed of a 5 km long transect with 5 plots of 250 x 20 m following the topographic contour at intervals of 1 km.

2.2 Coarse necromass stocks

Field measurements of coarse necromass were divided in two categories: line intersect sampling (van Wagner 1968) for fallen dead wood and belt transects for standing dead trees (Chao et al. 2008). For line intersect sampling, every piece of fallen dead woody material (trees, palms, lianas) with diameter≥10 cm that crossed the line was measured and classified into a decay class following Chao et al. (2008), dividing CWD into three categories. Necromass in class 1 is generally recently fallen, solid wood, sometimes presenting minor degradation. Material in class 2 is still sound but already presents rottenness features like the absence of bark. Class 3 is very rotten and can be easily broken. In cases where it was impossible to measure diameter because the piece was partly buried, two perpendicular measures were taken and their mean was the recorded diameter. In plots that followed the topographic contour, the central line of the plot, which is formed by regular, connected straight segments, was used as the intersect line. In square plots (100 x 100 m) the intersect line was also 250 m length but followed the plot perimeter. We treat all our line estimates as a single, connected intersection line and therefore each 250 m transect is an independent and unique measure of CWD per plot. However, as segmented transects are more sensitive to biased estimation arising from multiple crossing of necromass pieces and endpoint partial intersection (Affleck et al. 2005), we have adopted a set of conventions to avoid bias: 1) each particle crossed by intersection line was counted only once (Gregoire and Valentine 2003), and 2) when the intersect line endpoint terminates at a piece it was included only if 50% or more lay inside the transect line. We also note that when necromass orientation is randomly distributed in the sampling area (which we believe is a reasonable supposition for our forests), then there is no advantage associated with one line intersect design over another (Bell et al. 1996).

The belt transects for estimating coarse necromass (standing dead trees and broken snags) were 10 m wide on both sides of the 250 m transect line. Standing dead stems with diameter ≥ 10 cm were measured at 1.3 m height or at the lowest part of the snag above buttress roots in case these were present. If the snag was shorter than 1.3 m, the measurement was taken at the highest point possible. The snag height was measured with a digital hypsometer (Vertex Laser VL400 Ultrasonic-Laser Hypsometer III, Haglöf Sweden) to the point where the diameter was 10 cm. The length and diameter of attached branches in standing dead trees were visually estimated. To account for wood density variation following decay, standing dead trees and their occasional branches were also classified according to their decay classes in the same way as for the line intersect samples (described in detail in the next section).

2.3 Coarse necromass wood density

Samples of dead wood that crossed the line intersect in the plots were taken to measure the density of coarse necromass. A chain-saw was used to cut a wood disk sample from hard pieces. Softer wood pieces were sampled using a machete. When pieces were non-homogenous (partly hard and partly soft), samples were also taken with a machete but were inevitably irregular. Void spaces were taken into account by visually estimating their proportion.

Coarse necromass wood density was then determined by the ratio of oven dry mass and fresh wood volume. The water-displacement method was used to determine fresh volume as it is a reliable and simple method (Chave 2005). It consists of carefully sinking segments from the wood samples in a water recipient using a thin needle. This method is done with the recipient placed on a balance. In this study a balance of 0.01 precision and 4000 g capacity was used, and the weight of the displaced water indicated in the balance is equal to the volume of the wood sample. Before measuring, the volume segments of samples in classes 1 and 2 were pre-wetted for about 2 hours to fill wood pores with water. Dry wood would absorb more water resulting in overestimated density values. As material in decay class 3 is very friable, samples in this class were pre wetted for several minutes. After volume measurement the segment samples were oven dried at 60 ºC until constant weight. The density of each sample segment wase then calculated and used to average the density of each decay class in each site.

2.4 Vegetation data

Vegetation parameters (basal area, number of trees and palms per area, aboveground biomass and wood density of living individuals) were acquired using available data from the permanent vegetation plots. A recent analysis by Feldpausch et al. (2012) indicates that by not including tree height in biomass estimates, biomass may be overestimated, in comparison with an allometric pan-tropical model for moist forests (Chave et al. 2005) by up to 16% and 22% for central and southern Amazonia, respectively. Hence, we should expect that including height in biomass estimation should decrease error in areas north and south of the Rio Amazonas.As tree height data were unavailable for the permanent sample plots, an allometric model presented in Feldpausch et al. (2012) to estimate tree height (*H*) was applied.

$$H = 48.131 \times (1 - \exp(-0.0375 \times D^{0.8228}) \quad (1)$$

where *D* is the tree diameter.

To estimate plot-level dry aboveground biomass (AGB) we utilise an allometric model developed by Feldpausch et al. (2012), this model uses a pan-tropical dataset and includes new published destructive data from South America and Africa. The variables included in this model are tree diameter at breast height (*D*), wood density (ρ_T) and height (*H*) for tree *T*.

$$AGB = \exp(-2.9205 + 0.9894 \times \ln(D^2 \times \rho_T \times H)) \quad (2)$$

According to unpublished data from Niro Higuchi's research group and cited by Chambers et al. (2000), each tree in Amazon has ~85% of their mass $\geq$ 10 cm in diameter, so we multiplied AGB estimated values of each tree by 0.85 to account for only wood fragments greater than 10 cm diameter stocks.

The wood density from living trees was obtained from a wood density database (Chave et al. 2009; Zanne et al. 2009). The individuals in each plot were matched to wood density by species level. In cases where this information was unavailable matches were made by genus average or family (as in Baker et al. 2004). When missing information for tree identification occurs, mean density of known trees weighted by basal area of the plot was used. Species level identifications have been made for 53.7% of stems, with an additional 37.9% identified only to genus, 6.2% only to family and 2.2% of tree individuals unidentified. At the BR-319 transect plots (south from the Rio Amazonas), there were no floristic data available. For those sites an average living wood density was therefore estimated by sampling wood cores in at least 20 trees per plot, (trees$\geq$30 cm diameter only, with a total of 1,005 trees sampled in the region, unpublished data from Juliana Schietti).

2.5 Soil data

Soil sampling methods followed an international standard protocol (http://www.geog.leeds.ac.uk/projects/rainfor/pages/manualstodownload.html) and are only briefly summarised here. A complete description can be found in Quesada et al. (2010). The World Reference Bases for soil resources is used here to classify soils (IUSS Working group, WRB 2006). Three soil pits were dug at the Ducke Reserve, and three at the BDFFP sites. At the southern sites, one soil pit was dug in each of six modules along BR-319. To increase spatial coverage of soil properties, auger sampling was performed in plots without soil pits along the BR-319 and BDFFP. All pits were 2 m deep, even if the effective soil depth was shallower. Effective soil depth is defined here as the depth where clear impeding layers to root growth occur. Soil was sampled from the pit walls to estimate bulk density using specially designed container-rings of known volume in the following depths: 0-10, 10-20, 20-30, 30-50, 50-100, 100-150, 150-200 cm.

Soil physical conditions that could imply limitation for root growth were quantified by scoring the characteristics of each soil with the help of a table (Table 1) that provides a semi-quantitative assessment of key soil physical properties (Quesada et al. 2010). These included an evaluation of effective soil depth, soil structure quality, topography and anoxic conditions. The score for each category is then summed to form an index of soil physical quality (Π), in which highest values indicate the most constrained soils. Π_1 is represented by the sum of the four soil physical parameters and Π_2 is the sum of three parameters but excluding anoxia. Scores given to soil physical properties are semi – quantitative allowing conversion of soil descriptions to be used in statistical analysis. All classifications scores were made by Demetrius Martins and Carlos Alberto Quesada.

2.6 Environmental data

Mean annual precipitation and precipitation in the driest quarter were obtained from WorldClim global coverage at a 30 arc-seconds (approximately1 km) resolution (Hijmans et al. 2005).

The topography data was obtained using a Digital Elevation Model (DEM) of SRTM image of 90 m spatial resolution from Shuttle Radar Topography Mission (SRTM). A topographic index (TI) that estimates drainage of each SRTM pixel (Moore et al. 1991) was calculated using ArcMap®. The TI is derived by:

$$TI = \ln\left(\frac{\propto}{tan\beta}\right) \qquad (3)$$

where α is the contributing upslope drainage area and β is the slope. Sites with higher TI values have greater drainage constrains (e.g. water saturated). This seemed important as there is a relationship between TI and tree species distribution (Feldpausch et al. 2006) that could influence necromass distribution across the landscape.

2.7 Calculations

Volume of line intersect sampling (V_{LIS}) (m^3 ha^{-1}) and fallen volume in each decay class was estimated using the following equation (van Wagner 1968):

$$V_{LIS} = \frac{\pi^2 x \sum d_i^2}{8\ x\ L} \qquad (4)$$

d_i is the diameter (cm) of log *i* and *L* (m) is the length of the transect line.

For the estimation of standing dead volume (V_{Belt}, m^3 ha^{-1}), Smalian's formula was used:

$$V_{Belt} = H\left[\frac{\pi\left(\frac{D_1}{2}\right)^2 + \pi\left(\frac{D_2}{2}\right)^2}{2}\right] \qquad (5)$$

where *H* (m) is the height of the tree, D_1 and D_2 are the diameters (cm) at 1.3 m above the ground and on the top of the snag, respectively. To estimate D_2 a taper function was used (Chambers et al. 2000):

$$D_2 = 1.59 \times D_1(H^{-0.091}) \qquad (6)$$

where D_2 is the diameter at height *H* for a trunk of given D_1. This is a robust equation defined for Central Amazonian trees and has already been used in other studies (Clark et al. 2002; Palace et al. 2007) Necromass (*N*, Mg ha^{-1}) in each of the three decay classes was calculated as follows:

$$N_i = V_i \times \rho_i \qquad (7)$$

where, V (m^3 ha^{-1}) and ρ (Mg m^{-3}) correspond respectively to dead mass, volume and density in decay class *i*.

To calculate error for each N_i (E_N) the following equation was used:

$$E_N = E_\rho V + \rho E_V \qquad (8)$$

where E_ρ and E_V are the errors in density and volume, respectively. Equation (8) is valid when V and density of the material in the respective class are not correlated. In this study covariance between V and density although significant (P=0.0175) was very small (r^2_{adj}=0.01965). Total error was estimated conservatively for all classes as a sum of errors in mass.

2.8 Statistical analysis

Each plot was considered as a sample unit in linear regressions (n=79). Simple correlations were used to choose which non-collinear variables could be combined in the same regression model (Figure 2). Necromass relationships with environmental, climatic and edaphic variables were explored, resulting in a large number of tests. Therefore, a sequential Bonferroni adjustment of Hochberg (1988) was used to adjust P values and to prevent Type 1 errors by selecting spurious correlations. Necromass values were ln (natural logarithm) transformed to improve normality. In an attempt to better understand landscape-scale necromass patterns, a second regression analysis approach was performed using each local sampling area (modules) as a sample unit (n=12). Therefore the BDFFP, the Ducke Reserve, and each module along the BR-319 separated by 40-60 km were all considered as individual samples. To compare mean density of decay classes in each forest type a two-way ANOVA was used. To analyse differences between necromass stocks in each soil level restriction (soil–forest association) a one-way ANOVA was used. Post-hoc comparisons were made using Tukey HSD test. All analyses were carried out R version 2.14.2 (R Development Core Team, 2012)

3 Results

3.1 Variations in edaphic properties

Sites located north of the Rio Amazonas usually had no soil physical restriction, being located on flat or gentle undulating terrain (Figure 1-3, Figure 4a). All these soils were very deep, had low subsoil bulk density (0.8–1.2 g cm^{-3}, at the reference depth of 50 cm), good particle aggregation (good structure, friable) and were unsaturated (Table 2). Soils in the southern plots (BR-319) were generally shallow (maximum effective soil depth about 50 to 100 cm), with high subsoil bulk density (1.0–1.7 g cm^{-3}), little or no aggregation (deficient structure, very hard and compact), were generally root-restrictive and had varying levels of anoxic conditions (from seasonally flooded with patches of stagnated water to soils showing deep redox features) (Table 2). Anoxic conditions were clearly identifiable in the field when stagnating water was lying over the soil or when soil saturation and hydromorphic features were evident (Figure 4b). There was, however, some variation in soil restriction levels along the BR-319 plots, with soils at some modules being severely constrained (index Π_1 ranging from 6 to 11) while the remaining plots/modules had lower restriction levels (index Π_1 ranging from 2 to 6).

Level of soil anoxia was the most distinctive physical restrictions found across the study areas (Figure 3). Other parameters such as effective soil depth and soil structure were also important and may influence vegetation across the BR-319, but the large variation in anoxia scores across the entire study area suggest that it may be an important driver for vegetation in the region. After soil characterization, plots were separated into three groups according to their physical constraints:. (1) plots in soils with no physical restriction (NR, index Π_1 value$\leq$2), (2) plots in soils with lower restriction levels occurring only across the interfluve (LRL, index Π_1 value$\leq$6 and Anoxia value$\leq$1) and (3) plots in soils with higher restriction levels, also occurring only across the interfluve (HRL, index Π_1 value$\geq$6 and Anoxia value>1).

3.2 Stocks of Necromass

The volume of necromass varied significantly among the different soil-forest associations and between decay classes (Table 3, two-way ANOVA, forest type, $F_{[2,228]}$=17.48, P<0.001, decay class, $F_{[2,228]}$=11.46, P<0.001, with interaction, $F_{[4,228]}$=2.89, P=0.023). The volume of total CWD in forests growing on NR soils (69.5±11.1 m^3 ha^{-1}) was similar to the volume for forests on LRL soil (69.5±11.6 m3 ha-1). However, forests with higher soil constraints had significantly lower volumes of CWD (33.8 ±2.0 m^3 ha^{-1}) than both other soil groups. The volume of CWD was similar among decay classes except in NR soil forests, where CWD volume was lower in the first decay class (recently added CWD) than in classes 2 and 3.

Densities of CWD samples were significantly different among decay classes, decreasing considerably with degree of decomposition (Table 1). Nevertheless, there was no significant difference between soil-forest association types with different levels of soil physical constraints (two-way ANOVA, decay class, $F_{[2,668]}=156.6$, $P<0.001$, forest types, $F_{[2,668]}=1.49$, $P=0.22$, significant interaction, $F_{[4,668]}=4.0$, $P=0.003$)

Necromass stocks varied systematically across our study area (Figure 1), but also typically varied widely in each location. The northern sites showed the largest variation, for instance, necromass ranged from 6.7 to 72.9 Mg ha^{-1} at Ducke Reserve. On the other hand, necromass stocks varied little and were consistently lower at modules 1 to 5 along the BR-319 road (just south of Manaus), but being also low at the module 11, located far south at the end of the BR-319 road. Along the middle (modules 6 to 10), necromass was locally highly variable.

Total necromass stocks followed the same pattern as total CWD volume, since necromass stock estimates are derived from site-specific CWD density values and the density of decay classes did not vary significantly among forest types (Table 1). Forests in NR soil had a mean necromass stock of 33.1±7.1 Mg ha^{-1} (Table 5) and these values did not differ significantly from LRL forest soils (35.1±7.2 Mg ha^{-1}). However, necromass stocks for HRL forest soils (16.1±2.6 Mg ha^{-1}) were significantly and substantially lower than in both other soil types (two-way ANOVA, forest type, $F_{[2,228]}=15.7$, $P<0.001$, decay class, $F_{[2,228]}=8.3$, $P<0.001$, no interaction, $P=0.2$).

3.2.1 Standing and fallen fractions of necromass

Table 4 shows that standing necromass did not significantly differ between forests in NR soils (10.3±1.6 Mg ha^{-1}) and those with LRL (6.9±1.0 Mg ha^{-1}). Lower restriction level forests and higher restriction level forests (4.4±0.7Mg ha^{-1}) were also not significantly different. Significant differences were only found between NR and HRL (one-way ANOVA, $F_{[2,76]}=6.9$, $P=0.002$). Stocks of standing necromass represented 20-30% of total necromass in all types of forests and this percentage did not differ significantly among forest types (one-way ANOVA, $F_{[2,76]}=1.9$, $P=0.16$). Fallen dead wood accounted for 69-79% of necromass stocks, and were higher in NR and LRL forests than in HRL (Table 4). The proportion of fallen stocks to total necromass did not differ among forests. Also, the ratio of standing to fallen dead wood was not different among forests. The necromass to AGB ratio in the NR forests (0.13±0.01) and LRL (0.17±0.01) was significantly greater than in HRL forests (0.08±0.01) (one way ANOVA, $F_{[2,76]}=13.88$, $P<0.001$).

3.3 Vegetation data

Variation in key vegetation parameters across our soil-forest associations is shown in Table 5 (unpublished data from Juliana. Schietti). Each of the three soil groups was associated with a distinct forest structure. Above ground biomass was highest at the NR forests (248.2±6.1 Mg ha^{-1}) and lowest at HRL (198.8±7.0 Mg ha^{-1}), but with LRL not being significantly different from NR. However, the number of stems per hectare increases in the orderNR<LRL<HRL, being significantly higher at HRL (774.2±29.5) than at both NR and LRL (597±8.7 and 653.6±24.2, respectively). Parameters associated with individual tree size were usually significantly different between the soil-forest associations. For instance, the average biomass per tree (AGB divided by number of stems, AGB per tree), was significantly different at each soil-forest class, being highest at NR (0.42±0.01 Mg), intermediate at LRL (0.34±0.02 Mg) and lowest at HRL (0.27±0.01 Mg). Mean tree height (estimated from DBH) was also significantly different among the classes (Table 5) but mean DBH was only significantly different between HRL (20.3 ±0.3 cm) and both NR and LRL, although LRL had slightly lower mean DBH than NR forests (23.1±0.3 and 22.5±0.4 cm, for NR and LRL respectively).

3.4 Necromass determinants across landscape

Table 6 shows the relationships between environmental variables and necromass stocks across our study sites in Central and Southern Amazonia (*n*=79). As necromass stocks often varied considerably at local scales (i.e. at the module level, Figure 1) we also performed our analysis using local averages, with values in parenthesis in Table 6 representing the results for regression models using averaged sites of each sampling location (*n*=12, for BDFF and the Ducke Reserve, and 10 PPBio modules at BR-319).

Necromass was significantly related to forest structure measures such as biomass, average biomass per tree (AGB divided by the number of stems), stand basal area and number of stems per hectare, but the degree of association was generally low (Figure 2, 3 and Table 6). Live wood specific gravity on the other hand was not related to necromass stocks and was the vegetation parameter that showed the least variation across the landscape. However, we note that parameters associated with average individual tree size such as mean diameter, mean height, and average biomass per tree were particularly important in explaining necromass variations. Average biomass per tree (AGB per tree) had a clear positive relationship with necromass (Figure 3j) and was the vegetation parameter that best explained necromass variation (r^2_{adj}=0.20). Mean tree diameter and mean tree height were also good predictors of necromass stocks (Figure 3g and 3h), showing that trees at HRL forests generally had smaller height and DBH than LRL and NR forests, but with LRL showing an intermediary behavior. Considering further the relationship between necromass stocks and vegetation parameters related to average maximum tree size (mean tree diameter, height and AGB per tree, Figure 3), we observe a clear separation among the different forest-soil association groups, with forests consistently showing lower necromass on HRL where trees are smaller, and high necromass in NR where trees are larger. Forests on LRL consistently appear as an intermediary group, with some superposition on NR, but with a clear separation from HRL, despite the fact that these two groups occur in the same geographical area (HRL and LRL only occur along the BR-319 interfluvial area).

Multiple regression models showed little improvement when compared to simple regression models. Collinearity was often a problem in our dataset and, as only non-collinear variables were used in multiple regressions (Figure 2), only one multiple regression model was selected (including AGB and stem density). This model accounted for ~20% of the variation (r^2_{adj}=0.20), but another model with a single parameter (AGB per tree) explained the same amount of variation in necromass, this thus being the best vegetation predictor of necromass variation across the landscape. When local averages (n=12) of vegetation structure and necromass were used, no regression model attained significance.

Soil physical properties varied greatly across the study areas and were generally negatively related to necromass (Figure 3a to 3e; Table 6). Individual soil parameters were significantly related to necromass, with anoxia level being the best correlated variable (r^2_{adj}=0.35, P<0.001 for n=79 and r^2_{adj}=0.75, P=0.003 for n=12). For instance, once soil anoxia was added to multiple regression models, no other parameter provided additional explanatory value. Effective soil depth and structure were also significantly related to necromass (r^2_{adj}=0.30, P<0.001 for n=79, and r^2_{adj}=0.57 P<0.05 for n=12, for effective soil depth), however structure was not significantly related when analysing necromass using local averages (n=12). Topography had a much weaker relationship with necromass due to the characteristics of the study sites discussed above, but with this still being significant when the plots were used as independent measures (i.e. no averages, r^2_{adj}=0.10, P=0.002 n=79). Finally, the continuous topographic index (TI) computed from the satellite-based SRTM DEM was also negatively related to necromass (r^2_{adj}=0.12, P=0.001, Figure 3f), with this most likely representing the gradient of soil anoxia across the study sites. Such TI is a proxy for hydrological gradients, with larger TI numbers representing poorer drainage conditions. Furthermore, TI is strongly correlated with the anoxia estimated parameter (Figure 2).

Π_1, which represents the combination of all physical parameters, was strongly related to necromass (r^2_{adj}=0.29, P<0.001 for n=79, and r^2_{adj}=0.63, P=0.018 for n=12). This varied from score 0 (very good physical conditions) to 11 (higher restriction level, Figure 3a) with the soils having high levels of constraint (Π_1>6) showing much lower values of necromass. The index Π_2 showed a response similar to Π_1 (Figure 3b) but with this having lower capacity to explain variations in necromass (r^2_{adj}=0.21, P<0.001 for n=79, and r^2_{adj}=0.37, P=0.221 for n=12). The only difference between Π_1 and Π_2 is the absence of anoxia in Π_2. The reduction in explanatory power in Π_2 suggests that anoxia accounts for a large fraction of the relationship between necromass and Π_1, thus strengthening the interpretation that anoxia may be a prime driver of necromass in our study area.

Edaphic drivers of necromass stocks could be obscured by varying vegetation biomass stocks, whereby larger AGB stocks produce larger necromass stocks. We therefore, performed similar analyses by normalising data using a necromass/above ground biomass ratio (N/AGB, Table 6). In general, the N/AGB ratio resulted in much weaker relationships with all parameters studied. Also, although there is some variation in precipitation along the main north/south axis of the study area, we found no significant relationship between necromass and climatic variables (mean annual precipitation and precipitation in the driest quarter of the year, Table 6).

4 Discussion

4.1 General landscape patterns

We found that fallen necromass represents the largest fraction of necromass in all forest types, and Standing/Fallen proportions were not different between forests, suggesting that the main mode of death may be similar across the examined forest types in Central Amazonia. Standing/Fallen ratios in our plots (0.29-0.59) were greater than those found by Palace et al. (2007) in eastern Amazonia (0.14-0.17), but much lower than found by Delaney et al. (1998) in Venezuela (0.80). These differences between regions indicate how the ratio of fallen to standing necromass varies across Amazonian landscapes in response to large-scale variation in the dominant mode of death (Chao et al. 2009b). However, despite being unable to find clear signs of variation in standing to fallen stocks within our study region in Central Amazonia, we still found that total necromass stocks differ significantly among different soil-forest associations.

Low stocks in HRL forests are similar to the ones reported by Martius (1997) in fertile floodplain forests (Várzea) in Central Amazonia and by Chao et al. (2008) from a floodplain forest in Peru. Both studies suggested that the lower stocks of necromass in these areas may be a result of higher wood decomposition rates under the cycle of wetting and drying, and we recognize that this could be one source of variation in necromass stocks in our study, although we have not attempted to measure decomposition rates. However, decomposition rates are negatively related with wood density (Chambers et al. 2000) and it is commonly believed that wood density is the primary wood trait controlling decomposition (Chao et al. 2009a, Chave et al. 2009), nevertheless we found virtually no difference in wood density among our study sites. Differences in average tree diameter (DBH per tree) between our soil-forest associations may be a source of variation in wood decomposition rates (van Geffen et al. 2010) since stem thickness and surface area may exert controls on decomposition, with greatest rates where trees are smallest diameter, since smaller trees have a proportionally greater surface area for decomposition.

Another source of necromass variation in floodplain soils has been suggested by Martius (1997) who argued that flooding may redistribute CWD from higher to lower forests. This cannot be applied in our study area since plots are not located adjacent to large rivers. Of our 79 plots, only nine were located in flooding areas, but none of them were close to high energy - high volume rivers that could carry wood away. All of the other plots located in high values of anoxia (Anoxia value$\geq$2) do not show large scale flooding influence. As opposed to this redistribution effect, we infer a mechanistic role for anoxia, as stagnated soil water creates an anaerobic environment inhibiting deep root growth (Gale and Barfod 1999), which may limit survival for most tree species. Interactions between such soil characteristics and vegetation structure and dynamics are likely to explain variation in necromass in our study, and this will be discussed further in section 4.2.

We found a large variability of necromass within sample locations (plots) (Figure 1).. As most sites were 0.5 ha, it is likely that sporadic and largely stochastic mortality events impact substantially on necromass estimates at any one point in time. Mortality and forest dynamics may vary greatly on minor spatial scales. For instance, Keller et al. (2004) showed great differences in necromass stocks between their study sites and those of Rice et al. (2004), only 20 km away.

However, we also found very low necromass variation in a particular region located at the first 300 km of BR-319 road, as well as at its end. Those sites (modules 1 to 5, and module 11) had systematically lower necromass stocks. They all have in common very high levels of soil anoxia, suggesting that there may be a mechanism consistently driving necromass in waterlogged forest. Nevertheless, despite the large variation within individual locations, we were able to find significant relationships with soil and vegetation structure. Overall, the results support our prior expectation that soil characteristics would substantially affect necromass stocks in our study area. Mechanisms for such controls may involve direct influence of soil constraints on residence time of trees mediated by tree mortality in each soil condition, which may affect the shape of trees and subsequently the forest structure and, therefore, necromass stocks. These issues will be discussed in the next section.

4.2 Underlying causes of variation

4.2.1 Soil and necromass

Sites in the north had no physical soil restriction. There was no steep topography, neither restriction to deep root growth enabling good tree anchorage. Soil structure in those areas is also non-restrictive, allowing good soil aeration and easy root growth. Good drainage is another characteristic of those soils, since they have good structure and are distant from the water table. In those conditions necromass production may be driven by random patterns of tree mortality, mostly related to senescence and storms (Gale and Barfod 1999, Toledo et al. 2012). Also random mortality patterns associated with small plot sizes (0.5 ha) may be the reason for the large variance in necromass found in the northern sites, while the waterlogged southern sites had lower variance associated most likely to more homogeneous mortality among plots.

Although tree mortality and necromass production seem to be random in the northern sites, restrictive soil physical conditions seem to be important necromass predictors at the southern sites. Topography in these areas is flatter than in north, but the other soil parameters varied greatly and showed an important role influencing necromass. Shallow soils with high bulk density, poor aggregation and severe anoxic conditions characterise physical properties restricting deep root growth. These usually impose great influence on tree establishment increasing rates of tree mortality (Gale and Barfod 1999; Gale and Hall 2001; Quesada et al.

2012). From all edaphic variables, anoxia seems to be the most relevant controlling necromass in our study area (Table 6). However, we observed that instead of increasing the volume of CWD and necromass stocks, severe soil physical conditions act by decreasing necromass stocks. Different mechanisms could explain this observation. First, restrictive soil conditions could decrease necromass stocks due to lower wood density in these areas, since average plot wood density appears to decrease with increasing soil physical limitations in broader gradients in Amazonia (Quesada et al. 2012). Nevertheless, wood density in our restrictive soils was not significantly lower than at non-restrictive soils. Thus, in these areas, soil restrictions may affect necromass more by changing the overall forest structure – reducing average tree size and thereby accelerating decomposition - than by selecting low wood density species common to more dynamic forests. Effective soil depth appears to be also important in controlling necromass (Table 6). Shallow soils with poor aggregation are responsible for increasing the potential of anoxic conditions (smaller root space). Also, as soil saturation exerts controls on soil weathering and development, it may imply that properties such as soil depth and structure are actually correlated with soil anoxia level due to common dependences in pedogenetic processes (Quesada et al. 2011). In this case relationships between these soil variables (depth and structure) with necromass could be interpreted as reflecting their correlation with anoxia (Figure 2). The same explanation could be given to interpret the relationships found with the indices, as Π_1, which takes the anoxia parameter into account, is the second best model, while the Π_2, that does not include anoxia, show a large decrease on model fit. Hence, soil depth and structure seem to be indirectly related with necromass due to its correlation with anoxia level, but also being likely to increase the deleterious effect of anoxia on trees, which we assume is the major environmental driver at the southern sites.

The topographic index, as anoxia, also characterised as a terrain drainage predictor, but showed a slightly lower relationship with necromass. A reasonable explanation is that drainage characteristics predicted by the TI are essentially based on topography (Moore et al. 1991). Therefore the TI points to poor drainage as water accumulation due to the contribution of upslope area. As anoxic soil conditions in LRL and HRL forests are in great part due to low soil porosity and high bulk density, poor drainage may not require a large upslope area so thatthis topographic parameter is only weakly related with necromass. Despite these limitations, the TI appears to be potentially useful in estimating necromass stocks over large areas where vegetation and soil measurements are lacking, and warrants additional study.

4.2.2 Vegetation and necromass

In general, vegetation parameters had weak relationships with necromass. Above-ground biomass at the stand level only weakly predicted necromass (r^2_{adj}=0.12 for *n*=79 and 0.34 for *n*=12). Above-ground biomass associated with stem density resulted in some improvement (r^2_{adj}=0.20 for *n*=79). The relationship between necromass and biomass found here was very similar to those presented by Chao et al. (2009a), who also found weak relationships between necromass stocks and above ground biomass across a broader area in Amazonia. Above-ground biomass per tree was the best single vegetation parameter for necromass prediction, though still weak (r^2_{adj}=0.20 for *n*=79), with this being very important to understand the mechanistic process involving soil constraints, forest structure and dynamics and necromass stocks.

We note that different levels of soil physical restrictions appear to significantly affect forest structure (Table 5, Juliana Schietti in prep.) exerting an important influencein how, and for how long, living biomass is stored in forest ecosystems. We suggest that harsh soil physical conditions limit the size that trees can attain by establishing a threshold imposed by tree mortality. Thus, soils may control biomass storage by controlling the mean residence time of trees. As soil restrictions hamper tree establishment, increasing mortality (Quesada et al., 2012), average residence time of carbon decreases, resulting in a forest population of thinner and shorter trees that store individually less biomass (also with more individuals per hectare). On the other hand, forests on soils without physical limitations tend to be populated by larger trees, simply because they can live longer. As a consequence, the death of individuals with higher biomass results in higher mass mortality input, and if forest trees are substantially smaller such as observed in HRL forests, then mortality mass input is smaller, even if controlling for slightly higher mortality rates. For instance, NR and LRL have respectively 1.6 and 1.3 higher AGB per tree than HRL. Therefore, mass mortality inputs in both of these soil-forest associations should be greater than in HRL sites with this resulting in a twofold difference of necromass stocks between NR-LRL and HRL sites. Even if HRL have slightly higher stem mortality rates due to restrictive soil features, forests in these areas should add less to necromass stocks since their trees show individually lower biomass. Hence, we reinforce an important relation already pointed by Chao et al. (2009a) between mortality mass input and necromass, since the death of biomass (biomass basis) may be more important to necromass stocks than stem mortality (stem basis). Furthermore, trees with higher biomass also have larger diameter and, therefore, lower decomposition rates may be expected (van

Geffen et al. 2010). The balance of these factors should result in higher necromass stocks in NR and LRL soil-forest associations and lower in HRL. In addition, as LRL sites already present certain edaphic restrictions, we speculate that necromass stocks are similar to those found in NR because there are subtle differences in tree mortality rates and tree size between NR and LRL. Non- restrictive soil features in NR soil-forest association allow development of taller and thicker trees with higher average biomass per tree. On the other hand, forests in LRL, that already have certain edaphic restrictions, have similar AGB to NR, however with differences in forest structure. Those forests, although showing only slightly smaller average diameter and wood density than trees in NR, may present lower height resulting in lower biomass per tree. Such features should result in lower necromass stocks in LRL than in NR. Nevertheless, the presence of some edaphic restrictions may slightly enhance tree mortality in LRL (Quesada et al. 2012), thus equaling or surpassing necromass stocks between those two soil-forest associations. As a consequence, necromass input may be similar in those areas with NR presenting lower biomass mortality and LRL having a slightly higher mortality of somewhat smaller trees.

Tree crown size variation among forest type and region is other forest structural property that may affect necromass stocks. Trees are also taller in central Amazonia compared to southern Amazonia (Nogueira et al. 2008; Feldpausch et al. 2011) and tree maximum height are altered by environmental conditions, forest structure and wood density (Banin et al 2012). Wider crowns would create a wider path when falling, and thus generate more necromass. In contrast, shorter trees could cause less damage in their shorter falling arc. These variations in tree height are found in our study area; however, tree crown size was not assessed in this study. Variations in canopy structure may occur along our 700 km transect from the Rio Amazonas to Porto Velho, spanning central and southern Amazonian forests, and warrants additional study.

N/AGB ratio was found to not vary constantly across landscape. Necromass contributes proportionally less in HRL forests (0.085±0.007, Table 5) than in NR and LRL. Proportions of N/AGB presented by NR (0.132±0.012) and LRL (0.167±0.014) are larger than proportions in north-western Amazonia (0.103±0.011) and similar to eastern Amazonia (0.132±0.013, Chao et al. 2009a) respectively, and only the latter includes sampled areas in (Central) Brazilian Amazonia. Furthermore, proportions in this study are lower than those presented by Palace et al. (2007) (0.19–0.20). This points to the importance of including necromass measurement in carbon balance studies since it is not an invariant proportion of

AGB. Also, such differences in necromass contributions are an indication of shifts in environmental mechanisms such as variations in wood decomposition, forest structure and dynamics across the Amazon Basin. As HRL trees present significantly lower average diameter than trees in the other two soil-forest associations, decomposition rates in these forests may be increased since that diameter is negatively related with decomposition (van Geffen et al. 2010). Since wood density was on average similar across all soil-forest associations differences in decomposition are not due to variation of wood density but may exist through differences in average tree diameter.

Reasons by which wood density did not decrease with impeding soil physical conditions, as observed in broader scales in Amazon (Quesada et al. 2012), are still not clear. However, we believe that the similarity in wood density across the study area may result from the small variation in soil fertility between the regions, particularly in the availability of soil cations. Quesada et al. (2012) discuss the role of soil properties influencing stand wood density, and suggest a role of soil K, along with soil physical properties in modulating stand wood density. The authors reported that low wood density in Amazonia is associated with higher cation availability which is not present in the soils bordering the BR-319. Although the soils at the interfluve are less weathered than their northern counterparts, the level of soil fertility is similar to the Manaus region. For instance, there is very little variation in sum of bases (Σ_B) between the Manaus region and soils along the BR-319, with an average Σ_B of 0.5 $cmol_c\ kg^{-1}$ in the Manaus area and only 0.2 $cmol_c\ kg^{-1}$ along the BR-319 (average 0-30cm depth for 10 profiles around our study sites, RADAMBRASIL, 1978). Therefore, despite the pressure imposed by limiting physical conditions that could favour low wood density species, the lack of soil cations, particularly K, may limit the dominance of low wood density species in the area.

4.2.3 Climate and necromass

Previous studies showed that precipitation has a positive effect on AGB (Malhi et al. 2004) and an indirect effect on necromass stocks could be expected. As climate was relatively uniform across our landscape transect, climatic factors such as mean annual precipitation and precipitation in the driest quarter of the year were not related with necromass stocks. However, occasional extreme, unusual events such as large storms (Negrón-Juárez et al. 2010) and droughts (Phillips et al. 2009) have potential to increase forest disturbance and thus necromass stocks.

4.3 Final remarks

Finally, we note that plot size is a challenge for CWD studies, and determining the adequate scale is of prime importance. Using module averages as sample units instead of independent plots resulted in a significant decrease in the noise present in our data. In contrast, grouping plots within clusters generally resulted in a lower number of significant relationships between CWD stocks and vegetation properties. These results suggest, as expected, that there is less variation in edaphic than in vegetation properties at the scale of our module (several kilometers). Therefore, estimating necromass at a local scale of 0.5 ha plots may not be ideal, and larger plots or a greater number of replications in close proximity should be more efficient to capture variation in AGB and necromass (Chambers et al. 2000).

5 Conclusion

This study fills a gap in understanding the causes of necromass variation across Central Amazonia. Necromass is an important element in carbon cycling. Considering wood as ~50% carbon, NR, LRL and HRL forest had, respectively, 16.5±3.5 Mg ha^{-1}, 17.5±3.6 Mg ha^{-1} and 8.2±1.3 Mg ha^{-1} of carbon in necromass stocks. Furthermore, differences were found between necromass stocks across the landscape and were due to levels of soil constraint affecting forest structure and dynamics, which in turn affect necromass. Necromass is positively related to biomass per tree and covaries negatively with soil anoxic/saturated soil conditions (based either on soil property scores or a continuous topographic index). Such edaphic constraint should act on vegetation structure and dynamics, decreasing tree height, diameter, and individual biomass. Such shifts across the landscape may result in a reduction of mass mortality, but increased rates of stem mortality and decomposition. This study thus highlights the importance of soil properties and its modulating power over forest structure, so influencing necromass gradients at landscape–scales, and helping determine the overall forest carbon balance of Amazonian forests.

Indication of figures and tables

Figure 1 Spatial distribution of necromass stocks for 79 forest plots in Central Amazonia. Size of circles is proportional to variation in necromass stocks. Topographic index in different sites, see legend for details**.**

Figure 2 Pairplot for the vegetation, soil and environmental variables. The lower panel contains Pearson correlation coefficients between variables. The upper panel contains the scatterplots, **Pt**: total precipitation, **Pdm**: precipitation in the driest quarter **AGB:** AGB estimated by Feldpausch et al. 2012 model, **AGB_tree**: average AGB per tree, **DBH**: average diameter at breast height**, Height**: average height, **Wsg**: live wood density, **Stem**: number of stems per hectare, **BA**: Basal area, **TI**: topographic index, **Necro**: Necromass, **Depth:** soil depth parameter, **Struc**: soil structure parameter, **Topo**: soil topography parameter, **Anoxia**: soil anoxia parameter, **INDEX1**: Π_1, **INDEX2**: Π_2

Figure 3. Simple relationships between necromass and environmental variables. All necromass values were ln transformed.

Figure 4 a) Typical Ferralsol for NR sites (BDFF, Manaus): deep soils presenting good particle aggregation, low bulk density and no physical impediments to root growth such as hardpans and anoxic conditions. **b)** Typical Plinthosol occurring at BR-319 (Module 1): Soil having short effective depth, and very high bulk density restricting root growth. Soft orange colouration in the first 50 cm and deep mottling showing marks of water fluctuation common to these soils.

Table 1 Score table for physical soil constraints

Soil physical constraints rating categories	**Score**
Effective soil depth (soil depth, hardpans)	
Shallow soils (less than 20 cm)	4
Less shallow (20 to 50 cm)	3
Hardpan or rock that allows vertical root growth; other soils between 50 and 100 cm deep.	2
Hardpan, rocks or C horizon ≥ 100 cm deep	1
Deep soils ≥ 150 cm	0
Soil structure	
Very dense, very hard, very compact, without aggregation, root restrictive	4
Dense, compact, little aggregation, lower root restriction	3
Hard, medium to high density and/or with weak or block like structure	2
Loose sand, slightly dense; well aggregated in sub angular blocks, discontinuous pans	1
Good aggregation, friable, low density	0
Topography	
Very steep > 45º	4
Steep 20º to 44º	3
Gentle undulating 8º to 19º	2
Gentle sloping 1º to 8º	1
Flat 0º	0
Anoxic conditions	
Constantly flooded; patches of stagnated water	4
Seasonally flooded; soils with high clay content and very low porosity and/or dominated by plinthite	3
Deep saturated zone (maximum high of saturation 50 cm deep); redox features	2
Deep saturated zone (maximum high of saturation > 100 cm deep); deep redox features	1
Unsaturated conditions	0

Table 2. Range of soil physical conditions at the three different soil-forest associations.

Soil Parameter	NR	LRL	HRL
Soil type	Ferralsol/Acrisol	Plinthosol	Gleysol/Plinthosol
Anoxia	0	0-1	2-4
Depth	0	0-2	1-4
Strucutre	0-1	1-2	2-4
Topography	0-2	0-1	0-1
Bulk densitiy (g $cm^{-3)}$	0.8-1.2	1.0-1.6	1.2-1.7
Π_1	0-2	2-6	6-11
Π_2	0-2	2-6	4-8

Forest type initials: NR – No restriction, LRL – Low restriction level and HRL – High restriction level

Table 3. Volume of CWD (mean ± 1 standard error, m^3 ha^{-1}), densities (mean ± standard error, g cm^{-3}) of coarse woody debris, and necromass (mean ± 1 standard error, Mg ha^{-1}) in forests with three levels of soil restriction. In parentheses are the number of samples.

Forest type †	NR[a, m, x]	LRL[a, m, x]	HRL[a, n, y]
CWD volume			
Class 1[m]	12.3±3.0	19.8±3.8	6.9±1.2
Class 2[n]	26.1±4.7	29.9±3.4	15.7±1.3
Class 3[n]	31.1±3.4	19.8±4.4	11.1±1.2
Total	69.5±11.1	69.5±11.6	33.7±3.7
Density decay class			
Class 1[a]	0.68±0.02 (75)	0.67±0.04 (20)	0.61±0.02 (88)
Class 2[b]	0.55±0.02 (66)	0.53±0.03 (43)	0.48±0.01 (176)
Class 3[c]	0.32±0.01 (88)	0.34±0.02 (24)	0.33±0.02 (97)
Necromass			
Class 1[x]	8.4±2.3	13±3.3	4.2±0.9
Class 2[y]	14.4±3.1	15.3±2.7	7.7±0. 8
Class 3[x]	10.3±1.4	6.8±1.9	4.1±0.7
Total	33.1±6.8	35.1±7.9	16±2.4

Results of Tukey's HSD test are labeled by lowercase letters a, b and c for density decay classes; m and n for CWD volume; x and y for necromass.

†Forest types initials: NR – No physical soil restriction, LRL – Low physical soil restriction level, HRL – High physical soil restriction level.

Table 4. Necromass (mean ± standard error, Mg ha^{-1}) of fallen and standing CWD in forests with three levels of soil restriction in plots north and south of the Rio Amazonas

Forest types	NR $^{a, x}$	LRL $^{ab, x}$	HRL $^{b, y}$
Standing			
Class 1	3.8±1.1	2.7±0.9	1.2±0.3
Class 2	4.2±1.0	2.7±0.7	2.2±0.5
Class 3	2.4±0.5	1.6±0.7	1.0±0.2
Fallen			
Class 1	4.7±1.4	10.6±2.5	3.0±0.6
Class 2	10.2±2.3	13.1±1.4	5.5±0.6
Class 3	7.9±1.2	5.1±1.3	3.2±0.4

Results of Tukey's HSD test are labeled by lowercase letters a and b for total standing necromass; x and y for total fallen necromass

Table 5. Average vegetation parameters, necromass and Necromass/AGB ratio in the three soil-forest associations in plots north and south of the Rio Amazonas. Different letters indicate significant differences between means (Tukey HSD test, *P*<0.05).

Forest types	NR	LRL	HRL
AGB (Mg ha^{-1})	248.2±6.1^{a}	223.9±13.8^{a}	198.8±7.0^{b}
Stems	597.9±8.7^{a}	653.6±24.2^{a}	774.2±29.5^{b}
AGB per tree (Mg)	0.42±0.01^{a}	0.34±0.02^{b}	0.27±0.01^{c}
Mean height (m)	16.5±0.1^{a}	16.0±0.1^{b}	15.4±0.1^{c}
DBH (cm)	23.1±0.3^{a}	22.5±0.4^{a}	20.3±0.3^{b}
Necro (Mg ha^{-1})	33.1±7.1^{a}	35.1±7.2^{a}	16.1±2.6^{b}
Necro/AGB	0.13±0.01^{a}	0.17±0.01^{a}	0.09±0.01^{b}

†Necro/AGB: ratio of total necromass to above ground biomass (for trees>10 cm dbh).

Table 6. Relationships between independent variables and necromass stocks (*n*=79) across central and southern Amazonia. Results in parentheses are for regressions using averaged sites of each sampling location (*n*=12).

Variable	Intercept	Coefficient	r^2_{adj}	*P*
Necromass with soil physical constraints:				
Π_1	3.540 (3.712)	-0.086 (-0.100)	0.288 (0.629)	< 0.001 (0.018)
Π_2	3.518 (3.661)	-0.110 (-0.125)	0.206 (0.365)	< 0.001 (0.221)
Anoxia	3.456 (3.550)	-0.258 (-0.252)	0.350 (0.747)	< 0.001 (0.003)
Depth	3.414 (3.503)	-0.244 (-0.263)	0.295 (0.566)	< 0.001 (0.037)
Structure	3.433 (3.630)	-0.164 (-0.218)	0.198 (0.411)	< 0.001 (0.190)
Topography	3.016 (3.058)	0.243 (0.432)	0.101 (0.166)	0.017 (0.666)
N/AGB with soil physical constraints:				
Π_1	0.147 (-1.807)	-0.006 (-0.065)	0.096 (0.402)	0.016 (0.222)
Π_2	0.143 (-1.865)	-0.007 (-0.077)	0.052 (0.178)	0.148 (0.804)
Anoxia	0.143 (-1.889)	-0.019 (-0.181)	0.142 (0.591)	0.001 (0.031)
Depth	0.139 (-1.965)	-0.017 (-0.159)	0.108 (0.286)	0.008 (0.551)
Structure	0.138 (-1.912)	-0.010 (-0.119)	0.050 (0.143)	0.186 (0.804)
Topography	0.111 (-2.224)	0.018 (0.194)	0.040 (-0.035)	0.283 (0.804)
Necromass with TI:	4.327 (5.445)	-0.125 (-0.230)	0.120 (0.343)	0.009 (0.225)
Necromass with vegetation:				
AGB	2.170 (1.472)	0.004 (0.008)	0.119 (0.336)	0.009 (0.225)
AGB per tree	2.224 (2.916)	2.673 (0.095)	0.198 (0.147)	<0.001 (0.666)
Stems density	3.965 (3.674)	-0.001 (-0.001)	0.090 (-0.023)	0.025 (1.000)
Basal area	2.136 (1.333)	0.037 (0.069)	0.045 (0.171)	0.120 (0.602)
Wood specific gravity	3.403 (3.130)	-0.379 (0.001)	-0.011 (-0.1)	0.721 (1.000)
AGB + Stem density	3.001 (2.061)	-0.001 (-0.001)	0.203 (0.388)	0.001 (0.311)
DBH	1.181 (0.371)	0.089 (0.130)	0.108 (0.242)	0.012 (0.219)
Height	-1.769 (-4.004)	0.308 (0.453)	0.127 (0.316)	0.008 (0.208)
N/AGB with vegetation:				
AGB	0.127 (-2.658)	0.000 (0.002)	-0.012 (-0.045)	0.965 (0.804)
Stems density	0.215 (-1.619)	0.000 (-0.001)	0.094 (0.033)	0.042 (0.804)
Basal area	0.177 (-2.590)	-0.002 (0.015)	0.003 (-0.079)	0.965 (0.804)
Wood specific gravity	0.236 (-1.420)	-0.162 (-1.066)	0.012 (-0.061)	0.965 (0.804)
AGB + Stem densitiy	0.226 (-2.117)	0.000 (-0.001)	0.084 (0.005)	0.148 (0.804)
DBH	-3.327 (-4.102)	0.049 (0.090)	0.028 (0.159)	0.509 (0.804)
Height	-4.690 (-6.568)	0.153 (0.278)	0.026 (0.147)	0.509 (0.804)
Necromass with Climate:				
Total precipitation	2.256 (0.820)	0.000 (0.001)	0.000 (0.111)	0.632 (0.666)
Prec. in the driest quarter	2.779 (2.796)	0.001 (0.001)	0.009 (-0.053)	0.590 (1.000)
N/AGB with Climate:				
Total precipitation	0.067 (-3.727)	0.000 (0.001)	-0.009 (0.048)	0.965 (0.804)
Prec. in the driest quarter	0.121 (0.048)	0.000 (-2.295)	-0.013 (0.000)	0.965 (0.804)

Figure 1

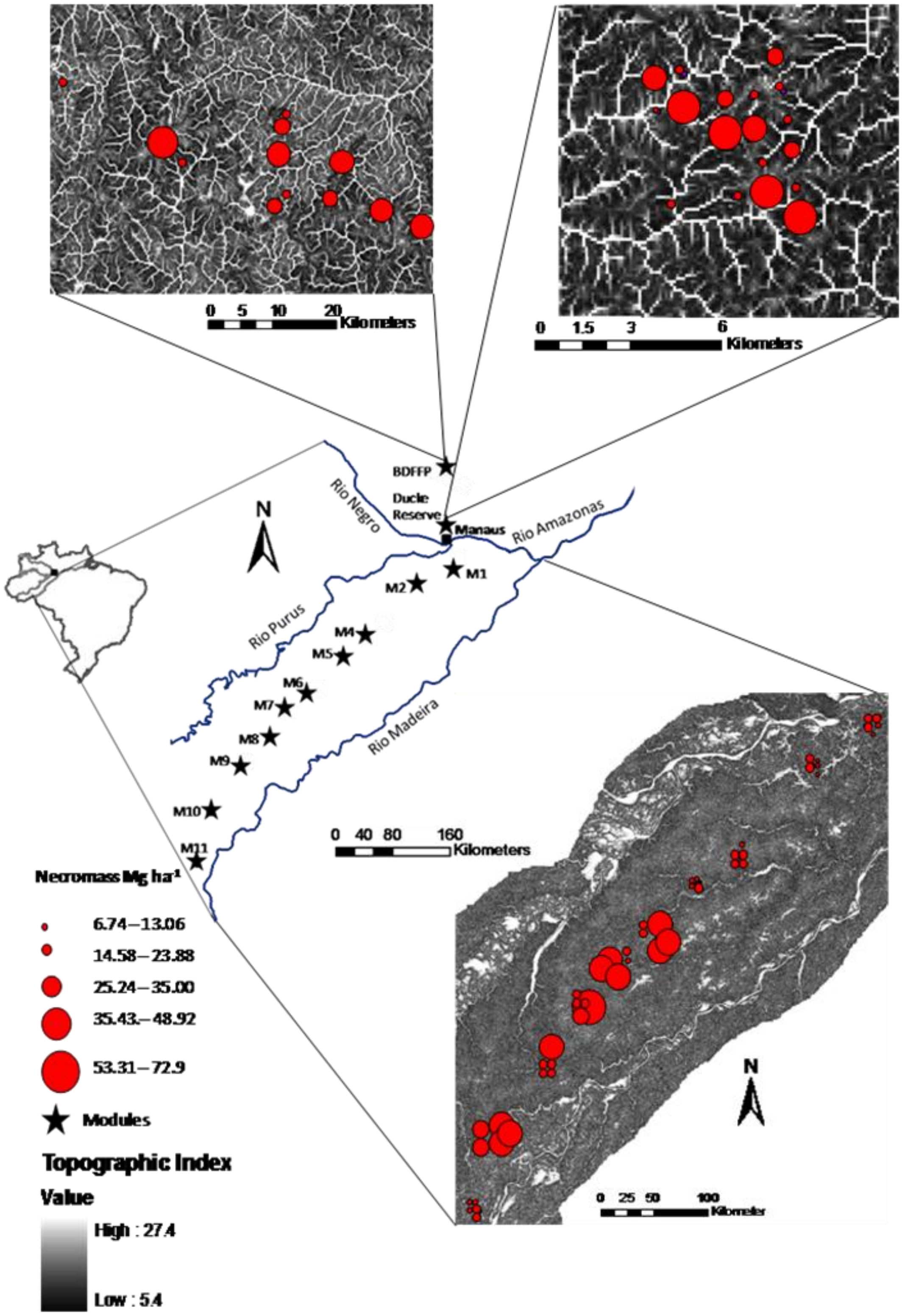

0 5 10 20 Kilometers
0 1.5 3 6 Kilometers
BDFFP
Ducke Reserve
Manaus
Rio Negro
Rio Amazonas
N
M1
M2
Rio Purus
M4
M5
M6
M7
M8
M9
M10
M11
Rio Madeira
0 40 80 160 Kilometers
Necromass Mg ha-1
6.74 – 13.06
14.58 – 23.88
25.24 – 35.00
35.43 – 48.92
53.31 – 72.9
Modules
Topographic Index
Value
High : 27.4
Low : 5.4
N
0 25 50 100 Kilometer

Figure 2

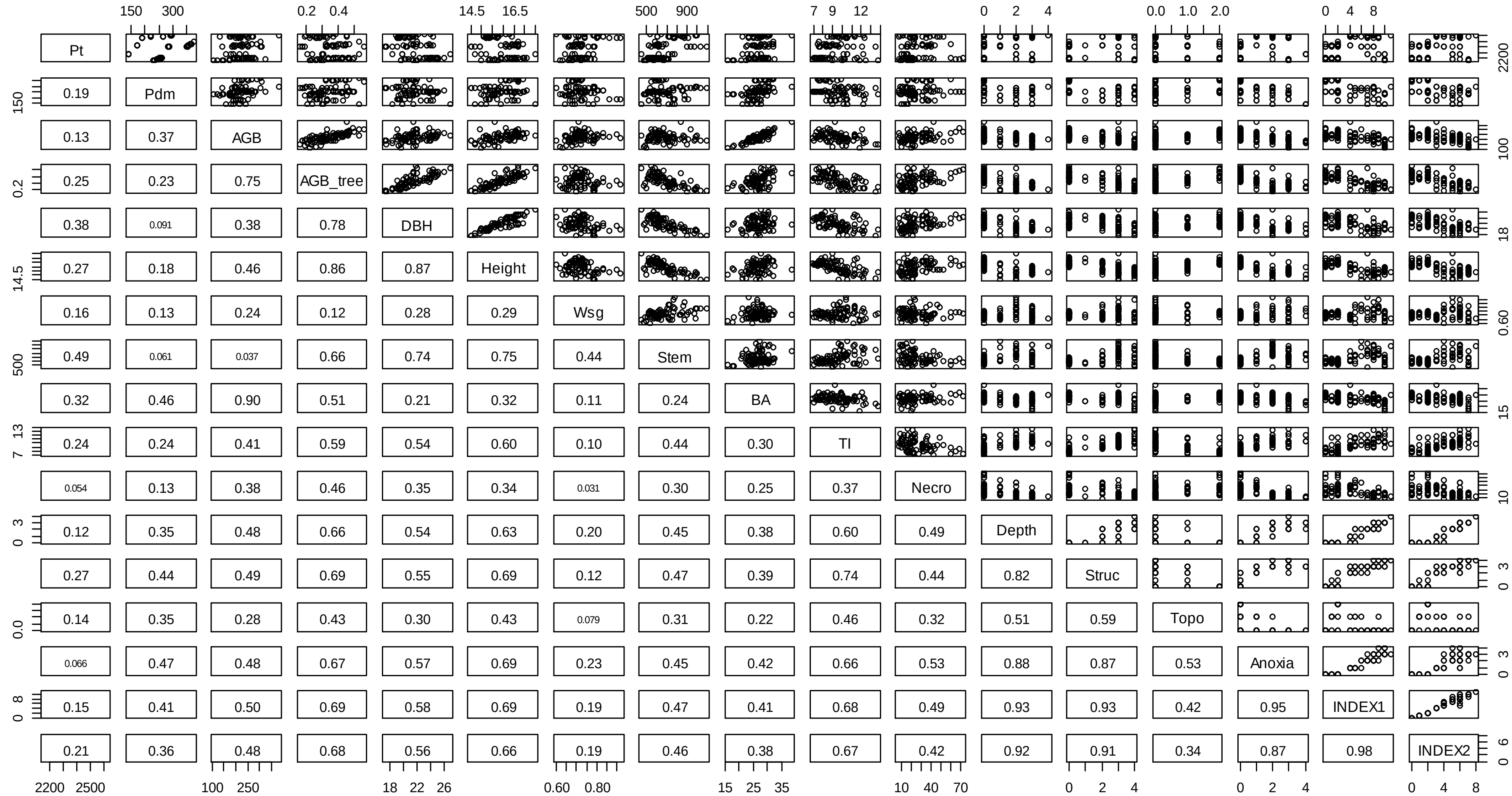
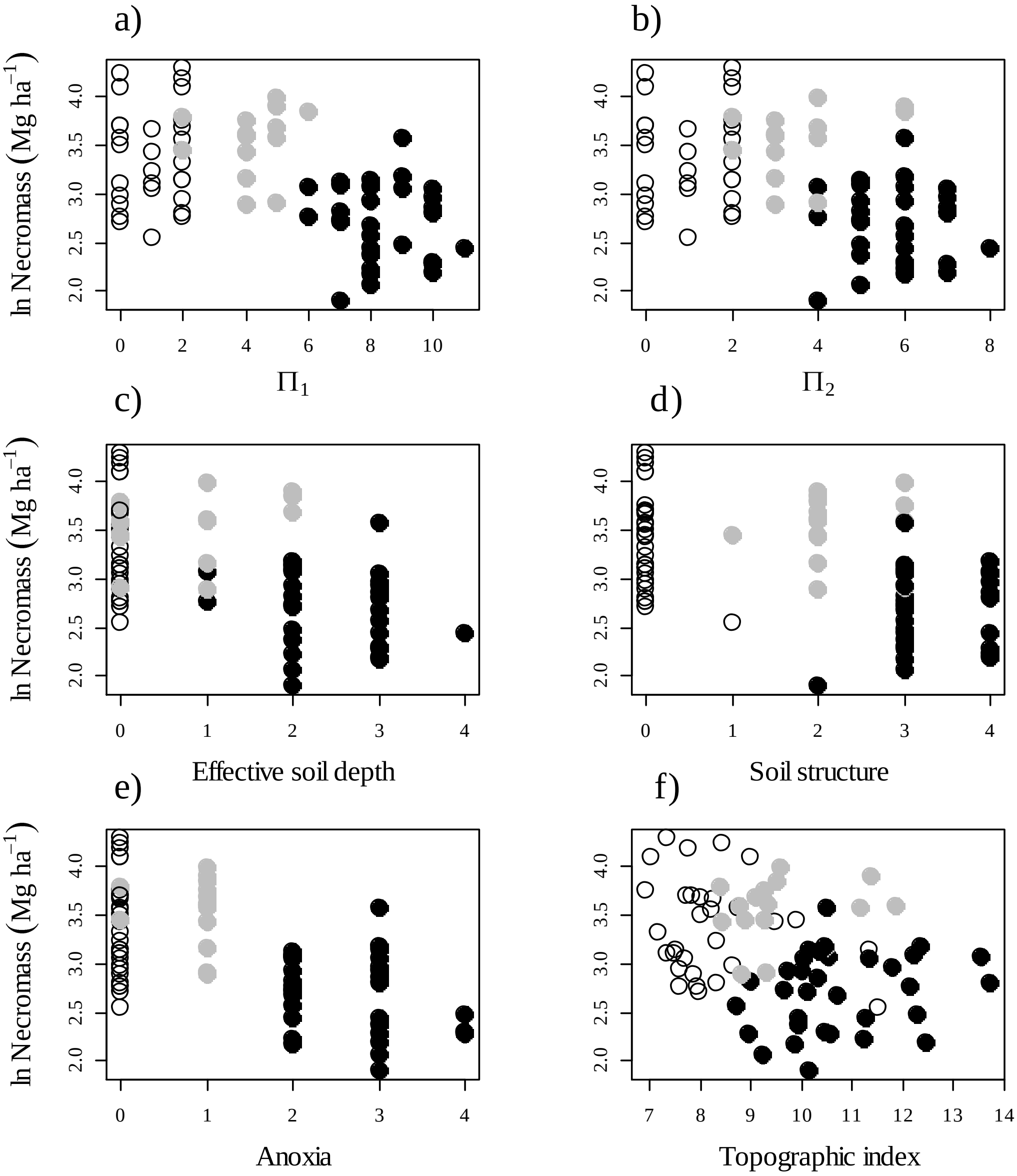
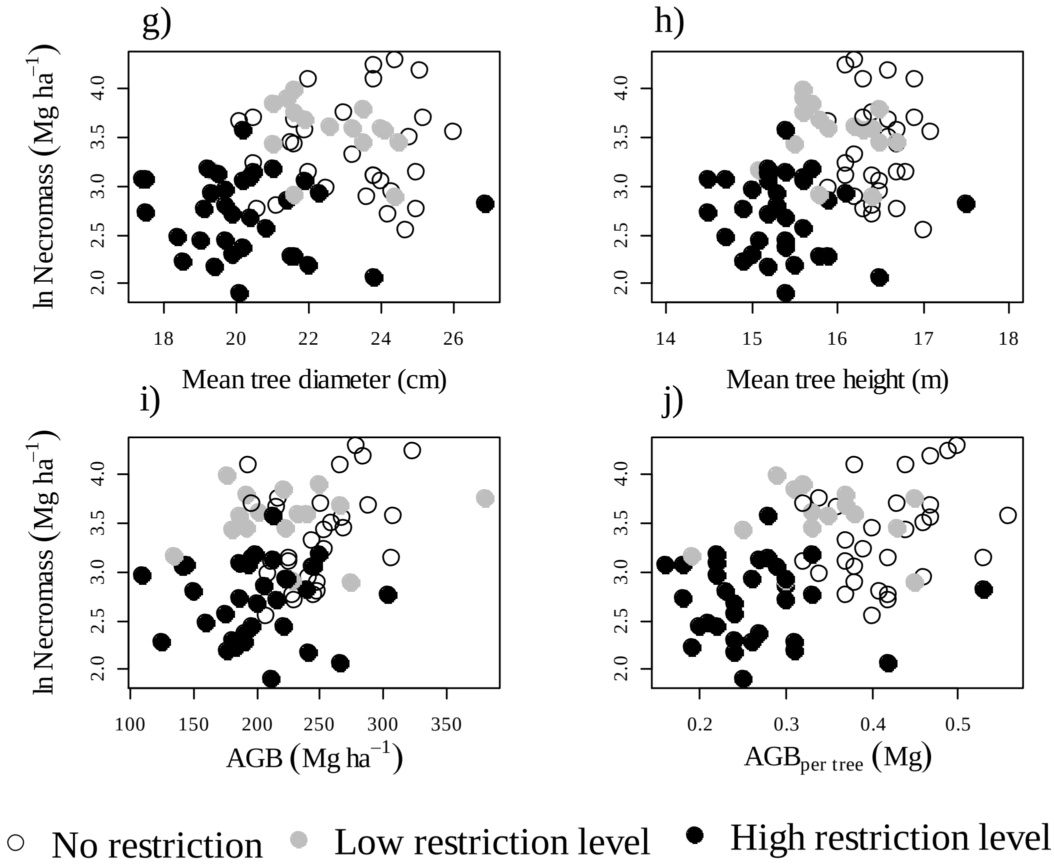

Pt
0.19 Pdm
0.13 0.37 AGB
0.25 0.23 0.75 AGB_tree
0.38 0.091 0.38 0.78 DBH
0.27 0.18 0.46 0.86 0.87 Height
0.16 0.13 0.24 0.12 0.28 0.29 Wsg
0.49 0.061 0.037 0.66 0.74 0.75 0.44 Stem
0.32 0.46 0.90 0.51 0.21 0.32 0.11 0.24 BA
0.24 0.24 0.41 0.59 0.54 0.60 0.10 0.44 0.30 TI
0.054 0.13 0.38 0.46 0.35 0.34 0.031 0.30 0.25 0.37 Necro
0.12 0.35 0.48 0.66 0.54 0.63 0.20 0.45 0.38 0.60 0.49 Depth
0.27 0.44 0.49 0.69 0.55 0.69 0.12 0.47 0.39 0.74 0.44 0.82 Struc
0.14 0.35 0.28 0.43 0.30 0.43 0.079 0.31 0.22 0.46 0.32 0.51 0.59 Topo
0.066 0.47 0.48 0.67 0.57 0.69 0.23 0.45 0.42 0.66 0.53 0.88 0.87 0.53 Anoxia
0.15 0.41 0.50 0.69 0.58 0.69 0.19 0.47 0.41 0.68 0.49 0.93 0.93 0.42 0.95 INDEX1
0.21 0.36 0.48 0.68 0.56 0.66 0.19 0.46 0.38 0.67 0.42 0.92 0.91 0.34 0.87 0.98 INDEX2

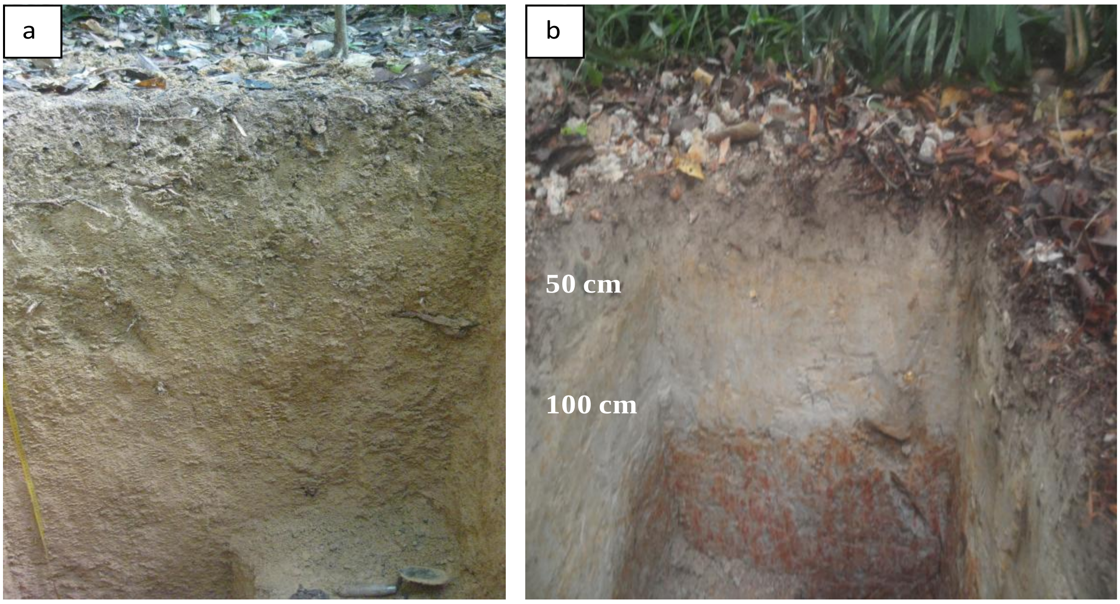
Figure 3


a)
b)
c)
d)
e)
f)
ln Necromass (Mg ha^{-1})
Π_1
Π_2
Effective soil depth
Soil structure
Anoxia
Topographic index



g)
h)
i)
j)
ln Necromass (Mg ha⁻¹)
2.0
2.5
3.0
3.5
4.0
18
20
22
24
26
Mean tree diameter (cm)
14
15
16
17
18
Mean tree height (m)
100
150
200
250
300
350
AGB (Mg ha⁻¹)
0.2
0.3
0.4
0.5
AGB per tree (Mg)
No restriction
Low restriction level
High restriction level

Figure 4



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7 Conclusão

Este estudo preenche uma lacuna na compreensão das causas de variação de necromassa ao longo da Amazônia Central. Necromassa é um elemento importante no ciclo do carbono. Ao considera-se a madeira com cerca de 50% de carbono, as florestas NR, LRL e HRL tinham 16,5 ± 3,5 Mg C ha^{-1}, 17,5 ± 3,6 Mg C ha^{-1} e 8,2 ± 1,3 Mg C ha^{-1} de carbono nos estoques de necromassa, respectivamente. Além disso, encontramos diferenças entre os estoques de necromassa ao longo de toda a paisagem devido aos níveis de restrição do solo afetando a estrutura da floresta e dinâmica, que por sua vez afetam necromassa. Necromassa é positivamente relacionada com a biomassa por árvore e covaria negativamente com as condições anóxicas/saturação do solo (baseadas nas pontuações das propriedades do solo ou de um índice contínuo topográfico). Tais restrições edáficas devem agir sobre a estrutura e dinâmica da vegetação diminuindo a altura média das árvores, diâmetro e biomassa individual. Tais mudanças ao longo da paisagem parecem resultar numa diminuição na mortalidade de massa e aumento das taxas de mortalidade e de decomposição (Figura 5). Finalmente, este trabalho destaca a importância das propriedades do solo e seu poder de modulação sobre a estrutura da floresta, atuando como fatores controladores dos gradientes de necromassa na escala de paisagem e influenciando todo o balanço de carbono das florestas amazônicas.

Apêndice I

PG-ECO-INPA
PÓS-GRADUAÇÃO EM ECOLOGIA

INPA
INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA

AULA DE QUALIFICAÇÃO

PARECER

Aluno(a): DEMÉTRIUS LIRA MARTINS
Curso: ECOLOGIA
Nível: MESTRADO
Orientador(a): FLÁVIO JESUS LUIZÃO
Co-orientador(es): CARLOS QUESADA e TED FELDPAUSCH

Título:

"Estoques de necromassa e densidade da madeira em função de fatores edáficos e ambientais no estado do Amazonas".

BANCA JULGADORA:

TITULARES:
Philip M. Fearnside (INPA)
Paulo Maurício Graça (INPA)
Jochen Schoengart (INPA)

SUPLENTES:
Euler M. Nogueira (INPA)
João Ferraz (INPA)

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Philip M. Fearnside (INPA)	(X) Aprovado	( ) Reprovado	[signature]
Paulo Maurício Graça (INPA)	(X) Aprovado	( ) Reprovado	[signature]
Jochen Schoengart (INPA)	(X) Aprovado	( ) Reprovado	[signature]
Euler M. Nogueira (INPA)	( ) Aprovado	( ) Reprovado	
João Ferraz (INPA)	( ) Aprovado	( ) Reprovado	

Manaus(AM), 18 de abril de 2011

OBS: O aluno apresentou a aula durante 43 minutos e respondeu às perguntas da banca. Foram feitas várias sugestões sobre a aula e sobre a metodologia e desenho do estudo.

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Apêndice II

INPA
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PG·ECO·INPA
PÓS-GRADUAÇÃO EM ECOLOGIA

GOVERNO FEDERAL
BRASIL
PAÍS RICO É PAÍS SEM POBREZA

ATA DA DEFESA PÚBLICA DA DISSERTAÇÃO DE MESTRADO DO PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA DO INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA.

Aos 13 dias do mês de agosto do ano de 2012, às 09:00 horas, na sala de aula do Programa de Pós Graduação em Ecologia PPG ECO/INPA, reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: o(a) Prof(a). Dr(a). **Bruce Walker Nelson**, do Instituto Nacional de Pesquisas da Amazônia -INPA, o(a) Prof(a). Dr(a). **Phillip Martin Fearnside**, do Instituto Nacional de Pesquisas da Amazônia - INPA e o(a) Prof(a). Dr(a). **Laszlo Nagy**, do Instituto Nacional de Pesquisas da Amazônia - INPA/LBA, tendo como suplentes o(a) Prof(a). Dr(a). Paulo Mauricio Lima de Alencastro Graça, do Instituto Nacional de Pesquisas da Amazônia - INPA e o(a) Prof(a). Dr(a). João Baptista Silva Ferraz, do Instituto Nacional de Pesquisas da Amazônia - INPA, sob a presidência do(a) primeiro(a), a fim de proceder a argüição pública do trabalho de **DISSERTAÇÃO DE MESTRADO** de **DEMÉTRIUS LIRA MARTINS**, intitulado "Variações nos estoques florestais de necromassa e densidade da madeira morta em função de fatores edáficos e ambientais na Amazônia Central", orientado pelo(a) Prof(a). Dr(a). Flávio Jesus Luizão, do Instituto Nacional de Pesquisas da Amazônia – INPA e co- orientado pelo(a) Prof(a). Dr(a). Carlos Alberto Nobre Quesada, do Instituto Nacional de Pesquisas da Amazônia - INPA.

Após a exposição, o(a) discente foi arguido(a) oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

[X] APROVADO(A) [ ] REPROVADO(A)

[X] POR UNANIMIDADE [ ] POR MAIORIA

Nada mais havendo, foi lavrada a presente ata, que, após lida e aprovada, foi assinada pelos membros da Comissão Examinadora.

Prof(a).Dr(a). Bruce Walker Nelson ______________________

Prof(a).Dr(a). Phillip Martin Fearnside ______________________

Prof(a).Dr(a). Laszlo Nagy ______________________

____
Coordenação PPG-ECO/INPA

Apêndice III

Instituto Nacional de Pesquisas da Amazônia - INPA
Graduate Program in Ecology

Referee evaluation sheet for MSc thesis

Title: **Forest necromass stocks and coarse woody debris density vary as a function of edaphic and environmental factors in Central Amazonia**

Candidate: **DEMETRIUS LIRA MARTINS**

Supervisor: **Flávio J. Luizão**
Co-supervisors: **Carlos Alberto N. Quesada** and **Ted Feldpausch**

Examiner: **Kuo-Jung Chao**

Please check one alternative for each of the following evaluation items, and check one alternative in the box below as your final evaluation decision.

	Excellent	Good	Satisfactory	Needs improvement	Not acceptable
Relevance of the study	( )	( )	( )	(√)	( )
Literature review	( )	(√)	( )	( )	( )
Sampling design	( )	(√)	( )	( )	( )
Methods/procedures	( )	(√)	( )	( )	( )
Results	( )	( )	( )	(√)	( )
Discussion/conclusions	( )	( )	( )	(√)	( )
Writing style and composition	(√)	( )	( )	( )	( )
Potential for publication in peer reviewed journal(s)	( )	( )	( )	(√)	( )

FINAL EVALUATION

( ) Approved without or minimal changes

( ) Approved with changes (no need for re-evaluation by this reviewer)

(√) Potentially acceptable, conditional upon review of a corrected version (The candidate must submit a new version of the thesis, taking into account the corrections asked for by the reviewer. This new version will be sent to the reviewer for a new evaluation only as acceptable or not acceptable)

( ) Not acceptable (This product is incompatible with the minimum requirements for this academic level)

Kuo Jung Chao

______________, __15th May, 2012____, ______________________

Place — Date — Signature

Additional comments and suggestions can be sent as an appendix to this sheet, as a separate file, and/or as comments added to the text of the thesis. Please, send the signed evaluation sheet, as well as the annotated thesis and/or separate comments by e-mail to pgecologia@gmail.com and claudiakeller23@gmail.com or by mail to the address below. E-mail is preferred. A scanned copy of your signature is acceptable.

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PG-ECO-INPA

Instituto Nacional de Pesquisas da Amazônia - INPA
Graduate Program in Ecology

INPA

Referee evaluation sheet for MSc thesis

Title: **Forest necromass stocks and coarse woody debris density vary as a function of adaphic and environmental factors in Central Amazonia**

Candidate: **DEMETRIUS LIRA MARTINS**

Supervisor: **Flávio J. Luizão**
Co-supervisors: **Carlos Alberto N. Quesada** and **Ted Feldpausch**

Examiner: Dr. Michael William Palace

Please check one alternative for each of the following evaluation items, and check one alternative in the box below as your final evaluation decision.

	Excellent	Good	Satisfactory	Needs improvement	Not acceptable
Relevance of the study	( )	(X)	( )	( )	( )
Literature review	( )	( )	(X)	( )	( )
Sampling design	( )	(X)	( )	( )	( )
Methods/procedures	(X)	( )	( )	( )	( )
Results	(X)	( )	( )	( )	( )
Discussion/conclusions	( )	(X)	( )	( )	( )
Writing style and composition	(X)	( )	( )	( )	( )
Potential for publication in peer reviewed journal(s)	(X)	( )	( )	( )	( )

FINAL EVALUATION

( ) Approved without or minimal changes

(X) Approved with changes (no need for re-evaluation by this reviewer)

( ) Potentially acceptable, conditional upon review of a corrected version (The candidate must submit a new version of the thesis, taking into account the corrections asked for by the reviewer. This new version will be sent to the reviewer for a new evaluation only as acceptable or not acceptable)

( ) Not acceptable (This product is incompatible with the minimum requirements for this academic level)

Durham, NH ___ 5/10/2012 ___ [signature]
Place ___ Date ___ Signature

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Instituto Nacional de Pesquisas da Amazônia - INPA
Graduate Program in Ecology

Referee evaluation sheet for MSc thesis

Title: **Forest necromass stocks and coarse woody debris density vary as a function of edaphic and environmental factors in Central Amazonia**

Candidate: **DEMETRIUS LIRA MARTINS**

Supervisor: **Flávio J. Luizão**
Co-supervisors: **Carlos Alberto N. Quesada** and **Ted Feldpausch**

Examiner: **Michael Keller**

Please check one alternative for each of the following evaluation items, and check one alternative in the box below as your final evaluation decision.

	Excellent	Good	Satisfactory	Needs improvement	Not acceptable
Relevance of the study	(X)	( )	( )	( )	( )
Literature review	(X)	( )	( )	( )	( )
Sampling design	( )	( )	( )	(X)	( )
Methods/procedures	( )	( )	( )	(X)	( )
Results	( )	( )	( )	(X)	( )
Discussion/conclusions	( )	(X)	( )	( )	( )
Writing style and composition	(X)	( )	( )	( )	( )
Potential for publication in peer reviewed journal(s)	( )	( )	( )	( )	(X)

FINAL EVALUATION

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Campinas, SP, May 22, 2012

Michael Keller

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