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ESTOQUE DE NUTRIENTES NA SERAPILHEIRA FINA E GROSSA EM FUNÇÃO DE FATORES EDÁFICOS EM FLORESTAS DO AMAZONAS, BRASIL

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Sinopse:

Estudaram-se os estoques de nutrientes na serapilheira fina e grossa em florestas de terra-firme da Amazônia Central localizadas em diferentes tipos de solo. As diferenças nas propriedades físicas e químicas do solo e sua influência no papel da serapilheira como fonte ou sumidouro de nutrientes na floresta foram abordadas.

Palavras-chave: Necromassa, ciclagem de nutrientes, fertilidade do solo, restrições físicas do solo, decomposição.

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“Sou um monte confuso de forças cheias de infinito
Tendendo em todas as direcções para todos os lados do espaço,
A Vida, essa coisa enorme, é que prende tudo e tudo une”
(Álvaro de Campos-Mensagem)

Resumo

O papel que a serapilheira grossa desempenha como fonte ou sumidouro de nutrientes e os processos que controlam a dinâmica desse compartimento tem grande influência na ciclagem de nutrientes no ecossistema florestal. A dinâmica e estrutura florestal amazônica estão associadas à variedade de solos ao longo da Bacia, no que se refere a propriedades físicas e químicas dos mesmos. A interação entre esses fatores pode, por sua vez, influenciar na quantidade de serapilheira fina (principalmente folhas sobre o chão da floresta) e grossa (troncos e galhos caídos com diâmetro ≥ 10 cm) produzida pela floresta, bem como controlar a taxa de liberação e estoque dos nutrientes retidos nesses resíduos. A relação entre propriedades dos solos e nutrientes na serapilheira foram avaliadas em 49 parcelas de 0.5 ha em florestas de terra firme localizadas ao norte e sul de Manaus. As florestas ao norte corresponderam à parcelas da Reserva Ducke e PDBFF, enquanto que ao sul, foram estudadas parcelas localizadas ao longo da BR-319 (módulos M1, M2, M4, M5, M8, M9 e M11), com diferentes graus de hidromorfismo. As parcelas foram agrupadas em nove módulos, de acordo com a proximidade e distribuição das mesmas, sendo sete ao longo do interflúvio Purus-Madeira (BR-319) e dois ao norte de Manaus (Reserva Ducke e PDBFF). Os solos foram classificados quanto às suas condições físicas, de acordo com o nível de restrição imposto ao desenvolvimento da vegetação, e também quanto à fertilidade nos primeiros 20 cm de solo. Foram avaliadas as concentrações e estoques de nutrientes na serapilheira fina e grossa, bem como o fluxo de nutrientes ao longo do processo de decomposição da madeira morta, por meio da avaliação de classes de decomposição. Florestas em áreas com maiores restrições físicas no solo apresentaram menor estoque de madeira morta (9,21 Mg ha^{-1} no M11 e 11,26 Mg ha^{-1} no M2) do que florestas com pouco ou nenhuma restrição física do solo (24,08 Mg ha^{-1} no M8 e 23,64 Mg ha^{-1} na Reserva Ducke). De modo oposto, módulos com solo mais restritivo apresentaram maior estoque de serapilheira fina (3,89 Mg ha^{-1} no M4 e 2,99 Mg ha^{-1} no M9) que florestas com pouca ou nenhuma restrição (1,87 Mg ha^{-1} na Reserva Ducke). As concentrações de Ca, Mg, K e P na serapilheira fina e grossa foram maiores ao longo do interflúvio, e apesar dos menores estoques de serapilheira, estas áreas apresentaram também os maiores estoques desses nutrientes, inclusive no solo. Maiores concentrações de Na, Al, Fe, Zn e N foram encontradas na serapilheira de áreas ao norte de Manaus. Análises de caminhos demonstraram que o estoque de nutrientes na serapilheira grossa é em grande parte controlado pela massa de serapilheira grossa, com excessão de K, Zn e N que podem ter seu estoque determinado pela associação da massa de serapilheira e concentração na madeira morta, e do Ca o qual teve seu estoque na serapilheira determinado por sua concentração na madeira morta, independente da massa de serapilheira. Ao longo do processo de decomposição, os padrões gerais de liberação ou imobilização de nutrientes foi similar em todos os módulos, com exceção do M1 e M11 para alguns elementos, como Ca e Mg, devido à alta concentração inicial nos tecidos dessas áreas. Variação substancial nos estoques de nutrientes na serapilheira pode ser estimada em grandes escalas através da associação entre propriedades físicas e químicas do solo.

Abstract

The role of coarse wood debris (CWD) such as nutrient sink or reservoir and the processes that control the dynamics of this compartment have large importance on nutrient cycling in forest ecosystems. The dynamic and structure of Amazonian forests are associated with a variety of soils across de Basin, with contrasting physical and chemical soil properties. The interaction between these factors may influence the amount of litter standing crop (LSC) and CWD (coarse wood debris, trunks and branches with diameter ≥ 10 cm) produced by the forest, as well as control nutrient release and/or nutrient stocks contained in their tissues. The relation between soil properties and nutrients in necromass were tested in 49 plots of 0.5 ha in *terra firme* forests located along a approximately 700 km transect extending north – south from Manaus-AM. Forests north of Manaus correspond to plots in Ducke Reserve and BDFFP project, while forests south of Manaus, are located along the Purus-Madeira interfluve (BR-319), in soils with varying degrees of hydromorphism. Plots were grouped in nine site clusters, according to their geographical distribution, being seven along Purus-Madeira interfluve (M1, M2, M4, M5, M8, M9 and M11 site clusters) and two north of Manaus (Ducke Reserve and BDFFP). Soils were classified by their physical properties, due to the restriction level imposed to vegetation growth and also for fertility in the first 20 cm of soil. We evaluated nutrient concentration and stocks in fine and coarse wood debris, and also nutrient concentrations among decay classes of CWD. Forests in site clusters with high soil restriction levels had lower stock of dead wood (9.21 Mg ha^{-1} at M11 and 11.26 Mg ha^{-1} at M2) than forests with little or no physical restriction soils (24.08 Mg ha^{-1} at M8 and 23.64 Mg ha^{-1} at Ducke Reserve). Conversely, site clusters with more restrictive soils had higher fine litter stock (3.89 Mg ha^{-1} at M4 and 2.99 Mg ha^{-1} at M9) than forests with little or no soil restriction (1.87 Mg ha^{-1} at Ducke Reserve). The concentrations of Ca, Mg, K and P in both fine and coarse litter were higher along interfluve, and despite lower stocks of litter, also had the largest stocks of these nutrients, including in the soil. Higher concentrations of Na, Al, Fe, Zn and N were found in areas north of Manaus. Path analysis suggest that, for most elements, the actual CWD nutrient stock is controlled by the mass of CWD, with dead wood tissue concentrations being secondary. However, K, Zn and N showed a simultaneous effect of wood tissue concentration and CWD mass. Ca was the only element where dead wood tissue concentration was determinant of CWD Ca stocks, with CWD mass being of secondary importance. Throughout the process of decomposition, the general patterns of nutrient release or immobilization were similar in all site clusters, with exception of M1 and M11 for some nutrients, (Ca and Mg) due to the high initial tissue concentration in these sites. Substantial variation in nutrient stocks in the litter can be estimated at large scales through the association between physical and chemical properties of the soil.

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Introdução

A árvore pode ser considerada uma produtora primária, um compartimento de estoque, além de sustentar o ecossistema florestal. Quando uma árvore morre, ela continua desempenhando ainda importantes papéis para o ecossistema, atuando no retorno de carbono e nutrientes ao ambiente, mas também facilitando a disponibilidade de outros recursos limitantes, como luz, água e energia (Franklin et al., 1987). Muitas dessas funções, no entanto, dependem da massa de madeira morta em um determinado momento, da taxa de mortalidade das árvores, bem como da velocidade do processo de decomposição (Harmon et al., 2000). Com relação aos nutrientes, as árvores vivas funcionam tanto como fonte quanto reservatório (Baker, 2007), imobilizando esses recursos por um período, mas eventualmente tornando-se componente importante dos ciclos biogeoquímicos da floresta, através da transferência desses elementos novamente ao ambiente. Poucos estudos têm focado em entender o que controla os estoques de nutrientes na serapilheira grossa e os processos que controlam sua dinâmica e subsequente liberação ou armazenamento de nutrientes essenciais (Kissing and Powers, 2010), sendo que os estudos a esse respeito nos trópicos são ainda mais escassos. A serapilheira pode ser classificada como serapilheira fina – folhas, gravetos e galhos finos com diâmetro inferior a 2 cm e serapilheira grossa – galhos e troncos com mais de 2 cm de diâmetro, sendo peças intermediárias com diâmetro entre 2 cm e 10 cm, e peças grossas com diâmetro maior que 10 cm (Pauletto, 2006).

A serapilheira grossa é reconhecida como um importante reservatório de carbono na Amazônia, armazenando cerca de 10 Pg C ao longo da Bacia (Chao et al., 2009). No entanto, os estoques de madeira morta encontram-se fortemente regionalizados na Amazônia, com estoques diminuindo ao longo de um gradiente de estrutura e dinâmica florestal de nordeste para sudeste (Chao et al., 2009). Do mesmo modo, áreas alagadas na Amazônia geralmente apresentam baixos estoques de serapilheira grossa (Chao et al., 2008). Uma grande contribuição para o entendimento dos mecanismos que possivelmente controlam os estoques de madeira morta foi recentemente feita por Martins et al., (submetido). Os autores investigaram a importância das propriedades físicas do solo no controle dos estoques de serapilheira grossa ao longo de várias áreas da Amazônia central. Uma importante descoberta desse trabalho foi a influência das propriedades físicas do solo, como por exemplo, profundidade efetiva, estrutura do solo e nível de anóxia (nível de saturação) na estrutura da floresta, que por sua vez, controla os estoques de madeira morta. Os autores relataram que florestas localizadas em solos sem restrições físicas (bem drenados, profundos e friáveis) tendem a apresentar árvores com elevada biomassa individual, enquanto solos com mais restrições ao estabelecimento e crescimento das árvores, tendem a apresentar florestas formadas por muitas e menores árvores.

Tais diferenças na biomassa individual das árvores geralmente resultam em menores estoques de madeira morta em solos mais limitantes, em que as árvores tendem a apresentar menor período de residência e por consequência contribuem com menos massa morta. O oposto ocorre em floresta que apresentam solos não restritivos, uma vez que quando uma árvore morre, ela contribui com muito mais massa morta. Os autores concluíram nesse estudo que a anóxia do solo foi o principal fator controlando a estrutura da floresta, levando a cerca de 33,1 Mg ha^{-1} de madeira morta estocada em áreas sem limitações físicas do solo e em contraste, 16,1 Mg ha^{-1} de madeira morta estocada em condições de solo, extremamente limitantes à floresta, principalmente relacionada à anoxia.

Essa grande variação no estoque de madeira morta ao longo da bacia amazônica, possivelmente reflete em diferentes estoques de nutrientes e taxa de aquisição e liberação desses nutrientes. Características da madeira morta, como tamanho e estrutura das moléculas que compõe o tecido vegetal, a toxicidade dos compostos secundários (Chambers et al., 2000; Chapin et al., 2002), o diâmetro no momento da morte e a densidade da madeira podem influenciar muito as taxas de decomposição desse material (van Geffen et al., 2010). Esses autores relatam que árvores de menor diâmetro decompõem-se muito mais rapidamente que aquelas com elevado diâmetro devido a um efeito de superfície exposta durante a decomposição. Entretanto, diferenças nas taxas de decomposição e tempo de retorno dos nutrientes da serapilheira grossa não são as únicas variáveis controlando os estoques de nutrientes nesse compartimento na bacia amazônica. Grandes diferenças na fertilidade dos solos são registradas ao longo da Amazônia e em associação com as propriedades físicas do solo e estrutura da vegetação (Phillips et al., 2004; Quesada et al., 2012) podem influenciar fortemente os estoques de nutrientes na serapilheira grossa, bem como sua importância relativa na ciclagem de nutrientes. Entretanto, até esse ponto existem poucas informações sobre esse assunto na região tropical.

Visando preencher essa lacuna no conhecimento dos papéis que a madeira morta desempenha no estoque e ciclagem de nutrientes, nós expandimos o trabalho de Martins et al., (submetido), analisando tanto a química do solo, a serapilheira fina e a serapilheira grossa (representada a partir desse momento como galhos e troncos caídos com diâmetro ≥ 10 cm) em locais selecionados sobre o mesmo gradiente. Nós trabalhamos com a hipótese de que os estoques de nutrientes na serapilheira grossa estão em função de dois processos complementares: (1) propriedades físicas do solo afetam os estoques de madeira morta, controlando a massa real de madeira morta (por exemplo, os estoques de nutrientes podem ser maiores mesmo que a concentração elementar do tecido vegetal seja baixa, porque há uma elevada quantidade de madeira morta); e (2) a fertilidade do solo impõe outro nível de controle, em que a concentração dos elementos na madeira morta é influenciada pela fertilidade local. Assim, é possível haver elevado estoque de nutrientes na serapilheira grossa em áreas com elevada concentração no tecido vegetal, mesmo que a quantidade de madeira morta seja pequena, com possíveis combinações desses dois processos sendo também possível.

Para avaliar essa suposição nós testamos a hipótese de que a concentração dos elementos no tecido vegetal é determinada pela fertilidade local do solo (em ambas, serapilheira fina e grossa) no nosso conjunto de dados, e associamos isso com os estoques de madeira morta encontrados por Martins et al., (submetido). Além disso, nós levantamos a hipótese de que florestas localizadas em solos com propriedades físicas favoráveis, que são geralmente menos férteis e apresentam em geral lento crescimento e árvores tolerantes ao sombreamento, terão maiores estoques de nutrientes na madeira morta, revelando um mecanismo conservacionista para essa área. O contrário é esperando em florestas sobre solos com condições físicas limitantes, que tendem a ser mais dinâmicas (Quesada et al., 2012) e devem ser mais eficientes na ciclagem de nutrientes por meio da serapilheira fina, apresentando menores estoques de nutrientes na madeira morta, favorecendo uma rápida taxa de retorno dos nutrientes ao ecossistema. Para avaliar tais ideias, relações estruturais entre as propriedades do solo e os estoques de nutrientes na serapilheira grossa, foi elaborado um modelo teórico simples incorporando quatro variáveis que supostamente influenciam os estoques de nutrientes na madeira morta.

Finalmente, nós avaliamos como a concentração dos nutrientes no tecido vegetal varia ao longo das classes de decomposição da madeira morta (madeira recém-caída, parcialmente decomposta e apodrecida, com melhor definição na seção de Material e Métodos) visando entender os padrões de liberação de nutrientes.

Objetivo

Avaliar a distribuição dos estoques e liberação de nutrientes na serapilheira fina e grossa em florestas sobre diferentes tipos de solo na Amazônia Central.

Objetivos específicos

Determinar como as propriedades físicas e químicas do solo podem afetar: (1) o estoque de nutrientes na serapilheira fina e grossa entre diferentes tipos de florestas e também (2) determinar como se dá o fluxo dos nutrientes ao longo do processo de decomposição da madeira morta, representado pelas classes de decomposição do material.

Capítulo 1

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1. Introduction

Tree is a primary producer, a storage compartment and the fundamental unit of the forest ecosystem. When a tree dies, it continues to play many roles as it returns resources to the environment such as carbon and nutrients but also making available other limiting resources such as light, water and energy (Franklin et al., 1987). Many of these functions, however, depend on the actual mass of wood detritus, the rate of tree mortality and decomposition process (Harmon et al., 2000). With respect to nutrients, living trees work both as a sink and reservoir (Harmon and Sexton, 1996), immobilizing this resource for a period of time, but eventually becoming an important part of forest biogeochemical cycles through the return of these elements in coarse wood debris (CWD). Few studies tried to understand what controls the stocks of CWD and the process that control its dynamics and subsequent release or storage of essential nutrients (Clark et al., 2002, Kissing and Powers, 2010), with the tropics being particularly poorly studied in that respect.

CWD is an important reservoir of carbon in Amazonia, storing circa 10 Pg C across the Basin (Chao et al., 2009). Nevertheless, CWD stocks were found to be much regionalized in Amazonia, decreasing along a gradient of forest structure and dynamics from northeast to southwest Amazonia (Chao et al., 2009). Chao et al., (2008) also reported that floodplain areas in Amazonia usually show low CWD stocks. A major contribution to the understanding of mechanisms behind CWD stocks in Amazonia has been recently reported by Martins et al., (submitted). The authors investigated the importance of soil physical properties in controlling CWD stocks along a large area across central Amazonia. Their most important finding was that soil physical properties such as effective soil depth, soil structure and level of soil anoxia (degree of water saturation), could influence forest structure which in turn could exert a control on CWD stocks. The authors reported that forests on soils with non limiting physical properties (well drained, deep and friable) tended to have trees with larger individual biomass, while soils imposing physical constraints to tree establishment and growth tended to have forests dominated by many, smaller trees. Such differences on individual tree biomass generally resulted in smaller CWD stocks in the most limiting soils (shallow, root restrictive and/or waterlogged) since that trees stock individually less biomass and therefore contribute with a small mass mortality. The opposite occurs on forests with non limiting soils that support bigger trees which stock individually more biomass, therefore contributing with a much higher mass mortality. The authors concluded that soil anoxia was the most likely attribute to shape forest structure in their study, leading to a CWD stock of 33.1 Mg ha^{-1} in areas without soil physical limitations and a contrasting stock of 16.1 Mg ha^{-1} in areas where soil conditions and particularly anoxia were strongly limiting.

Such large regional variation in dead wood stocks across the Basin is also likely to reflect in different CWD nutrient stocks and turnover. Characteristics of dead wood such as the size and structure of the tissue molecules, toxicity of secondary compounds (Chambers et al., 2000; Chapin et al., 2002), tree diameter at the moment of death and xylem density can strongly influence decomposition rates (van Geffen et al., 2010). For instance, van Geffen et al., (2010) report that small, thin trees decompose much faster than trees with large diameter due to an effect of wood surface area on decomposition. Also CWD with 2-10 cm of diameter showed higher nutrient concentrations than CWD above 10 cm of diameter (Pauletto, 2006). However, differences in decomposition rates and CWD turnover times are not the only reason for a large variation in CWD nutrient stock across the Amazon Basin. Large variations in soil fertility occur in Amazonia and associated with soil physical properties and vegetation structure (Phillips et al., 2004; Quesada et al., 2012) these are likely to strongly influence both the CWD nutrient stocks and its relative importance on the biogeochemical function of Amazonia. However, to this point there is very limited information on this matter.

In order to fill the existing gap in knowledge on the role of CWD in the nutrient storage and cycling, we have extended on the work of Martins et al., (submitted) analyzing both soil, litter and CWD chemistry across selected sites on the very same gradient. We worked with the assumption that nutrient stocks in CWD are a function of two complementary processes: (1) soil physical properties affect CWD nutrient stocks by determining the actual mass of dead wood in the pool (for example nutrient stocks can be high even if actual tissue elemental concentration is low because their stocks can be controlled by high wood mass); (2) soil fertility imposes another level of control, with CWD tissue concentrations being influenced by local soil fertility. Thus it is possible to have a high CWD nutrient stock in areas with high tissue concentrations even if actual pool of dead wood is small, with further combinations of these two processes also been possible. To evaluate this assumption we tested the hypothesis that plant tissue nutrient concentration is determined by local soil fertility (in both fine and coarse debris) in our dataset, and associate this with the CWD stocks reported by Martins et al., (submitted). In addition, we hypothesized that forests with favorable soil physical properties, which are usually nutrient poor and dominated by slow growing and shade tolerant trees will have larger nutrient stocks as CWD, this being a nutrient conserving mechanism. The opposite is expected in forests under limiting soil physical conditions, which tend to be more dynamic (Quesada et al., 2012) and should rely more on cycling nutrients through leaf litter, having lower CWD nutrient stocks, and thus favoring a faster turnover of nutrients. Structural relationships between soil properties and nutrient stocks in CWD were built by a simple theoretical model incorporating the four variables that are likely to influence CWD nutrient stocks.

Finally we evaluate how tissue nutrient concentration varies among wood decomposition classes (rotten, partially decomposed and recent dead wood, with these classes being properly defined in the Methodology) with a view to understand patterns of nutrient release from CWD.

2. Methods

2.1. Study sites

Data were collected in permanent plots located north and south of the Negro River in the state of Amazonas, Brazil (Fig. 1). The northern sites are in the *Reserva Florestal Adolfo Ducke* (hereafter called 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 (TEAM). The southern sites are located in the Purus – Madeira inter-fluvial zone along the Manaus – Porto Velho road (BR-319). The permanent plots at these sites are also monitored by PPBio.

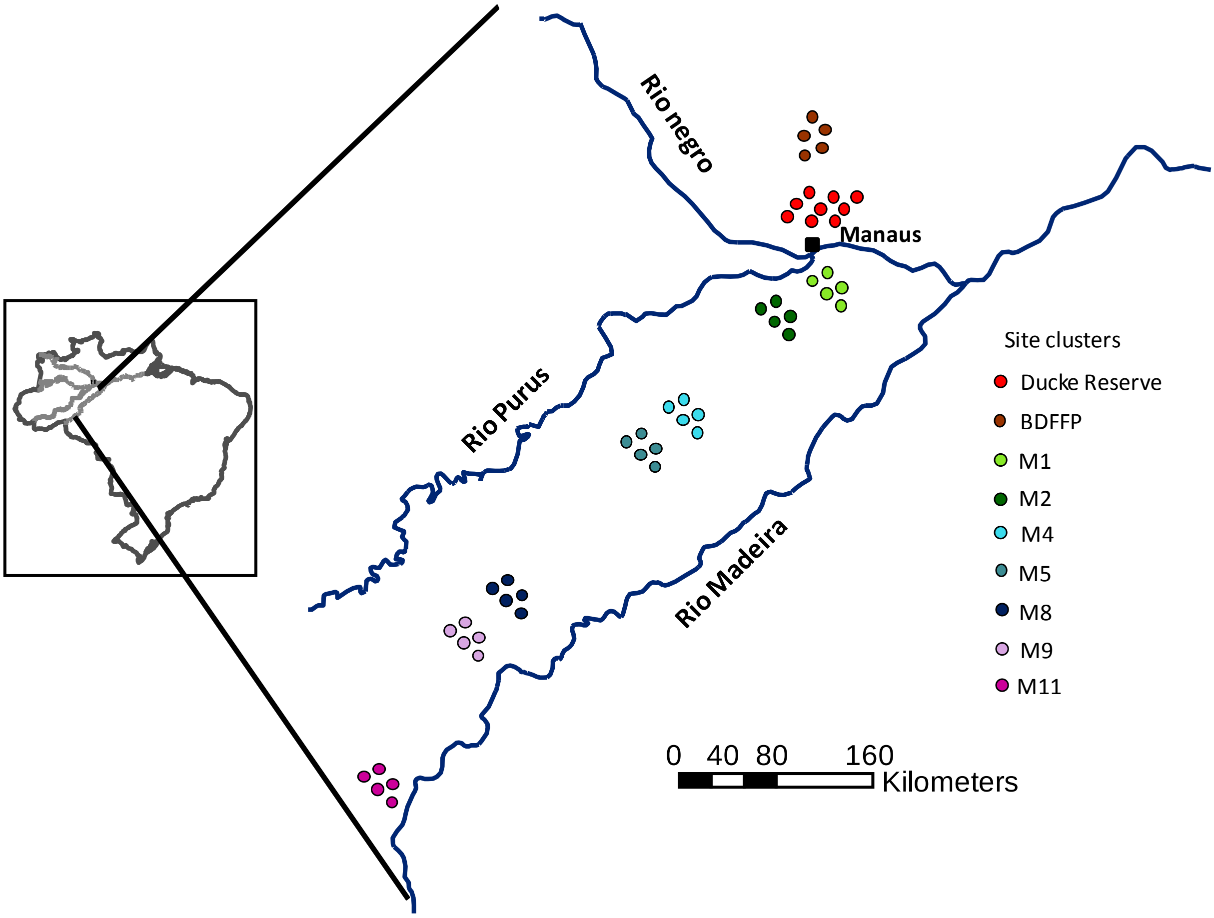

Figure 1. Distribution of study sites across central Amazonia.

2.2 Site characteristics and sampling design

The Ducke Reserve is managed by the National Institute for Amazon Research (Instituto Nacional de Pesquisas da Amazonia - INPA), spanning 10,000 ha of mature *terra firme* tropical moist forest in 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 km^2 area. The soils in the area are Ferralsols and Acrisols along the slopes and plateaus, which are highly weathered and thus have well developed physical conditions (Quesada et al., 2010). In general soils are deep, well drained, and low bulk density soils. The Ducke Reserve also has wet, sandy soils (Podzols) in the low positions of the terrain, but these were not included in this study. From the 25 vegetation plots available at the Ducke Reserve, nine (09) were sampled, being all above Acrisols and Ferralsols. All sampled plots are at least 1 km from one another and are 250 m long and 20 m wide (0.5 ha) following the topographic contour (Magnusson et al., 2009).

The BDFFP study site is located 80 km north of Manaus (2º30´S, 60ºW). There data were collected in five (05) plots of mature *terra firme* tropical moist forest, at least 1 km away from border and in forest fragments greater than 500 ha (Laurance et al., 1998). Forest canopy is a 30-37 m tall with emergent trees reaching up to 55 m. Average precipitation is 2200 mm (Nascimento and Laurance, 2002). Similar to the Ducke Reserve, all samples were collected on permanent plots over Ferralsols and Acrisols with good soil physical structure. The plots located in the BDFFP Conservation Unity are 100 x 100 m and do not follow any specific topographic feature (Laurance et al., 1998).

The plots located south of the Amazon river are placed along the BR-319 Highway on an interfluvial zone between Purus and Madeira rivers. We have sampled on thirty five (35) permanent plots along the interfluve, with permanent plots distributed into seven (07) site clusters, scattered along approximately 600 km. Each site cluster is composed of a 5 km length transect with 5 plots of 250 x 20 m following the topographic contour at intervals of 1 km. Along that road, plots which are located closer to Manaus have a somewhat dense lowland evergreen forest while at plots located closer to Porto Velho a lowland open evergreen forest occurs (IBGE, 1997). Therefore forest structure varies across our sampling plots. The region is characterized by a very flat topography varying between 30 and 50 m in altitude along large distances. Mean annual precipitation of the area varies from 2624-2155 mm (WorldClim global coverage). The soils on the interfluve are predominantly Plinthosols and Gleysols (Sombroek, 2000, Martins et al., submitted), generally showing varying degrees of soil water saturation. Soil physical structure is generally restrictive, with very high bulk density in the subsoil, resulting in varying degrees of hardness and effective soil depth (Martins et al., submitted). Subsoil layers that limit root penetration vary from 30-100 cm deep in these plots (RADAMBRASIL, 1978; Sombroek, 2000)

Soils located north of the Amazon River are found on an old and geologically stable area, most likely from the Tertiary-Cretaceous period (approximately 65-100 million years old). Soils along the interfluve (southern sites) are located over a much younger geological surface, varying in age from the Holocene to the Pleistocene. Soils located close to the Amazon and Madeira Rivers (site clusters M1 and M11, respectively, Figure 2) are essentially alluvial terraces formed on deposits laid by recent river meandering (Holocene, <10.000 years old). The remaining areas (site clusters M2, M4, M5, M8 and M9, Figure 1) are located over Pleistocene sediments (<1.8 million years old).

2.3. Coarse wood debris

Coarse wood debris stocks, were measured by Martins D. L. and are described in detail in Martins et al., (submitted), therefore will be only briefly described here. Field measurements of fallen coarse necromass were made with line intersect sampling (LIS, van Wagner, 1968). 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 have initial rottenness features like the absence of bark. Class 3 is very rotten and can be easily broken. This classification in decomposition class was used to adjust wood density in stock calculation to avoid overestimations.

For each piece of dead wood that crossed the intersect line samples were taken to measure the density of coarse necromass and for determining tissue nutrient concentration (with bark, sapwood and heartwood). A chain-saw was used to cut a wood disk sample from hard pieces. Softer wood pieces were sampled using a machete. 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. After volume measurement the segment samples were oven dried at 65 ºC until constant weight. The density of each sample segment was then calculated and used to average the density of each decay class in each site. Separate subsamples were taken to determine the nutrient concentrations. At BDFFP, 146 CWD samples were collected in five plots. At BR-319, 444 samples were collected in 35 plots and 136 samples were collected in nine plots at the Ducke Reserve. Our samples covered many different species, which were not identified.

2.4. Litter standing crop

Litter standing crop (LSC) was sampled in plots where CWD was sampled. Litter standing crop represents the litter accumulated in the soil surface in a given moment. As LSC can vary through the year, we have made efforts to sample all plots in the same time window (October and November). For measuring the LSC, we collected ten (10) samples per plot, using a square frame of 20 cm x 20 cm in size, randomly distributed within the plots. The material obtained was separated between leaves and others (fruits, twigs and unidentified material). These ten samples were amalgamated into one compound sample per plot. Only leaves were used to determine nutrient concentration and subsequent calculation of nutrient stocks.

2.5 Chemical analysis of plant material

Both LSC and the CWD samples were dried in an oven at 65 ° C to constant weight, with all samples being subsequently ground by a Wiley Mill. For the determination of cations, phosphorus and micronutrients (Ca, Mg, K, Na, Al , Fe, Zn, Mn and P), we performed wet digestions using a nitric + percloric acid mixture as described in detail by Malavolta et al., (1989). Concentrations of Ca, Mg, K, Na, Al , Fe, Zn and Mn were determined by Atomic Absorption Spectrophotometer (Model 1100b, Perkin Elmer, Norwalk, CT, USA) as prescribed by Anderson and Ingram, (1993). On the same extracts, phosphorus was determined colorimetrically (Olsen and Sommers, 1982) using a UV spectrophotometer (Model 1240, Shimadzu, Kyoto, Japan). The contents of C and N were determined by a CN automatic analyzer (CN VARIO MAX, Elementar, Germany) as described in detail by Pella, (1990).

2.6 Soil data

2.6.1 Soil fertility

Soil chemistry data was obtained from available databases. At Ducke Reserve and BDFFP, total nutrient concentration was obtained from the RAINFOR soils database (C.A. Quesada unpublished data). At the BR-319 information about total and exchangeable nutrient in soil was obtained from the PPBio database (T. Emilio unpublished data). Soil carbon and nitrogen were analyzed by L. F. Lugli. Exchangeable nutrient data at BDFFP sites were obtained, from P. M. Fearnside (unpublished data) and at Ducke Reserve, from T. Pimentel (unpublished data). Soils were analyzed for exchangeable cations (Ca, Mg, K, Fe, Al and Zn) using the KCl 1M and Melich 1 extraction procedures (Pleysier and Juo, 1980) and determined by Atomic absorption technique as prescribed by Anderson and Ingram, (1993). Total phosphorus was analyzed by H_2SO_4 + H_2O_2 extraction followed by colorimetric determinations (Tiessen and Moir, 1993), but also being determined in exchangeable form in Melick 1 extracts. C and N concentrations were analyzed in an automatic CN analyzer (Pella, 1990). Total elemental composition was also determined in the H_2SO_4 + H_2O_2 extracts. Due to logistic limitations not all plots were sampled, so we have restricted our analysis of soil fertility to the site cluster level. All data about exchangeable nutrients of soil refer to 0-20 cm soil layer, while total nutrients refer to 0-30 cm.

2.6.2 Soil descriptions and determination of soil physical properties

Soil physical properties used in this study were determined by Martins et al., (submitted) and are only briefly summarised here. 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 A1) 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. Index 1 (Π_1) is represented by the sum of the four soil physical parameters and Index 2 (Π_2) is the sum of three parameters excluding anoxia. Scores given to soil physical properties are semi – quantitative allowing conversion of soil descriptions to be used in statistical analysis. For the determination of soil physical properties, 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 seven site clusters 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 occurs. 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.

2.7. Calculations

Nutrient stocks in CWD, LSC and soils were calculated as:

$$CWD_N = \mathrm{CWD_S} \times \mathrm{CWD_C}$$

where $\mathrm{CWD_N}$ is the nutrient stock in coarse wood debris in kg ha^{-1}, $\mathrm{CWD_S}$ is the coarse wood debris stock in Mg ha^{-1}and $\mathrm{CWD_C}$ is the coarse wood debris concentration of each nutrient in g kg^{-1}.

$$LSC_N = \mathrm{LSC_S} \times \mathrm{LSC_C}$$

where $\mathrm{LSC_N}$ is nutrient stock at litter standing crop in kg ha^{-1}, $\mathrm{LSC_S}$ is the litter standing crop stock in Mg ha^{-1}and $\mathrm{LSC_C}$ is the litter standing crop concentration of each nutrient in g kg^{-1}.

$$S_N = \mathrm{S_C} \times 10000 \times \rho \times l$$

where $\mathrm{S_N}$ is the soil nutrient stock in kg ha^{-1}, $\mathrm{S_C}$ is the soil nutrient concentration in g kg^{-1}, ρ is soil bulk density in g cm^{-3}, 10000 is a constant to determine nutrient stocks in kg ha^{-1} and *l* is the layer depth, also constant in this case, 0.2 m.

2.8. Statistical analysis

Each plot was considered as a sample unit to compare means of nutrient concentrations and stocks in soil (n=35), CWD (n=49) and LSC (n=35) and also in linear regressions (n=35). Relationships between nutrient in CWD and LSC with edaphic variables were explored using mixed models (nlme package) with a random intercept, since our dataset shows a cluster/hierarchical design. Hierarchical groups consisted in BDFFP, Ducke Reserve and all of seven site clusters along BR-319. Mixed models were also used to compare mean concentration and stock of nutrients in soil, LSC and CWD among site clusters. Post-hoc comparisons were made using Tukey HSD test. Nutrient concentrations in the compartments were square root or log transformed to improve normality. To understand the variance explained by linear regressions we used a method suggested by Nakagawa and Shiekzeth, (2013) for obtaining a marginal R^2 (R^2_m) which describes the proportion of variance explained by the fixed factor and conditional R^2 (R^2_c) that describes the proportion of variance explained by both the fixed and random factors. A path analysis was made to test the validity of a theoretical model using soil physical and chemical properties to explain nutrient stock in CWD. All analyses were carried out in R version 3.0 (R Development Core Team, 2013).

3. Results

3.1. Variation in edaphic properties

Exchangeable nutrient concentration in soil did not vary much among site clusters (Table 1). Mg, Al and Fe were not significantly different (one way ANOVA, $F_{[8,26]} = 0.63$, $p = 0.74$; $F_{[8,26]} = 1.18$, $p = 0.34$; $F_{[8,26]} = 1.75$, $p = 0.13$ respectively). Ca, K and P concentrations were higher at Purus-Madeira interfluve sites, where soils are much younger and less weathered (Pleistocene and Holocene age) than soils north Manaus (Tertiary-Cretaceous period). Ca was significantly higher at M1 site cluster, with about 0.16 ± 0.03 $\mathrm{cmol_c\ kg^{-1}}$ (one way ANOVA, $F_{[8,26]} = 3.40$, $p < 0.05$), followed by Ducke Reserve, with half of its Ca content, 0.08 ± 0.03 $\mathrm{cmol_c\ kg^{-1}}$. The other sites north and south Manaus, have less than 0.05 $\mathrm{cmol_c\ kg^{-1}}$ of Ca in soil. M4 and M5 showed higher K concentration (one way ANOVA, $F_{[8,26]} = 4.82$, $p < 0.001$). K concentration tended to decrease from M4 to M11, the later area being more recent (Holocene), with K concentration in such area reaching values close to those found in M1 and M2 site clusters. Exchangeable P concentration was lowest in Ducke Reserve, with only 1.54 ± 0.11 mg $\mathrm{kg^{-1}}$. Exchangeable P generally decreases from northeast to southwest, along the BR-319 road (from M1 to M9), but it was considerably higher at the M11 site cluster (Holocene area), with about 4.03 ± 0.60 mg $\mathrm{kg^{-1}}$ (one way ANOVA, $F_{[8,26]} = 14.69$, $p < 0.001$). The M1 site cluster, also from Holocene period, showed the higher exchangeable P concentration, with 6.81 ± 0.60 mg $\mathrm{kg^{-1}}$. Zn concentrations were significantly higher at sites north Manaus and also at M4 and M5 sites (one way ANOVA, $F_{[8,26]} = 13.85$, $p < 0.001$).

Site clusters north Manaus generally showed higher C content in soil, while all sites along BR-319 showed lower and similar content with exception of M2, which showed the lowest content of all sampled areas, 0.98 ± 0.05 % (one way ANOVA, $F_{[8,26]} = 2.58$, $p = 0.03$). Following this trend, N concentration was also higher in BDFFP and Ducke Reserve when compared to all BR-319 site clusters, which showed lower N concentrations (one way ANOVA, $F_{[8,26]} = 6.74$, $p < 0.001$).

Regarding total nutrient concentrations (Table A2), P, Mg and K concentrations were much lower in Ducke Reserve and BDFFP (one way ANOVA, $F_{[8,26]} = 40.04$, $p < 0.001$; $F_{[8,26]} = 145.65$, $p < 0.001$ and $F_{[8,26]} = 52.11$, $p < 0.001$ respectively) about three times lower for P and ten times lower for K and Mg. In these areas, however, Ca total concentration was similar to some site clusters of the interfluve. Likewise, the Total Reserve of Bases (TRB), which is a chemically based weathering index (Quesada et al., 2010), was much higher at BR-319 site clusters, reflecting their recent formation and consequent less intense expression of weathering.

Table 1. Exchangeable element concentration, C and N content in the soil 0-20, cm (mean ± standard error) in two site clusters north Manaus and seven south Manaus, in Purus-Madeira interfluve.

Element concentration	**Ducke**	**BDFFP**	**M1**	**M2**	**M4**	**M5**	**M8**	**M9**	**M11**
$cmol_c\ kg^{-1}$									
Ca	0.1±0.0	0.03±0.0	0.2±0.05	0.04±0.0	0.03±0.0	0.04±0.02	0.03±0.0	0.05±0.0	0.03±0.0
Mg	0.1±0.0	0.04±0.0	0.09±0.0	0.06±0.0	0.07±0.0	0.07±0.0	0.06±0.0	0.08±0.0	0.07±0.0
K	0.08±0.0	0.06±0.0	0.05±0.0	0.04±0.0	0.1±0.0	0.09±0.0	0.07±0.0	0.08±0.0	0.05±0.0
Al	2.5±0.2	1.4±0.1	3.0±1.0	2.4±0.1	1.8±0.4	2.5±0.3	2.6±0.3	2.4±0.3	2.4±0.5
$mg\ kg^{-1}$									
Fe	340±68.8	144±14.1	288±19.0	162±44.8	103±34.6	144±53.4	193±61.7	198±72.1	126±30.1
Zn	1.2±0.1	2.3±0.0	1.0±0.0	0.5±0.1	1.6±0.2	1.2±0.1	0.9±0.1	0.8±0.1	0.6±0.1
P	1.5±0.1	NA*	6.8±0.6	3.8±1.5	2.9±0.4	2.7±0.2	1.9±0.4	1.6±0.4	4.0±0.6
%									
C	2.1±0.1	1.8±0.3	1.5±0.1	0.9±0.05	1.3±0.1	1.7±0.2	1.6±0.3	1.3±0.1	1.4±0.1
N	0.2±0.0	0.2±0.0	0.1±0.0	0.1±0.0	0.1±0.0	0.1±0.0	0.1±0.0	0.1±0.0	0.1±0.0
*n***	3	2	4	3	3	5	5	5	5

* No available data about exchangeable P concentration in BDFFP soils; ** *n* number of plots sampled for each site cluster.

Nutrient stocks in the soil, on the other hand, are the product of soil bulk density and each nutrient concentration (Table 2). However, despite the usually higher bulk density of soils along the BR-319 road, which could result in greater differences among site clusters, the general pattern of nutrient stock distributions was similar to those of simple concentrations. Soil bulk density was higher at the BR-319 site clusters and lower in BDFFP and Ducke Reserve. The elements with higher stocks in soil were C and N, followed by Al, Fe, K, Mg, Ca, P and Zn. In general, M1 tended to show higher stocks for most of the elements. Due to the high Ca concentration and also high soil bulk density, M1 showed a much larger Ca stock in soil, with 80.63 ± 26.27 kg ha^{-1} (one way ANOVA, $F_{[8,26]} = 2.70$, $p = 0.02$) followed by Ducke Reserve with 28.51 ± 9.94 kg ha^{-1} and M9 plots, which showed high soil bulk density resulting in 28.75 ± 3.75 kg ha^{-1}. The BDFFP and M8 sites showed lower Ca stocks, due to low Ca concentration and soil bulk density of these sites (eventually also occurring in some M8 plots). There were no differences in Mg stocks between site clusters (one way ANOVA, $F_{[8,26]} = 1.72$, $p = 0.14$).

Exchangeable P stocks were considerably higher in the BR-319 sites than in plots north Manaus, with the M1 site cluster showing the highest stock with 18.13 ± 1.57 kg ha^{-1} (one way ANOVA, $F_{[8,26]} = 13.63$, $p < 0.001$). K concentration in the soil did not vary substantially among studied sites, but the stocks of K followed soil bulk density and so were significantly higher in M4 and M5 site clusters with 123.26 ± 6.05 and 109.54 ± 9.58 kg ha^{-1} respectively (one way ANOVA, $F_{[8,26]} = 9.09$, $p < 0.001$). Similar pattern was also found for Zn, where M4 showed the highest stocks (one way ANOVA, $F_{[8,26]} = 4.21$, $p = 0.02$). Al stocks were also higher at M4 and M5 with 726.11 ± 74.05 and 677.28 ± 69.65 kg ha^{-1} (one way ANOVA, $F_{[8,26]} = 5.23$, $p < 0.001$) also reflecting the higher bulk density. There were no differences in Fe concentrations and stocks among plots (one way ANOVA, $F_{[8,26]} = 0.78$, $p = 0.62$), and there were no significant differences in C (one way ANOVA, $F_{[8,26]} = 2.30$, $p = 0.052$) and N stocks among site clusters (one way ANOVA, $F_{[8,26]} = 1.98$, $p = 0.08$).

Table 2. Element stock in the soil 0-20, cm (mean ± standard error), soil bulk density and index of soil physical quality in two site clusters north Manaus and seven south Manaus, in Purus-Madeira interfluve.

Element stock	**Ducke**	**BDFFP**	**M1**	**M2**	**M4**	**M5**	**M8**	**M9**	**M11**
kg ha^{-1}									
Ca	28.2±9.6	9.8±0.0	80.6±26.3	22.7±2.6	23.0±3.0	23.3±9.9	17.1±2.2	28.7±3.7	20.9±3.0
Mg	21.6±8.1	8.2±0.0	26.2±4.8	23.8±1.3	26.4±3.4	26.6±7.6	19.1±1.8	29.0±4.6	26.2±5.0
K	53.4±15.6	36.9±2.5	52.5±7.7	49.76±3.7	123.3±6.0	109.5±9.6	80.4±7.7	91.6±7.4	62.6±3.1
Al	415±36.4	202±20.5	680±223.1	668±26.6	526±119.6	726±74.0	677±69.6	655±80.6	632±101.6
Fe	613±124.1	236±22.9	724±51.6	519±154.4	342±109.2	456±166.7	507±166.6	599±222.1	358±78.4
Zn	2.4±0.6	3.3±0.0	2.5±0.0	2.1±1.0	5.5±1.1	5.2±0.8	2.8±0.1	2.9±0.1	1.8±0.7
P	2.4±0.2	NA	18.1±1.6	12.3±4.5	9.9±1.859	8.4±0.8	5.7±1.3	4.8±1.3	11.4±1.8
Mg ha^{-1}									
C	38.7±1.3	30.6±5.4	38.4±3.4	30.6±1.8	44.8±2.6	54.7±7.6	43.6±5.2	38.7±2.7	40.6±4.6
N	3.0±0.2	2.7±0.4	3.2±0.4	2.3±0.0	2.7±0.1	3.5±0.3	2.7±0.2	2.8±0.2	3.3±0.2
Soil density *(g cm*$^{-3}$*)*	0.9	0.8	1.2	1.5	1.6	1.6	1.4	1.5	1.5
Index 1*	1	1	10	8	7	8	4	9	9
*n***	3	2	4	3	3	5	5	5	5

*Index 1: index of soil physical quality; ** *n* number of plots sampled for each site cluster.

Sites located north of the Amazon River usually had no soil physical restriction, being found on flat or gentle undulating terrain. The soils were very deep, had low subsoil bulk density (0.8 – 1.2 g cm^{-3}, for the reference depth 50 cm), and had good particle aggregation (good structure, friable) with very deep water table (Martins et al., submitted). On the other hand, soils in the southern plots (BR-319) were shallow (maximum effective soil depth about 30–100 cm), with high subsoil bulk density (1.0 – 1.7 g cm^{-3}), little or no aggregation (deficient structure, very hard and compact), being generally root restrictive and showing varying levels of anoxic conditions (from seasonally flooded with patches of stagnated water to soils showing only deep redox features) (Martins et al., submitted). There was however, some variation on soil restriction levels along the interfluve plots, with all sites sampled in this study being severely constrained (index Π_1 ranging from 6 to 11) with exception of M8, which averaged lower restriction levels (index $\Pi_1 = 4$). It is worth to note though that all soils at the interfluve (Plinthosols/Gleysols) had worse physical conditions when compared to Ferralsols/Acrisols from the northern plots. Soils at the interfluve were generally hydromorphic, but with this occurring for different reasons. Rising of the water table, poor soil drainage and impoundment of the water that accumulates in the plot due to rivers inundation are the main reasons for water logging.

3.2. Nutrient concentrations and stocks in CWD

CWD nutrient content varied widely and systematically across our study sites (Table 3). Ca concentration in CWD was higher in areas from the Holocene, where the M1 site showed the highest concentration, with 5.95 ± 0.85 g kg^{-1} (one way ANOVA, $F_{[8,40]} = 16.27$, $p < 0.001$), followed by M11, with 1.29 ± 0.25 g kg^{-1}. The lowest Ca concentration was found at M8, with only 0.44 ± 0.07 g kg^{-1}. M1 and M11 site clusters also showed the highest Mg and K concentration in CWD (one way ANOVA, $F_{[8,40]} = 12.28$, $p < 0.001$ and $F_{[8,40]} = 8.94$, $p < 0.001$), with 0.87 ± 0.11 and 0.85 ± 0.12 g kg^{-1} for Mg, and 0.96 ± 0.14 and 1.35 ± 0.21 g kg^{-1} for K in M1 and M11 respectively.

Na concentration was higher at the BDFFP site cluster, with 0.22 ± 0.02 g kg^{-1} (one way ANOVA, $F_{[8,40]} = 3.23$, $p = 0.006$) but not significantly different among the other sites. Al concentration in CWD on the other hand, was much higher in both site clusters north Manaus, with 1.10 ± 0.27 g kg^{-1} at Ducke Reserve and 1.54 ± 0.27 g kg^{-1} at BDFFP (one way ANOVA, $F_{[8,40]} = 7.69$, $p < 0.001$), while Fe concentration did not vary significantly between sites (one way ANOVA, $F_{[8,40]} = 2.04$, $p = 0.06$). P concentrations were higher in CWD from

Holocene areas, showing 0.09 ± 0.01 g kg^{-1} at M1 and 0.08 ± 0.01 g kg^{-1} at M11 (one way ANOVA, $F_{[8,40]} = 10.59$, $p < 0.001$). Zn concentration in CWD was significantly higher at M2 with 30.57 ± 15.52 mg kg^{-1}, followed by BDFFP with 15.19 ± 2.08 mg kg^{-1} (one way ANOVA, $F_{[8,40]} = 12.91$, $p < 0.001$). BDFFP also showed high Mn concentration, with 36.68 ± 3.67 mg kg^{-1}, but M11 had significantly higher Mn concentration among all site clusters, with 113.32 ± 22.73 mg kg^{-1} (one way ANOVA, $F_{[8,40]} = 10.11$, $p < 0.001$). Ducke Reserve had considerably higher C content in CWD, with 48.20 ± 0.73 % (one way ANOVA, $F_{[8,40]} = 5.84$, $p < 0.001$), without wide variation among the other site clusters. N concentration, however, tended to be higher in plots north Manaus than in Purus-Madeira interfluve. The higher N concentration was found at BDFFP with 0.61 ± 0.03 % (one way ANOVA, $F_{[8,40]} = 4.00$, $p = 0.0015$), contributing to the low CN ratio at this site, only 101.21 ± 5.00 (Table 3).

Table 3. Element concentration in CWD (mean ± standard error) in two site clusters north Manaus and seven south Manaus, in Purus-Madeira interfluve.

Element concentration	**Ducke**	**BDFFP**	**M1**	**M2**	**M4**	**M5**	**M8**	**M9**	**M11**
g kg^{-1}									
Ca	0.9±0.1	1.1±0.1	5.9±0.8	0.5±0.0	0.5±0.1	0.5±0.1	0.4±0.1	0.7±0.2	1.3±0.2
Mg	0.3±0.0	0.4±0.0	0.9±0.1	0.3±0.0	0.3±0.0	0.3±0.0	0.3±0.0	0.5±0.1	0.8±0.1
K	0.2±0.0	0.4±0.0	0.9±0.1	0.7±0.1	0.4±0.0	0.4±0.1	0.6±0.1	0.4±0.1	1.3±0.2
Na	0.1±0.0	0.2±0.0	0.2±0.02	0.1±0.0	0.1±0.0	0.1±0.0	0.2±0.0	0.1±0.0	0.2±0.0
Al	1.1±0.3	1.5±0.3	0.1±0.1	0.5±0.2	0.5±0.1	0.8±0.3	0.3±0.0	0.2±0.0	0.6±0.3
Fe	0.1±0.0	0.2±0.0	0.1±0.0	0.2±0.1	0.1±0.0	0.2±0.0	0.1±0.0	0.1±0.0	0.2±0.0
P	0.0±0.0	0.1±0.0	0.1±0.0	0.07±0.0	0.05±0.0	0.05±0.0	0.04±0.0	0.03±0.0	0.08±0.0
mg kg^{-1}									
Zn	8.3±1.3	15.2±2.1	6.9±1.3	30.6±15.5	5.0±0.6	4.5±0.7	12.1±3.9	6.9±1.5	13.3±2.0
Mn	20.6±4.4	36.7±3.7	33.7±9.6	18.1±2.7	16.2±2.2	17.8±2.0	21.8±2.4	23.3±3.2	113.3±22.7
%									
C	48.2±0.7	45.9±0.2	45.5±0.3	45.8±0.9	47.8±0.2	47.2±0.5	47.3±0.2	45.3±0.3	46.2±0.2
N	0.5±0.0	0.6±0.0	0.4±0.0	0.5±0.0	0.5±0.0	0.5±0.0	0.5±0.0	0.4±0.0	0.5±0.0
CN*	116±5.2	101±5.0	137±10.2	109±7.1	127±7.0	107±6.9	136±9.8	138±7.2	123±11.3
n**	136	146	59	60	77	64	87	60	37

*CN is the ratio between C and N contents; ** *n* number of CWD sampled for each site cluster.

The CWD stock for a given element is the product of its concentration and the amount of CWD mass. CWD mass stocks tended to decrease from north to south, specifically from Ducke Reserve to M11 (Table 4), the exception being the higher amount of fallen dead wood found in M8 site, comparable to high CWD stocks found north Manaus. CWD stocks were significantly higher at Ducke Reserve and M8 site cluster, with 23.64 ± 2.25 Mg ha^{-1} and 24.08 ± 5.54 Mg ha^{-1} (one way ANOVA, $F_{[8,40]} = 3.27$, $p = 0.0058$). For instance, CWD Ca stocks were higher at M1 where tissue Ca concentration was high and CWD stocks were low. This resulted in the highest Ca stock, with 63.65 ± 19.34 kg ha^{-1} (one way ANOVA, $F_{[8,40]} = 6.77$, $p < 0.001$). However, we observed that Ca stocks were also high in plots north Manaus, but due to the large amount of CWD mass stock in these areas.

Mg stocks, did not vary significantly among plots, despite all the variation in Mg concentration and CWD stocks variability (one way ANOVA, $F_{[8,40]} = 1.96$, $p = 0.07$). No variation was also detected for K (one way ANOVA, $F_{[8,40]} = 1.09$, $p = 0.38$), Na (one way ANOVA, $F_{[8,40]} = 1.09$, $p = 0.38$) and Fe stocks (one way ANOVA, $F_{[8,40]} = 1.21$, $p = 0.31$), in CWD. Al stock was much higher at BDFFP 20.78 ± 3.31 kg ha^{-1}, followed by Ducke Reserve, which showed 10.75 ± 2.96 kg ha^{-1} (one way ANOVA, $F_{[8,40]} = 3.79$, $p = 0.002$). Sites in the Purus-Madeira interfluve showed lower Al stocks than plots north Manaus. P stock in CWD was not different between sites (one way ANOVA, $F_{[8,40]} = 2.00$, $p = 0.07$). But it was possible to note elevated stocks where CWD mass stocks were also higher, with exception of M1 site, which showed higher P concentration in CWD. Zn stocks were higher in BDFFP and M2 site cluster, with 0.29 ± 0.12 and 0.25 ± 0.11 kg ha^{-1} respectively (one way ANOVA, $F_{[8,40]} = 3.74$, $p = 0.002$). Ducke Reserve had higher Mn stock in CWD with 0.97 ± 0.44 kg ha^{-1}, as did the BDFFP sites, due to the high amount of CWD mass, and M11, because of its high Mn concentration in CWD (one way ANOVA, $F_{[8,40]} = 3.07$, $p = 0.008$).

Sites which showed high stocks of CWD also showed higher N stocks. Ducke Reserve had 125.34 ± 13.30 kg ha^{-1}, followed by BDFFP with 119.84 ± 28.35 kg ha^{-1} and M8 with 109.59 ± 20.08 kg ha^{-1} (one way ANOVA, $F_{[8,40]} = 3.88$, $p = 0.0018$). C stocks followed the same trend and the highest values were also found in Ducke Reserve with 10.34 ± 1.11 Mg ha^{-1} and M8, with 11.45 ± 2.70 Mg ha^{-1} (one way ANOVA, $F_{[8,40]} = 2.63$, $p = 0.02$) (Table 4).

Table 4. Total CWD mass stock and element stock in CWD (mean ± standard error) in two site clusters north Manaus and seven south Manaus, in Purus-Madeira interfluve.

Element stock	**Ducke**	**BDFFP**	**M1**	**M2**	**M4**	**M5**	**M8**	**M9**	**M11**
Mg ha^{-1}									
CWD stock *	23.6±2.2	18.6±2.9	12.9±2.0	11.3±2.8	12.7±2.3	14.0±4.6	24.1±5.5	12.9±3.9	9.2±1.2
kg ha^{-1}									
Ca	24.7±4.4	16.7±4.6	63.6±19.3	5.8±2.3	6.7±1.4	7.6±3.1	9.1±1.3	7.4±3.3	10.8±3.2
Mg	8.3±1.6	7.4±2.0	9.9±2.5	4.5±2.1	3.8±0.7	4.0±1.3	7.9±1.2	5.5±2.1	7.3±1.7
K	6.8±1.9	5.2±1.3	11.5±4.3	7.5±3.5	4.1±0.7	6.3±1.9	10.9±2.0	9.5±5.7	11.4±2.2
Na	8.0±3.5	4.0±1.2	1.8±0.4	2.0±0.8	1.2±0.3	1.7±0.7	4.1±1.0	1.6±1.1	1.8±0.5
Fe	3.9±1.6	3.3±1.0	1.4±0.4	1.8±0.5	1.4±0.2	1.9±0.4	2.1±0.4	1.0±0.3	1.4±0.6
Al	10.7±2.9	20.8±3.3	6.8±2.2	2.2±0.8	7.9±3.5	9.4±4.5	4.9±1.8	3.9±1.9	3.0±1.0
P	1.3±0.3	1.0±0.2	1.1±0.3	0.7±0.2	0.6±0.1	0.7±0.2	1.0±0.2	0.5±0.2	0.6±0.1
N	125.3±13.3	119.8±28.3	51.0±8.8	56.6±11.5	54.1±11.9	79.5±28.6	109.6±20.1	51.7±18.6	43.2±12.6
Zn	0.1±0.0	0.3±0.1	0.1±0.0	0.2±0.1	0.1±0.0	0.05±0.0	0.2±0.0	0.1±0.0	0.1±0.0
Mn	1.0±0.4	0.8±0.3	0.3±0.1	0.2±0.0	0.2±0.0	0.3±0.1	0.5±0.1	0.4±0.2	0.9±0.2
Mgha^{-1}									
C	10.3±1.1	7.7±1.9	5.9±0.9	5.2±1.3	5.6±1.0	6.6±2.2	11.4±2.7	5.6±1.7	4.1±0.6
*n***	9	5	5	5	5	5	5	5	5

* CWD stock is the amount of CWD mass; ***n* number of plots sampled for each site cluster.

3.3. CWD density and nutrient concentration among decomposition classes

Figure 2 and 3 showed changes in CWD density and the flux of nutrients along the decomposition process, estimated by the differences on nutrient concentration for the three decay classes studied. We found a wide variation in density of CWD among the three decomposition classes, with density decreasing as the decomposition process advances (Figure 2). CWD density in class one, two and three were significantly different, but not within each class among site clusters.

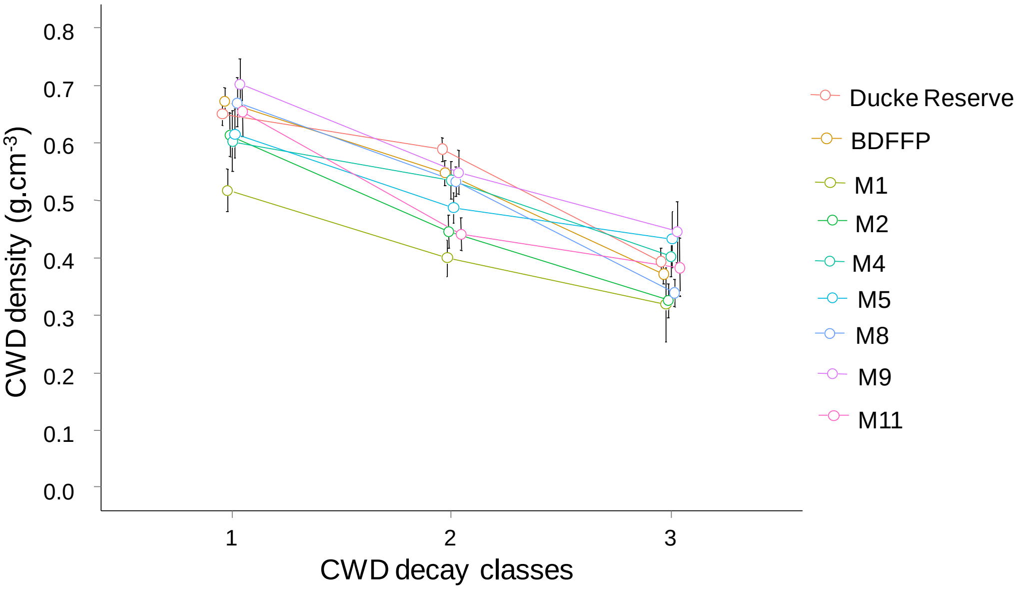

Figure 2. CWD density (g cm^{-3}) among decay classes in nine site clusters north and south Manaus.

Ca concentration did not vary significantly among decomposition classes in any of the sampled sites (Figure 3a), with the exception of M1. For most sites, the initial concentration of this nutrient in class one remained almost the same in class two and three of decomposition. In M1 Ca concentration increased from class one to two, and decreased from class two to three, remaining with almost the same initial concentration, which is also much higher than at other sites. Similar pattern, was found in Mg concentration (Fig. 3b), but besides M1, M11 also showed different trend in Mg release during decomposition. Mg concentration at the M11 site cluster increased from class one to class two, decreasing sharply from class two to three. At M1, Mg concentration increased from class one to two and remained constant in class three. Mg concentration in all other sites tended to decrease with the advance of decomposition, or to remain the same, with exception of M9 site cluster, which showed a slight accumulation from class two to three. For both Ca and Mg, the sites which had higher initial concentrations, remained with higher concentrations along the progress of decomposition. K concentrations showed practically the same trend of release in all sites (Fig. 3c). Again, M11 and M1 showed high initial K concentration. In class three K concentration was similar for all areas, with exception of M11, which showed higher remaining K concentration.

Na concentrations did not vary between decomposition classes in all site clusters, except for Ducke Reserve. In this site the difference in Na concentration between the three classes is large, with an abrupt decrease from class one to class two, and an increase, from class two to class three (Fig. 3d). Al concentration in CWD in general, tended to increase (Fig. 3e) in all site clusters, following decomposition. Although the general pattern is for accumulation, in some sites Al concentration did not vary among three decay classes, and in others it increased from class one to two and remained the same in class three. At BDFFP, Ducke Reserve, M11 and M2 sites, Al concentration increased from class two to three, considerably. These four sites showed higher remaining Al concentration, while M1 showed the lowest. Fe concentration in CWD had the same accumulation pattern found for Al, in all site clusters, except for M1 (Fig. 3f). Zn concentration also increased with the advance of decomposition classes, but the differences are not notably wide (Fig. 3g). BDFFP and M11 sites showed higher initial Zn concentration and also remained with the highest ones. Initial Mn concentration in CWD tended to be similar to the final concentration in all sites, but not in M11 (Fig. 3h). Some sites showed slightly increase in Mn concentration from class one to two, while others showed a small decrease among classes, but all reached class three with almost the same concentration of class one. P concentration (Fig. 3i) tended to increase slightly among decay process in all site clusters, but not for M1, which showed higher initial P concentration and had a constant decrease in P, reaching similar values of other sites in class three. In Figure 3i we note that despite the slightly increase, the initial, intermediate and final P concentration in CWD did not change much.

Carbon concentration did not vary widely among decomposition classes in any of our sites (Fig. 3j) and the sites with higher initial C content in CWD remained with high C also in class three. N concentration however increased along decay classes (Fig. 3k), with exception of M1, which showed increase in N concentration from class one to two, which did not change in class three. Because there were no difference in C content among classes, but there was a slightly increase in N concentration, CN ratio generally decrease in most sites (Fig. 3l).

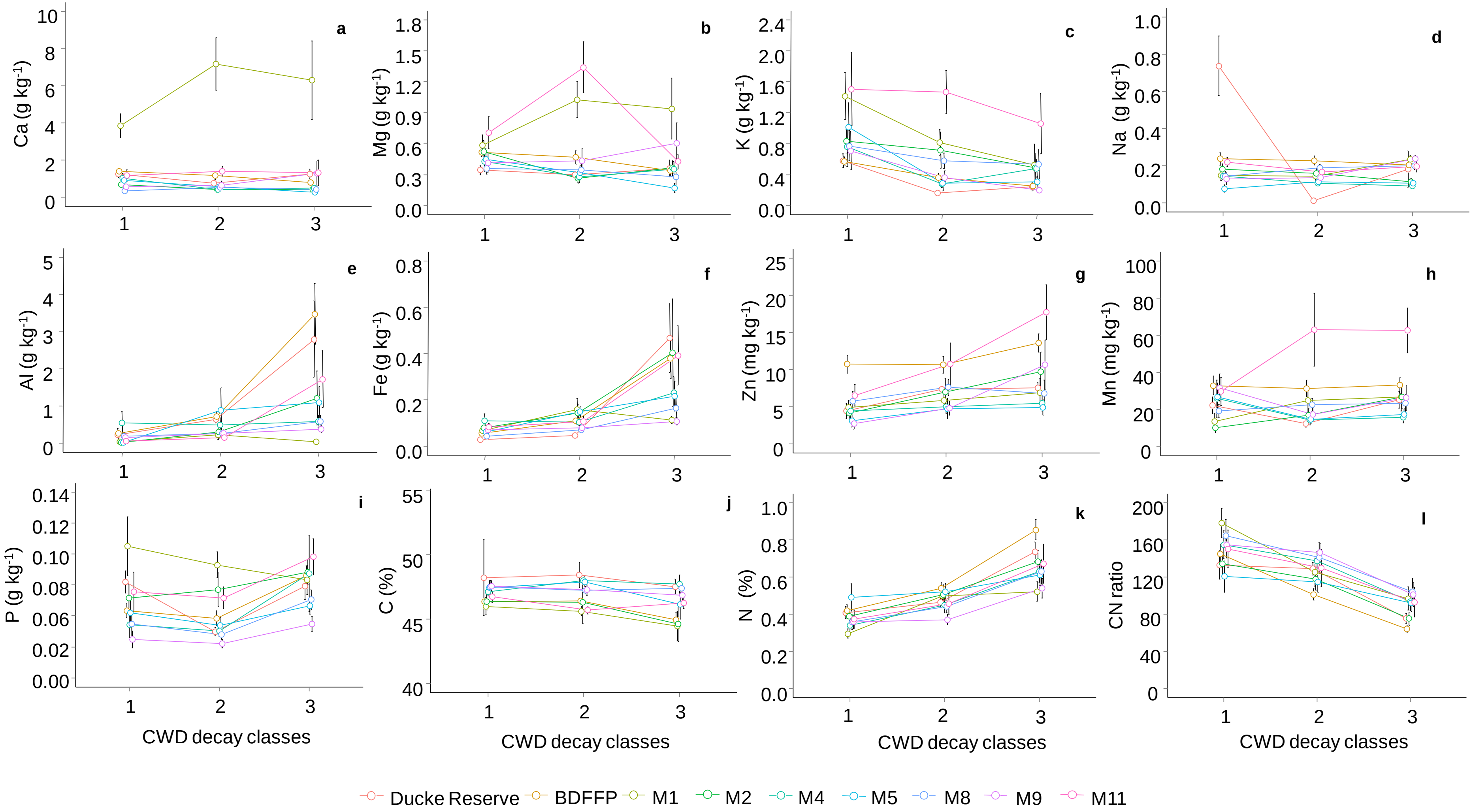

Figure 3. Nutrient flux (mean ± standard error, g kg^{-1}, mg kg^{-1} or %) in CWD by three decay classes in nine site clusters north and south Manaus. (a) Ca, (b) Mg, (c) K, (d) Na, (e) Al, (f) Fe, (g) Zn, (h) Mn, (i) P, (j) C, (k) N and (l) CN.

3.4. Nutrient concentration and stock in LSC

LSC generally showed higher nutrient concentration than CWD. Ca concentration in LSC tended to be higher in plots north of Manaus, than in plots from BR-319 (Table 5), with the exception of M1 which showed much higher Ca concentration than any other site, with about 12.49 ± 0.89 g kg^{-1} (one way ANOVA, $F_{[8,26]} = 9.06$, $p < 0.001$). The second higher Ca concentration was found in Ducke Reserve, with only 3.07 ± 0.23 g kg^{-1}. Mg concentration was also higher at M1 site cluster, but with some variation 1.57±0.79 g kg^{-1} (one way ANOVA, $F_{[8,26]} = 6.73$, $p < 0.001$). It was possible to note an increasing gradient of Mg concentration from M4 to M11 site, reaching concentrations as high as the one found at M1 site cluster. Site clusters north Manaus and also M1 had significantly lower K concentration in LSC (one way ANOVA, $F_{[8,26]} = 20.73$, $p < 0.001$), with Ducke showing the lowest concentration, 0.74 ± 0.05 g kg^{-1} and M11, the highest, 1.97 ± 0.07 g kg^{-1}. BDFFP and Ducke Reserve also showed much higher Na concentrations with 0.40 ± 0.05 and 0.34 ± 0.01 g kg^{-1} respectively (one way ANOVA, $F_{[8,26]} = 30.09$, $p < 0.001$), while Na did not vary significantly among the Purus-Madeira interfluve sites, where the highest value found was 0.09 ± 0.04 g kg^{-1} at M4. Higher Al concentration was found at M1 site cluster, but with large local variation among plots, with about 2.31 ± 1.15 g kg^{-1} (one way ANOVA, $F_{[8,26]} = 5.23$, $p < 0.001$) and there was no significant differences in Fe concentration among site clusters (one way ANOVA, $F_{[8,26]} = 2.05$, $p = 0.08$).

Zn and P concentrations in LSC were significantly higher at M1 site cluster, one of the Holocene soils area, with 0.017 ± 0.002 mg kg^{-1} for Zn and 0.42 ± 0.03 g kg^{-1} for P (one way ANOVA, $F_{[8,26]} = 7.11$, $p < 0.001$ and $F_{[8,26]} = 10.13$, $p < 0.001$ respectively). Mn concentrations in LSC were also higher in Holocene areas (M1 and M11) as well as in the very weathered ones, formed in Tertiary period (Ducke and BDFFP). The other sites at BR-319 showed low Mn concentrations. In contrast, C content in LSC were significantly lower at M1 and M11 sites, with 45.42 ± 0.09 % and 46.06 ± 0.66 % (one way ANOVA, $F_{[8,26]} = 3.95$, $p = 0.003$) but being similar among all other sites. However, N concentration in LSC was significantly higher in plots north Manaus, with 1.72 ± 0.04 % at Ducke Reserve and 1.55 ± 0.06 % at BDFFP (one way ANOVA, $F_{[8,26]} = 12.64$, $p < 0.001$), resulting in lower CN ratio in these two areas (Table 5). It was also possible to note a north – south decreasing in N concentration in LSC from Ducke Reserve to M9.

Table 5. Element concentration in LSC (mean ± standard error) in two site clusters north Manaus and seven south Manaus, in Purus-Madeira interfluve.

Element concentration	**Ducke**	**BDFFP**	**M1**	**M2**	**M4**	**M5**	**M8**	**M9**	**M11**
g kg^{-1}									
Ca	3.1±0.2	2.7±0.1	12.5±0.9	1.3±0.1	1.4±0.1	1.4±0.1	1.2±0.1	1.8±0.2	2.4±0.7
Mg	1.4±0.0	1.7±0.1	1.6±0.8	1.4±0.0	1.2±0.1	1.2±0.0	1.2±0.0	1.5±0.1	1.6±0.1
K	0.7±0.0	0.8±0.1	1.0±0.2	1.3±0.0	1.2±0.0	1.3±0.0	1.7±0.1	1.5±0.1	2.0±0.1
Na	0.40±0.0	0.34±0.0	0.08±0.0	0.09±0.0	0.09±0.0	0.06±0.0	0.07±0.0	0.08±0.0	0.07±0.0
Al	1.8±0.4	1.9±0.6	2.3±1.1	0.4±0.2	2.1±0.4	0.9±0.4	0.5±0.1	0.4±0.1	1.2±0.2
Fe	0.3±0.08	0.2±0.04	0.2±0.07	0.1±0.02	0.2±0.11	0.7±0.61	0.1±0.02	0.1±0.0	0.2±0.0
P	0.2±0.0	0.2±0.0	0.4±0.0	0.2±0.0	0.2±0.0	0.1±0.0	0.2±0.0	0.2±0.0	0.3±0.0
mg kg^{-1}									
Zn	0.01±0.0	0.01±0.0	0.02±0.0	0.01±0.0	0.013±0.0	0.01±0.0	0.01±0.0	0.01±0.0	0.01±0.0
Mn	0.1±0.0	0.14±0.0	0.1±0.0	0.04±0.0	0.04±0.0	0.05±0.0	0.05±0.0	0.06±0.0	0.2±0.0
%									
C	48.3±0.4	48.7±0.5	45.4±0.1	47.7±1.9	49.2±0.9	49.5±0.3	48.8±0.6	49.2±0.4	46.0±0.6
N	1.7±0.0	1.5±0.0	1.4±0.1	1.2±0.2	1.2±0.0	1.1±0.0	1.2±0.1	1.1±0.0	1.3±0.0
CN	28.3±0.7	31.5±1.5	31.9±2.2	38.7±7.0	38.9±0.8	43.2±1.9	40.4±2.3	43.5±2.6	34.9±0.6
*n**	9	3	2	2	2	2	5	5	5

* *n* number of plots sampled for each site cluster.

Nutrient stock in LSC is a function of both amount of dead material on the floor and nutrient concentration in the tissue. LSC mass stock was significantly different among site clusters (one way ANOVA, $F_{[8,26]}$ =3.35, $p = 0.009$) (Table 6). M4, M5, M8, M9 and M11 showed the higher amounts of LSC mass, while Duke, BDFFP, M1 and M2 showed lower stocks. Despite showing LSC stock three times lower, M1 had the highest Ca stock because of the high Ca concentration, with 22.31 ± 2.18 kg ha^{-1} (one way ANOVA, $F_{[8,26]}$ =4.81, p = 0.001). M11 also had a significantly higher Ca stock with 6.92 ± 1.84 kg ha^{-1}. In the other site clusters, Ca stocks did not vary a lot. M9 and M11 had higher Mg stocks with 4.61 ± 0.22 and 4.60 ± 0.36 kg ha^{-1} (one way ANOVA, $F_{[8,26]}$ = 3.37, $p = 0.008$) respectively. This was associated with high Mg concentration and also large LSC stocks. These two site clusters also showed higher K stock in LSC, with 4.61 ± 0.45 and 5.71 ± 0.31 kg ha^{-1} (one way ANOVA, $F_{[8,26]}$ =18.20, $p < 0.001$). K stocks tended to increase in LSC in the north-south gradient, from Ducke Reserve to M11 site. Na stocks, however, were much higher in sites north of Manaus, with about 0.80 kg ha^{-1}, and very low among all plots in the interfluve (one way ANOVA, $F_{[8,26]}$ =6.81, $p < 0.001$). There was no significant difference in Fe stocks among site clusters (one way ANOVA, $F_{[8,26]}$ =1.93, $p = 0.09$), while Al stocks were higher where large amounts of LSC were found, with 7.65 ± 1.20 kg ha^{-1} at M4 (one way ANOVA, $F_{[8,26]}$ =5.73, $p <$ 0.001).

P stocks in LSC followed the high concentrations of this element found in M11 and M1 (Table 6), with 0.96 ± 0.06 and 0.75 ± 0.03 kg ha^{-1} respectively (one way ANOVA, $F_{[8,26]}$ =6.85, $p < 0.001$), while M4, due to the large amount of LSC mass, almost reaches similar stocks from M11 and M1. Higher LSC stock in M4 also led to higher Zn and C stocks in this site cluster (one way ANOVA, $F_{[8,26]}$ =3.29, $p = 0.009$ and $F_{[8,26]}$ =3.30, $p = 0.009$), with 0.06 ± 0.03 and 1.90 ± 0.60 kg ha^{-1} respectively. Mn stocks were also mostly related to its tissue concentration, being significantly higher at M11, with 0.51 ± 0.04 kg ha^{-1} (one way ANOVA, $F_{[8,26]}$ =10.56, $p < 0.001$). There were no differences in N stocks among site clusters (one way ANOVA, $F_{[8,26]}$ =6.85, $p < 0.001$), despite sites north of Manaus showed higher N concentrations.

Table 6. Element stock in LSC (mean ± standard error) in two site clusters north Manaus and seven south Manaus, in Purus-Madeira interfluve.

Element stock	**Ducke**	**BDFFP**	**M1**	**M2**	**M4**	**M5**	**M8**	**M9**	**M11**
Mg ha^{-1}									
LSC stock	1.9±0.2	2.3±0.2	1.8±0.0	2.1±0.2	3.9±1.3	2.5±0.4	2.5±0.2	2.9±0.2	2.9±0.1
kg ha^{-1}									
Ca	5.5±0.7	6.2±0.6	22.3±2.2	2.8±0.6	5.7±2.4	3.5±0.8	2.9±0.4	5.3±0.6	6.9±1.8
Mg	2.7±0.3	3.9±0.3	2.8±1.5	2.9±0.3	4.3±0.9	2.9±0.6	3.1±0.3	4.6±0.2	4.6±0.3
K	1.4±0.2	1.8±0.1	1.7±0.3	2.9±0.3	4.6±1.3	3.2±0.7	4.2±0.2	4.6±0.4	5.7±0.3
Na	0.8±0.1	0.8±0.1	0.1±0.0	0.2±0.0	0.4±0.2	0.1±0.0	0.2±0.0	0.2±0.0	0.2±0.0
Fe	0.4±0.1	0.5±0.1	0.3±0.1	0.2±0.0	0.9±0.7	1.4±1.2	0.2±0.0	0.2±0.0	0.6±0.1
Al	3.0±0.6	4.3±1.1	4.0±1.9	0.8±0.3	7.6±1.2	2.1±0.6	1.4±0.5	1.2±0.2	3.7±0.6
P	0.4±0.0	0.4±0.0	0.7±0.0	0.4±0.0	0.7±0.2	0.4±0.1	0.4±0.0	0.5±0.0	0.9±0.0
N	31.9±4.1	35.8±1.9	25.5±1.1	26.5±0.5	48.6±14.4	28.4±3.9	30.7±1.6	34.1±12.3	38.1±1.0
Zn	0.02±0.0	0.02±0.0	0.03±0.0	0.02±0.0	0.06±0.0	0.03±0.0	0.02±0.0	0.03±0.0	0.03±0.0
Mn	0.2±0.0	0.3±0.0	0.2±0.0	0.1±0.0	0.1±0.0	0.1±0.0	0.1±0.0	0.2±0.0	0.5±0.0
Mg ha^{-1}									
C	0.9±0.1	1.1±0.1	0.8±0.0	1.0±0.2	1.9±0.6	1.2±0.2	1.2±0.1	1.5±0.1	1.3±0.0
*n**	9	3	2	2	2	2	5	5	5

* *n* number of plots sampled for each site cluster.

3.5. Nutrient determinants in CWD and LSC across landscape

We evaluated the influence of soil fertility and physical properties in the amount of CWD mass stocks. Soil physical properties were represented by Π_1 (Index 1), which correspond to the sum of the scores given to effective soil depth, structure, anoxia and topography to form an index of soil physical quality. There was a significant and negative relation between CWD mass stocks and Index 1 (Figure 4a) ($p = 0.029$, $R^2_m = 0.14$ and $R^2_c = 0.14$), as was already shown by Martins et al., (submitted). Soil physical properties explain 14% of CWD mass stocks variation for both fixed and random factors. Higher CWD stocks were found in sites with low index 1 values, which represent better soil physical conditions. The relationship between CWD mass stocks and soil fertility is represented here by soil exchangeable P which was the best correlated fertility parameter (Figure 4b). No significant relationship was found between soil P and CWD mass stock ($p = 0.14$, $R^2_m = 0.07$ and $R^2_c = 0.11$). The sum of exchangeable bases showed the second best relationship with CWD mass stock (not shown) but again no clear relation was found ($p = 0.74$, $R^2_m = 0.003$ and $R^2_c = 0.09$).

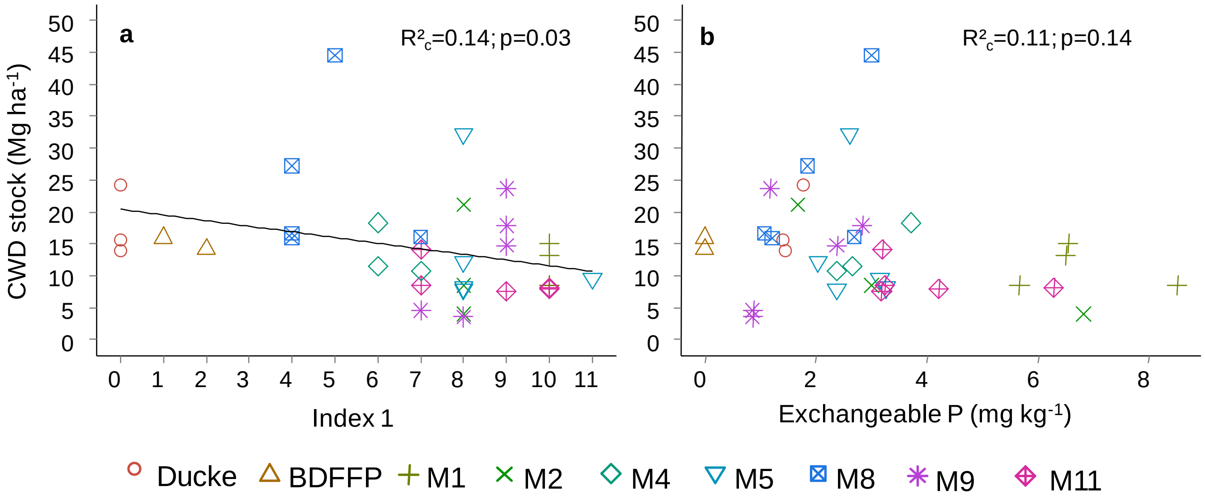

Figure 4. Simple relationships between CWD mass stock (Mg ha^{-1}) and (a) soil physical properties (Index 1) and (b) soil fertility (represented by exchangeable P concentration).

In general, relationships between soil elemental concentration and LSC were stronger than with CWD (Figures 5, 6 and 7). There was a significant and positive relation between exchangeable Ca in soil and Ca concentration in CWD and LSC ($p = 0.03$, $R^2_m = 0.15$ and $R^2_c = 0.29$; and $p = 0.03$, $R^2_m = 0.17$ and $R^2_c = 0.49$ for CWD and LSC respectively) and the highest values for soil, CWD and LSC Ca concentration were found at M1 site cluster (Figure

5a, 5b). The Ducke Reserve also shows a comparatively high concentration (Figure 5a, 5b). The relationship between Ca in soil and LSC was stronger (49%) than the one found for CWD (29%). Mg concentration in soil however, was not related to CWD ($p = 0.82$, $R^2_m = 0.001$ and $R^2_c = 0.31$) and LSC concentrations ($p = 0.10$, $R^2_m = 0.11$ and $R^2_c = 0.13$) (Figure 5c and 5d). K concentration in soil and in CWD showed significant and negative relation ($p = 0.00$, $R^2_m = 0.32$ and $R^2_c = 0.66$) (Figure 5e). It was possible to note however, that all plots at M11 site cluster had low K concentration in soil, and high K concentration in CWD. No significant relation was found for K in soil and LSC ($p = 0.63$, $R^2_m = 0.003$ and $R^2_c = 0.77$) (Figure 5f).

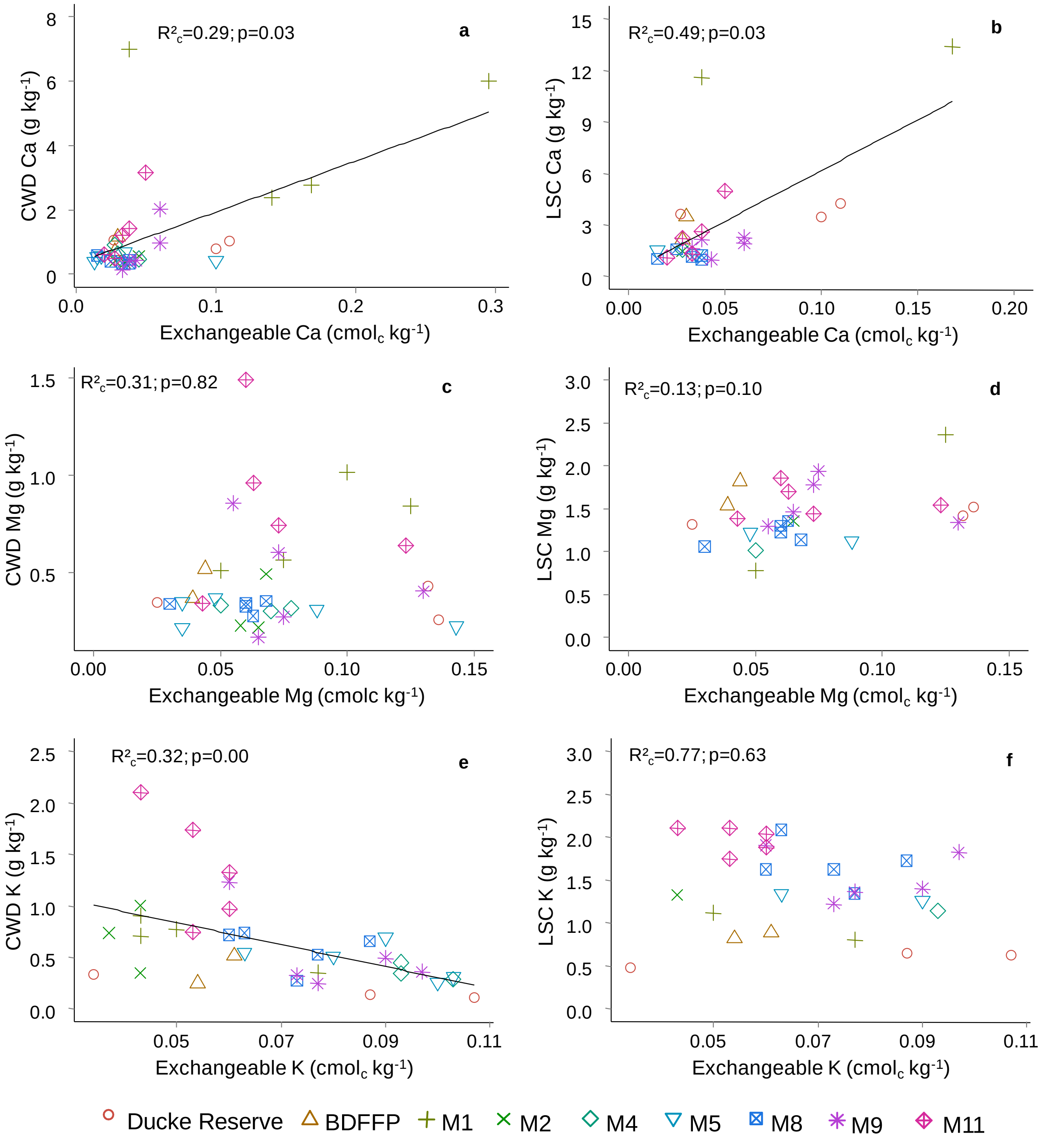

Figure 5. Simple relationships between exchangeable nutrient concentration in soil ($cmol_c\ kg^{-1}$) and nutrient concentration in CWD and LSC ($g\ kg^{-1}$). Note variables were transformed for analysis but not in figures.

There was also no relation between Al in soil and CWD ($p = 0.86$, $R^2_m = 0.00$ and $R^2_c = 0.28$), however, a negative relation between this element in soil and LSC was found ($p = 0.006$, $R^2_m = 0.093$ and $R^2_c = 0.84$) (Fig. 6a and 6b). Again, there was no relation between Fe concentrations in soil and in CWD ($p = 0.87$, $R^2_m = 0.00$ and $R^2_c = 0.00$), but Fe concentration in LSC was positive related to its concentration in soil ($p = 0.01$, $R^2_m = 0.18$ and $R^2_c = 0.62$) (Fig. 6c and 6d). Zn in soil was not related to Zn concentration in both CWD ($p = 0.37$, $R^2_m = 0.03$ and $R^2_c = 0.47$) and LSC ($p = 0.35$, $R^2_m = 0.04$ and $R^2_c = 0.49$) (Figure 6e and 6f).

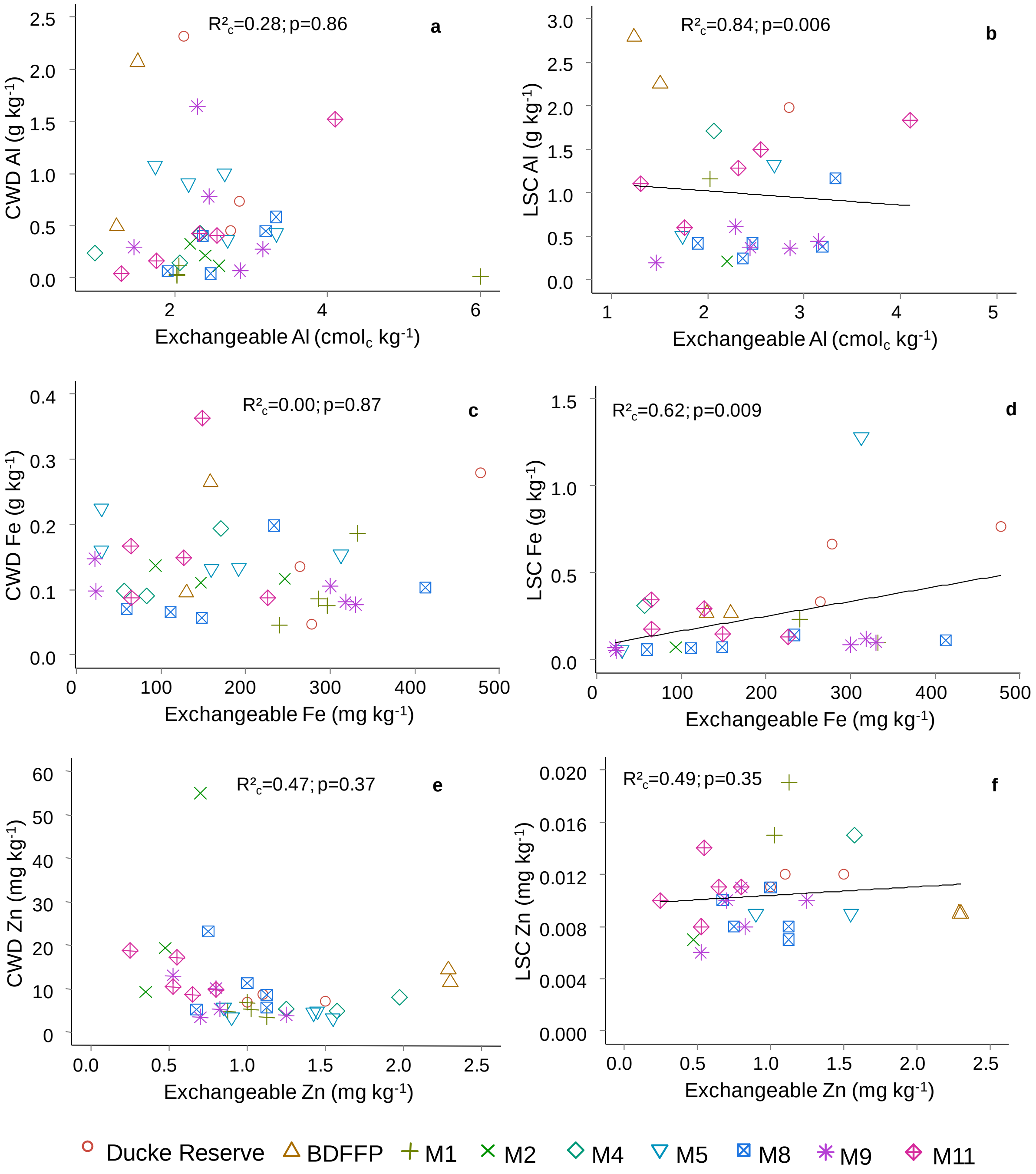

Figure 6. Simple relationships between exchangeable nutrient concentration in soil (cmol$_c$ kg^{-1} and mg kg^{-1}) and nutrient concentration in CWD and LSC (g kg^{-1} and mg kg^{-1}). Note variables were transformed for analysis but not in figures.

C content in CWD and LSC tended to vary similarly, with expected no relation to soil C content (for CWD: p = 0.76, R^2_m = 0.00 and R^2_c = 0.42 and for LSC: p = 0.32, R^2_m = 0.03 and R^2_c = 0.54) (Figure 7a and 7b). However, N content in soil was strongly related to both N concentration in CWD and LSC. There was a significant and positive relation between N content in soil and in CWD (p = 0.00, R^2_m = 0.23 and R^2_c = 0.40) and the complete model, with fixed and random effects was even better (Figure 7c). There was also a positive relation between N content in soil and in LSC ($p = 0.00$, $R^2_m = 0.61$ and $R^2_c = 0.69$) with both models with fixed effects and the complete model, with fixed and random effects explain more than 60% of its relationship (Figure 7d). We also note a trend in site cluster distribution based on N concentration, where sites north Manaus, represented by Ducke and BDFFP showed higher N concentration in soil, as well as in CWD and LSC, while sites from Purus-Madeira interfluve had low N concentration in all three compartments (Figures 7c and 7d). P concentration in soil was also strongly and positively related to P concentration in CWD ($p = 0.02$, $R^2_m = 0.18$ and $R^2_c = 0.47$) and in LSC ($p = 0.02$, $R^2_m = 0.24$ and $R^2_c = 0.68$) (Figure 7e and 7f). Together, fixed and random effects explained more than only fixed effects and again, the relation between soil and LSC P concentrations was stronger than the relation between soil and CWD. Distinct distribution of site clusters is also seem in Figures 7e and 7f, where plots from M1 and M11 tended to have higher P concentration in soil and also in CWD and LSC.

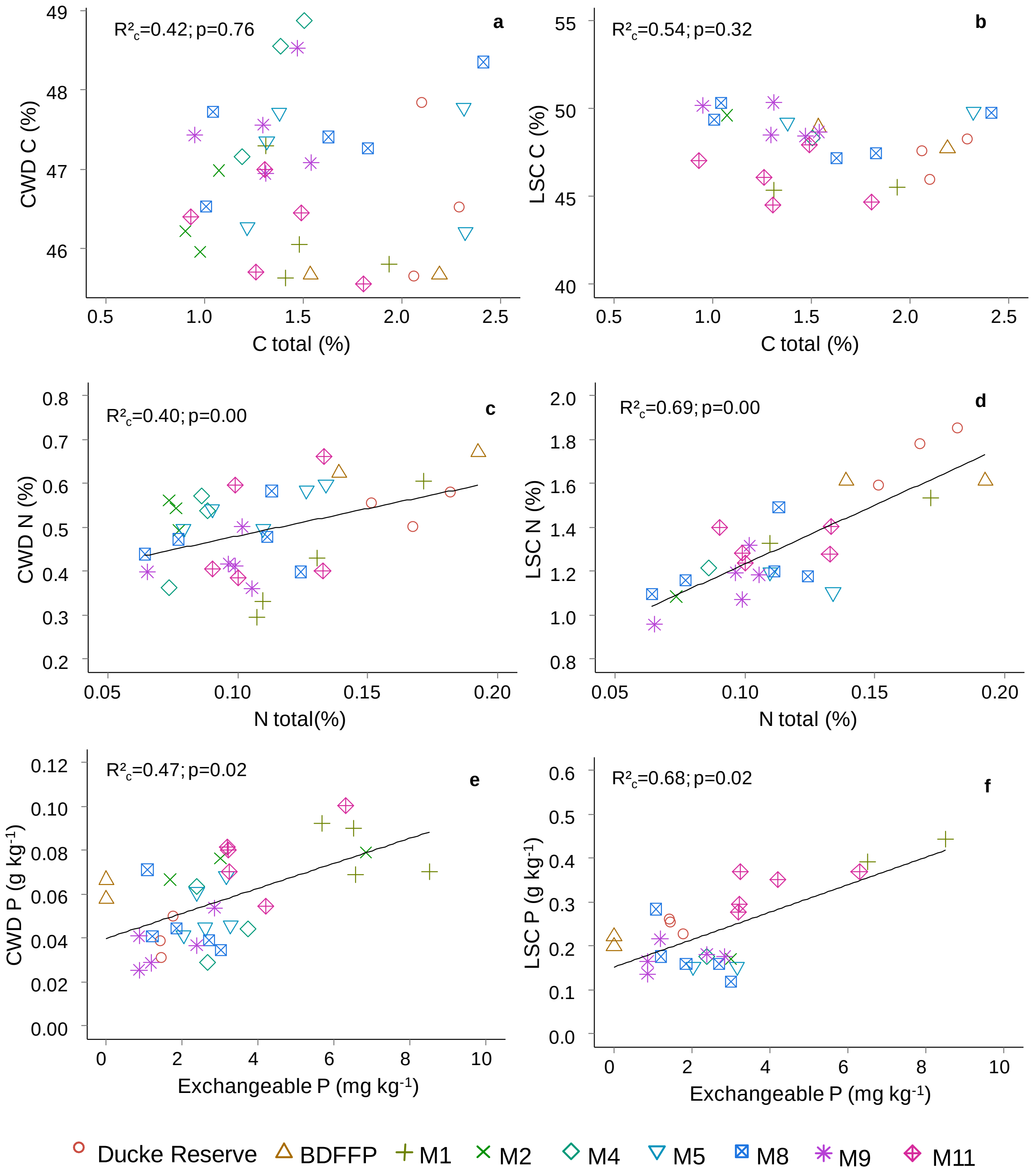

Figure 7. Simple relationships between exchangeable nutrient concentration in soil (cmol$_c$ kg^{-1}) and nutrient concentration in CWD and LSC (g kg^{-1}). Note variables were transformed for analysis but not in figures.

3.6. Relation between edaphic properties, mass of CWD and its nutrient stocks

We hypothesized that nutrient stocks in CWD are a function of two complementary processes: soil physical properties affect CWD nutrient stocks by determining the actual mass of dead wood in the pool (Martins et al, submitted) and soil fertility on the other hand imposes another level of control through the effect of CWD elemental concentration, which is ultimately influenced by local soil fertility. The structural model (Figure 8), shows soil physical properties represented in our analysis by Index 1 and nutrient concentrations in soil represented by the concentration of each exchangeable nutrient and also total N content in separate models. Path coefficients from direct effects, indirect and general effects between variables are shown in Table 7. Path analyses were performed for eight elements were nutrient concentrations were available for both soil and CWD.

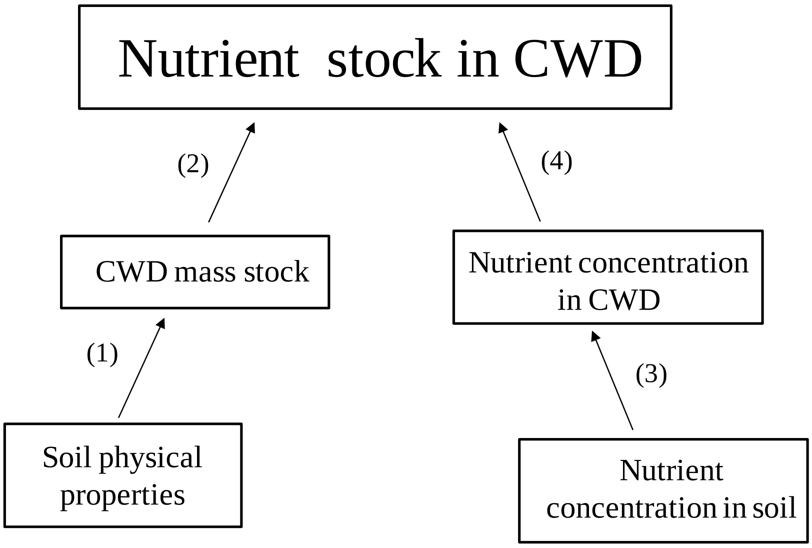

Figure 8. Path diagram showing causal relationships between soil physical and chemical properties on nutrient stock in CWD. Numbers in parenthesis and arrows represent direct relation between variables.

We observed that Index 1 was significantly and negatively related to the amount of CWD stock in our sampling areas (Table 7), as already shown by Martins et al., (submitted). In our sites soil physical properties explain 32% of CWD stock variance. The actual CWD stock was the main control of CWD nutrient stocks in all elements with the exception of Ca. Ca was the one element which showed higher path coefficients direct effects (paths 3 and 4, Figure 8) and was the nutrient that showed the strongest relationship between soil fertility, nutrient concentration in CWD and through that overall Ca stock. For this reason, general effect of the path model for Ca was high (0.43), and the only positive general effect found that was related to the importance of soil chemical properties in CWD nutrient stocks.

Mg, Al and Fe and P showed almost exclusively controls from the CWD mass path (i.e. nutrient stocks determined by the amount of CWD), with very little or no influence from elemental tissue concentration (Table 7) as evidenced by their path's indirect effects. Although a relationship exists between stocks of Al and Fe and their concentration in CWD, there was no relationship between soil and CWD tissue concentrations for these elements. Indirect effects for the CWD mass path where 0.12 and 0.13 for Al and Fe, while the indirect effect for the fertility path was only 0.01 for both Al and Fe. P, on the other hand, was the only element showing no significant relationship between CWD tissue concentration and P CWD stocks, this despite a strong positive relationship between soil exchangeable P and CWD P concentration. Indirect effects suggest that P stocks in CWD depend mostly on CWD mass, with little direct influence from wood tissue concentration.

Simultaneous influence from the CWD mass path and the fertility path (defined here as the influence of soil fertility on CWD tissue nutrient content and its consequent influence on CWD nutrient stock) occurred for K, Zn and N, suggesting that the stock of these elements is controlled both by the amount of CWD mass and the variation in wood tissue nutrient concentration. Indirect effects for these elements suggest that stocks of K and Zn may be proportionally more affected by soil fertility and CWD elemental concentration (-0.28 and -0.26, for K and Zn respectively), but also being influenced by the amount of CWD (-0.12 and -0.13, for K and Zn respectively). N also seems to be influenced by both effects, but with the amount of CWD explaining a larger fraction of CWD N stocks. Also worth to note is that K and Zn CWD concentrations were the only ones which showed negative relationships with soil fertility, where the higher the nutrient concentration in soil had lower concentration in CWD.

Table 7. Direct, indirect and general effects of soil physical and chemical properties from path model showed in Figure 9 on nutrient stock in CWD. Direct effects represent path coefficients.

	Physical soil path			Chemical soil path			
Nutrient	Index 1 on CWD stock (1)	CWD stock on Nutrient CWD stock (2)	Indirect Effect	[Soil] nutrient on [CWD] nutrient (3)	[CWD] nutrient on CWD nutrient stock (4)	Indirect Effect	General Effect
Ca	-0.32*	0.09	-0.03	0.58**	0.76**	0.43	0.39
Mg	-0.32*	0.53**	-0.17	0.09	0.32*	0.03	-0.14
K	-0.32*	0.39*	-0.12	-0.52**	0.54**	-0.28	-0.4
Al	-0.32*	0.42*	-0.13	-0.04	0.41*	-0.02	-0.15
Fe	-0.32*	0.39*	-0.12	0.02	0.56**	0.01	-0.11
Zn	-0.32*	0.40*	-0.13	-0.32*	0.83**	-0.26	-0.39
P	-0.32*	0.78**	-0.25	0.55**	0.06	0.03	-0.22
N	-0.32*	0.85**	-0.27	0.42*	0.41*	0.17	-0.1

Direct effects are in parenthesis; Index 1 represents soil physical properties; Indirect effect from the physical soil path is the multiplication of direct effect (1) and (2), while indirect effect from chemical soil path is the multiplication of direct effect (3) and (4); General effect is the sum of indirect effects both from physical and chemical soil path. Significance of the direct effects are indicated as * $P < 0.05$ and ** $P < 0.001$.

4. Discussion

4.1. Landscape variation in CWD nutrient stocks

Nutrient stocks in CWD and LSC in our study were a function of the effect of both physical and chemical soil properties, acting at various levels. For most elements, stocks followed total mass stocks of dead material, while some elements showed a combined effect of wood mass and local soil fertility. Ca was the only nutrient where the effect of soil concentration (and consequent dead wood Ca concentration) was more important than the contribution of dead wood mass. Thus Ca stocks in CWD ranged widely, showing high values even when these areas showed low CWD mass stocks. In general we found that, as shown by Martins et al., (submitted), lower stocks of CWD were found in soils with higher restriction levels to tree growth and survival, and higher stocks were found in forests over soils with good soil physical conditions. In contrast, our results indicate that LSC usually has lower mass stocks where CWD stocks are higher, while higher LSC stocks were found in areas with low CWD mass stocks.

It is important to constrain those results to our study area. The amplitude of variation for soil fertility in our study sites was rather small, despite the large area covered here. For instance, exchangeable Ca in our study sites range from 0.03 to 0.16 $\text{cmol}_c\ \text{kg}^{-1}$, with most of our sites below the lower end observed by Quesada et al., (2010) across Amazonia, where exchangeable Ca was found to vary between 0.1 and 10 $\text{cmol}_c\ \text{kg}^{-1}$. Similar paucity of nutrients in our soils is also observed for all major elements such as Mg (range from 0.04 to 0.1 $\text{cmol}_c\ \text{kg}^{-1}$), K (range from 0.04 to 0.1 $\text{cmol}_c\ \text{kg}^{-1}$), P (range from 1.54 and 6.81 mg kg^{-1}) and N (0.08 – 0.17%). This contrasts with the observed ranges for these elements across Amazonia (Quesada et al., 2010) which are much wider (Mg 0.03 - 2.5 $\text{cmol}_c\ \text{kg}^{-1}$, K 0.02 - 0.4 $\text{cmol}_c\ \text{kg}^{-1}$ and P 1.3 - 21.8 mg kg^{-1} and N 0.05 – 0.9%). Considering such large variation in soil fertility it seems likely that larger variation in CWD nutrient concentration occur throughout Amazonia, which potentially may be reflected in CWD nutrient stocks in a similar fashion to the relationship observed here for Ca, where CWD stocks were a function of tissue concentration, instead of simply being controlled by the amount of wood mass. Elements that are directly absorbed by roots in soil water are potentially the most likely to attain high concentrations in CWD in fertile soils (such as nitrate and exchangeable bases). However not all elements in CWD would reflect soil fertility, since some of them appear to have rather fixed amounts in wood (Fe, Al, Zn and Mn). Another explanation to the variation in CWD nutrient concentrations and stocks could be related to differences in tree species composition following changes in soil chemical and physical properties (Wilcke et al., 2005).

The relationship between soil physical properties and CWD mass stocks (Martins et al., submitted) reflects the influence of soil physical conditions on the residence time of trees (Galbraith et al., 2013). Soils with favorable physical conditions usually sustain forests with long living trees, heavier trees, which contribute with considerable mass to the necromass pool when they die. Similarly, soils with limiting conditions to root growth and tree establishment tend to have more dynamic forests (Quesada et al., 2012), and shorter tree residence time, being occupied predominantly by smaller trees which contribute with less necromass when they die. Decomposition is also related to tree size at moment of death, and is another factor influencing CWD stocks. Wood density is an important trait controlling decomposition (Chambers et al., 2000; Chave et al., 2009) but CWD diameter also exert large influence in this process (van Geffen et al., 2010). Differences in thickness and surface area may partially control CWD decay, with faster decomposition where trees have smaller diameters, and consequently, greater surface area for decomposition. Therefore, CWD stocks in forests showing favorable soil physical conditions should have a slower decomposition rate, and may be an important long term reservoir compartment for nutrient cycling. This might be of high importance to some Central Amazonian forests as a nutrient conserving mechanism. LSC turnover is fast and compensate the slower cycling of CWD, but a large amount of nutrients is stored in CWD for the long term.

CWD nutrient stocks may be critical for the maintenance of site fertility and productivity, serving as a long-term sink for nutrients thus protecting the ecosystem from disturbance-related nutrient losses, as well as being a source of nutrients. However, the nutritional importance of CWD relative to other types of debris has been suggested to be insignificant in some environments. For instance, Laiho and Prescott, (2004) working on coniferous forests on North America have suggested that CWD nutrient stocks are of minor importance since they store low concentration of nutrients and decomposition is temperate forests is slow. The authors reported that although CWD accounts for up to 54% of accumulated organic matter (including forest floor litter and soil), it contributes with <5% of the N, <10% of the P, and <25% of the K, Ca, and Mg. They conclude that CWD is of minor importance in the nutrient cycles of northern coniferous forests (Laiho and Prescott, 2004). However, their result was based in temperate ecosystems in which CWD turnover is very low.

Wilcke et al., (2005) studying nutrient stock and turnover in a montane forest in Ecuador also found that CWD only play a minor role in nutrient cycle, contributing less than 1.8% to the nutrient stock in total dead organic matter.

However, Amazon forests potentially cycle more nutrients in CWD than temperate and montane forests since decomposition is much faster. Also, the general paucity of nutrients in central Amazonian soil may result in increased importance of CWD nutrient pools. In our study, CWD nutrient stocks represent a somewhat higher proportion of total nutrient pools (defined here as top soil exchangeable stocks + LSC + CWD). Proportion of nutrient stocks in CWD ranges from 18-42% for Ca, 14-38% for Mg, 3-14% for K and from 5-32% for P total nutrient pool (Table A3). Other elements such as N, Fe and Zn have much lower proportions (1-4%, 0.2-1.4% and 1-9% for N, Fe, Zn, respectively). However, as pointed out by Laiho and Prescott, (2004), the interpretation of these pool ratios is somewhat ambiguous, because the forest floor and soil organic matter pools contain unknown proportions of nutrients derived from CWD, and the CWD pool may include nutrients imported from the surroundings.

Very few studies attempted to measure CWD nutrient stocks in Amazonia, and therefore comparison with other geographical areas is limited. Summers, (1998) and Pauletto, (2006) have quantified nutrient stocks in CWD in forest management areas in the Amazon region, attempting to compare the differences in nutrient stocks in this compartment between explored and pristine forests. For pristine forests of Mato Grosso, Brazil, Pauletto, (2006) found an average CWD stock of 33.7 Mg kg^{-1}, much higher than the highest stock found in our study, which was 24.08 Mg ha^{-1}. Summers, (1998), also for pristine forests near Manaus, found 25.5 Mg ha^{-1} similar to the maximum stocks found in this study.

4.2. Nutrient fluxes in CWD decay classes

The constant concentration throughout de decay classes observed for many elements in our study may reflect the mass loss occurring during decomposition, primarily as microbially respired CO_2 but also through organic matter leaching (Harmon et al., 1994; Wilcke et al., 2005). This overall mass loss tends to increase nutrient concentrations (i.e., g nutrient / kg CWD) by decreasing the denominator and can therefore hide actual nutrient gain or loss (Holub et al., 2001). This implies that CWD mass loss is greater than or equal to the loss of these nutrients or that the nutrients are being imported into CWD. Increases in CWD nutrient content can also be a result of potential inputs through precipitation or throughfall

(Harmon et al., 1986), dry deposition, root ingrowth, fungal translocation (Frey et al., 2000), animal inputs, and asymbiotic N_2 fixation (Silvester et al., 1982; Sollins et al., 1987). Soil could also become easily mixed with CWD in highly decomposed wood (class 3). Nutrient losses from CWD on the other hand involve pathways that could include leaching (Fahey and Yavitt, 1985), animal transfer out (Edmonds and Eglitis, 1989), fungal translocation (Harmon et al., 1994), nutrient volatilization (e.g., ammonia loss or denitrification), plant uptake and CWD fragmentation. Accumulation can also be a result from low mobility of some elements. For instance Al (and potentially Fe, Zn and Mn) has high ionic charge and tend to form strong bonds to cation exchange sites in CWD (Holub et al., 2001). Some elements are also only sparingly soluble in water, which should reduce losses from CWD favoring their accumulation. Conversely, concentrations of K decrease rapidly, indicating that K is lost at a greater rate than CWD mass (Harmon et al., 1994; 1986).

Summers, (1998) and Pauletto, (2006) also studied nutrient concentration among decomposition classes of CWD in Amazonian forests. The observed flux of nutrients was similar between their studies and ours, despite some differences found in initial element concentration. Pauletto, (2006) in general, found higher concentrations of base cations and P for all decay classes in comparison to Summers, (1998) and our study. Our results hold greater similarities to those found by Summers, (1998), particularly regarding to Ca and Mg concentrations (with an average 1.46 and 0.36 g kg^{-1}, respectively), but with K and P concentration in his study being lower than ours (0.21 and 0.03 g kg^{-1} respectively).

4.3. Variation in edaphic properties and its relation to LSC and CWD chemistry

Soils across our Central Amazonian transect are fundamentally a function of their geomorphology and geological substrate age. Soils north of Manaus (BDFFP and Ducke Reserve) are located in very old and highly weathered surfaces from the Terciary-Cretaceous, approximately 100 million years old (Chauvel, 1987; Quesada et al., 2011). Physical properties found on these soils reflect the high levels of weathering, which have resulted in very deep and well structured soil horizons. As a consequence of such intense weathering, nutrients have been lost throughout soil formation and most of remaining nutrients come from recycling of organic matter (Quesada et al., 2010; 2011). On the other hand, soils along the BR-319 road are much younger (Sombroek, 2000). Areas close to Manaus and Porto Velho are of Holocene age (<10.000 years) and may have recently suffered sediment deposition from meandering rivers (Solimões and Madeira Rivers) which could explain the somewhat higher fertility when compared to other soils along the BR-319 road. However, most of the Purus – Madeira interfluve area is formed by sediments from the Pleistocene (<1.8 million years), likely to be reminiscent from an ancient internal lake, which have very infertile, hydromorphic soils with rather poor physical conditions (Sombroek, 2000).

It is interesting to note that despite of the BR-319 soils are much younger than their northern counterparts, their concentration of exchangeable soil nutrients is lower than at BDFFP and Ducke reserve. However, once the Total Reserve Bases weathering index is compared among these areas, it is possible to note a much higher concentration of elements in the BR-319, which likely represent a major abundance of primary minerals in these soils (Quesada et al., 2011, Delvaux et al., 1989). The product of weathering in these soils is Al, which explain the extreme infertility of exchangeable bases. In addition, total phosphorus, which is also a good proxy of pedogenetic process (Smeck, 1985), is considerably higher at the BR-319 soils, consistent to their lower pedogenetic development.

The abundance of exchangeable nutrients along our study area is very low, representing the extreme lower end of soil fertility in Amazonia (Quesada et al., 2010). Nevertheless, despite the small range of soil fertility, both LSC and CWD nutrient concentration reflected the abundance of soil nutrients, particularly for Ca, P and N which showed slightly wider ranges in soil. K showed a distinct pattern with a negative relationship where soils with more K had lower concentrations in LSC and CWD. K is known to be highly vulnerable to leaching during decomposition (Harmon, 1986; Laiho and Prescott, 2004), and higher transport out of CWD may occur where K is more available and initial K concentrations are higher (Holub et al., 2001). Mg, Al, Fe, and Zn in CWD were not related to soil exchangeable concentration. Mg has been reported to shown correlations with soil Mg content (Laiho and Prescott, 2004) and therefore the lack of relationship in our study area may result from the narrow variation in exchangeable Mg in soil. The other elements seem to vary little in wood, which could be related to low active absorption of such elements (Fe, Al and Zn) or low allocation to wood. Generally, LSC were associated more clearly to soil conditions than CWD.

5. Conclusions

Soil physical constrains have been associated to forest dynamic in Amazon basin, determining forest dynamics and structural characteristics, that in turn influence CWD stocks.

By determining the amount of dead wood, soil physical properties are also important in controlling nutrient stocks in CWD. We found that the mass of CWD in a given area exerts large influence over CWD nutrient stocks, with the exception of some elements. Nutrient concentration in CWD can also influence CWD nutrient stocks, particularly in regard to Ca. Finally, our results suggest that nutrient stocks in CWD could be more important to nutrient storage in oligotrophic forests in central Amazonia than previously assumed. The relative importance of CWD increases as soil weathering advances. In younger soils that are less weathered, forests tend to show higher mortality rates, shorter residence of trees which become lower and thinner and consequently accumulate less biomass by tree. When a tree from this type of forest dies, it generates less CWD stocks and also less nutrient stock in this compartment, becoming relatively less important to nutrient stocks than the soil itself. On the other hand, where the soils are very weathered and also less fertile, nutrient stock in CWD becomes relatively more important. The forests in this kind of soils usually have lower mortality rates, longer residence of trees, with higher and thicker trees, which accumulate higher biomass by tree. When the trees from this kind of ecosystem die, they generate higher stocks of CWD and consequently higher nutrients stocks, if compared to the very weathered soil. This work highlights the importance of soil physical and chemical characteristics in determining forest functioning, and nutrient storage in landscape scale in central Amazonia.

6. Conclusões

As restrições físicas do solo tem sido associadas à dinâmica florestal na Amazônia, determinando características estruturais e a dinâmica da floresta, o que por sua vez influencia no estoque de serapilheira grossa. Ao determinar a quantidade de madeira morta, as propriedades físicas do solo são também determinantes no controle dos estoques de nutrientes na serapilheira grossa, comparando-se ao controle exercido pela fertilidade do solo. Entretanto, a concentração de nutrientes na madeira morta não pode ser usada como variável preditora do controle dos estoques de nutrientes nesse compartimento, estando esses associados em grande parte apenas com a massa de madeira morta. Os resultados desse estudo demonstram ainda que em alguns casos, existe a combinação da massa e do conteúdo de nutrientes determinando seus estoques na serapilheira grossa. A concentração da maioria dos elementos na serapilheira fina e grossa variou em função da fertilidade do solo. A grande amplitude na concentração de cálcio encontrada na serapilheira grossa sugere que alguns elementos podem ter seus estoques controlados mais fortemente pelas concentrações na madeira morta do que pelo estoque de massa de madeira morta. O fluxo de nutrientes representado pelas classes de decomposição da serapilheira grossa indica que, apesar das diferenças edáficas e também na estrutura das florestas estudadas, a liberação ou acúmulo de nutriente na madeira morta é relativamente constante, apesar das diferenças nas concentrações iniciais dos elementos. Finalmente, os resultados encontrados aqui sugerem que estoques de nutrientes na madeira morta podem ser mais importantes para a retenção de nutrientes em florestas oligotróficas da Amazônia central do que assumido anteriormente. A serapilheira grossa torna-se relativamente mais importante no estoque de nutrientes em florestas sob solos muito intemperizados e menos férteis, enquanto que em florestas com solos jovens e menos intemeprizados, o solo é ainda um reservatório importante de nutrientes, se comparado com a serapilheira grossa. Este trabalho destaca a importância das características físicas e químicas do solo na modulação das florestas, afetando dessa forma a quantidade de nutrientes estocados e ciclados pela serapilheira grossa em escala de paisagem na Amazônia central.

7. Appendix

Table A1. 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 A2. Total element concentration and TRB (Total Reserve Bases) in the soil 0-30, cm (mean ± standard error) in two site clusters north Manaus and seven south Manaus, in Purus-Madeira interfluve.

Element concentration	**Ducke**	**BDFFP**	**M1**	**M2**	**M4**	**M5**	**M8**	**M9**	**M11**
cmol$_c$ kg^{-1}									
Ca	1.1±0.1	1.8±0.0	0.8±0.2	0.6±0.2	1.2±0.1	1.3±0.1	0.8±0.1	0.6±0.1	1.0±0.0
Mg	0.4±0.0	0.4±0.0	5.6±1.3	4.6±0.3	3.3±0.4	3.9±0.5	4.6±0.5	4.6±0.6	5.8±0.5
K	0.4±0.0	0.3±0.0	4.4±0.8	4.9±0.6	3.9±0.9	4.8±0.8	5.8±0.5	6.5±0.7	7.0±0.3
Na	0.7±0.2	1.4±0.0	0.7±0.1	1.0±0.2	0.9±0.1	0.9±0.1	1.5±0.2	1.2±0.1	1.3±0.1
TRB*	2.7±0.2	3.9±0.0	11.5±2.3	11.1±1.3	9.4±1.5	11.0±1.3	12.7±1.0	12.9±1.4	15.2±0.8
mg kg^{-1}									
P	55.4±3.2	45.8±0.0	134.9±19.6	155.3±9.0	108.8±3.5	120.6±2.4	129.5±6.9	130.3±8.3	162.8±9.4
*n***	3	2	4	3	3	5	5	5	5

* TRB (Total Reserve Bases) is the sum of Ca, Mg, K and Na concentrations. *** *n* number of plots sampled for each site cluster.

Table A3. Element stock proportion in CWD (%) in relation to total stocks in top soil exchangeable stocks + LSC + CWD in two site clusters north Manaus and seven south Manaus, in Purus-Madeira interfluve.

Element proportion in CWD (%)	**Ducke**	**BDFFP**	**M1**	**M2**	**M4**	**M5**	**M8**	**M9**	**M11**
Ca	42.29	51.01	38.21	18.58	19.03	21.99	31.17	17.78	27.96
Mg	25.48	38.10	25.43	14.37	11.08	12.00	26.39	14.17	19.21
K	11.05	11.91	17.46	12.45	3.13	5.29	11.39	8.96	14.25
Al	2.50	9.13	0.98	0.33	1.46	1.27	0.73	0.59	0.47
Fe	0.63	1.39	0.19	0.34	0.40	0.42	0.41	0.18	0.40
Zn	5.47	8.08	2.32	10.59	1.24	0.95	5.59	2.28	4.74
P	31.82	NA	5.79	5.54	5.29	7.20	14.72	8.93	4.63
C	20.70	19.50	13.08	14.08	10.71	10.61	20.33	12.32	8.94
N	3.97	4.17	1.54	2.33	1.91	2.23	3.82	1.82	1.27

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