



INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA - INPA

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA – PPG-ECO

Distribuição das frações do carbono orgânico nos solos de florestas maduras na Bacia Amazônica: o papel das propriedades do solo, da qualidade da liteira e do clima

CLAUDIA PANDOLFO PAZ

Manaus, Amazonas
Setembro, 2011

CLAUDIA PANDOLFO PAZ

Distribuição das frações do carbono orgânico nos solos de florestas maduras na Bacia Amazônica: o papel das propriedades do solo, da qualidade da liteira e do clima

REGINA C. C. LUIZÃO

Carlos Alberto Quesada

Dissertação apresentada ao Instituto Nacional de Pesquisas da Amazônia como parte dos requisitos para obtenção do título de Mestre em Biologia (Ecologia).

Manaus, Amazonas

Setembro, 2011

Banca Examinadora do Trabalho Escrito

Gustavo Saiz - James Cook University

Parecer: *Aprovada com correções*

Steel Silva Vasconcelos - EMBRAPA Amazônia Ocidental

Parecer: *Aprovada*

Plínio B. Camargo – Universidade de São Paulo

Parecer: *Aprovada*

Banca Examinadora da Defesa Oral Pública

Adriana M. C. Horbe - Universidade Federal do Amazonas

Parecer: *Aprovada*

Lucerina T. Cabrera – Instituto Nacional de Pesquisas da Amazônia

Parecer: *Aprovada*

Fernanda T. Villani - Instituto Federal de Educação, Ciência e Tecnologia do Amazonas

Parecer: *Aprovada*

P348

Paz, Claudia Pandolfo

Distribuição das frações do carbono orgânico nos solos de florestas maduras na Bacia Amazônica: o papel das propriedades do solo, da qualidade da liteira e do clima / Claudia Pandolfo Paz. --- Manaus : [s.n.], 2011. vii, 78f. : il. color.

Dissertação (mestrado) -- INPA, Manaus, 2011

Orientador : Regina C. C. Luizão

Co-orientador : Carlos Alberto Quesada

Área de concentração : Ecologia

1. Solos tropicais – Amazônia. 2. Carbono orgânico. 3. Solos – Fracionamento da matéria orgânica. I. Título.

CDD 19. ed. 631.41

Sinopse: Analisamos a distribuição das frações do carbono orgânico no solo em 30 parcelas de florestas maduras na Bacia Amazônica. Foram avaliados dez diferentes tipos de solos, em quatro profundidades. Foram consideradas as variáveis de solo, a qualidade da liteira e o clima para investigar o controle ambiental sobre a concentração de carbono nos solos destas florestas tropicais.

Palavras-chave: Ecologia de florestas tropicais, fracionamento da matéria orgânica no solo, RAINFOR, funcionamento de ecossistemas.

AGRADECIMENTOS

Meus sinceros agradecimentos aos meus orientadores Regina Luizão e Beto Quesada que me proporcionaram a oportunidade de trabalhar nesse projeto. Obrigada pelo aprendizado, confiança, liberdade e apoio em todos os sentidos.

Ao professor Flávio Luizão (coordenador do RAINFOR/Moore Foundation) pelo apoio e confiança. Obrigado a Betty & Gordon Moore Foundation e FDB pela bolsa de estudo concedida.

Ao Beto Quesada e toda a família RAINFOR (Raimundo, Jonas, Erick, Lita, Zalina, Sidney, Erison, Renato e Antônio) pela ajuda dispensada ao longo de meses de laboratório. Com certeza eu não teria condições de fazer tudo sozinha. Obrigada pela amizade e pelas risadas mesmo nas horas mais difíceis.

À coordenação do PPG Ecologia, especialmente à coordenadora do programa Claudia Keller, pelo apoio e esforço para manter tudo organizado.

À Tânia Pimentel, por toda a ajuda desde o início do trabalho, pelas ótimas conversas, pela experiência de laboratório, pela amizade.

À todas as pessoas que passaram pelo LTSP (Laboratório Temático de Solos e Plantas) durante o período que estive lá, principalmente aos técnicos Orlando Cruz e Edivaldo sempre dispostos a ajudar e tornar a convivência entre todos muito agradável.

Obrigada aos meus colegas da turma da Ecologia 2009 pela ótima convivência. Com certeza amigos para sempre.

Não posso deixar de agradecer os coordenadores, professores, monitores e colegas do EFA 2009 e 2010. Essa experiência foi incrível. Participar desse curso foi fundamental para o meu crescimento durante o mestrado.

Agradeço aos amigos Flávio Rodrigues, Camila Anjos, Juliana Menger, Ursula Andres, Igor Kaeffer, Cristian Dambros, Vinícius Moraes, Patrícia Torres e Lara Silva com quem compartilhei moradia nesses anos e que se tornaram a minha família em Manaus.

Agradeço a minha mãe, pai e irmãos que foram fundamentais na realização do meu sonho amazônico. Sem o apoio de vocês nada disso seria possível.

Agradeço ao Carlos Renato Boelter (Leléo) que encarou junto comigo esse desafio, pela companhia e aprendizado.

RESUMO

A estabilidade do carbono orgânico no solo (SOC) é dependente das condições do ambiente, como o clima, fatores edáficos e qualidade da matéria orgânica. Assim, considerando-se que existe uma ampla variação destas condições na Bacia Amazônica, espera-se que a concentração de SOC em frações lábeis e estáveis varie também. Investigar esses processos em sistemas florestais naturais é importante para compreender os mecanismos de funcionamento do ecossistema e produzir modelos ecológicos de dinâmica do carbono com um grau maior de precisão. Neste estudo foram respondidas as seguintes questões: (i) como estão distribuídas as frações do SOC em diferentes tipos de solos e profundidades? (ii) como as frações do SOC estão inter-relacionadas? (iii) qual é o papel das propriedades do solo, da qualidade das folhas da liteira e das variáveis climáticas sobre a distribuição das frações do SOC ao longo da Bacia Amazônica? O estudo foi realizado em 30 parcelas de 1h de florestas maduras no Brasil, Peru, Colômbia e Guiana Francesa. Foram utilizadas técnicas de fracionamento da matéria orgânica do solo e análises químicas e físicas padronizadas do solo e liteira. Os resultados mostraram uma variação na concentração de SOC nas frações ao longo do gradiente de intemperismo do solo. Os solos mais jovens e férteis tenderam a apresentar maiores concentrações de SOC associada às frações minerais estáveis (silte+argila), enquanto os solos altamente intemperizados como Ferralsols e Acrisols apresentaram maiores concentrações de SOC nos agregados do solo. Os solos arenosos e altamente inférteis tenderam a apresentar maiores concentrações de SOC nas frações leve, entretanto a labilidade dessa fração da MOS pode variar dependendo da qualidade da matéria orgânica. A concentração de SOC nas frações do solo demonstrou ser principalmente controlada pelos fatores edáficos, com exceção da fração leve que apresentou relação forte com a qualidade da liteira. Nós encontramos poucas evidências do efeito direto do clima sobre as frações de SOC.

ABSTRACT

Distribution of soil organic carbon fractions in old-growth forests in the Amazon Basin: the role of soil properties, leaf litter quality and climate

Soil organic carbon (SOC) stability is a function of environmental and biological conditions such as edaphic factors, climate and organic matter quality. Considering that a wide variation occurs in all these parameters across Amazonia, one could expect that there should be systematic variations in SOC fractions across the area. Understand the processes involved in carbon stabilization in tropical pristine forests is very important to improve our understanding of ecosystem function and to allow the preparation of better and more accurate models of soil carbon dynamics. We used soil carbon fractionation techniques to answer the following questions: (i) How the different soil carbon fractions are distributed among the different soil types, at varying depths (ii) How they are inter-related and (iii) What is the role of soil properties, climate and litter quality in modulating SOC fractions across the Amazon Basin. This study was carried out on 30 1 hectare pristine rainforest plots located at Brazil, Peru, Colombia and French Guyana. Our results show that SOC concentration in the different fractions vary following a soil weathering gradient, where soil carbon on young, more fertile soils is predominantly associated to relatively stable pools (silt+clay fraction) while highly weathered soils such as Ferralsols and Acrisols have large proportion of their soil carbon associated with stable aggregates. Very sandy and infertile soils have organic matter mainly associated with the maintenance of particulate organic matter on soil surface, which is clearly associated to poor organic matter quality and low decomposability. Concentration of SOC on most fractions was found to be mainly associated to edaphic properties, with the exception of the light fraction which is related to litter quality. We have found little evidence of climate influence on SOC fractions.

SUMÁRIO

Agradecimentos.....	iv
Resumo	vi
Abstract	vii
Introdução.....	01
Objetivos.....	05
Capítulo 1: Distribution of soil organic carbon fractions in old-growth forests in the Amazon Basin: the role of soil properties, leaf litter quality and climate	06
Title page	07
Abstract.....	08
1. Introduction	09
2. Methods	11
2.1 Study site	11
2.2 Soil and leaf litter samples.....	11
2.3 Soil organic matter fractionation	12
2.4 Soil and litter quality analysis	13
2.5 Data analysis.....	15
3 Results.....	16
4 Discussion	25
5 Final remarks	32
Acknowledgments.....	32
References	32
Tables.....	41
Table legends	46
Figures.....	47
Figure legends	53
Supplementary material	54
Supplementary material legends.....	62
Conclusão.....	63
Apêndice I – Ata de aula de qualificação.....	65
Apêndice II – Ata de defesa presencial.....	66
Apêndice III – Pareceres dos revisores da versão escrita.....	67

INTRODUÇÃO

1.1 Carbono orgânico e ecossistemas

Atualmente, estudos envolvendo a ciclagem de carbono em ecossistemas terrestres tem sido o foco de muita discussão, principalmente por causa do aumento da concentração de gases do efeito estufa na atmosfera nas últimas décadas (Fearnside, 1985; Lal, 2004). Mudanças globais causadas principalmente pela queima excessiva de combustíveis fósseis e pelas derrubadas e queima de florestas tropicais aceleram o aquecimento terrestre, mas os efeitos em longo prazo dessas mudanças ainda são incertos (Nepstad et al., 1999; Cochrane, 2003; Achard et al., 2002). No entanto, já estão ocorrendo alterações nos ciclos biogeoquímicos, na biodiversidade e na vida dos seres humanos. Assim, no intuito de aprimorar as previsões em relação aos efeitos das mudanças no clima, têm sido feitos esforços para entender a dinâmica do carbono entre biosfera e atmosfera (Achard et al., 2004). Como resultado, têm sido realizadas muitas estimativas dos estoques de carbono na atmosfera e biosfera (Tian et al., 1998; Malhi & Phillips, 2004; Malhi et al., 2008).

A quantificação da biomassa acima do solo tem ajudado a entender alguns padrões na distribuição do carbono nos ecossistemas, e estimam que as florestas tropicais maduras como a floresta amazônica acumulam 93 ± 23 Pg C acima do solo, incluindo lianas e pequenas árvores (Malhi et al., 2006). Como consequência, a perda dessas florestas implicaria bilhões de toneladas de carbono lançados na atmosfera. Porém, estudos recentes mostraram que as camadas mais superficiais dos solos são responsáveis por um estoque de carbono até três vezes maior do que a vegetação sobre eles (Swift 2001; Silver *et al.* 2000). Isso fornece motivos suficientes para querer quantificar os estoques de carbono nos solos sob florestas, bem como investigar o controle exercido por fatores ambientais sobre a sua distribuição.

1.2 Matéria orgânica no solo (MOS)

A matéria orgânica no solo exerce um papel fundamental nos estoques de carbono. Os resíduos de organismos são depositados e incorporados às partículas minerais do solo e em florestas tropicais contribui com cerca de 700 Gt de C nos primeiros 3 m do solo (Jobbagi e Jackson, 2000). Há muito se sabe que a matéria orgânica tem um papel muito importante para o funcionamento dos ecossistemas (Hattenschwiler *et al.* 2005; Vitousek & Sanford, 1986, Russel, 1977). Estudos voltados para agricultura revelam que a MOS

interfere na disponibilização dos nutrientes para as plantas, além de apresentar funções de estruturação do solo e retenção de água (Wander 2004). Em sistemas florestais a queda das folhas, galhos e partes reprodutivas das plantas é uma das principais vias de entrada de matéria orgânica no solo, por causa da constante renovação de suas estruturas fotossintéticas e reprodutivas. Por exemplo, Jobbagi e Jackson (2000) mostraram que as camadas mais superficiais do solo (de 0-20 cm) em diferentes biomas, são as que contêm as maiores quantidades de carbono com tendência a uma diminuição gradativa da concentração de C conforme aumenta a profundidade. As reservas de matéria orgânica no solo são fundamentais para o balanço do carbono no solo e para a manutenção da vegetação (Oades 1988; Wander 2004).

1.3 Mecanismos de estabilização da MOS

A matéria orgânica pode apresentar variações quanto ao tempo que permanece nos solo. Dado que grande parte da matéria orgânica (30-70%) é consumida pela fauna de solo, fungos e bactérias o carbono pode voltar para a atmosfera como CO₂ em pouco tempo. Assim, a labilidade depende de mecanismos que mantêm a matéria orgânica estabilizada nos compartimentos do solo. Conhecidos como mecanismos de estabilização, alguns processos físicos e químicos ocorrem no solo e atrasam a decomposição da matéria orgânica. Além disso, a qualidade da matéria orgânica pode favorecer sua estabilização no solo. Mecanismos físicos estão mais relacionados com o processo pedológico, no qual a qualidade e a quantidade de minerais afetam a adsorção dos compostos orgânicos (Oades, 1988; Mikkuta et al., 2006). Além disso, o solo pode conter macro e microagregados que envolvem a matéria orgânica particulada e dificultam a ação dos organismos decompositores (Oades, 1988).

Da mesma forma, materiais muito recalcitrantes (lignina, tanino, polifenóis) podem atrasar a decomposição por serem de baixa qualidade para os principais decompositores (Schulten & Leinweber 2000). Qualquer um desses mecanismos, atuando sozinho ou em conjunto, afeta negativamente o processo de decomposição e, portanto, contribui para a manutenção de um certo estoque de matéria orgânica no solo (Schulten & Leinweber 2000 Six et al. 2002; Christensen 2002; Zimmerrmann et al., 2007; Ahn et al., 2009). Considerando que os mecanismos são altamente dependentes das condições do ambiente, tais como clima, principalmente temperatura e precipitação, bem como fatores edáficos e pedológicos, é possível que haja uma interação entre esses fatores o que torna sua compreensão um desafio (Oades, 1988; Swift, 2006; Six et al., 2002).

No solo, a matéria orgânica pode ser encontrada sob diferentes formas, as quais são responsáveis pelas diferenças na qualidade e tamanho dos reservatórios de carbono. Os reservatórios de carbono no solo são classificados em três categorias principais de acordo com o tempo envolvido na decomposição da matéria orgânica e retorno dos nutrientes para o sistema (Zimmermann et al., 2007). A reserva de matéria orgânica no solo pode ser ativa, de rápida decomposição ou pode ter uma decomposição mais lenta quando associada aos agregados organo-minerais. Por outro lado, a reserva passiva, é o reservatório de matéria orgânica que permanece no solo por muitos anos, até milênios, sem ser decomposta (Derenne and Largeau, 2001). A partir do fracionamento da matéria orgânica do solo pode-se determinar e quantificar cada fração e estimar a taxa de substituição do carbono nos solos sob diferentes condições ambientais (Christensen, 2002; Wander, 2004). Nesse sentido, o método desenvolvido por Zimmermann et al. (2007) nos permite obter cinco frações da matéria orgânica. Esse é considerado um método promissor já que une fracionamento físico/densimétrico com reações termo-químicas o que nos permite discutir aspectos da dinâmica do carbono em diversos tipos de solo (Christensen, 2002; Wander, 2004; Zimmermann, 2007).

1.4 Fatores que influenciam na dinâmica do carbono

Muitos fatores afetam o acúmulo de C no solo, sendo que o clima, concentração de CO₂ na atmosfera, fertilidade do solo (ex. concentração de N e P), hidrologia e composição das espécies são os principais controladores da entrada de carbono nos solos (Davidson and Janssens, 2006). Segundo esses autores, a saída seria mais afetada pela temperatura, água, oxigênio, qualidade do substrato, incidência de fogo, proteção física da matéria orgânica no solo e ação de enzimas e inibidores da decomposição. Seriam estes os fatores que determinariam a capacidade de um solo funcionar como fonte ou sumidouro de carbono. Dessa forma, estudos sobre os mecanismos que afetam a estabilização do carbono no solo tornam-se fundamentais para a compreensão da sua dinâmica e dos efeitos que as alterações nas condições ambientais poderiam causar.

Em geral, estudos das relações entre solo, vegetação e clima são realizados para fins de produção agrícola, principalmente em regiões temperadas. Por isso, em relação à dinâmica do carbono orgânico no solo em florestas tropicais úmidas, especialmente na floresta amazônica, há muito ainda para ser estudado. Investigar esses processos em sistemas florestais naturais é importante para prever as consequências das alterações no

uso da terra bem como, compreender os mecanismos de funcionamento do ecossistema e produzir modelos ecológicos com um grau maior de precisão.

1.5. Gradientes ambientais na Amazônia

A região amazônica é um ecossistema muito heterogêneo em relação às condições ambientais encontradas ao longo de sua extensão. Além de uma variação no clima, existe uma ampla variação nos tipos de solos, que apresentam características químicas e físicas diversas e produzem um gradiente de fertilidade do solo (Quesada et al., 2011; Quesada et al., 2010). Na Bacia Amazônica, estudos recentes mostraram que a estrutura e a dinâmica da vegetação acompanham essas variações nas condições do solo e do clima (Quesada et al., 2009; Phillips et al., 1998; Malhi et al., 2004; Baker et al. 2004b; Phillips et al., 2004; Stephenson and Van Mantgen, 2005). No entanto, a influência desses gradientes sobre a distribuição do carbono orgânico no solo em diferentes frações e suas relações com a vegetação ainda são pouco conhecidos.

É possível que as frações de carbono orgânico no solo variem ao longo dos gradientes de fertilidade e de clima e estejam correlacionadas com a qualidade da liteira e outros aspectos da vegetação (Quesada et al., 2010). Informações sobre a distribuição do carbono orgânico em diferentes compartimentos do solo poderiam auxiliar na compreensão dos mecanismos que atuam sobre a estabilização do carbono nos solos da maior floresta tropical do mundo. Os resultados deste estudo serão importantes também para aprimorar os modelos ecológicos de dinâmica de carbono e trazer maior grau de certeza às previsões associadas às mudanças climáticas nos próximos anos.

Assim, o presente estudo foi realizado no âmbito do projeto RAINFOR com a justificativa de fornecer dados para aprimorar os modelos de dinâmica de carbono e trazer maior grau de certeza às previsões de potenciais alterações no clima, solos e vegetação na região amazônica.

OBJETIVO GERAL

Avaliar a distribuição das frações do carbono orgânico no solo (SOC) em diferentes solos ao longo da Bacia Amazônica. Com esse estudo pretendemos fazer inferências sobre os principais mecanismos de estabilização da MOS que apresentam um papel importante nos solos da Amazônia, relacionando variáveis de solo, qualidade das folhas da liteira e clima com os conteúdos de SOC em diferentes frações.

OBJETIVOS ESPECÍFICOS

Responder as seguintes questões: (i) como estão distribuídas as frações do carbono orgânico no solo (SOC) em diferentes tipos de solos e profundidades; (ii) como as frações do SOC estão inter-relacionadas; (iii) qual é o papel das propriedades do solo, da qualidade das folhas da liteira e das variáveis climáticas sobre a distribuição das frações do SOC ao longo da Bacia Amazônica.

CAPÍTULO 1

Paz, C. P.; Quesada, C. A. & Luizão, R. C. C. 2011. Distribution of soil organic carbon fractions in old-growth forests in the Amazon Basin: the role of soil properties, leaf litter quality and climate. Manuscrito formatado para *Biogeosciences*

Distribution of soil organic carbon fractions in old-growth forests in the Amazon Basin: the role of soil properties, leaf litter quality and climate

Claudia P. Paz, Carlos A. Quesada & Regina C. C. Luizão

Instituto Nacional de Pesquisas da Amazônia – INPA, Av. André Araújo, 2936, Aleixo, CEP 69060-001, Manaus - AM, Brazil, Phone: (+55) 92 3643-1818.

Correspondence to: C. P. Paz (claudiappaz@gmail.com)

Abstract

Soil organic carbon (SOC) stability is a function of environmental and biological conditions such as edaphic factors, climate and organic matter quality. Considering that a wide variation occurs in all these parameters across Amazonia, one could expect that there should be systematic variations in SOC fractions across the area. Understanding the processes involved in carbon stabilization in tropical pristine forests is very important to improve our understanding of ecosystem function and to allow the development of better and more accurate models of soil carbon dynamics. We used soil carbon fractionation techniques to answer the following questions: (i) How the different soil carbon fractions are distributed among the different soil types, at varying depths (0-5, 5-10, 10-20, 20-30 cm), (ii) How they are inter-related and (iii) What is the role of soil properties, climate and litter quality in modulating SOC fractions across the Amazon Basin. This study was carried out on 30 1 hectare pristine rainforest plots located at Brazil, Peru, Colombia and French Guyana. We use a physical-chemical fractionation method to answer our questions. Results show that SOC concentration in the different fractions vary following a soil weathering gradient, where soil carbon on young, more fertile soils is predominantly associated to relatively stable pools (silt+clay fraction) while highly weathered soils such as Ferralsols and Acrisols have large proportion of their soil carbon associated with stable aggregates. Very sandy and infertile soils have organic matter mainly associated with the maintenance of particulate organic matter on soil surface, which is clearly associated to poor organic matter quality and low decomposability. Concentration of SOC on most fractions was found to be mainly associated to edaphic properties, with the exception of the light fraction which is related to litter quality. We have found little evidence of climate influence on SOC fractions.

1 Introduction

Motivated by concerns over the climate change, carbon has become subject of many studies around the world (Fearnside, 1985; Achard et al., 2004; Lal, 2004). Increasing levels of carbon in the atmosphere are associated with fossil fuel combustion, deforestation and forests fires, with these leading to acceleration of Greenhouse effects. Biogeochemical cycles, biodiversity and human life will be modified (Fearnside, 2003; 2004), however, the long-term alterations are quite unpredictable yet (Heiman & Reichstein, 2008; Nepstad et al., 1999; Cochrane, 2003; Achard et al., 2002) The understanding of carbon dynamics in ecosystems tends to be crucial for scientific predictions and governmental actions involving the global change (Achard et al., 2004). In this context, forest soils are valuable, because they store a huge amount of carbon, up to 3-fold more than forests above-ground biomass (Jobbagi and Jackson, 2000; Tian et al., 1998; Malhi et al., 2006; Barlow et al., 2003; WBGU, 1988 (www.ipcc.ch/ipccreports); Swift 2001; Silver et al., 2000). These facts provide us sufficient reasons to quantify the soil organic carbon (SOC) and to understand the carbon dynamics between biosphere and atmosphere. Soil organic carbon has been extensively studied, especially for agricultural purposes which provide a wealth of information about the SOC in a large variety of soils. These studies show the importance of the SOM to fertility, soil water retention and structure. However, natural ecosystems largely lack these information and basic studies in tropical forest soils become necessary.

A large amount of organic carbon is stored in soils, but it can be originating from organic residuals with different quality and can be found in different soil compartments. These variations lead to SOC with different lability, which influences its mineralization rate. Some stabilization mechanisms are involved in the maintenance of organic carbon in soils (Six et al., 2002; Christensen, 2002; Zimmermann et al., 2007; Ahn et al., 2009), these mechanisms may be physical, chemical or biochemical, and they promote delay in SOM decomposition process. Chemical mechanisms are related to the quantity and quality of minerals that affect the adsorption of organic compounds and their decomposition (Baldock and Skjemstad, 2000; Bruun et al., 2010). As physical mechanisms we consider the soil macro- and micro-aggregation of particles, that occlude the SOM and protects it from decomposition, similar to what occurs in chemical protection. These processes prevent soil microorganisms to decompose SOM, increasing the residence time of the organic carbon in soils. In addition, biochemical mechanism promotes SOC stabilization by decreasing the quality of organic material (Coley et al., 1985; Coley and Barone 1996) as the higher

proportion of recalcitrant compounds (e.g. lignin, tannins, polyphenols) in SOM hinders the decomposition process, causing the accumulation of organic carbon in soils (Schulten and Leinweber, 2000). The understanding of SOC stabilization under natural conditions is a challenge considering the mechanisms are highly dependent on environmental factors (climatic, pedological and biological characteristics) and their interactions (Oades, 1988; Swift, 2006; Six et al., 2002).

According to the time involved in SOM decomposition, three categories of SOC pools may be recognized (Zimmermann et al., 2007). SOM pools may be: (i) active, when its decomposition is fast, which means that SOM remains in soils for days or months; generally this SOM fraction is not associated with mineral soil particles; (ii) slow, when SOM is not readily available for decomposers, because it is chemically associated with fine soil particles (silt and clay) or protected in stable aggregates or coarse particles (sand), consequently the carbon remains for some years or few decades in soils, and (iii) passive; when SOM is highly stable and provide conditions to the persistence of carbon for thousands of years in soil, because complex chemical structure of compounds that form organic residuals (Derenne and Largeau, 2001). Through SOM fractionation techniques is possible to determine the size of SOC content in different fractions and pools to evaluate the SOC distribution along a variety of soils under different environmental conditions (Christensen, 2002; Wander, 2004).

Soils in the Amazon basin are originated from different geologic formations, which include different material ages and mineral composition. These wide variations generate a gradient of soil fertility across this region (Quesada et al., 2011; Quesada et al., 2010). Because of the different weathering level, soils in this region tend to decrease in concentrations of nutrients in the western-eastern direction. Despite the lower nutrient content, older soils may have more favorable physical properties for vegetation growth. This trade-off results in wide variations in environmental conditions, which lead to a large diversity of plant species as well as variations in structure and vegetation dynamics (Malhi and Phillips, 2004; Phillips et al., 1998; Malhi et al., 2004; Baker et al., 2004b; Phillips et al., 2004; Stephenson and Van Mantgen, 2005). However, we do not know how the SOC fractions are distributed along these gradients of soil properties, vegetation characteristics and climate.

Therefore, information about SOC distribution in different soil compartments would help to understand the stabilization mechanisms in soils of the Amazon Basin that comprises the largest tropical forest of the world. The present study aims to improve the understanding of soil carbon dynamics in tropical forests and to generate basic information to be incorporated in ecological models of SOC dynamics. Following the general aims of

RAINFOR project for increasing knowledge about Amazon ecosystem processes, we will use soil organic matter fractionation techniques to achieve the following specific aims: (i) evaluate the distribution of soil organic carbon (SOC) fractions in different soil types and at varying depths; (ii) analyze inter-relations between SOC fractions and processes involved in them; (iii) investigate the role of soil properties, leaf litter quality, and climatic variables on SOC fractions distribution across the Amazon Basin.

2 Methods

2.1 Study sites

We conducted this work on 30 1-ha forest plots in the Amazon Basin which are part of the RAINFOR network (www.rainfor.org). Study sites are located in Brazil, Colombia, French Guyana and Peru (Table 1). All study sites are under pristine, mature and non-inundated forests only. To account for the wide variation on nutrient content, texture and mineralogy occurring on Amazonian soils, we have sampled ten different reference soil groups, as defined by the World Reference Base (WRB) classification. These varied from the less developed and recently formed soils (i.e. Regosols and Cambisols) to soils occupying the most weathered groups (such as Ferralsols and Acrisols) that have been intensively weathered and leached (Quesada et al., 2011).

With regard to climate, sites experience wide variation of conditions with mean annual temperature ranging from 25 to 27 °C, and mean annual precipitation ranging from 1900 to 2850 mm per year. Dry season length, measured through the months with less than 100 mm of rainfall, also varies widely ranging from 0 to 5 months. Figure 1 shows the geographic distribution of study sites in Amazonia, with arrows indicating the dominant gradients in soil fertility and rainfall occurring in Amazonia. Data on mean annual temperature and annual precipitation were obtained through the interpolation techniques. Finally, study sites were chosen to maximize the geographical distance and minimize the effect of spatial autocorrelation.

2.2 Soil and leaf litter sampling

Soil and litter sampling were conducted according to a standard protocol (www.geog.leeds.ac.uk/projects/rainfor/projdocs.html) which is briefly described here (Quesada et al, 2010; Quesada et al 2011). In each 1-ha plot, five soil cores were collected

using an undisturbed soil sampler (Eijkelkamp Agrisearch Equipment BV, Giesbeek, The Netherlands). Soil and litter were collected in the end of the rainy season for all the sites. In each plot, one soil pit was dug in a location that represents the dominant soil of that site. Sampling points followed a random stratified distribution in order to obtain representative soil collections of each area. Although the soils were sampled up to 2 m deep, for this study we used only surface samples for soil physical-chemical analysis and organic matter fractionation, separated in four soil layers, 0-5, 5-10, 10-20, 20-30 cm. Soil classification followed the World Reference Base – WRB (IUSS Working Group WRB, 2006).

After sampling, samples were immediately dried at room temperature, cleaned of all detritus and plant remains and sieved (2 mm), being then ready for chemical and physical analysis. Leaf litter was collected next to each soil cores using a 50 x 50 cm quadrat. Plant material was also dried in order to stop the decomposition process. At the laboratory, leaves, branches and reproductive parts were dried in 40 °C oven until constant weight. For this study, only leaves were used. They had the central vein removed and were milled and saved for laboratory analysis.

2.3 Soil organic matter fractionation

Considering that the organic matter fractionation procedure is laboratory intensive and time consuming, for each site we have made composite samples for each depth, thus resulting in four samples per site.

To obtain the soil organic carbon fractions we applied the techniques of soil organic matter physical fractionation in air dried soil samples (Zimmermann et al., 2007). In this method, the soil samples were separated into five fractions: two fractions of the active pool (Light fraction and Dissolved Organic Carbon), two organic matter fractions of slow decomposition pool (Silt+Clay and Sand+Stable Aggregates or Heavy fraction) and organic matter from a passive pool (Resistant organic matter), which represents the more stable organic matter pool (Wander, 2004). Hereafter we will call Light fraction or LF, Dissolved Organic Carbon or DOC, Silt+Clay fraction or S+C, Heavy fraction or HF and resistant fraction or rSOC. The Total SOC is the total concentration of soil organic carbon not fractionated.

In the fractionation procedure, we first sonicated 30 g soil sample in a beaker with 161 ml of distilled water using a calibrated ultrasonic probe for 3'25". After the sonication, the soil sample was wet sieved to separate <63 µm particles (silt and clay) from >63 µm soil particles (particulate organic matter and sand + soil stable aggregates, i.e. the heavy and

light fractions). Three fractions were obtained from the <63 μm portion: the dissolved organic carbon (DOC), the total organic carbon associated to silt and clay particles (S+C) and the chemically resistant carbon (rSOC). To obtain these fractions, the entire solution containing sediment smaller than 63 μm was centrifuged for 4 min at 1,200 rpm in 50 ml centrifuge tubes. The material deposited at the bottom of the tube (Silt+Clay fraction) was dried in an oven at 40 °C for 48 hours and subsequently weighed. A homogeneous aliquot of 50 ml from the total water volume used in the wet sieving after centrifugation was filtered under vacuum suction through a membrane filter of 0.45 μm to obtain the DOC sample.

To obtain the resistant carbon fraction, we weighed 1 g of the dried Silt+Clay fraction and submitted to thermal oxidation by adding, 150 ml of sodium hypochlorite 6% (adjusted to pH 8 with concentrated HCl). In this process the carbon associated with the less resistant silt+clay was released as CO_2 , remaining only the more resistant organic matter. After this reaction, the remaining material was washed with distilled water, oven dried at 40°C for 48 hours when it became ready to be taken to the CHNS combustion analyzer (Elementar Vario Max, Germany). Therefore, the Silt+Clay fraction was determined as total carbon on the Silt+Clay fraction minus the resistant SOC fraction.

To obtain the sand + aggregate fractions (Heavy fraction) and particulate organic matter (Light fraction) we added a 25 ml solution of sodium polytungstate (density of 1.8 g/cm^3 , Sometu, Germany) on the >63 μm dried sample into 50 ml centrifuge tubes. Samples were then centrifuged for 15 min at 1,800 rpm and left to rest overnight. After this time, sample was left in the freezer for approximately 3 hours. After that, the Light fraction (basically plant residuals not complexed with minerals) and the Heavy fraction (sand + stable aggregates) could be easily separated by washing the frozen supernatant with distilled water. Both fractions were rinsed with distilled water to remove any residue of polytungstate solution. After drying (40 °C for 48 h), all samples were analyzed for organic C content in an automated CN analyzer.

2.4 Soil and litter quality analysis

Exchangeable cations

Exchangeable Ca, Mg, K, Na and Al were determined by the silver thiourea method (Ag-TU, Pleysier and Juo, 1980) as described in detail in ISRIC (1995), with extracts analyzed by AAS. Samples dilutions for Ca, Mg and Al were done using a 0.55% lanthanum suppressant solution, while K and Na also had their detection improved by addition of 0.2% CsCl. Details of solutions and standard series preparation as well as other information can be obtained in

Van Reeuwijk (2002). In this study effective cation exchange capacity (ECEC) and sum of bases (SB) were calculate (ignoring any exchangeable $[H^+]$) as follows:

$$ECEC = [Ca] + [Mg] + [K] + [Na] + [Al] \quad (1)$$

$$[SB] = [Ca] + [Mg] + [K] + [Na] \quad (2)$$

where the bracketed terms represent the exchangeable concentrations of each element expressed as $cmol_c kg^{-1}$.

Soil phosphorus

To achieve a comprehensive assessment of available phosphorus a standard phosphorus fractionation method was adopted (Hedley et al., 1982). The method consists of a sequential extraction with reagents of increasing strength. The first step being resin extractable P, followed by 0.5 M $NaHCO_3$, 0.1 M NaOH and 1M HCl. Total phosphorus was also determined by acid digestion using concentrate sulphuric acid followed by H_2O_2 as described in Tiessen and Moir (1993). The extraction results in eight different fractions named as resin P, bicarbonate inorganic, bicarbonate organic, sodium hydroxide inorganic, sodium hydroxide organic, hydrochloric acid, residual and total phosphorus. The residual fraction was determined as the difference between the total pool and the sum of all other labile fractions. In this study, we have only considered the effect of total phosphorus (P total) and the “available P” which consists of the adding up of organic and inorganic phosphorus from resin, bicarbonate, hydroxide and hydrochloric acid (or simply total – residual). More details on the extraction methods can be obtained in Quesada et al. (2010).

Chemical weathering index

To investigate the weathering levels of soils within the dataset, the weathering index Total Reserve Bases (TRB) was calculated. This index is based on total cation concentration in the soil and is considered to give a chemical estimation of weatherable minerals (Delvaux et al., 1989). Soils samples were extracted for total elemental concentrations (Ca, Mg, K, Na, Al, P) by strong acid digestion using concentrate sulphuric acid followed by H_2O_2 . Concentrations were determined by AAS. The weathering index TRB was calculated as:

$$[TRB] = [Ca_T] + [Mg_T] + [K_T] + [Na_T] \quad (5)$$

where $[X_T]$ represents the total concentration of each element in $mmol_c kg^{-1}$ soil.

Carbon and Nitrogen

Soil samples and SOC fractions were milled to less than 50 μm and subsequently analyzed using an automated elemental analyser (Pella, 1990; Nelson and Sommers, 1996).

Litter lignin concentrations

Litter lignin concentration was determined by the ADF-sulfuric method (Van Soest, 1963; Rowland and Roberts, 1994). The method consists of application of acid-detergent, followed by acid attack of cellulose using H₂SO₄ 72%, with lignin and ash residual being subsequently determined by loss of weight on ignition. Litter lignin was considered as a measure of quality of organic matter input to soil.

Particle size analysis

Particle size analyses were done following the pipette method (Gee & Bauder, 1986), where 10 g of fine earth was first treated with physical and chemical dispersants and then separated into sand (particle sizes between 0.05 and 2 mm), silt (particle sizes between 0.002 mm and 0.05 mm) and clay contents (particle sizes < 0.002 mm). Sand was first separated by wet sieving, and then clay content was determined gravimetrically in a 20 ml aliquot.

2.5 Data analysis

Each plot was considered as an independent sample unit for statistical analysis. To respond our first question we use soil types as categories and SOC fractions and SOC pools as continuous response variables. Data were analyzed with percentage SOC values and elemental concentration (mg g⁻¹ SOC). Because percentage values have low interpretative power among soil categories this measure were not used in other analysis. We present in this study the average data found in four different layers of each soil type and average values between the layers of different depths for each soil type. For the second question Shapiro-Wilk's *W* normality test was run with all soil fractions and data were log-transformed to obtain normal distributions. We use Kendall's τ to test correlations between fractions and correlations between fractions and the environmental variables (soil properties, litter and climate). We used R version 2.9.2 (R *Development Core Team* 2009) to run correlations and regression tests.

Spatial autocorrelation

Analyses of ecological processes are usually been done using multiple regressions in which a desired response variable is regressed against sets of environmental variables (see Quesada et al., 2009 for recent relevant examples). However, the lack of independence

between pairs of observations across geographical space (spatial autocorrelation), results in the need for more complex strategies for data analyses (Legendre, 1993). This occurs because spatial autocorrelation generates redundant information on data, thus overestimating the actual degrees of freedom (Dutilleul, 1993). Autocorrelation in multiple regression residuals ultimately results in the underestimation of standard errors of regression coefficients, consequently inflating Type I errors. Regression models that incorporate the spatial structures into their structure or regression residuals should then be used to provide unbiased regression coefficients (Diniz-Filho and Bini, 2005). Eigenvector-based spatial filtering (extracted by Principal Component of Neighbour Matrices: PCNM, Bocard and Legendre, 2002) was used to help us understand our observed spatial patterns in soil organic carbon. Spatial filters were then used in multiple partial regressions in order to exclude pure geographical effects from our analysis. Moran's *I* correlograms were performed for each variable of interest to aid the detection of spatial structures in the data. All spatial statistics were performed using the software Spatial Analysis in Macroecology – SAM (Rangel et al., 2006). Relationships here were considered significant to the $P < 0.05$ level. However, we have accepted relationships up to $P < 0.1$ as an indication of marginally significant relationships.

3 Results

3.1 Distribution of SOC fractions among different soil types

3.1.1 Vertical variations of soil organic carbon fractions

All soils in this study have shown a gradual decrease in total soil organic carbon (SOC) with depth (Fig. 2). In general, the largest concentration of SOC occurs on the 0-5 cm layer which usually had about twice as much carbon than the deeper layers. Exception were Plinthosols, Acrisols and Ferralsols which had a more homogeneous distribution of SOC with depth (Fig. 2). Subtle differences on the vertical distribution of SOC fractions occur along the soil development gradient. Also to be noted is that for most soils, large amounts of SOC on the light fraction (L) only occur on the soil surface (0-5 cm), with the exception of the very sandy soils such as Arenosols and Podzols where this fraction dominates upon the others.

On the least developed soils (Regosols), most of SOC is found on the heavy fraction (HF), with the proportion of SOC on HF not changing with increasing depth. At Gleysols, which are also poorly developed soils, SOC is evenly distributed among the different

fractions when close to soil surface (at 0-5 and 5-10 cm deep), while the deeper layers show a complete dominance of SOC on the finer textured fractions (Silt+Clay and Resistant fractions). Relatively similar distribution of SOC fractions occur in Fluvisols, Cambisols and Alisols but with increasing domination of fine textured fractions as weathering levels advance.

In general, the contribution of the heavy fraction (HF) to store SOC decrease sharply along the soil development gradient (Fig. 2 and 3) while the proportion of SOC in the finer textured fractions increases (Resistant and Silt+Clay fraction). This pattern changes abruptly in soils with advance stages of soil development such as in Acrisols and Ferralsols where a gradual increment of SOC on the heavy fraction occurs, both at the soil surface and deeper layers. It is however worth to note that this increment on SOC on the heavy fraction of Acrisols and Ferralsols is associated with an increasing amount of stable aggregates while for the remaining soils it was more commonly associated to sand texture.

On the more weathered end of the soil development gradient, the Arenosols and Podzols showed distinct distribution of SOC among fractions. Both soils have SOC dominated by the light fraction, with most soil carbon occurring on the soil surface, and strongly decreasing C concentrations with depth (Fig. 2). Independent of the soil layer, the contribution of mineral soil fractions to SOC storage is very low in these soils, but a small increment of SOC in the heavy fraction can be seen at the 5-10 cm layer in both soil types. Finally, the dissolved organic carbon fraction (DOC) had the least contribution to SOC among all soils (2% on average), being usually found on the soil surface. The largest concentrations of DOC occurred on Ferralsols.

3.1.2 Distribution of SOC fraction along a soil development gradient

The distribution of SOC concentration varied systematically across a gradient of soil development as proposed by Quesada et al. (2011; 2010). Two distinct patterns can be observed along the soil age gradient (Fig. 3a). First, at the early and intermediate stages of soil development, SOC concentrations tend to increase from Regosols to Gleysols and Fluvisols. After this first peak, SOC concentration shows a gradual decrease until the lowest values of SOC are obtained in the Plinthosols. A second pattern emerges on the most weathered soils with SOC showing a tendency of increased concentration as weathering level advances. SOC concentration increases from Acrisols to Ferralsols, peaking on Podzols, and then decreasing towards the Arenosols.

The proportion of SOC in the different fractions studied here has also varied along the soil age gradient (Fig 3b and Supplementary material S1). The resistant fraction (rSOC) contributed to an average 22.8% of SOC but this ranging from 10.7% in Podzols to as much as 42.4% in Plinthosols. Gleysols had the largest amount of SOC on the resistant fraction (Fig 3a), while the largest proportion of SOC in that fraction occurred in Plinthosols (Fig.3b). The proportion of SOC in the heavy fraction decreased along the soil development gradient (Fig. 3 a - b). While the HF contain about 48% of SOC in Regosols, the proportion of SOC on HF decreases gradually along the gradient of soil development being 14.9, 15.5, 9.0, 4.1 and 6.8% for Gleysols, Fluvisols, Cambisols, Alisols e Plinthosols respectively. As pointed out in section 3.1, this pattern changes in Acrisols and Ferralsols which have an important portion of SOC associated to the heavy fraction. On average the heavy fraction corresponded to 24.7% of SOC for all soils, with this ranging from 4.1% on Alisols up to 50.8% on Ferralsols.

While the importance of the HF to store SOC decreases, the proportion of SOC in the finer textured fractions increases (Resistant and Silt+Clay fraction). The S+C fraction represents on average 31.9% of SOC in all soils, with this ranging from 14.25% to 57.58% in Arenosols and Alisols, respectively. The proportion of soil carbon on the S+C fraction vary remarkably along the soil age gradient, being small on younger substrates, while tend to gradually increase until it peaks on intermediate age soils, and then gradually decreases as soil weathering levels increase.

The light fraction varied little between most soils but there is a high contrast between Arenosols and Podzols and the remaining soils. The average SOC associated to the light fraction in Arenosols and Podzols was 46.8% while this make up to an average 12.5% in the remaining soils (overall average 19.2% for all soils). Ferralsols had the lowest proportion of SOC on the light fraction (7.91%). The dissolved organic carbon had the lowest concentrations among all fractions, occurring as trace for most soils. On average it makes up to 1.3% of SOC, ranging from 0.8 to 2.91% (Alisols and Ferralsols at the extremes, respectively).

3.1.3 Interrelations among soil organic carbon fractions

Figure 4 shows bivariate relationships between each different soil organic carbon fractions, with the view to provide a better understanding of the interrelationships between them. Different soil type clusters can be identified throughout the relationships (i.e. all Ferralsols appearing together), which show that soils sharing similar morphological characteristics also

behave similarly in relation to soil carbon. Kendall's τ rank correlation for these relationships is shown on Table 2.

There is a relationship between the rSOC and S+C fractions (Kendall's $\tau = 0.478$, $p < 0.001$). However, a close look at the relationship reveals that most highly weathered soils tend to occupy the upper part along the almost straight line, while the young and intermediate age soils tend to predominate in the lower part of such line (Figure 4). This may be understood as the more weathered soils having systematically more resistant carbon to a given S+C content. This notion gets support if we plot rSOC as a proportion of total silt+clay fraction (i.e. S+C + rSOC) as shown in Figure 6. It shows that rSOC proportion increases with weathering, with low and intermediate age soils having rSOC ranging from 20 to 50% of the entire S+C fraction while soils with advanced weathering level such as Ferralsols, Acrisols and Plinthosols have rSOC ranging from 40 to 60%.

Similar relationship occurs between S+C and DOC fractions (Kendall's $\tau = 0.347$, $p < 0.01$), where there is also an apparent division with the most weathered soils having systematically more DOC to a given S+C fraction SOC content. The relationship between the Silt+Clay and Light fractions (Kendall's $\tau = 0.374$, $p < 0.01$) suggest that most non-sandy soil types have SOC in LF fraction increasing as S+C SOC increases. The same occurs for the sandy soils but with a different magnitude. Arenosols and Podzols seem to be offset to the upper part of the relationship, thus showing a much larger LF to a given S+C content. No clear relationship was found between the S+C fraction and HF SOC (Kendall's $\tau = -0.144$, not significant), suggesting that these are not complementary fractions despite that these fractions are associated to contrasting particle size (note that the HF is formed by both sand particles and stable aggregates).

The rSOC behaved in a similar way of the S+C fraction. No clear relationship was found with the rSOC and HF (Kendall's $\tau = 0.036$, not significant) and similar relationship was found with the LF (Kendall's $\tau = 0.128$, not significant) and DOC (Kendall's $\tau = 0.396$, $p < 0.01$).

The DOC fraction appeared to be strongly related to the heavy fraction (Kendall $\tau = 0.417$, $p < 0.001$), with the largest values of DOC being associated to Ferralsols. It is worth to point out that both Silt+Clay and heavy fractions are well correlated with DOC, this probably occurring due to gradients on clay aggregation along the heavy fraction (i.e. most Ferralsols in this study have high clay contents and HF is basically formed by stable aggregates). The relationship between LF and HF (Kendall's $\tau = -0.034$, not significant) shows that although the LF appear to be related to HF in many soil types, there is a different behavior

occurring on the most weathered soils which tend to have lower proportion of SOC in the light fraction.

Finally, the relationship between DOC and LF (Kendall's $\tau = 0.194$, not significant) also seem to have different controls acting on different soils. DOC increases as SOC content in LF increases in all sand rich soils (Arenosols and Podzols) while this do not occur with the same intensity on other soil types. Instead, DOC seems to be controlled by clay content and amount of stable aggregates.

3.2. Environmental controls of soil carbon

3.2.1 Correlations between soil carbon fractions and the environment

Kendall τ correlations (Table 3) were performed between the soil carbon fractions and a set of environmental variables such as climate (annual precipitation and mean annual temperature), edaphic factors (texture, soil chemistry and weathering index) and organic matter quality (soil C:N ratio and litter lignin concentration). Graphical representation of such relationships is available as supplementary material (S2, page 53-58). No single environmental variable could explain variation in all SOC fractions, suggesting that different fractions may be related to distinct specific factors or combination of factors.

The Silt+Clay fraction was significantly correlated with the edaphic variables sum of bases (Kendall's $\tau = 0.249$; $p < 0.05$), effective cation exchange capacity (Kendall's $\tau = 0.400$; $p < 0.001$), total reserve bases (Kendall's $\tau = 0.351$; $p < 0.01$) and phosphorus (Kendall's $\tau = 0.400$; $p < 0.001$ and 0.328 ; $p < 0.01$ for available P and total P respectively), suggesting that the proportion of carbon on this fraction may be dependent on soil nutrient availability and soil weathering level. No clear relationship was found with litter lignin (a surrogate for the quality of organic matter input to soil) and climate factors (precipitation and temperature).

The Resistant fraction, which is thought include only very stable forms of carbon, resulted significantly correlated with soil clay content (Kendall's $\tau = 0.290$ $p < 0.05$) being also negatively correlated with sand (Kendall's $\tau = -0.334$ $p < 0.01$). In addition, rSOC had significant correlation with ECEC (Kendall's $\tau = 0.382$ $p < 0.01$) and phosphorus (Kendall's $\tau = 0.249$ $p < 0.05$ and 0.249 $p < 0.05$ for available P and total P respectively). The proportion of S+C that is dominated by rSOC (Fig. 6) was also correlated with sum of bases (Kendall's $\tau = -0.295$ $p = 0.023$) and Olsen P (Kendall's $\tau = -0.285$ $p = 0.028$).

The HF was correlated with clay content (Kendall's $\tau = 0.299$ $p < 0.05$) and negatively correlated with total reserve bases (Kendall's $\tau = -0.337$ $p < 0.01$) which is a chemical

weathering index that represent the availability of easily weatherable minerals in the soil (Quesada et al. 2011, Delvaux et al., 1989). This indicates that the carbon associated to soil coarse fractions (stable aggregates and sand) increases along with soil weathering. Similar explanation can be given to the relationship with soil C:N ratio (Kendall's $\tau = 0.434$ $p < 0.001$) since high C:N ratio is reported for ancient Amazonian soils, with lower ratios occurring on younger substrates (Quesada et al., 2010). The HF was also positively correlated with litter lignin concentration (Kendall's $\tau = 0.291$ $p < 0.05$) suggesting that the quality of the organic matter that enters the soil may be responsible for variations in this fraction.

The Light fraction (or particulate organic residuals) was the only fraction showing significant correlation with climate factors (annual precipitation, Kendall's $\tau = 0.329$ $p < 0.01$). It was however, also related to the quality of organic matter entering the soil (litter lignin, (Kendall's $\tau = 0.278$ $p < 0.05$) and the overall lability of such carbon on the soil matrix (C:N ratio, Kendall's $\tau = 0.255$ $p < 0.05$). It is however possible that the nature of particulate organic matter itself may have influence on bulk soil C:N ratio, thus soil C:N ratio will not be considered on the regression analysis for the LF.

The dissolved organic carbon fraction (DOC) was strongly correlated with soil clay content (Kendall's $\tau = 0.496$ $p < 0.001$), being also negatively correlated with sand content (Kendall's $\tau = -0.344$ $p < 0.01$). It was also highly correlated with soil C:N ratio (Kendall's $\tau = 0.335$ $p < 0.01$) and total soil carbon (Kendall's $\tau = 0.680$ $p < 0.001$), thus suggesting that the proportion of carbon that is dispersible in water may be a function of soil texture and bulk soil carbon content. Finally, total carbon (bulk soil carbon, i.e. not fractionated) was also highly correlated with soil texture (Kendall's $\tau = 0.340$ $p < 0.01$ and 0.383 $p < 0.01$ for clay and sand, respectively), but also showing a reasonable correlation with soil effective cation exchange capacity (Kendall's $\tau = 0.257$ $p < 0.05$). Again soil C:N ratio appears as well correlated (Kendall's $\tau = 0.278$ $p < 0.05$ but see bivariate relationship on Supplementary information S2, page 53), but this is assumed here to occur because soil C:N ratio is directly derived from soil carbon values (the total carbon used here). Therefore soil C:N ratio shall not be used in regression analysis of total carbon. Although not appearing as a significant correlation in Table 3 (Kendall's $\tau = 0.111$), the litter lignin concentration is well correlated to total soil carbon if Pearson correlations are used (Pearson $r = 0.399$ $p < 0.05$, see also bivariate relationship on Supplementary information S2, page 53).

3.2.2 Soil organic carbon fractions on the geographic space

Soil carbon concentration and its partitioning among the different fractions were shown to vary widely across Amazonia. Considering that distinguishable patterns occur among the different soils (Fig. 2 and 3), and with an apparent systematic variation, we aimed to investigate the potential environmental controls that may influence the amount and partitioning of SOC in different forms or pools. However, data collected on such geographically sparse area (Fig. 1) is generally subjected to the effect of spatial autocorrelation. Therefore, prior to performing any statistical analyses of environmental effects acting over soil carbon fractions, there is a need to account for the potential effect of spatial structures on the data.

Figure 5 shows that the different soil carbon fractions have different levels of correlation in space with varying levels of correlation with latitude and longitude. This observation suggests that spatial structures have influence on the data, and for some soil carbon fractions, spatial autocorrelation might be responsible for a reasonable fraction of the observed variation across neighboring areas. This occurs because closely spaced samples may essentially be replicate measures of the same conditions (i.e. soil carbon fractions may be affected by edaphic conditions which may vary regionally). Moran's I correlograms in Figure 5 confirm that all but one response variable analyzed here are spatially autocorrelated, with the level of spatial correlation varying among the different SOC fractions. The highest level of spatial autocorrelation occurred on the Heavy fraction, followed by the Clay+Silt and Light fractions. The level of spatial autocorrelation on Total C and DOC fractions was lower, with these being mostly correlated in relatively short distances (<1000 km) while the Resistant fraction did not show significant levels of spatial correlation. This observation reveals the necessity for adequate strategies to perform statistical analysis in autocorrelated data. The usual statistical protocols such as ordinary multiple regressions would generate autocorrelated residuals, underestimating the errors of regression coefficients and consequently inflating Type I errors, therefore resulting in too liberal tests of hypothesis (Legendre, 1993; Diniz-Filho and Bini, 2005).

To account for spatial autocorrelation, eigenvector-based spatial filters (Bocard and Legendre, 2002) were calculated for each soil carbon fractions analyzed in this study, and then used in the multiple regression framework as additional predictors to describe the spatial structure of the region. This approach, based on principal coordinate analysis of truncated geographical distance matrices, provides in principle unbiased regression coefficients (Diniz-Filho and Bini, 2005). Following that method, two eigenvector filters were extracted to account for the spatial structures on the Clay+Silt and Total C fractions, while one filter was able to describe and remove the effects of spatial autocorrelation in the Heavy,

Light and DOC fractions. The extraction of filters for the resistant fraction did not result in any improvement of regression residuals suggesting that rSOC is free of the effects of spatial structures on the data. The selection of eigenvector filters was done according to the framework suggested by Diniz-Filho and Bini (2005). The application of spatial filters resulted in effective removal of spatial autocorrelation from regression residuals as seen in the Moran's I correlograms in figure 5. This should allow for the correct estimation of the effects of each variable, unbiased by spatial autocorrelation in residuals.

3.2.3 Regression analysis

On this work we chose to show results for ordinary least square multiple regressions (i.e. without corrections for spatial autocorrelation) side by side with its corrected version (i.e. with PCNM spatial filters included). This was done to stress the importance of considering the presence of spatial structure on the data collected. Results for both regressions are found on Table 4 (see *a/so* S3, page 55). The selection of predictors to be included on the regression analysis was based on the correlation level between the variables (Table 3), but also taking into account the ecological meaning of such relationships.

The regression model that best described the variation on the Silt+Clay fraction SOC included total phosphorus and sand content. Sand was included in this analysis to counteract the effect of finer soil particles that make up to this fraction (basically this fraction is soil carbon associated to silt and clay, so if clay content is a background driver of such C concentrations, there should be a negative interaction with sand content). The ordinary least square regression (OLS) resulted significant for the overall model ($F = 5.6$ $p < 0.01$), explaining about to 24% of variation ($R^2 = 0.24$). The only predictor significant was total phosphorus. The spatially corrected regression (spatial regression from now on), also resulted significant for the whole model ($F = 6.0$ $p < 0.001$) with and R^2 of 0.41. The inclusion of spatial filters did not change the significance of any predictor but did increase the regression coefficient for total phosphorus, also improving its p value. Total phosphorus emerged as the single predictor influencing the Silt+Clay carbon fraction in our study, suggesting that the proportion of carbon present on that fraction might be associated to nutrient availability and soil weathering stage.

The Resistant fraction (rSOC) is apparently free of major effects of spatial structure on the data and therefore only OLS regressions are shown on Table 4. The model that best described the variation on the rSOC fraction included total reserve bases, sand content and soil C:N ratio, with these variables explaining about to 29% of variation. All predictors came

out significant ($p < 0.05$; $p < 0.01$; $p = 0.07$, for total reserve bases, sand and C:N ratio respectively), as did the whole model ($F = 4.9$ $p < 0.01$). Although the p value for C:N ratio is above the 0.05 threshold, it is accepted here as an indication of positive relationship. It is however noticeable that the R^2 of these regression analysis are relatively modest, evidencing that other controlling factors may be of importance to explain the variations on both the Silt+Clay and rSOC fractions. This will be detailed further on the discussion section.

As for the Heavy fraction (HF), the best model to describe its variation included clay content and soil C:N ratio ($p < 0.001$ for both clay and C:N ratio), with the whole model being high significant ($F = 30.0$ $p < 0.001$) and explaining about 67% of variation on the Heavy fraction (data for the OLS regression). The inclusion of a spatial filter did not change the significance of any predictor, but did slightly decrease regression coefficients and t test values. After the inclusion of the spatial filter, the regression R^2 increased to 0.79, an evidence that the existing spatial structures have been incorporated into the model. The regression model for the Light fraction included litter lignin and total phosphorus. The OLS regression was significant for the whole model ($F = 9.3$ $p < 0.001$) with an R^2 of 0.36.

Litter lignin came out as an important predictor of SOC in Light Fraction (coefficient of regression 4.2 $p < 0.001$) while total phosphorus only appeared as marginally significant ($p = 0.07$). However, once that the spatial filter was included into the regression, soil total phosphorus became highly significant ($p < 0.01$), while litter lignin remained significant. The overall spatial regression F value increased to 12.9 ($p < 0.001$) with an R^2 of 0.55.

The best regression model for the dissolved organic carbon fraction included clay content and bulk soil carbon as predictors. The overall regression was highly significant ($F = 103.4$ $p < 0.001$) with a R^2 of 0.88. Both clay and bulk soil carbon content emerged as significant factors affecting DOC (data for OLS regression). The inclusion of spatial filters did not change the level of significance of predictors, but decreased the overall spatial regression F value to 85.3 ($p < 0.001$).

The best regression model to predict total soil carbon included litter lignin, soil ECEC and sand content. The OLS regression model explained 40% of the variation in soil total carbon and was significant to the whole model ($R^2 = 0.40$; $F = 7.5$ $p < 0.001$). All three predictors resulted significant ($p < 0.01$, $p = 0.04$ and $p = 0.03$ for lignin, ECEC and sand respectively). The inclusion of spatial filters did not change the overall regression fit significantly ($F = 4.8$ $p = 0.003$) but did change slightly the level of significance of the predictors ($p = 0.02$, $p = 0.03$ and $p = 0.05$ for lignin, ECEC and sand respectively). The spatial regression R^2 did not change significantly ($R^2 = 0.39$).

4. Discussion

4.1 Distribution of SOC fractions across different soil types in Amazonia

Soil organic carbon fractions varied systematically across the different soil types studied here. The proportion that each SOC fraction takes at the different soil types, seem to be related with a weathering continuum as proposed by Quesada et al. (2011). This occurs because soils having different levels of weathering show specific combination of conditions which influence soil carbon stabilization and partitioning among SOC fraction. Edaphic factors such mineral composition, Fe and Al oxide content, particle surface area; the amount of stable aggregates and nutrient availability vary considerably along a gradient of soil development. In addition, changes in soil conditions also affect living organisms growing on these soils which in turn influence back on soil through feedback mechanisms (Lathwell and Grove, 1986; Aerts, 1999; Dent et al., 2006). This is of particular importance to SOC since the quality of organic matter that enters the soil is largely controlled by nutrient availability (Coley, 1985) as is its decomposability (Vitousek 2004). The interaction of these specific conditions with climate (i.e. temperature and moisture) may control the amount of SOC stabilized in a soil and its distribution among SOC fractions (Aerts, 1997; Davidson and Janssens, 2006).

Variations on soil morphology and associated mineral composition that occur along the soil development gradient will determine the soil capacity to stabilize organic matter (Kaiser and Guggenberger, 2003). For instance, at early stages of soil development, restrictions in soil depth may conditionate soil carbon, maintaining large amounts close to soil surface. As the mineral fraction of such soils is still coarse, the surface area of soil particles is small and show less affinity to organic matter (Uehara and Gilman, 1981). This may be the reason for young soils such as Regosols and Gleysols having their carbon mostly associated to the heavy fraction (Fig. 2).

The surface area of clay minerals and its affinity to organic matter increases with soil development, peaking on intermediate age soils (Uehara and Gilman, 1981; Kaiser and Guggenberger, 2003). The data shown on section 3.1 gives good representation of such changes. The carbon associated to soil coarse fraction (the Heavy fraction) decreases gradually along the soil age gradient while the importance of the finer fraction increases. It is also to note that the partitioning of SOC occupying the Silt+Clay and Resistant fractions may be dependent on nutrient availability, throughout feedback linkage with plant investment in defense and structural compounds (Vitousek 2004; Coley et al., 1985; Cortez et al., 2007). In

other words, the soil fertility influences the quality of organic matter that enters the soil, which in turn would influence the balance between the Resistant and Silt+Clay SOC fractions (Lathwell and Grove, 1986). This has implication for the maintenance of soil C stocks, and for some it may intuitively suggest that highly weathered soils should hold more carbon in less labile forms (i.e. resistant fraction). This is however not necessarily the truth for two reasons. First, in younger and more fertile soils, the nature of their clay minerals holds large quantities of less labile carbon, in particular on amorphous Fe and Al minerals, which have great affinity to organic matter (Oades 1988; Mikkuta et al., 2006), so comparatively these soils may have even more Resistant carbon than their highly weathered counterparts. Second, highly weathered soils such as Ferralsols and Acrisols tend to form large amounts of stable aggregates where most of its soil carbon is held and recycled. This change in soil structure makes the heavy fraction an important reservoir of soil carbon in these soils. However, highly weathered soils tend to proportionally hold more carbon on the Resistant fraction in relation to total C associated to clay and silt (Fig.3 and 6).

The amount of aggregates is another important soil property that changes along soil development. The formation and stabilization of soil aggregates is influenced by several factors, such as content of clay and Fe and Al oxides (Lynch and Bragg, 1985) and the amount and quality of organic substances (Six et al., 2000; Bossuyt et al., 2001). While soils are young and fertile, the clay particles tend to flocculate, and formation of large size, stable aggregates is restricted to soil surface, that occur in Regosols, for exemple. As weathering advances, most soil cations are lost and clay particles tend to aggregate, often having organo-mineral complexes as cementing substances. This process is characteristic of Ferralsols and Acrisols where a large portion of SOC is found associated to stable macroaggregates on the Heavy fraction, including deeper layers.

The distribution of carbon on the sand rich soils (Arenosols and Podzols) was very distinct from the remaining soil types. These soils are dominated by sand and therefore lack conditions that favor the stabilization of organic matter such as a large surface area and available electrical charges to bind with carbon (Ahn et al., 2009). Nutrient availability is also very low (Quesada et al., 2011; 2010) and this almost invariably results in the vegetation investing in lignified plant structures of very slow decomposition. It is therefore the recalcitrance of organic residues and the lack of binding sites for organic matter that conditionate the distribution of SOC fractions in these soils (Ahn et al. 2009), doing so by favoring the accumulation of particulate organic matter on soil surface. Drainage restriction is another factor conditioning organic matter in these soils since it is an additional constraining decomposition. Most Podzols in Amazonia are water saturated for large part of

the year (Quesada et al., 2011). Arenosols are generally better drained, but sometimes they are in fact giant Podzols (i.e. diagnostic spodic horizon is too deep to allow classification as Podzol). In this situation Arenosols also suffer from water saturation as is the case for one Arenosol in this study (ALP-04), this condition resulted in the two Arenosols sites (one well drained and one water saturated) having contrasting levels of Light fraction (Supplementary material S1).

The interrelationships between the different SOC fractions provide insights about the mechanisms controlling soil organic matter function. For instance, the relationship between S+C and rSOC suggests that carbon stabilized in both fractions may be conditioned by similar drivers, such as clay and Fe and Al oxide content. Nevertheless, the proportion that rSOC occupy within the total S+C fraction (i.e. S+C and Resistant, Fig. 6) may be related to differences in soil organic matter quality as influenced by large variations in soil fertility along the soil development gradient (Quesada et al., 2010). This notion gets support by the positive significant relationship between S+C and total phosphorus (Table 4), which is the single most important element limiting plant production in Amazonia (Quesada et al., 2009).

The amount of dissolved organic carbon also seems to be related to gradients of amount and quality of clay as evidenced by the relationship between S+C, rSOC and DOC fractions. But we also observed that DOC is remarkably related to the Heavy fraction, in especial to the most clay rich and well aggregated soils (Fig. 5, Ferralsols and Acrisols). This observation is connected with the relationship between the Heavy and Light fractions (Fig. 5). Although most soils seem to have an almost linear relationship between HF and L fractions, a distinct behavior is observed in highly weathered soils, particularly at the Ferralsols and Acrisols group. In a simplistic view, soil organic matter may be simply greater at these soils due to its higher aggregate content. The mechanism behind this idea is that particulate organic matter (POM) may be encapsulated within macroaggregates in these soils, implying that the Light fraction may not have been effectively separated by the high density solution, and that the macroaggregates in these soils may require more energy to be disrupted by sonication. In support to this, it has been suggested that POM may serve as a core for the formation of large aggregates through process of physical entrapping and production of metabolic binding substances by soil microorganisms, which attach primary particles and small aggregates to the organic materials, thus leading the formation of stable macroaggregates (Golchin et al., 1997).

Organic matter is protected within such aggregates because aggregation serves as a physical barrier to microorganisms and their enzymes, but also being protected against aerobic decomposition due to restricted oxygen diffusion (Hassink et al., 1993). However,

protection of soil organic matter within aggregates is not permanent, with the turnover of macroaggregates being close to that of plant residues in the soil (Golchin et al., 1997; Gale 2000; Puget et al., 2000; John et al., 2005). This may partially explain the relationship between HF and DOC where the most well aggregated soils (Ferralsols and Acrisols) also had the highest DOC. The inference here being that slow but continuous turnover of soil aggregates may supply DOC at higher concentrations.

4.2 Accounting for spatial autocorrelation

Environmental data collected over wide areas such as the Amazon Basin is likely to produce correlated spatial structures. This is of great importance, since inclusion of spatial filters into statistical analyses have demonstrated that spatial autocorrelation creates a bias in regression coefficients which inflates tests of hypothesis and thus may eventually change interpretations of ecological processes in question (Diniz-Filho and Bini, 2005). For instance, Quesada et al. (2009) studying the effect of soil chemical and physical properties over forest structure and dynamics in Amazonia, have shown that at least two central results of their study would have been completely misjudged if no correction for spatial autocorrelation had been applied. In our study, the inclusion of spatial filters did not change the level of significance of regression predictors in most cases, but there would be at least the rejection of one truly significant predictor (total P on Light fraction analysis) if no correction was applied to it.

4.3 Environmental controls on the partitioning of soil organic matter among fractions

Organic matter fractions are known to vary as a function of soil management (i.e. tillage, cultivar type and rotation), climate variation and quality of organic matter input, with a number of agricultural studies detailing these observations (Cambardella & Elliott, 1994; Wander & Traina, 1996; Kong et al. 2005). However, to our knowledge there has been no systematic evaluation of the effect of natural environment gradients on the distribution of soil carbon fraction in native soils at continental scales. The understanding of how SOC fractions respond to natural environment variations furnishes important basic knowledge about the existing mechanisms controlling SOC dynamics, its turnover times and sensitivity to climate change.

For instance, there seems to be a response of SOC fractions to variations in soil fertility, with the carbon associated to S+C fraction being significantly related to total soil

phosphorus and well correlated with other edaphic variables related to soil fertility and weathering degree. We also observe that rSOC seems to be related to soil weathering level and its texture proportions. In addition, a significant relationship with bulk soil C:N ratio suggests that rSOC is related to gradients of soil C lability in Amazonia. The rSOC fraction is usually reported to be made up by very stable carbon with turnover times of thousands of years (Six and Jastrow, 2002; Brunn et al., 2008). Our evidences here suggest that the proportion occupied by rSOC in the total S+C fraction is related to soil weathering level and nutrient availability, with rSOC taking a larger proportion of SOC on the most weathered and infertile soils.

Despite of these interesting mechanistic findings, we observe that the fraction explained by environmental variables is relatively small for both S+C and rSOC. This occurs because we have not yet included measures of the importance of clay size mineral fractions (such as Fe and Al hydroxides) in our analysis. Fe and Al hydroxides are of great importance to describe variations in SOC fractions, but in particular to those related to finer soil particles (S+C and rSOC). Most of soil organic matter (SOM) is associated to soil's mineral matrix (John et al., 2005) and association between SOM and soil minerals and metal ions result in stabilized SOM pools, with older mean age (Scharpenseel and Becker-Heidmann, 1989; Eusterhues et al., 2003) and longer turnover times (Balesdent, 1996; Ludwig et al., 2003). The main inorganic soil constituents involved into interactions between SOM and the mineral soil are the fine clay minerals and amorphous hydroxides of Fe and Al (Zech and Guggenberger, 1996) through organo-mineral interactions with their larger surface charge density. As the importance and proportion of such minerals should vary significantly in Amazonia, due to wide variation in soil age and types (Quesada et al., 2010), it is expected that hydroxides of Fe and Al would explain a significant portion of variation in SOC associated to the S+C and rSOC fractions. Analysis of Fe and Al oxides are being made for this study but were not available in time for the writing of this thesis. This will though be included in the final version for publication.

Our regression model for predicting the Heavy fraction included the bulk soil C:N ratio and clay content, with this explaining a large proportion of the variation in SOC associated to the Heavy fraction ($R^2 = 0.79$). We interpret the relationship with soil clay content as to represent the proportion of stable aggregates in the soil. The relationship with soil C:N ratio is taken here to represent a proxy for the quality of soil C associated to the mineral matrix. It has been show that soil C:N ratio in Amazonia is strongly related to soil phosphorus content, with an indication that soil C:N ratio in Amazonia should reflect broad variations in soil fertility

and different levels of investment in defense and structural compounds by the vegetation (Quesada et al., 2010).

These variations on clay and aggregation level of our soils also seem to be related to DOC fraction. We were able to effectively model the DOC fraction using clay and bulk SOC content with our regression explaining approximately 90% of the variation on DOC fraction. However, in addition to the effect of soil texture and carbon pool size, we also observe that there is an interesting relationship between DOC and light fraction at the sand rich soils, which may indicate that particulate organic matter may have some importance as source of dissolved organic carbon, at least for these soils. There is considerable discussion in the literature regarding the importance of fresh litter and older SOM as sources of DOC in forest soils (reviewed by Kalbitz et al., 2000). For example, studies on the chemical composition of dissolved organic matter, suggest that most of it is an end product of microbial metabolism (Guggenberger et al., 1994). Yet, short-term experimental manipulations of organic matter sources show that fresh litter also contributes significantly to the production of DOC (Park et al., 2002). These two views are not necessarily mutually exclusive (McDowell, 2003), and might indicate that different mechanisms may drive DOC production in soils with contrasting characteristics.

However, simple predictors of DOC concentration in soil solution may not provide mechanistic understanding of DOC production and losses and therefore our predictors may need to be tested in additional datasets. Also, it should be considered that bulk extract DOC analyses reflect the net result of competing processes (i.e. sorption and production of DOC) and thus they may mask the actual pathways involved in dissolved organic carbon production and transformation (McDowell, 2003).

The light fraction showed little variation in most soils but there is a high contrast between Arenosols and Podzols and the remaining soils. The average SOC associated to the light fraction in Arenosols and Podzols was 46.8% while this make up to an average 12.5% in the remaining soils in this study. These findings indicate that conditions particular to these soils promoted the accumulation of particulate organic matter. Results from our regression analysis confirmed that litter quality is one factor promoting the accumulation of undecomposed plant residues. Further, our analysis indicates that such accumulation may be related to soil fertility effects on the investment in defense compounds (Coley 1985), in particular as a response to soil phosphorus limitation. These observations gain support if the usual litter lignin concentration in plants occurring on these soils is considered. Lignin makes up to remarkable 60% of leaf litter in Arenosols and Podzols (Quesada, 2008). The same applies to total soil P which attains the lowest values in Amazonia, being usually about to 30

mg kg⁻¹ (Quesada et al., 2010). As mentioned above, the effect of water saturation that is commonly associated to these soils can not be discarded as a potential influence to the decomposition process.

The best regression model for predicting bulk soil carbon (or total carbon) included ECEC, sand content and litter lignin concentration as predictors. While sand content reflects the influence of soil texture on soil carbon stabilization, the ECEC is used here as a proxy for variations in specific surface area (SSA) and chemical and morphological changes occurring along soil development. Also, the significant relationship with litter lignin suggests the importance of the quality of organic matter input to soil. However, our analysis here would strongly benefit from the inclusion of more study sites. Also, the evaluation of correlations with Fe and Al hydroxides may prove to be of significance since these are likely to explain a large portion of total soil organic carbon (Mikkuta et al, 2006).

Finally, we found little evidence on support of climate factors influencing SOC fractions in Amazonia. The importance of precipitation in our dataset was limited to some correlation with the particulate organic matter fraction, but its effect was weak when compared to edaphic properties or litter quality (Amelung et al. 1998; Meentemeyer 1978). This runs against several studies that point to climatic factors as the main drivers of soil carbon dynamics (Amelung et al., 1998; Davidson and Janssens, 2006; Garten et al. 1999; Leifeld and Fuhrer, 2005). It seems that the short range of variation in mean temperature found in our dataset (from 24 to 27 °C) do not allow for significant influence over factors that potentially could be temperature directed. Temperature is known to influence SOC through its control on decomposition process (and for chemical reaction activation), but as mean temperature in Amazonia is well above any limitation to decomposition this may be of low meaning to our study area. Similar argument applies for rainfall which does vary more widely in Amazonia (from 1,700 – 3,400 mm yr⁻¹). Although there is a wider range of precipitation in Amazonia, we can generalize that for about all of Amazonia the conditions are just about the optimum for microorganism communities and therefore for decomposition process (Hattenschwiler et al., 2005). Indeed, the effect of climate is a major issue on temperate zones where temperature may become a limiting factor for decomposition of SOM (Amelung et al., 1998). Anyway, the effect of climate factors over soil carbon dynamics are still under debate (Knorr et al., 2005; Reichstein et al., 2005; Fang et al., 2006; Plante et al., 2010) and far from consensus. For instance, some studies point to a greater sensitivity of labile SOC fractions to increase temperature while others suggest that the most recalcitrant fractions may be more affected by climate change (Leifeld and Fuhrer, 2005).

5 Final Remarks

The fractionation of soil organic carbon from different Amazonian soils demonstrated that there is considerable variation on SOC quantities and its partitioning among SOC fractions. This variation reflects the role of environmental conditions in influence the stabilization of SOC, with certain key soil characteristics being of importance to influence on the partitioning of SOC among the different fractions. On the other hand, our study found little evidence that could support significant influence of climate variables on SOC fractions in Amazonia, this despite of climate being of clear significance elsewhere.

Future work on this subject should expand the number of observations, but preferentially including other soil types not analyzed here. Also, future studies should stress the importance of clay properties and their changes along the gradient of soil development; in particular the role of Fe and Al oxides deserves investigation.

Acknowledgements

We thank Gordon & Betty Moore Foundation for the scholarship by C. P. Paz and financial support to carry out field and laboratory activities. We thank INPA by institutional support and provision of laboratories. We are grateful to the reviewers of earlier versions of the manuscript for their contribution.

References

- Achard, F., Eva H. D., Stibig H. J., Mayaux P., Gallego J. Richards T., and Mallinreau J.P. Determination of deforestation rates of the world's humid tropical forests, *Science*, 297, 999-1002, 2002.
- Achard, F., Eva, H. D., Mayaux, P., Stibig, H. J., and Belward, A. Improved estimates of net carbon emissions from land cover change in the tropics for the 1990s, *Global Biogeochemical Cycles*, 18, 1-11, 2004.
- Aerts, R. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos*, 79, 439-449, 1997.
- Aerts, R. Interspecific competition in natural in plant communities: mechanisms, trade-offs and plant-soil feedbacks. *Journal of Experimental Botany*, 50, 29-37, 1999.
- Ahn, M. Y., Zimmermann, A. R., Comerford, N. B., Sickman, J. O., and Grunwald, S. Carbon mineralization and labile organic carbon pools in the sandy soils of a North Florida Watershed, *Ecosystems*, 12, 672-685, 2009.

- Amelung, W., Zech, W., Zhang, X., Follet, R. F., Tiessen, H., Knox, E., and Flach, K. W. Carbon, nitrogen, and sulfur pools in particle-size fractions as influenced by climate, *Soil Sci. Soc. Am*, 62, 172-181, 1998.
- Baker, T. R., Phillips, O. L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Killeen, T. J., Laurance, S. G., Laurance, W. G., Lewis, S., Lloyd, J., Momteagudo, A., Neill, D. A., Patiño, S., Pitman, N. C. A., Silva, J. M. N. and Martines, R. V. Variation in wood density determines spatial patterns in Amazonian forest biomass, *Global Change Biology*, 10, 545-562, 2004.
- Baldock, J. A, and Skjemstad, J. O. Role of the soil matrix and minerals in protecting natural organic materials against biological attack, *Organic Geochemistry*, 31, 697-710, 2000.
- Balesdent, J. The significance of organic separates to carbon dynamics and its modelling in some cultivated soils, *European Journal of Soil Science*, 47, p. 485-493, 1996.
- Balesdent, J., Besnard, E., Arrouays, D., and Chenu, C. The dynamics of carbon in particle-size fractions of soil in a forest-cultivation sequence, *Plant & Soil*, 201, 49-57, 1998.
- Bocard, D., and Legendre, P. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices, *Ecological Modelling* 153, 51-68, 2002.
- Bossuyt, H., Deneff, K., Six, J., Frey, S.D., Merckx, R., and Paustian, K. Influence of microbial populations and residue quality on aggregate stability, *Appl. Soil Ecol.* 16, 195–208, 2001.
- Brunn, S., Thomsen, I. K. Christensen, B. T., and Jensen, L. S. In search of stable soil organic carbon fractions: a comparison of methods applied to soils labelled with ^{14}C for 40 days or 40 years, *European Journal of Soil Science*, 59, 247-256, 2008.
- Bruun, T. B., Elberling, B., and Christensen, B. T. Lability of soil organic carbon in tropical soils with different clay minerals, *Soil Biology & Biochemistry*, 42, 888-895, 2010.
- Cambardella, C. A., and Elliott, E. T. Carbon and nitrogen dynamics of soil organic matter fraction from cultivated grasslands soils, *Soil Science Society of America*, 58, 123-130, 1994.
- Cochrane, M. A. Fire science for rainforests, *Nature*, 421, 913-919, 2003.
- Coley, P. D., and Barone, J. A. Herbivory and plant defenses in tropical forests. *Annu. Rev. Ecol. Syst*, 27, 305-35, 1996.
- Coley, P. D., Bryant, J. P., and Chapin, F. S. Resource availability and plant antiherbivore defense. *Science*, 230, 895-899, 1985.
- Cortez, J., Garnier, E., Pérez-Harguindeguy, N., Debussche, M., and Gillon, D. Plant traits, litter quality and decomposition in a Mediterranean old-field succession, *Plant Soil*, 296, 19–34, 2007.

- Christensen, B. T. Physical fractionation of soil and structural and functional complexity in organic matter turnover, *European Journal of Soil Science*, 52, 345-353, 2002.
- Davidson, E., A., and Janssens, I., A. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change, *Nature*, 440,165-173, 2006.
- Dent, D. H., Bagchi, R., Robinson, D., Majalap-Lee, N., and Burslem, D. F. R. P. Nutrient fluxes via litterfall and leaf litter decomposition vary across a gradient of soil nutrient supply in a lowland tropical rain forest, *Plant Soil*, 288, 197–215, 2006.
- Derenne, S., and Largeau, C. A review of some important families of refractory macromolecules: composition, origin, and fate in soils and sediments, *Soil Science*, 166, 833-847, 2001.
- Delvaux, B., Herbillon, A. J., and Vielvoye, L. Characterization of a weathering sequence of soils derived from volcanic ash in Cameroon. Taxonomic, mineralogical and agronomic implications. *Geoderma* 45, 375-388, 1989.
- Diniz-Filho, J. A. F., and Bini, L. M. Modelling geographical patterns in species richness using eigenvector-based spatial filters, *Global Ecology & Biogeography*, 14, 177-185, 2005
- Dutilleul, P. Spatial heterogeneity and the design of ecological field experiments. *Ecology* 74, 1646-1658, 1993.
- Eusterhues, K., Rumpel, C., and Kögel-Knabner, I. Organo-mineral associations in sandy acid forest soils: importance of specific surface area, iron oxides and micropores, *European Journal of Soil Science*, 56, 753-763, 2005.
- Fang, C., Smith, P., Moncrieff, J. B., and Smith, J. U. Similar response of labile and resistant soil organic matter pools to changes in temperature, *Nature*, 433, 57-59.
- Fearnside, P. M. Brazil's Amazon forest and the global carbon problem. *Interciencia*, 10, 179-186, 1985.
- Gale, N. The relationship between canopy gaps and topography in a western Ecuadorian rain forest. *Biotropica*, 32, 653-661, 2000.
- Garten Jr, C. T., Post, W. M., Hanson, P. J., and Cooper, L. W. Forest soil carbon inventories and dynamics along an elevation gradient in the southern Appalachian Mountains, *Biogeochemistry*, 45, 115-145, 1999.
- Gee, G. W., and Bauder, J. W. Particle-size analysis. In: *Methods in Soil Analysis. Part 1. Physical and Mineralogical Methods* (ed A Klute), pp 383-409. American Society of Agronomy and Soil Science Society of America, Madison, Wisconsin, USA. 1986.
- Golchin A., Baldock, J. A., Clark, P., Higashi T., and Oades J. M. The effects of vegetation and burning on the chemical composition of soil organic matter of a volcanic ash soil

- as shown by ^{13}C NMR spectroscopy. II. Density fractions. *Geoderma*, 76, 175-192, 1997.
- Guggenberger G. , Christensen B. T., and Zech W . Land-use effects on the composition of organic matter in particle-size separates of soil. I. Lignin and carbohydrate signature, *Eur J Soil Sci* 45, 449–458, 1994.
- Guggenberger, G., and Zech, W. Composition and dynamics of dissolved organic carbohydrates and lignin degradation products in two coniferous forests, N.E. Bavaria, Germany. *Soil Biology and Biochemistry* 26, 19–27, 1994.
- Hassink J., Bouwman L. A., Zwart K. B., Bloem J. and Brussard L. Relationships between soil texture, physical protection of organic matter, soil biota, and C and N mineralization in grassland soils, *Geoderma*, 57, 105-128, 1993.
- Hedley, M. J., Stewart, J. W. B., and Chauhan, B. S. Changes in inorganic and organic soil phosphorus fractions induced by cultivation practices and by laboratory incubations, *Soil Science Society of America*, 46, 970-976, 1982.
- Heiman, M., and Reichstein, M. Terrestrial ecosystem carbon dynamics and climate feedbacks, *Nature*, 451, 289-292, 2008.
- Hattenschwiler, S., Tiunov, A. V., and Scheu, S. Biodiversity and litter decomposition in terrestrial ecosystems, *Ann. Rev. Evol. Syst.*, 36, 191-218, 2005.
- ISRIC (International Soil Reference and Information Centre) Global and national soils and terrain digital databases (SOTER), *World Soil Resources Report No. 74*, FAO, Rome, 1995.
- IUSS Working Group WRB. World reference base for soil resources: A framework for international classification, correlation and communication, *World Soil Resources Report*, 10, 103, FAO, Rome. 2006.
- Jobbagi, E. G., and Jackson, R. B. The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecological Applications*, 10 (2), 423-436, 2000.
- John, B., Yamashita, T., Ludwig, B. & Flessa, H. Storage of organic carbon in aggregate and density fractions of silty soils under different types of land use, *Geoderma*, 128, 63–79, 2005.
- Kaiser, K., and Guggenberger. Mineral surfaces and soil organic matter. *European Journal of Soil Science*, 54, 219-236, 2003.
- Kalbitz, K., Solinger, S., Park, J.-H., Michalzik, B., and Matzner, E., Controls on the dynamics of dissolved organic matter in soils: a review, *Soil Science*, 165, 277– 304, 2000.
- Knorr, W., Prentice, I. C., House, J. I., and Holland, E. A. Long-term sensitivity of soil carbon turnover to warming, *Nature*, 433, 298-301, 2005.

- Kong, A. Y. Y., Six, J., Bryant, D. C., Denison, R. F., and Kessel, C. van. The relationship between carbon input, aggregation, and soil organic carbon stabilization in sustainable cropping systems, *Soil Biology & Biochemistry*, 69, 1078-1085, 2005.
- Lal, R. Soil carbon sequestration to mitigate climate change, *Geoderma*, 123, 1-22, 2004.
- Lathwell, D. J., and Grove, T. L. Soil-plant relationships in the tropics. *Ann. Rev. Ecol. Syst.*, 17, 1-16, 1986.
- Legendre, P. Spatial autocorrelation: Trouble or new paradigm? *Ecology*, 74, 1659-1673, 1993.
- Legendre, P. and Legendre, L. *Numerical ecology*. Elsevier, 853 p., 1998.
- Leifeld, J., and Fuhrer, J. The temperature response of CO₂ production from bulk soils and soil fractions is related to soil organic matter quality, *Biogeochemistry*, 75, 433-453, 2005.
- Ludwig, B., John, B., Ellerbrock, R., Kaiser, M., and Flessa, H. Stabilization of carbon from maize in a sandy soil in a long-term experiment. *European Journal of Soil Science*, 54, 117-126. 2003.
- Lynch, J. M., and Bragg, E. Microorganism and soil aggregate stability, *Advances in Soil Science*, 2, 133-171, 1985.
- Malhi, Y and Phillips, O. L. Tropical forests and global atmospheric change: a synthesis, *Phil. Trans. R. Soc. Lond. B.*, 359, 549-555, 2004.
- Malhi, Y., Wood, D., Baker, T., Wright, J., Phillips, O., Cochrane, T. Meir, P., Chave, J., Almeida, S., Arroyo, L. M., Higuchi, N., Killeen, T. J., Laurance, S. G., Laurance, W. F., Lewis, S. L., Monteagudo, A., Neil, D. A., Vargas, P. N. Pitman, N. C. A., Quesada, C. A., Salomão, R., Silva, J. N. M., Lezama, A. T., Terborgh, J., Martínez, R. V., and Vinceti, B. The regional variation of aboveground live biomass in old-growth Amazonian forests, *Global Change Biology*, 12, 1107-1138, 2006.
- McDowell R. W., Monaghan, R. M., and Morton, J. Soil phosphorus concentrations to decrease potential P loss to surface waters in Southland, *New Zealand Journal of Agricultural Research*, 46, 239-253, 2003.
- Meentemeyer, V. Macroclimate the lignin control of litter decomposition rates, *Ecology*, 59, 465-472.
- Mikutta, R., Kleber, M., Torn, M. S., and Jahn, R. Stabilization of soil organic matter: association with minerals or chemical recalcitrance? *Biogeochemistry*, 77, 25-56, 2006.
- Nelson, D. W., and Sommers, L. E. Total carbon and total nitrogen. In: *Methods of Soil Analysis: Part 3 - Chemical Methods*. (ed. D L Sparks), pp 961-1010. SSSA Book Series No 5, SSSA and ASA, Madison, WI, 1996.

- Nepstad, D., Veríssimo, A. Alencar, A., Nobre, C., Lima E. Lefebvre, P., Schlesinger, P., Potter, C., Moutinho, P., Mendoza, E., Cochrane, M., and Vanessa Brooks. Large-scale impoverishment of Amazonian forests by logging and fire, *Nature*, 398, 505-508, 1999.
- Oades, J. M. The retention of organic matter in soils, *Biogeochemistry*, 5, 35-70, 1988.
- Park, J. H., Kalbitz, K., and Matzner, E. Resource control on the production of dissolved organic carbon and nitrogen in a deciduous forest floor, *Soil Biology and Biochemistry*, 34, 813-822, 2002.
- Pella, E. Elemental organic analysis. Part 1. Historical developments. *Am. Lab.*, 22, 116–125, 1990.
- Phillips, O. L., Malhi, Y., Higuchi, N., Laurance, W. F., Nuñez V. P., Vásquez M. R., Laurance, S. G., Ferreira, L. V., Stern, M., Brown, S. and Grace, J. Changes in the carbon balance of tropical forests: evidence from long-term plots, *Science*, 282, 439-442, 1998.
- Phillips, O. L., Baker, T., Arroyo, L., Higuchi, N., Killeen, T., Laurance, W. F., Lewis, S. L., Lloyd, J., Malhi, Y., Monteagudo, A., Neill, D., Núñez Vargas, P., Silva, N., Terborgh, J., Vásquez Martínez, R., Alexiades, M., Almeida, S., Brown, S., Chave, J., Comiskey, J. A., Czimczik, C. I., Di Fiore, A., Erwin, T., Kuebler, C., Laurance, S. G., Nascimento, H. E. M., Olivier, J., Palacios, W., Patiño, S., Pitman, N., Quesada, C. A., Saldias, M., Torres Lezama, A. and Vinceti, B. Patterns and process in Amazon tree turnover, 1976-2001, *Philosophical Transactions of the Royal Society of London Series B*, 359, 437-462, 2004.
- Plante, A. F., Conant, R. T., Carlson, J., Greenwood, R., Shulman, J. M., Haddix, M. L., and Paul, E. A. Decomposition temperature sensitivity of isolated soil organic matter fraction, *Soil Biology & Biochemistry*, 42, 1991-1996, 2010.
- Pleysier, J. L., and Juo, A. S. R. A single-extraction method using silver-thiourea for measuring exchangeable cations and effective CEC in soils with variable charges, *Soil Science*, 129, 205-211, 1980.
- Puget, P., Chenu, C., and Balesdent, J. Dynamics of soil organic matter associated with particle-size fractions of water-stable aggregates. *Eur. J. Soil Sci.* 51, 595–605, 2000.
- Quesada, C. A., Lloyd, J., Schwarz, M., Patiño, S., Baker, T. R., Czimczik, C., Fyllas, N. M., Martinelli, L., Nardoto, G. B., Schmerler, J., Santos, A. J. B., Hodnett, M. G., Herrera, R., Luizão, F. J., Arneith, A., Lloyd, G.; Dezzio, N.; Hilke, I.; Kuhlmann, I.; Raessler, M.; Brand, W. A.; Geilmann, H.; Moraes-Filho, J. O.; Carvalho, F. P.; Araujo Filho, R. N.; Chaves J. E.; Cruz Junior, O. F.; Pimentel, T. P. and Paiva, R. Variations in

- chemical and physical properties of Amazon forest soils in relation to their genesis. *Biogeosciences*, 7, 1515–1541, 2010.
- Quesada, C. A., Lloyd, J., Schwarz, M., Baker, T. R., Phillips, O. L., Patiño, S., Czimczik, C., Hodnett, M. G., Herrera, R., Arneeth, A., Lloyd, G., Malhi, Y., Dezzeo, N., Luizão, F. J., Santos, A. J. B., Schmerler, J., Arroyo, L., Silveira, M., Priante Filho, N., Jimenez, E. M., Paiva, R., Vieira, I., Neill, D. A., Silva, N., Peñuela, M. C., Monteagudo, A., Vásquez, R., Prieto, A., Rudas, A., Almeida, S., Higuchi, N., Lezama, A. T., López-González, G., Peacock, J., Fyllas, N. M., Alvarez Dávila, E., Erwin, T., di Fiore, A., Chao, K. J., Honorio, E., Killeen, T., Peña Cruz, A., Pitman, N., Núñez Vargas, P., Salomão, R., Terborgh, J., and Ramírez, H. 2010. Regional and large-scale patterns in Amazon forest structure and function are mediated by variations in soil physical and chemical properties. *Biogeosciences Discussions*, 6, 3993–4057, 2009.
- Quesada, C. A., Lloyd, J., Anderson, L. O., Fyllas, N. M., Schwarz, M. and Czimczik, C. I. Soils of Amazonia with particular reference to the RAINFOR sites. *Biogeosciences*, 8, 1415-1440, 2011.
- R Development Core Team. 2009. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Viena, Austria. Acessível em: <http://www.R-project.org>
- Rangel, T. F., Diniz-Filho, J. A., and Bini, L. M. Towards an integrated computational tool for spatial analysis in macroecology and biogeography, *Global Ecology and Biogeography*, 15, 321-327, 2006.
- Reichstein, M., Katterer, T., Andren, O., Ciais, P., Schulze, E. D., Cramer, W., Papale, D., and Valentini, R. Temperature sensitivity of decomposition in relation to soil organic matter pools: critique and outlooks, *Biogeosciences*, 2, 317-321, 2005.
- Rowland, A. P., and Roberts, J. D. Lignin and cellulose fractionation in decomposition studies using acid-detergent fibre methods. *Communications in Soil Science and Plant Analysis* 25, 269-277, 1994.
- Scharpenseel, H.-W. and Becker-Heidmann, P. Shifts in ¹⁴C patterns of soil profiles due to bomb carbon, including effects of morphogenetic and turbation processes, *Radiocarbon*, 31, 627–636, 1989.
- Schulten, H. R. and Leinweber, P. New insights into organic-mineral particles: composition, properties and models of molecular structure. *Biol. Fertil. Soils*, 30, 399-432, 2000.
- Silver, W. L., Neff, J., McGroddy, M., Veldkamp, E., Keller, M. and Cosme, R. Effects of soil texture on belowground carbon and nutrient storage in a lowland amazonian forest ecosystem, *Ecosystems*, 3, 193-209, 2000.

- Six, J., Elliot, E. T., and Paustian, K. Soil macroaggregate turnover and microaggregate formation: a mechanism for C sequestration under no-tillage agriculture, *Soil Biology & Biochemistry*, 32, 2099-2103, 2000.
- Six, J., Conant, R. T., Paul, E. A., and Paustian, K. Stabilization mechanisms of soil organic matter: implications for C-saturation of soils, *Plant and Soil*, 241, 155–176. 2002.
- Six, J., and Jastrow, J. D. Organic matter turnover. *Encyclopedia of Soil Science* (Ed. M. Dekker), 936-942, 2002.
- Sombroek, W. G. A reconnaissance of the soils of the Brazilian Amazon region. Centre for Agricultural Publications and Documentation, Wageningen. 1966.
- Stephenson, N., and Van Mantgen, P. J. Forest turnover rates follow global and regional patterns of productivity, *Ecology Letters* 8, 524-531, 2005.
- Swift, R. S. Sequestration of carbon by soil. *Soil Science*, 166, 858-871, 2001.
- Tian, H., Melillo, J. M., Kicklighter, D. W., McGuire, A. D., Helfrich III, J. V. K., Moore III, B. and Vörösmarty, C. J. Effect of interannual climate variability on carbon storage in Amazonian ecosystems. *Nature*, 396, 664-667, 1998.
- Tiessen, H., and Moir, J. O. Total and Organic Carbon. In: *Soil Sampling and Methods of Analysis* (ed. M R Carter), pp 187-199. Leis Publ., Boca Raton, FL. 1993.
- Uehara, G. and Gilman, G. *The Mineralogy, Chemistry, and Physics of Tropical Soils with Variable Charge Clays*. Westview Press, Boulder, Colorado. 1981.
- Van Reeuwijk, L.P. *Procedures for soil analysis*. International Soil Reference Information Centre, ISRIC, sixth edition. Wageningen, Netherlands, 120p., 2002.
- Van Soest, P. J. Use of detergents in the analysis of fibrous feeds. II. A rapid method for the determination of fiber and lignin. *J Assoc of Agric Chem*, 46, 829-835, 1963.
- Vitousek, P. M. *Nutrient Cycling and Limitation: Hawai'i as a Model System*. Princeton University Press, 223 pp., 2004.
- Wander, M. Soil organic matter fractions and their relevance to soil function. In: *Soil Organic Matter in Sustainable Agriculture*, CRC Press. p. 68-90. 2004.
- Wander, M., and Traina, S. J. Organic matter fractions from organically and conventionally managed soils: II characterization of composition, *Soil Science Society of America*, 60, 1087-1094, 1996.
- Zech, W., and Guggenberger G. Organic matter dynamics in forest soils of temperate and tropical ecosystems. In A. Piccolo, editor. *Humic substances in terrestrial ecosystems*. Elsevier. 1996.

Zimmermann, M., Leifeld, J., Schmidt, M. W. I., Smith, P. and Fuhrer, J. Measured soil organic matter fractions can be related to pools in the RothC model. *European J. Soil Science*, 58, 658–667, 2007.

Table 1.

Plot code	Plot name	WRB Soil Type	lat	long	Mean Annual Temperature (°C)	Annual Precipitation (mm)	Country
AJR-01	Rio Juruá, plot 1	Cambisol	-4,8300	-66,3667	26.0	2,681.3	Brazil
ALF-01	Alta Floresta, plot 1	Acrisol	-9,5983	-55,9369	25.0	2,349.6	Brazil
ALF-02	Alta Floresta, plot 2	Regosol	-9.5784	-55,9176	25.0	2,353.8	Brazil
ALP-30	Allpahuayo, plot C	Alisol	-3,9544	-73,4258	26.0	2,762.7	Peru
ALP-40	Allpahuayo, plot D	Arenosol	-3,9411	-73,4394	26.0	2,770.3	Peru
BNT-04	Bionte, plot 4	Ferrasol	-2,6275	-60,1531	26.8	2,239.2	Brazil
CAX-02	Caxiuanã, plot 2	Acrisol	-1,7433	-51,4615	26.0	2,188.6	Brazil
CAX-06	Caxiuanã, tower plot	Ferrasol	-1,7198	-51,4582	26.0	2,203.5	Brazil
CUZ-03	Cuzco Amazonico, plot 2E	Cambisol	-12,499	-68,9630	25.5	2,082.9	Peru
JEN-11	Jenaro Herrera, A Terraza Alta	Acrisol	-4,8778	-73,6299	26.0	2,632.5	Peru
JEN-12	Jenaro Herrera, B Varillal	Podzol	-4,8989	-73,6290	26.0	2,640.1	Peru
JEN-13	Jenaro Herrera,	Gleysol	-4,9237	-73,5278	26.0	2,645.3	Peru
JRI-01	Jari, EMBRAPA control plots	Ferrasol	-0,8944	-52,1903	26.0	2,384.8	Brazil
MAN-03	Manaus, Jacarandá "campinarana"	Podzol	-2,6086	-60,2142	27.0	2,250.0	Peru
MAN-12	Manaus, Jacaranda plateau & slope	Ferrasol	-2,6069	-60,2089	26.9	2,250.0	Brazil

Plot code	Plot name	WRB Soil Type	lat	long	Mean Annual Temperature (°C)	Annual Precipitation (mm)	Country
MNU-03	Manu, terra firme terrace, TM	Cambisol	-11,900	-71,4000	25.0	2,473.7	Peru
MNU-04	Manu, terra firme ravine, TQ	Fluvisol	-11,904	-71,4016	25.0	2,478.2	Peru
MNU-05	Manu, alluvial Cocha Cashu, T12	Fluvisol	-11,878	-71,4083	25.0	2,456.9	Peru
MNU-06	Manu, alluvial Cocha Cashu	Fluvisol	-11,886	-71,3972	25.0	2,465.6	Peru
NOU-21	Nouragues Petit Plateau 21E	Ferralsol	4,0833	-52,6667	24.2	3,336.9	French Guyana
NOU-02	Nouragues Grand Plateau 11L	Acrisol	4,0833	-52,6667	24.2	3,336.9	French Guyana
POR-01	Seringal Porongaba, plot 1	Plinthosol	-10,818	-68,7762	25.0	1,690.8	Brazil
POR-02	Seringal Porongaba, plot 2	Plinthosol	-10,799	-68,7728	25.0	1,698.6	Brazil
RST-01	Restauração, Resex Alto Juruá, plot 1	Cambisol	-9,0387	-72,2669	25.0	1,805.0	Brazil
SIN-01	Sinop, plot 1	Ferralsol	-11,411	-55,3247	25.8	2,180.0	Brazil
TAM-06	Tambopata Explorers Inn, plot 4	Alisol	-12,838	-69,2960	25.0	2,502.3	Peru
TAP-123	Tapajós, EMBRAPA control plots	Ferralsol	-3,3096	-54,9419	25.0	1,878.9	Brazil
TAP-04	Tapajós, LBA tower	Ferralsol	-3,3089	-54,9503	25.0	1,879.1	Brazil
ZAR-01	El Zafire, Varillal	Podzol	-4,0068	-69,9061	25.0	2,800.7	Colombia
ZAR-02	El Zafire, Rebalse	Gleysol	-4,0020	-69,9035	25.0	2,797.2	Colombia

Table 2.

	Kendall's τ correlation			
	Silt + clay	Resistant	Heavy	Light
Resistant	0.478 ***			
Heavy	-0.144 ^{ns}	0.036 ^{ns}		
Light	0.374 **	0.128 ^{ns}	-0.034 ^{ns}	
DOC	0.347 **	0.396 **	0.417 ***	0.194 ^{ns}

*** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$, ns=not significant

Table 3.

	Kendall's τ correlation					
	SOC fractions					
	Silt+clay	Resistant	Heavy	Light	DOC	Total C
Clay	0.028 ^{ns}	0.290*	0.299*	-0.179 ^{ns}	0.496***	0.340**
Sand	-0.182 ^{ns}	-0.334**	-0.135 ^{ns}	0.016 ^{ns}	-0.344**	-0.383**
SB	0.249*	0.027 ^{ns}	-0.170 ^{ns}	0.152 ^{ns}	-0.077 ^{ns}	0.115 ^{ns}
ECEC	0.400**	0.382**	-0.064 ^{ns}	0.170 ^{ns}	0.165 ^{ns}	0.257*
TRB	0.351**	0.182 ^{ns}	-0.337**	0.016 ^{ns}	-0.144 ^{ns}	0.029 ^{ns}
Total P	0.328**	0.260*	-0.140 ^{ns}	0.112 ^{ns}	0.079 ^{ns}	0.218 ^{ns}
Available P	0.400***	0.249*	-0.234 ^{ns}	0.207 ^{ns}	-0.011 ^{ns}	0.188 ^{ns}
Litter lignin	-0.002 ^{ns}	-0.034 ^{ns}	0.291*	0.278*	0.111 ^{ns}	0.172 ^{ns}
Soil C:N ratio	-0.052 ^{ns}	0.006 ^{ns}	0.434***	0.255*	0.335**	0.278*
Temperature	0.098 ^{ns}	0.137 ^{ns}	0.170 ^{ns}	0.226 ^{ns}	0.181 ^{ns}	0.103 ^{ns}
Rainfall	0.108 ^{ns}	0.006 ^{ns}	0.145 ^{ns}	0.329**	0.037 ^{ns}	0.228 ^{ns}

*** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$, ns=not significant

Table 4.

	Unfiltered				Filtered			
	Coefficients	F - test (<i>t</i> - test)	<i>P</i> value	Adjusted R ²	Coefficients	F - test (<i>t</i> - test)	<i>P</i> value	Adjusted R ²
Silt + clay		5.606	0.009	0.241		6.04	0.001	0.410
Intercept	-2.417	(-1.417)	0.168		-3.597	-1.845	0.077	
Total P	0.549	(3.203)	0.003		0.7523	3.635	0.001	
Sand	0.080	(-0.556)	0.582		0.0240	0.173	0.864	
Filter 1					0.3675	0.309	0.759	
Filtro 2					3.2633	3.098	0.005	
Resistant		4.881	0.008	0.286				
Intercept	-0.161	(-0.103)	0.9190					
TRB	0.163	(2.414)	0.0231					
Sand	-0.261	(-2.768)	0.0103					
Soil C:N	0.762	(1.908)	0.0675					
Heavy		30.02	<0.001	0.667		37.3	<0.001	0.789
Intercept	-9.567	(-6.388)	<0.001		-5.495	-3.544	0.001	
Clay	0.549	(5.511)	<0.001		0.371	4.099	<0.001	
Soil C:N	2.623	(6.926)	<0.001		1.655	4.325	<0.001	
Filter					0.004	4.097	<0.001	
Light		9.3	<0.001	0.364		12.89	<0.001	0.551
Intercept	-23.828	(-3.896)	<0.001		-17.224	-3.148	0.004	
Litter lignin	4.175	(4.274)	<0.001		2.789	3.063	0.005	
Total P	0.379	(1.857)	0.074		0.483	2.775	0.011	
Filter					0.004	3.505	0.002	
DOC		103.4	<0.001	0.876		85.27	<0.001	0.897
Intercept	-7.947	(-19.146)	<0.001		-7.689	(-19.647)	<0.001	
Clay	0.284	(5.349)	<0.001		0.259	(5.258)	<0.001	
C total	1.170	(11.492)	<0.001		1.130	(12.023)	<0.001	
Filter					0.001	(2.556)	0.017	
C Total		7.5	<0.001	0.401		4.8	0.003	0.396
Intercept	-8.316	(-2.644)	0.014		-5.079	-1.270	0.216	
Litter lignin	2.479	(4.202)	<0.001		1.855	2.423	0.023	
ECEC	0.292	(2.157)	0.040		0.332	2.248	0.034	
Sand	-0.238	(-2.332)	0.028		-0.231	-2.076	0.049	
Filter 1					0.700	0.729	0.473	
Filter 2					1.221	1.281	0.212	

Table legends

Table 1. List of studied sites for soil carbon fractions in the Amazon Basin with type soil (World Reference Base -WRB), geographic position and climate data.

Table 2. Relationship among Soil Organic Carbon (SOC) fractions. Values for Kendall's τ correlation test are shown.

Table 3. Relationship among Soil Organic Carbon (SOC) fractions and Total C with (i) soil properties: clay and sand content, sum of bases (SB), effective cation exchange capacity (ECEC), total reserve bases (TRB), total phosphorus concentration (Total P), total available phosphorus (Available P); (ii) organic matter quality variables: leaf litter lignin and soil C:N ratio; climatic variables: (iii) mean annual temperature and annual rainfall for study sites in Amazon Basin. Values for Kendall's τ correlation test are shown.

Table 4. Summary of multiple regression models (OLS) between soil organic carbon fractions and environmental variables as predictors. Results from unfiltered and spatial autocorrelation filtered analysis are shown.

Figure 1.

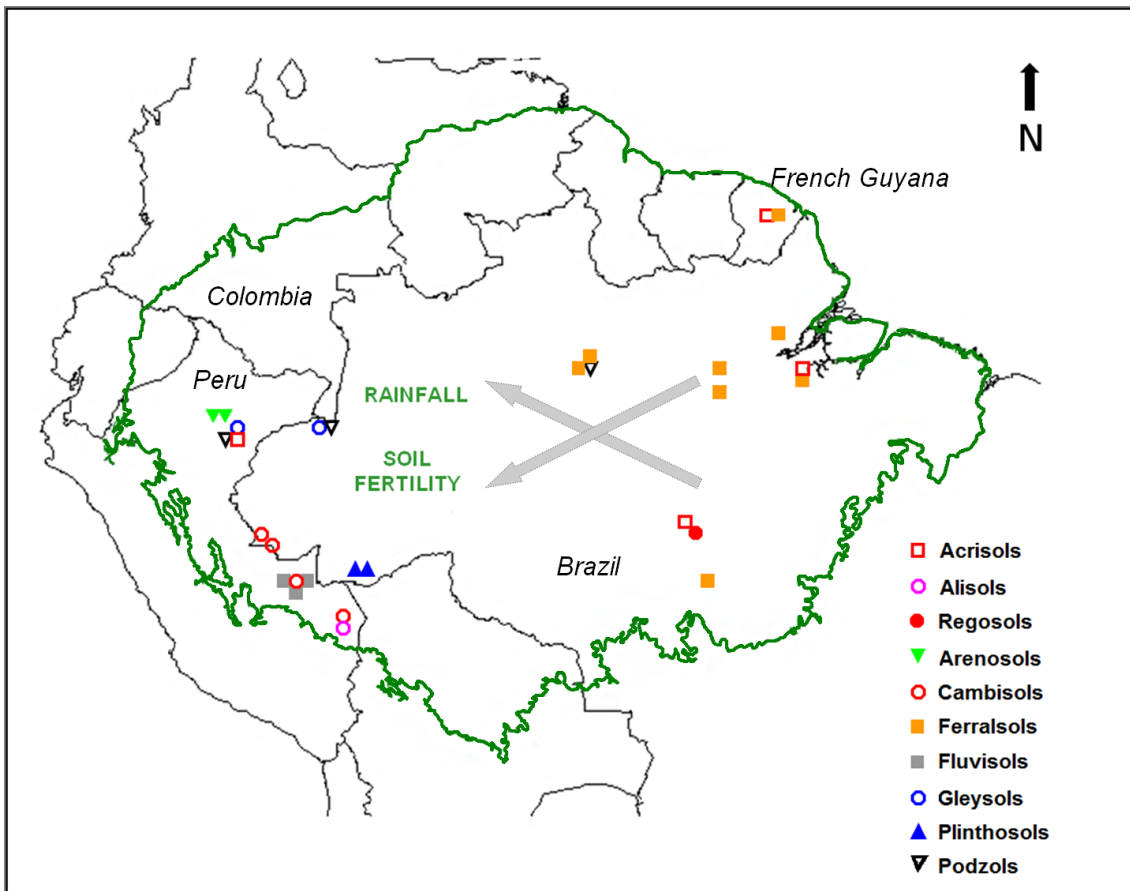


Figure 2.

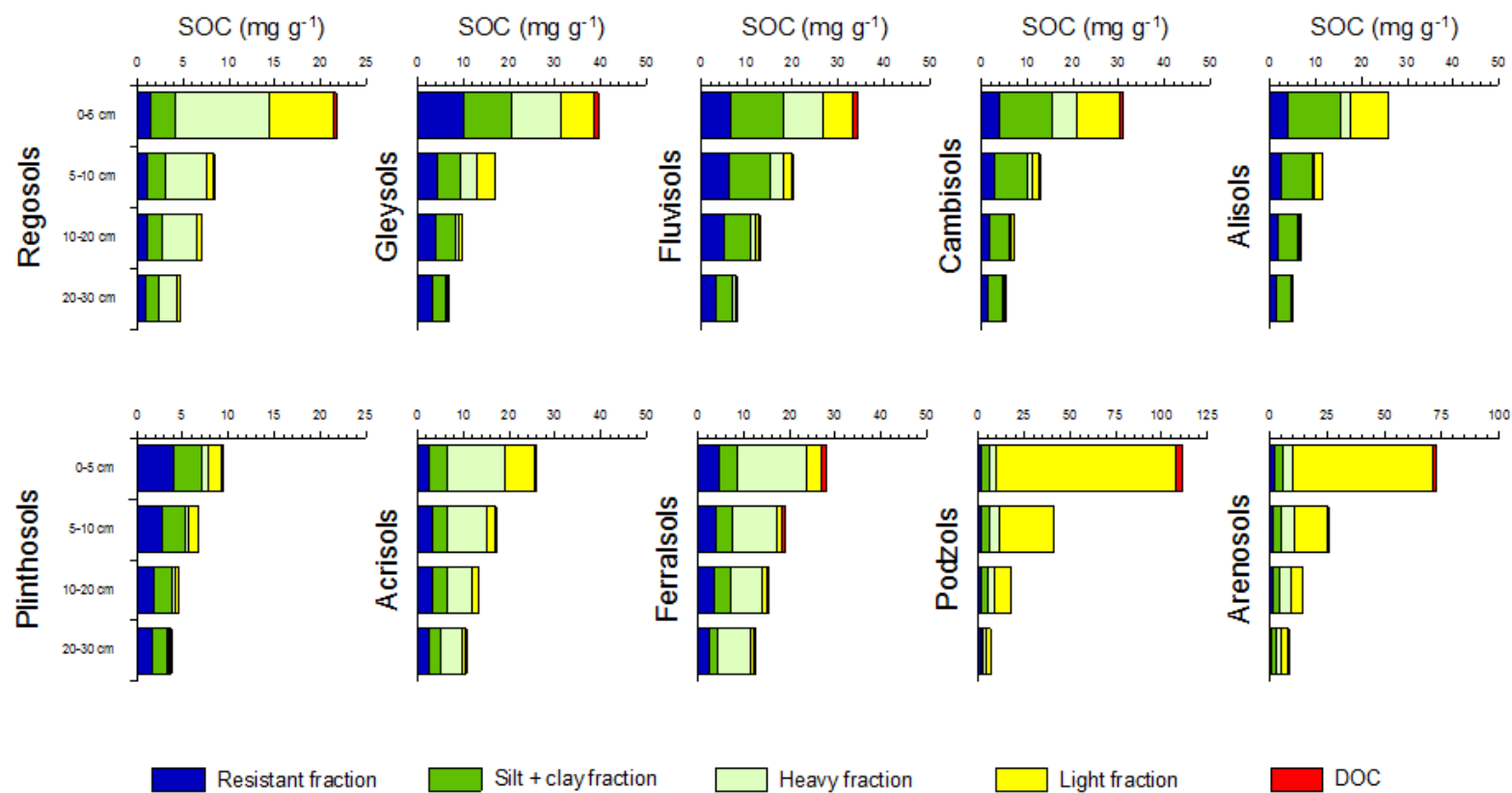


Figure 3.

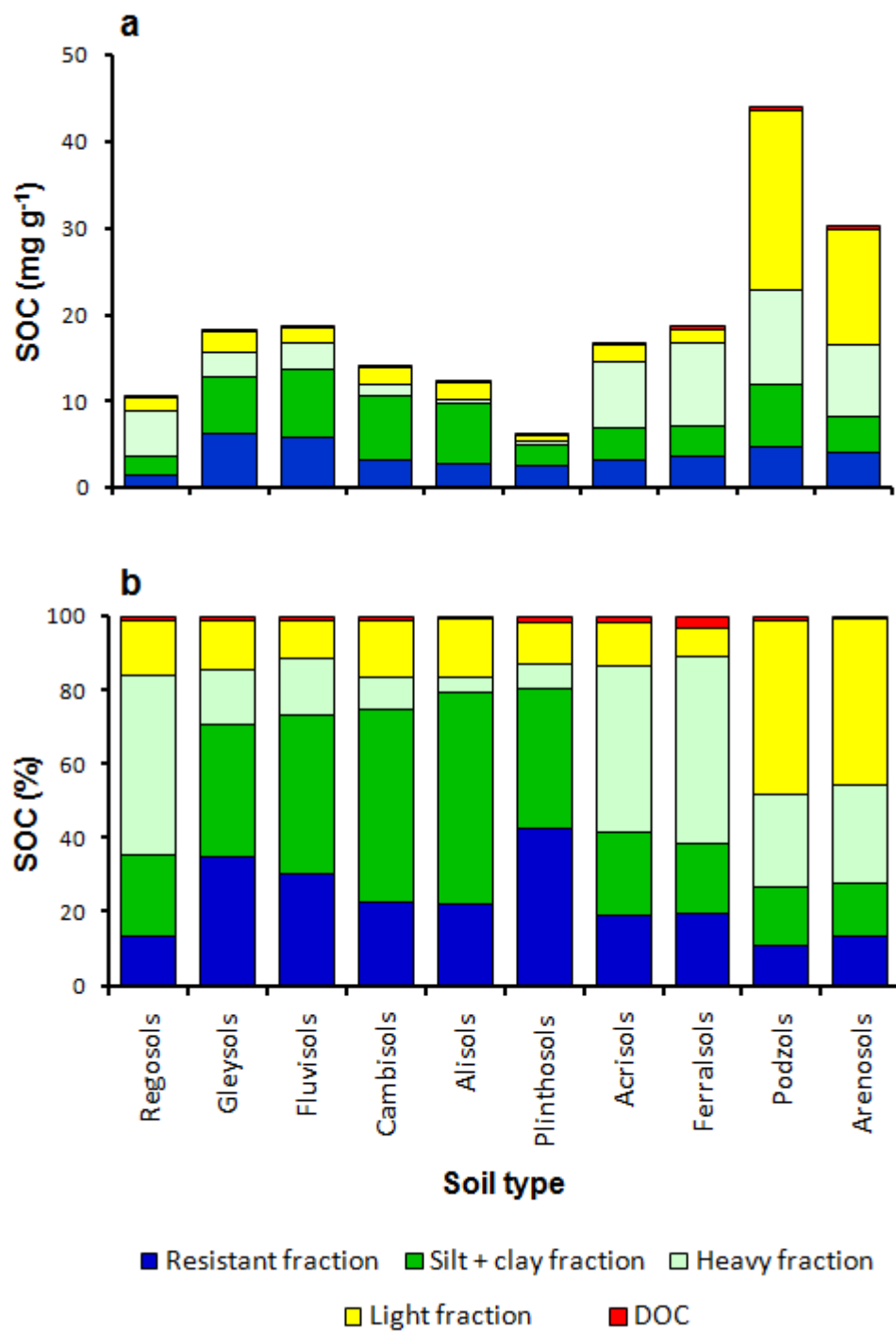


Figure 4.

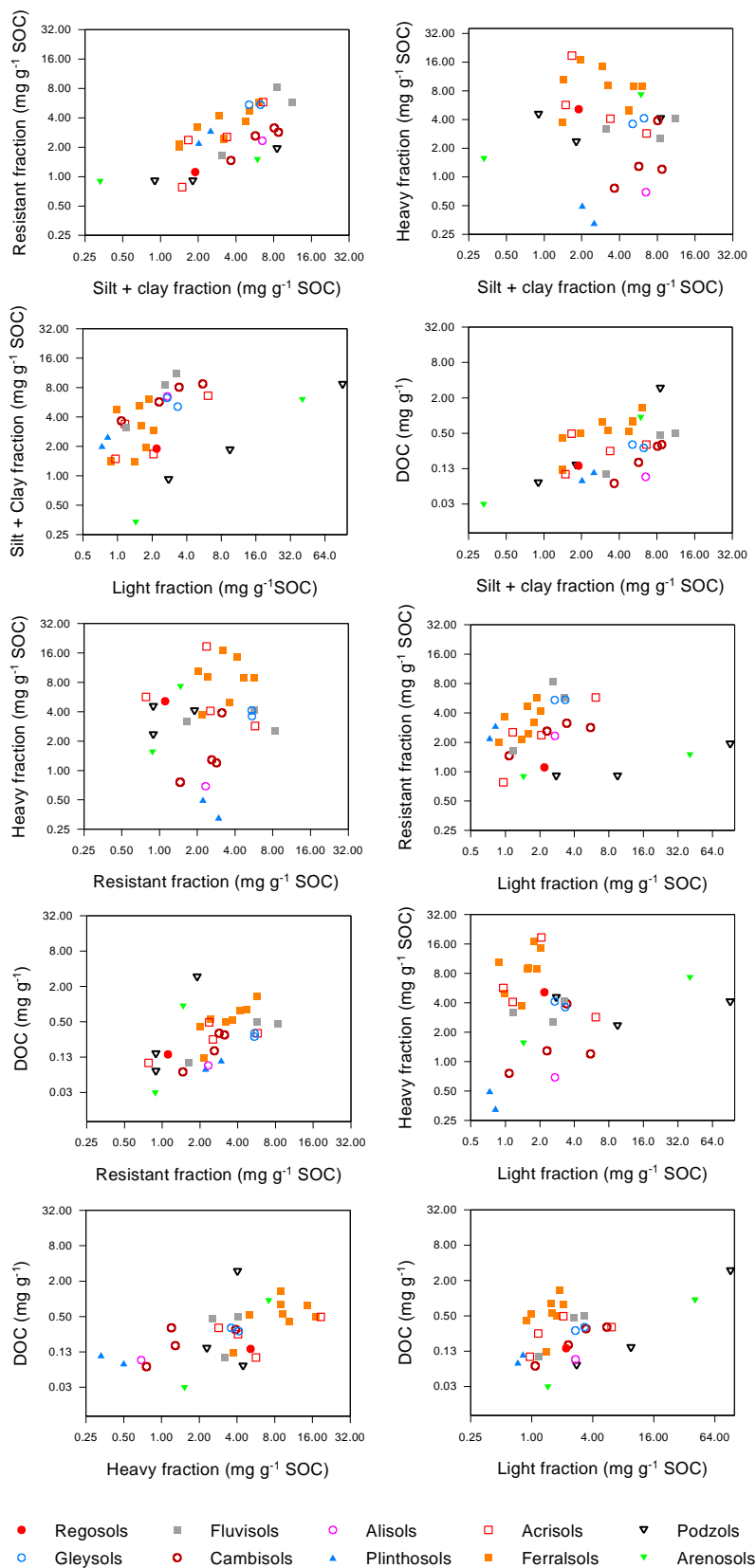


Figure 5

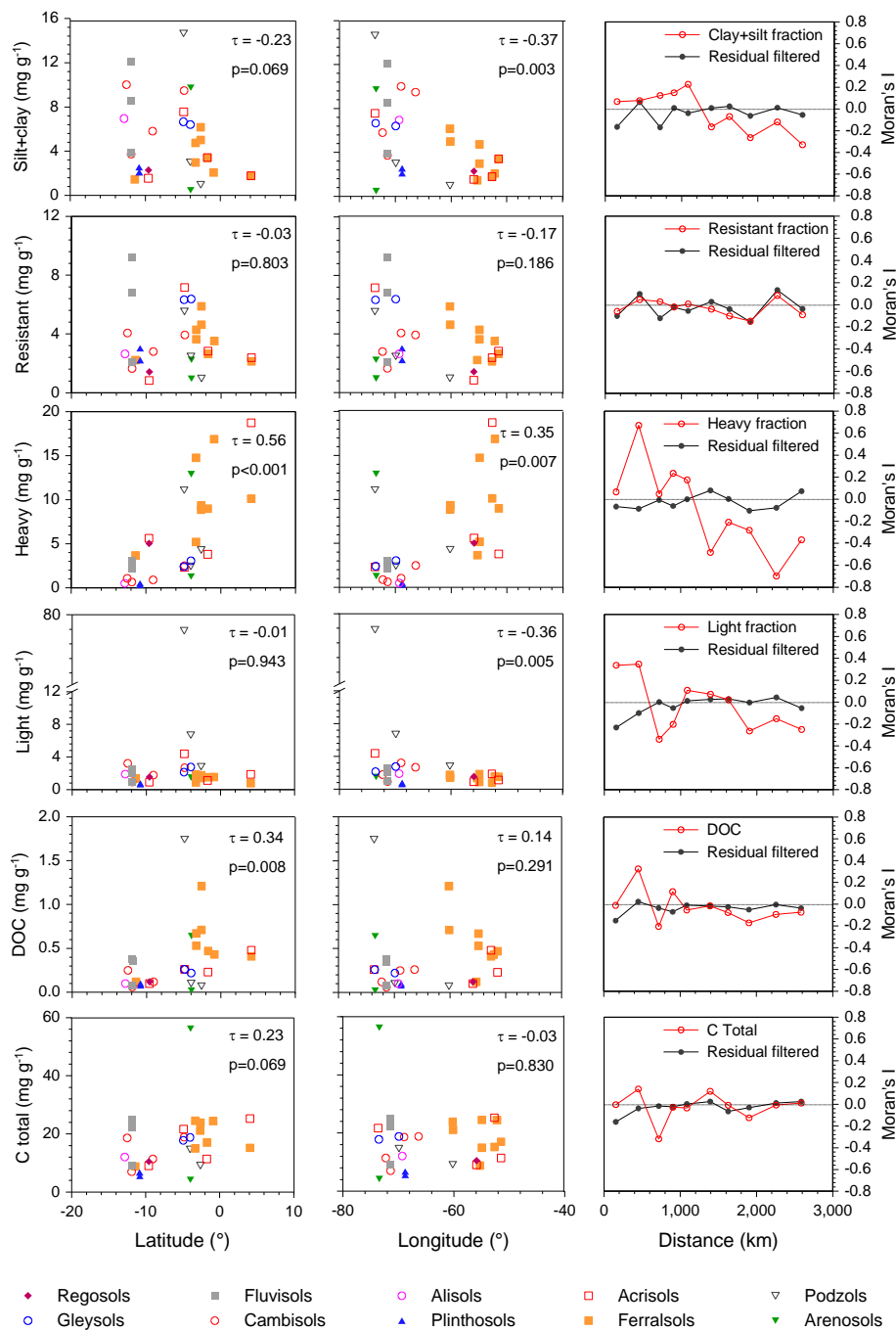


Figure 6.

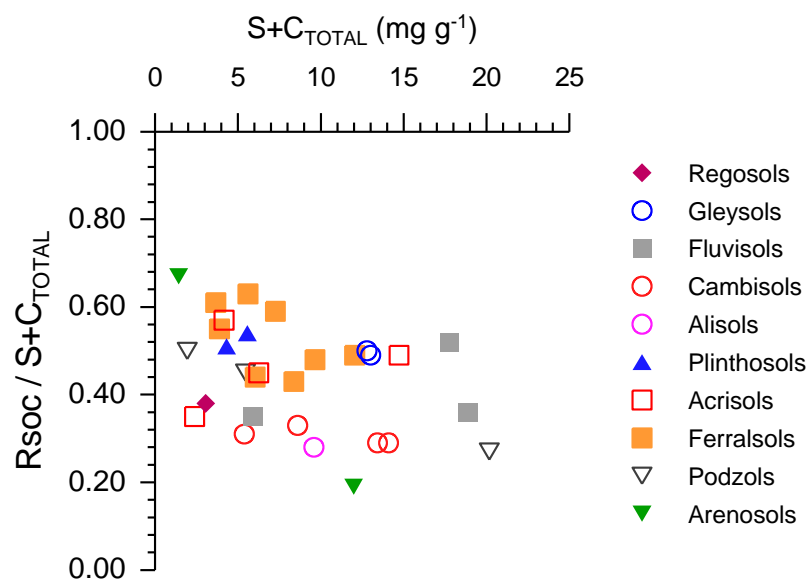


Figure legends

Figure 1: Distribution map of study sites in the Amazon Basin. Arrows indicate the direction of environmental gradients (soil fertility and rainfall) along the region. Symbols (combination of shape and color) indicate the geographical position of each study site and the respectively soil type associated.

Figure 2: Vertical distribution of the soil organic carbon (SOC) fraction in the ten different soil types studied along the Amazon Basin. Soil types are arranged in the sequence of development proposed by Quesada et al. (2010). Blue and green colors represent the more stable SOC fraction, while yellow and red represent the more labile SOC fractions. Note that SOC concentrations scale vary among graphs.

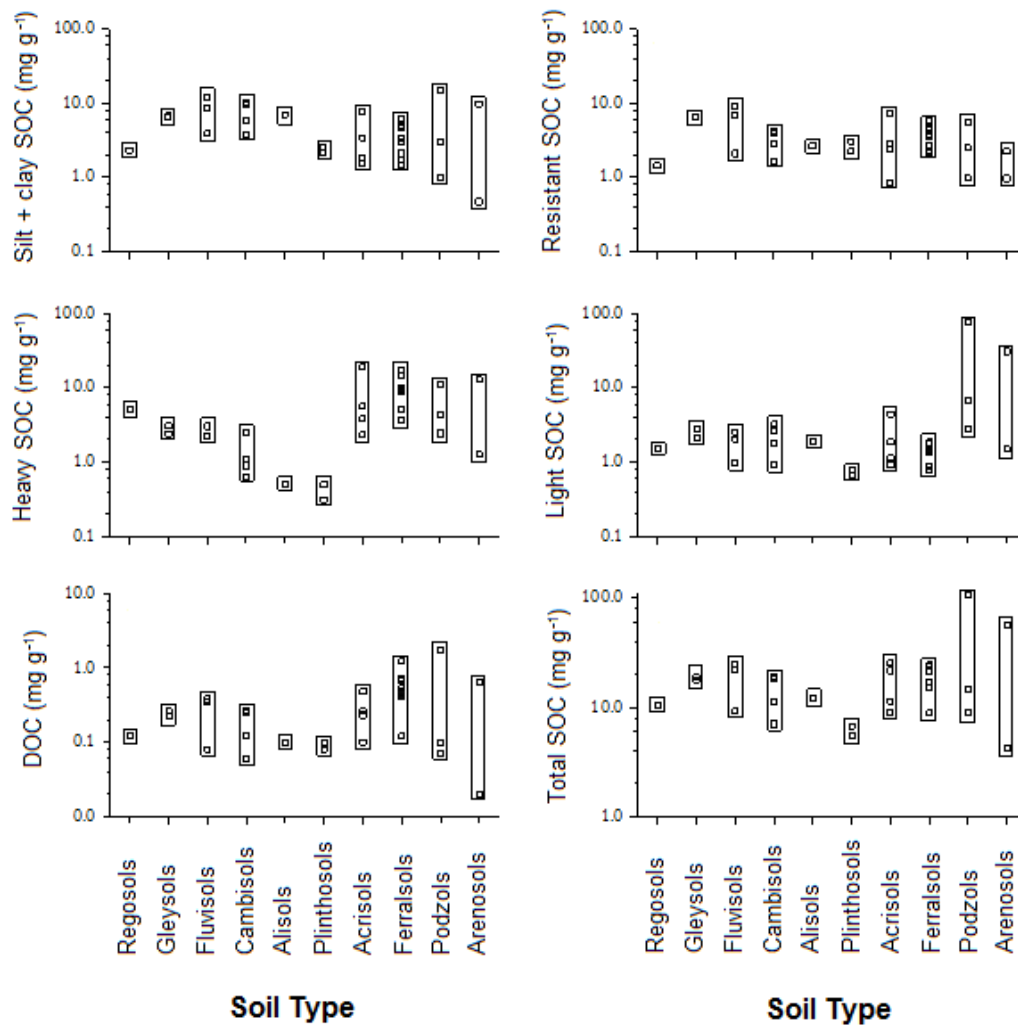
Figure 3: Soil organic carbon (SOC) distribution (average among depths) in soil types studied in Amazon Basin. Soil types are arranged in the sequence of development proposed by Quesada et al. (2010). Blue and green colors represent the more stable SOC fraction, while yellow and red represent the more labile SOC fractions.

Figure 4: Bivariate plots showing the relationship among soil organic carbon (SOC) fraction. Symbols represent the different soil types studied in Amazon Basin.

Figure 5: Correlations of soil carbon fractions with the geographic space. Moran's I correlograms are also given showing spatial autocorrelation but with spatial filters being able to effectively remove its effect from regression residuals

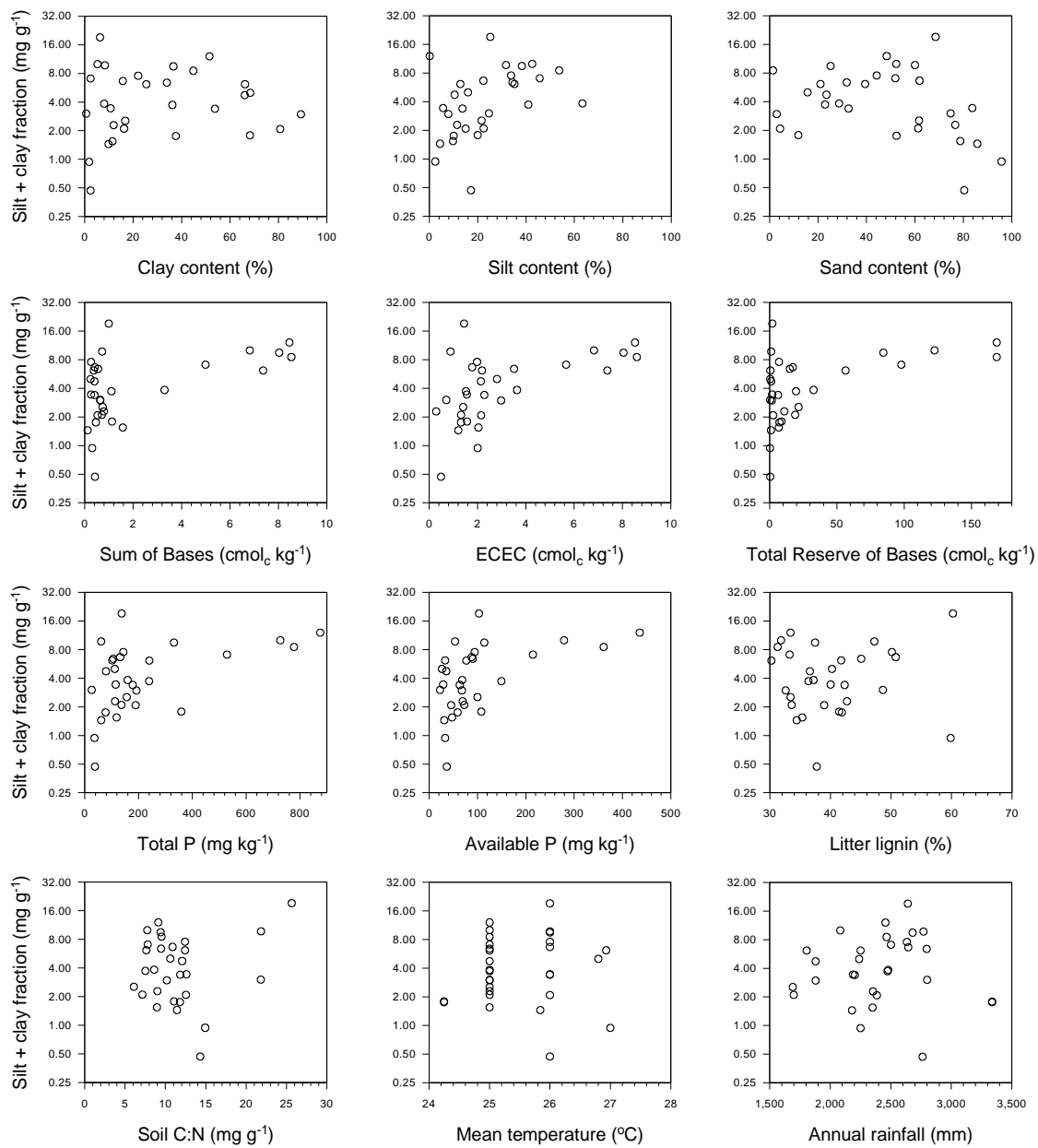
Figure 6: Resistant SOC as a proportion of total Silt + Clay fraction.

Supplementary material S1:



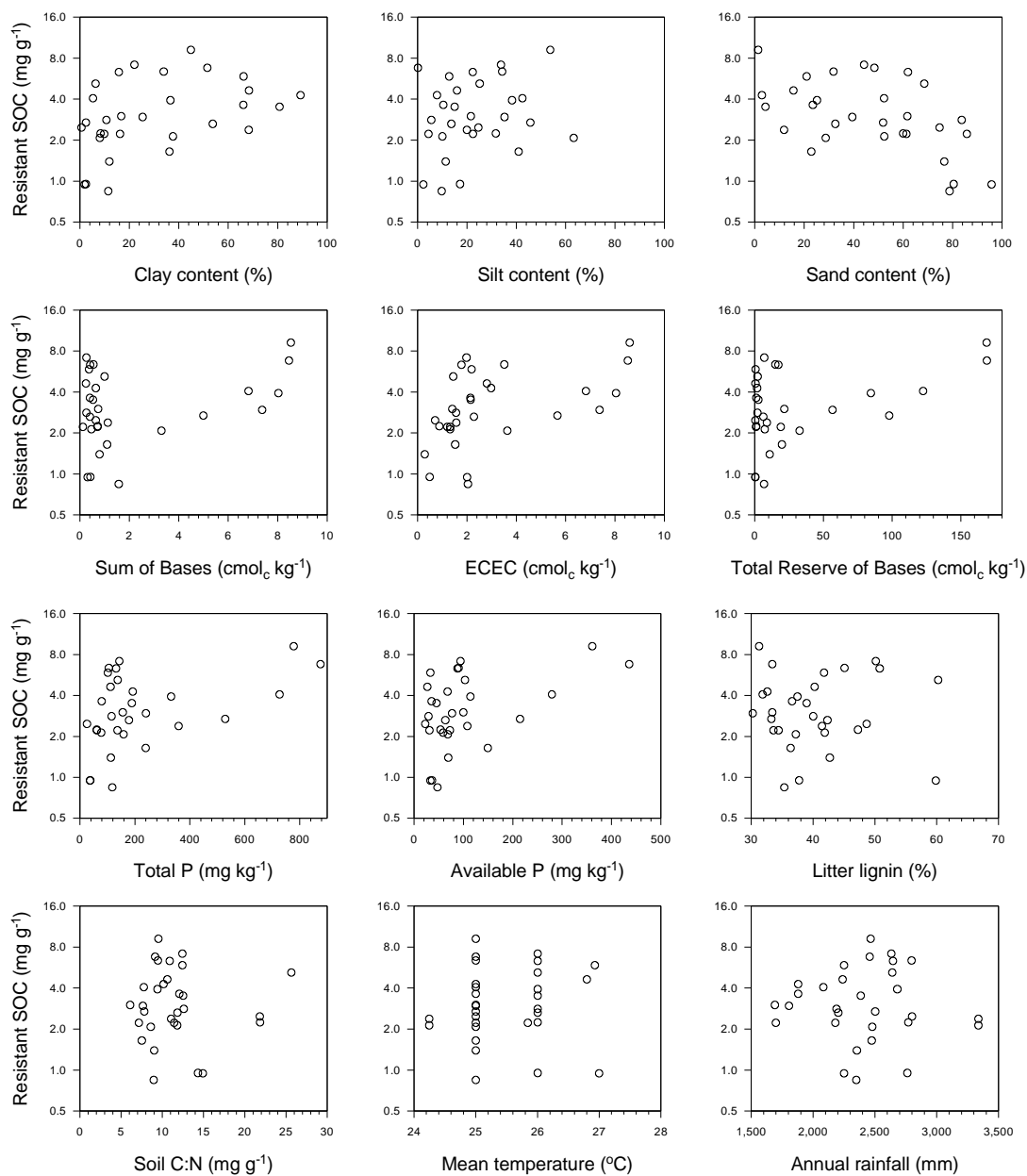
Supplementary material 2:

A



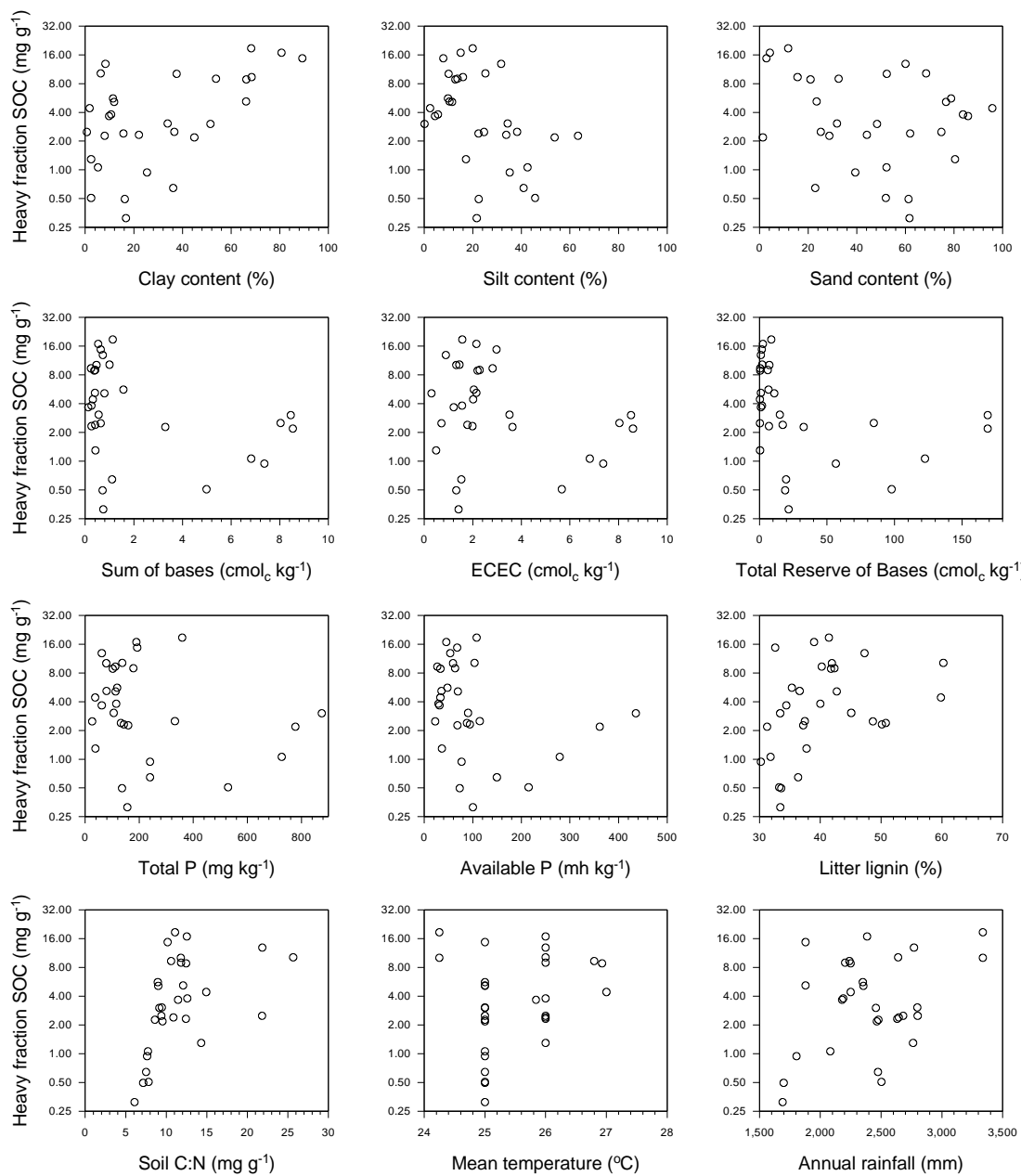
Supplementary material 2

B



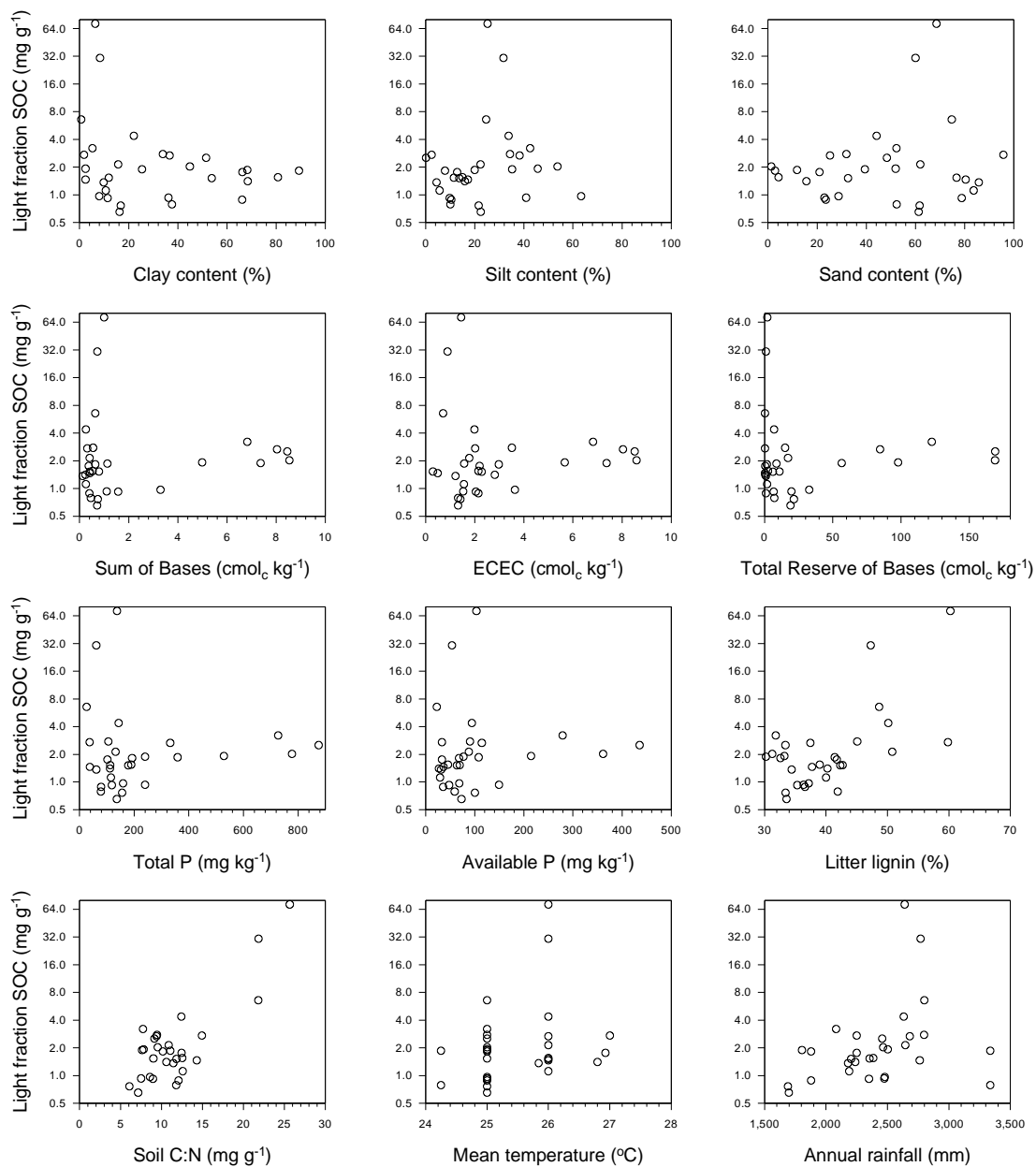
Supplementary material 2

C



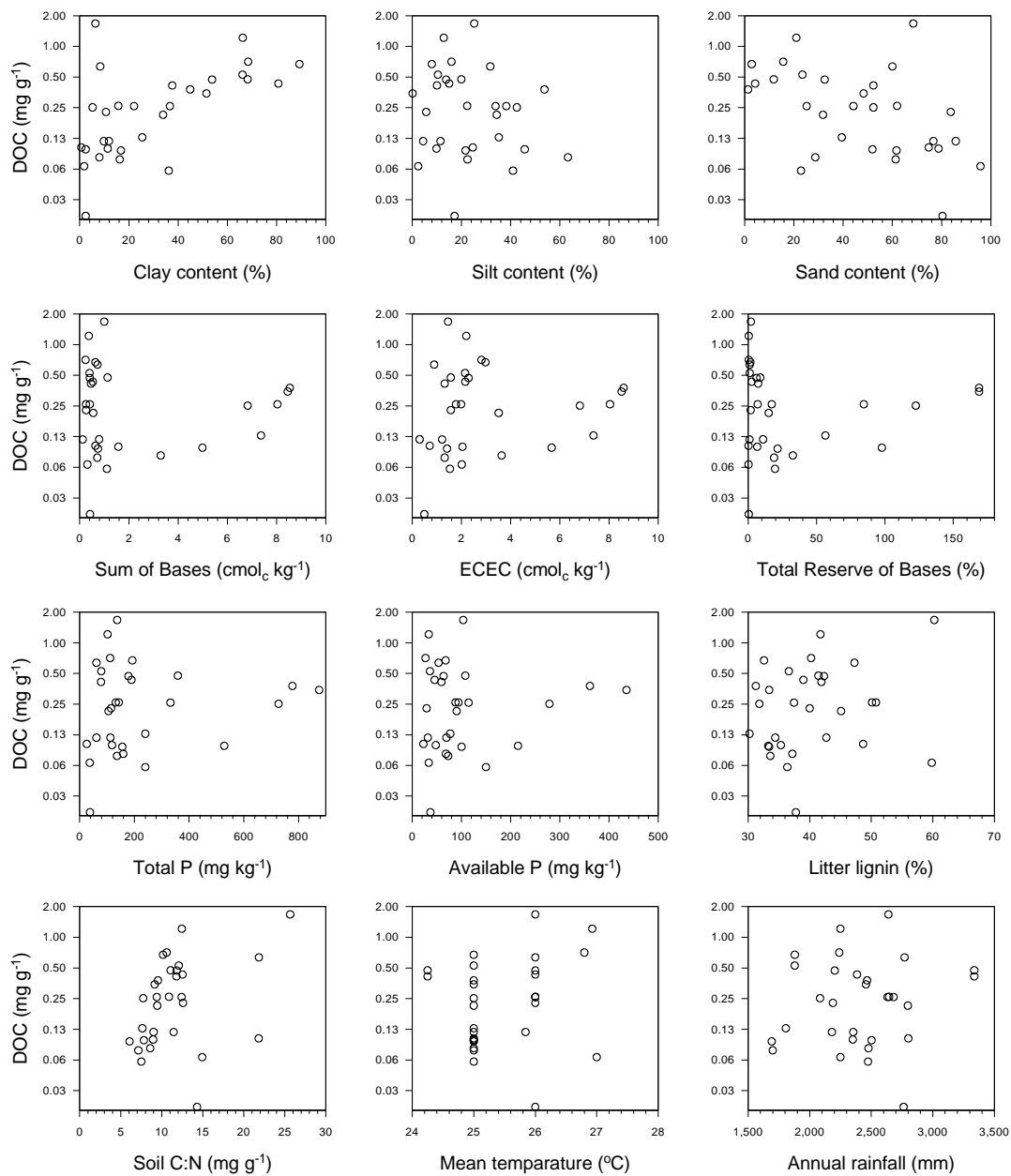
Supplementary material 2

D



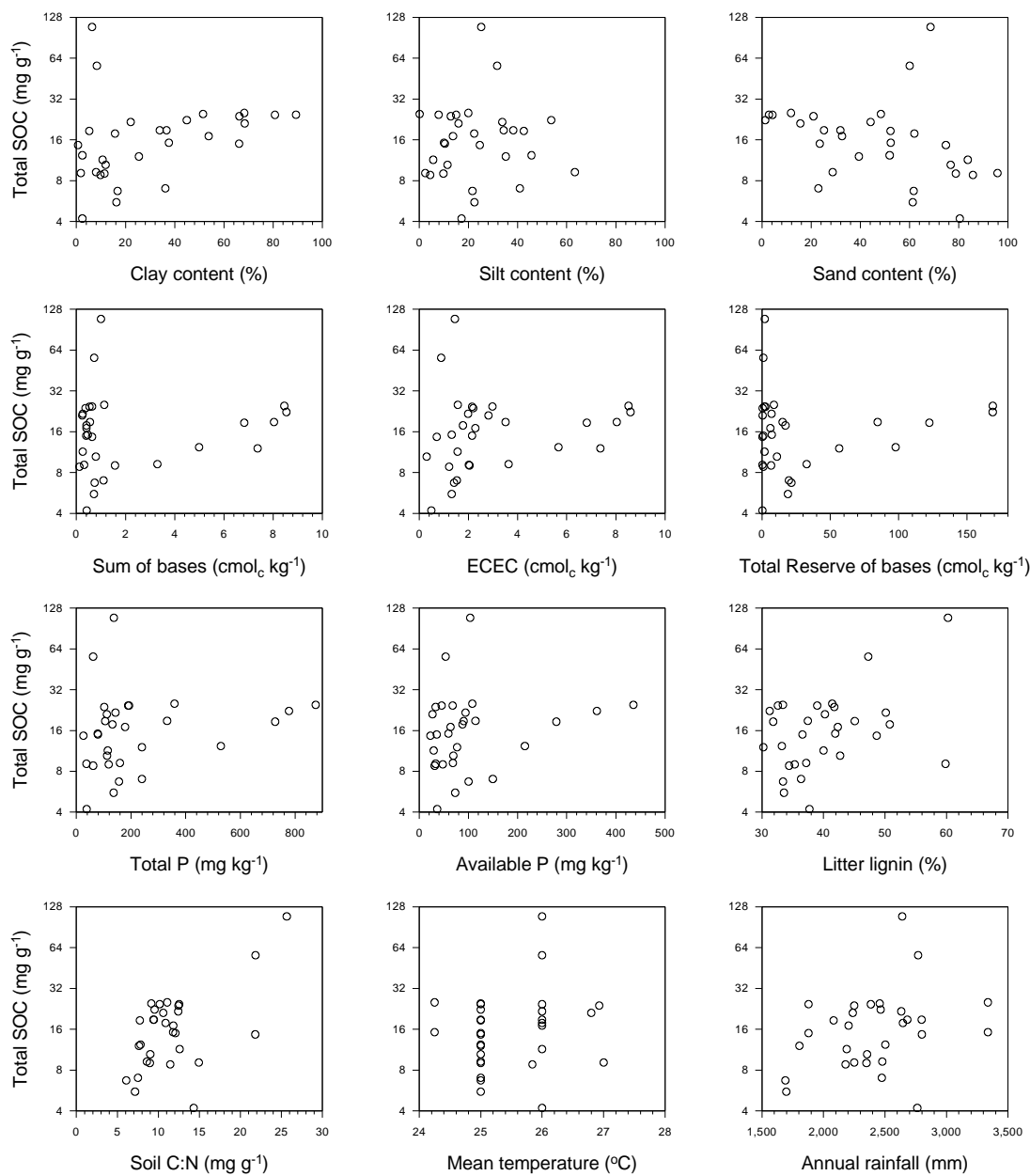
Supplementary material 2

E

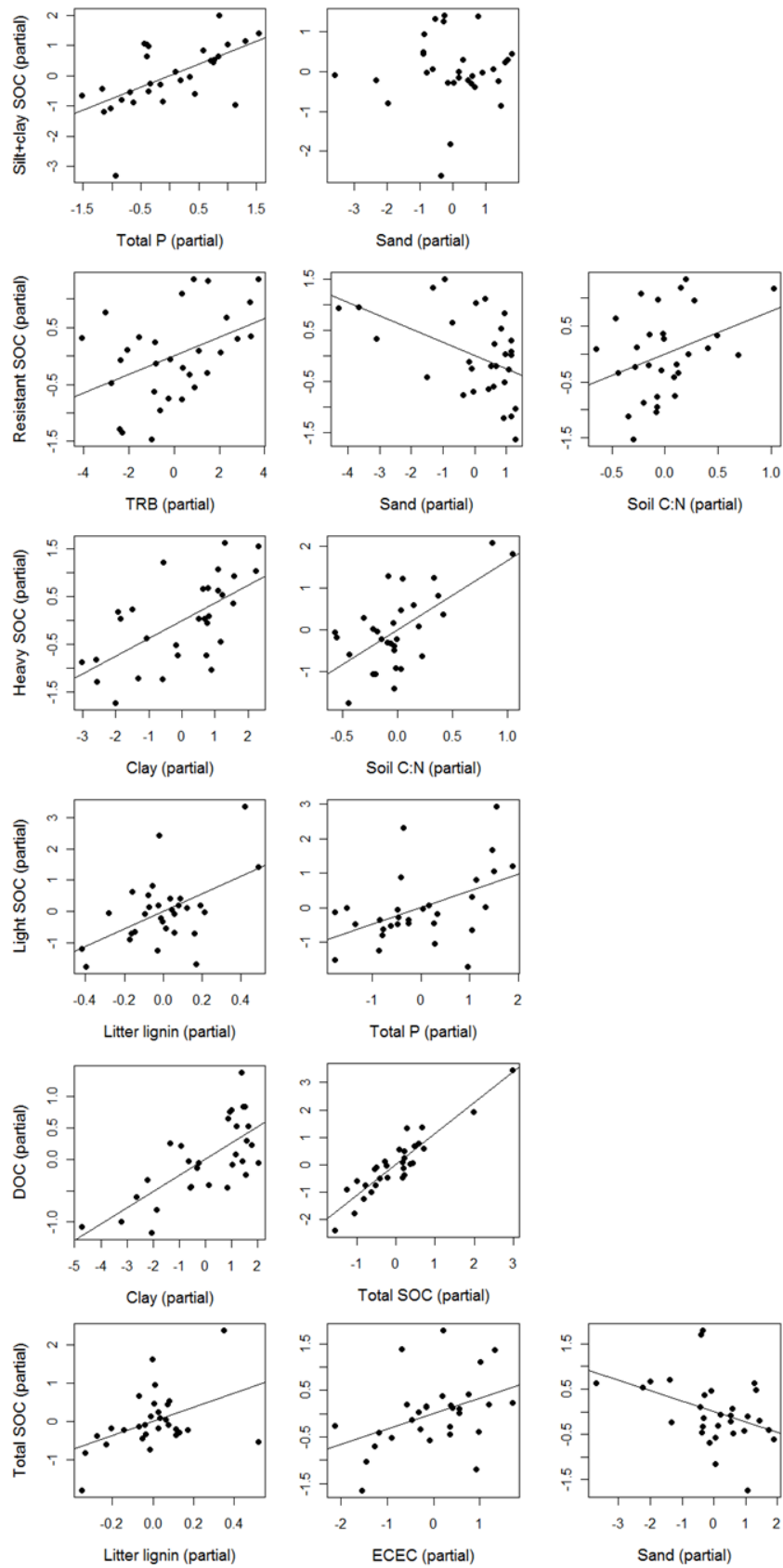


Supplementary material 2

F



Supplementary material 3



Supplementary material legends

S1: Variation of soil organic carbon (SOC) in the soil types across the Amazon Basin. Bars size indicate the internal variation around the average for each soil type. Soil types are arranged in the sequence of soil development proposed by Quesada et al. (2010).

S2: Bivariate plots from soil properties, litter quality and climate variables and the concentration of soil organic carbon (SOC) in (A) Silt + Clay fraction; (B) Resistant fraction; (C) Heavy fraction; (D) Light fraction; (E) Dissolved Organic Carbon; (F) Total SOC. Both x and y axis values were log transformed.

S3: Graphic results of Ordinary Least Squared (OLS) models showing the biplot results of individual effects (partials) of soil or litter quality variables on soil organic carbon (SOC) fractions.




Conclusão

O fracionamento da matéria orgânica em diferentes solos da Amazônia mostrou que existe uma ampla variação na qualidade e na quantidade de carbono orgânico armazenado nesses solos. Essa variação reflete a sensibilidade da matéria orgânica a diversos fatores ambientais que conseqüentemente afetarão a dinâmica do carbono no sistema. Apesar de não investigarmos todos os possíveis fatores que influenciam nessa dinâmica, nossos dados revelam o papel fundamental das propriedades do solo sobre a retenção de SOC nos solos tropicais. Por outro lado, apesar de bem documentada na literatura, as variáveis climáticas não mostraram um efeito direto sobre o conteúdo de SOC nas diferentes frações. Mesmo assim, não descartamos que a temperatura e a precipitação tenham um papel controlador na estabilização do SOC. Contudo, na Amazônia, a faixa de variação de temperatura, essencial para a ativação das reações químicas que envolvem o processo de decomposição, não é muito ampla e é relativamente alta (25,5 °C). Enquanto que a precipitação, apesar de haver uma variação maior ao longo da Bacia Amazônica, também não ultrapassa a faixa ideal para a atividade microbiológica. De qualquer forma, a temperatura e a quantidade de chuva acumulada em um ano são elevadas, o que não restringe a decomposição da matéria orgânica, tornando as propriedades do solo, como fertilidade e grau de intemperismo, e a qualidade da liteira, variáveis mais importantes no controle do carbono orgânico no solo.

Nossos dados revelaram também que uma análise de padrões gerais em um amplo gradiente geográfico deve ser feita com cuidado. Em primeiro lugar não se pode ignorar o efeito da distância geográfica nas análises. Nesse extenso ecossistema, em centenas de quilômetros de distância, o que na maioria das vezes é considerada suficiente para se ter amostras independentes em outros lugares do mundo, podemos ainda encontrar autocorrelação espacial, que pode interferir bruscamente na interpretação de resultados. Em segundo lugar, determinar padrões gerais com tanta variação ambiental pode mascarar processos ecológicos importantes que estão ocorrendo em escalas menores. No nosso caso, a análise da distribuição do conteúdo de SOC nas frações poderia ter uma interpretação diferente se não levássemos em consideração os tipos de solos (Fig. 4). A partir dessa informação pudemos observar, em casos de relação nula, que existem solos com características muito similares, que apresentam-se agrupados nos gráficos, ou em outros casos, formam um gradiente em escala menor.

Os nossos resultados sugerem que a inclusão de novas áreas de amostragem, que amplie os tipos de solos e condições ambientais encontradas na Bacia Amazônica, é necessária em estudos similares futuros. Além disso, existem outros fatores físicos, como a mineralogia do solo, ou biológicos, como a diversidade e atividade de decompositores, que não foram abordados e que podem ter um efeito complementar na distribuição das frações do SOC. Dessa forma, nossa meta é incorporar novas variáveis nos próximos trabalhos, buscando ampliar a compreensão sobre a dinâmica do carbono nos solos para prever com maior precisão o impacto de possíveis mudanças ambientais.

APÊNDICE I

 PG-ECO-INPA <small>PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA</small>	 INPA <small>INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA</small>	Ministério da Ciência e Tecnologia  <small>UM PAÍS DE TODOS</small>
----------------------------------------------------------------------------------------------------------------------------------------------------------	---------------------------------------------------------------------------------------------------------------------------------------------------------	--------------------------------------------------------------------------------------------------------------------------------------------------------------

AULA DE QUALIFICAÇÃO

PARECER

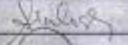
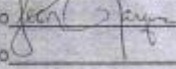
Aluno(a): CLAUDIA PANDOLFO PAZ
 Curso: ECOLOGIA
 Nível: MESTRADO
 Orientador(a): REGINA LUIZÃO
 Co-orientador(a): CARLOS ALBERTO QUESADA

Título:

"Relações das frações de carbono orgânico no solo com a fertilidade do solo, o clima e a vegetação na Amazônia".

BANCA JULGADORA:


TITULARES: Elisa Wandelly (EMBRAPA) Flávia Costa (INPA) Jean Dalmo Marques (INPA)	SUPLENTES: Henrique Nascimento (INPA) João Ferraz (INPA)
---------------------------------------------------------------------------------------------------	-----------------------------------------------------------------------

EXAMINADORES	PARECER	ASSINATURA
Elisa Wandelly (EMBRAPA)	<input checked="" type="checkbox"/> Aprovado () Reprovado	
Flávia Costa (INPA)	<input checked="" type="checkbox"/> Aprovado () Reprovado	
Jean Dalmo Marques (INPA)	<input checked="" type="checkbox"/> Aprovado () Reprovado	
Henrique Nascimento (INPA)	<input type="checkbox"/> Aprovado () Reprovado	
João Ferraz (INPA)	<input type="checkbox"/> Aprovado () Reprovado	

Manaus(AM), 23 de março de 2010

BS: A ALUNA FEZ UMA ÓTIMA APRESENTAÇÃO EM 40 MINUTOS, ESTA BEM PREPARADA PARA DESENVOLVER SUA DISSERTAÇÃO, MAS DEVERIA OBSERVAR AS SUGESTÕES DA BANCA.

PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA TROPICAL E RECURSOS NATURAIS - PPG BTRN
 PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA PPG-ECOINPA
 Av. Efigênio Sales, 2239 - Bairro: Adrienópolis - Caixa Postal: 478 - CEP: 69.011-970, Manaus/AM.
 Fone: (+55) 92 3643-1909 Fax: (+55) 92 3643-1909
 site: <http://pg.inpa.gov.br> e-mail: pgeco@inpa.gov.br

Pbc-24/03/2010


APÊNDICE II



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

Aos 16 dias do mês de setembro do ano de 2011, às 10:00 horas, na sala de aula do Programa de Pós-Graduação em Ecologia – PPG ECO/INPA, reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: o(a) Prof(a). Dr(a). **Adriana Maria Coimbra Horbe**, da Universidade Federal do Amazonas, o(a) Prof(a). Dr(a). **Fernanda Tunes Villani**, do Instituto Federal de Educação, Ciência e Tecnologia do Amazonas e o(a) Prof(a). Dr(a). **Lucerina Trujillo Cabrera**, do Instituto Nacional de Pesquisas da Amazônia, tendo como suplentes o(a) Prof(a). Dr(a). Yoko Françoise Ishida, do Instituto Nacional de Pesquisas da Amazônia e o(a) Prof(a). Dr(a). Renato Cintra, do Instituto Nacional de Pesquisas da Amazônia /LBA, sob a presidência do(a) primeiro(a), a fim de proceder a arguição pública da DISSERTAÇÃO DE MESTRADO de **CLAUDIA PANDOLFO PAZ**, intitulada "Distribuição das frações do carbono orgânico nos solos de florestas maduras na Bacia Amazônica: o papel das propriedades do solo, da qualidade da liteira e do clima", orientado(a) pelo(a) Prof(a). Dr(a). Regina Celi Costa Luizão, do Instituto Nacional de Pesquisas da Amazônia e co-orientado(a) pelo(a) Prof(a). Dr(a). Carlos Alberto Quesada, do Instituto Nacional de Pesquisas da Amazônia.

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

APROVADO(A) REPROVADO(A)
 POR UNANIMIDADE POR MAIORIA

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

Prof(a).Dr(a). Adriana Maria Coimbra Horbe

Prof(a).Dr(a). Fernanda Tunes Villani

Prof(a).Dr(a). Lucerina Trujillo Cabrera






Coordenação PPG-ECO/INPA

APÊNDICE III



Instituto Nacional de Pesquisas da Amazônia - INPA
Programa de Pós-graduação em Ecologia



Avaliação de dissertação de mestrado

Título: **Distribuição das frações do carbono orgânico nos solos da Bacia Amazônica: o papel das propriedades do solo, da qualidade da liteira e do clima**

Aluno: **CLAUDIA PANDOLFO PAZ**

Orientador: **Regina C. C. Luizão**

Co-orientador: **Carlos Alberto Quesada**

Avaliador: Plínio Barbosa de Camargo

Por favor, marque a alternativa que considerar mais apropriada para cada item abaixo, e marque seu parecer final no quadro abaixo

	Muito bom	Bom	Necessita revisão	Reprovado
Relevância do estudo	(x)	()	()	()
Revisão bibliográfica	(x)	()	()	()
Desenho amostral/experimental	(x)	()	()	()
Metodologia	(x)	()	()	()
Resultados	(x)	()	()	()
Discussão e conclusões	(x)	()	()	()
Formatação e estilo texto	(x)	()	()	()
Potencial para publicação em periódico(s) indexado(s)	(x)	()	()	()

PARECER FINAL

- Aprovada** (indica que o avaliador aprova o trabalho sem correções ou com correções mínimas)
- Aprovada com correções** (indica que o avaliador aprova o trabalho com correções extensas, mas que não precisa retornar ao avaliador para reavaliação)
- Necessita revisão** (indica que há necessidade de reformulação do trabalho e que o avaliador quer reavaliar a nova versão antes de emitir uma decisão final)
- Reprovada** (indica que o trabalho não é adequado, nem com modificações substanciais)

Piracicaba,
Local

08 de agosto,
Data

Assinatura

Comentários e sugestões podem ser enviados como uma continuação desta ficha, como arquivo separado ou como anotações no texto impresso ou digital da tese. Por favor, envie a ficha assinada, bem como a cópia anotada da tese e/ou arquivo de comentários por e-mail para pgecologia@gmail.com e claudiakeller23@gmail.com ou por correio ao endereço abaixo. O envio por e-mail é preferível ao envio por correio. Uma cópia digital de sua assinatura será válida.

Endereço para envio de correspondência:

Claudia Keller
DCEC/CPEC/INPA
CP 478
69011-970 Manaus AM
Brazil



Instituto Nacional de Pesquisas da Amazônia - INPA
Programa de Pós-graduação em Ecologia



Avaliação de dissertação de mestrado

Título: Distribuição das frações do carbono orgânico nos solos da Bacia Amazônica: o papel das propriedades do solo, da qualidade da liteira e do clima

Aluno: CLAUDIA PANDOLFO PAZ

Orientador: Regina C. C. Luizão

Co-orientador: Carlos Alberto Quesada

Avaliador: Steel Silva Vasconcelos

Por favor, marque a alternativa que considerar mais apropriada para cada item abaixo, e marque seu parecer final no quadro abaixo

	Muito bom	Bom	Necessita revisão	Reprovado
Relevância do estudo	(x)	()	()	()
Revisão bibliográfica	(x)	()	()	()
Desenho amostral/experimental	(x)	()	()	()
Metodologia	(x)	()	()	()
Resultados	(x)	()	()	()
Discussão e conclusões	()	(x)	()	()
Formatação e estilo texto	()	(x)	()	()
Potencial para publicação em periódico(s) indexado(s)	(x)	()	()	()

PARECER FINAL

(x) **Aprovada** (indica que o avaliador aprova o trabalho sem correções ou com correções mínimas)

() **Aprovada com correções** (indica que o avaliador aprova o trabalho com correções extensas, mas que não precisa retornar ao avaliador para reavaliação)

() **Necessita revisão** (indica que há necessidade de reformulação do trabalho e que o avaliador quer reavaliar a nova versão antes de emitir uma decisão final)

() **Reprovada** (indica que o trabalho não é adequado, nem com modificações substanciais)

Belém
Local

5 de agosto de 2011
Data

Steel Silva Vasconcelos
Assinatura

Comentários e sugestões podem ser enviados como uma continuação desta ficha, como arquivo separado ou como anotações no texto impresso ou digital da tese. Por favor, envie a ficha assinada, bem como a cópia anotada da tese e/ou arquivo de comentários por e-mail para pgecologia@gmail.com e claudiakeller23@gmail.com ou por correio ao endereço abaixo. O envio por e-mail é preferível ao envio por correio. Uma cópia digital de sua assinatura será válida.

Endereço para envio de correspondência:

Claudia Keller
DCEC/CPEC/INPA
CP 478
69011-970 Manaus AM
Brazil



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



Referee evaluation sheet for MSc thesis

Title: **Distribution of soil organic carbon fractions in the Amazon Basin: the role of soil properties, leaf litter quality and climate**

Candidate: **CLAUDIA PANDOLFO PAZ**

Supervisor: **Regina C. C. Luizão**

Co-supervisor: **Carlos Alberto Quesada**

Examiner: **Dr Gustavo Saiz**

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

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

FINAL EVALUATION

() Approved without or minimal changes

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

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

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

_____ Cairns (Australia), _____ 4 August 2011 _____, _____ Gustavo Saiz
Place Date Signature

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

Mailing address:

Claudia Keller
DCEC/CPEC/INPA
CP 478
69011-970 Manaus AM
Brazil