INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

EFEITO DO CLIMA E SOLOS NA PRODUÇÃO DE SERAPILHEIRA EM FLORESTAS DE TERRA FIRME NA AMAZÔNIA CENTRAL

MARIA PIRES MARTINS

MANAUS – AM
Dezembro, 2023

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EFEITO DO CLIMA E SOLOS NA PRODUÇÃO DE SERAPILHEIRA EM FLORESTAS DE TERRA FIRME NA AMAZÔNIA CENTRAL

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Dissertação de mestrado apresentada à Coordenação do Programa de Pós-Graduação em Biologia/Ecologia (PPG-ECO) do Instituto Nacional de Pesquisas da Amazônia (INPA) como parte dos requisitos para obtenção do título de Mestra em Ecologia.

MANAUS – AM
Dezembro, 2023

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INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA

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Aos 29 dias do mês de setembro do ano de 2023, às 09h00min, via videoconferência, reuniu-se a Comissão Examinadora de Defesa Pública composta pelos seguintes membros: o Dr. **Bruce Walker Nelson**, do Instituto Nacional de Pesquisas da Amazônia – INPA, a Drª. **Sabrina Garcia**, do Instituto Nacional de Pesquisas da Amazônia – INPA e o Dr. **Jochen Schöngart**, do Instituto Nacional de Pesquisas da Amazônia – INPA, tendo como suplentes a Drª. Terezinha Monteiro, do Instituto Nacional de Pesquisas da Amazônia – INPA e a Drª Rosimeire Araújo Silva, do Instituto Nacional de Pesquisas da Amazônia – INPA, sob a presidência do orientador, a fim de proceder à arguição pública do trabalho de **DISSERTAÇÃO DE MESTRADO** de **MARIA PIRES MARTINS**, intitulado: **"EFEITO DO CLIMA E SOLOS NA PRODUÇÃO DE SERAPILHEIRA EM FLORESTAS DE TERRA FIRME NA AMAZÔNIA CENTRAL"**, orientada pelo Dr. Carlos Alberto Nobre Quesada e coorientada pela Drª. Izabela Fonseca Aleixo, ambos do Instituto Nacional de Pesquisas da Amazônia – INPA.

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

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☒ POR UNANIMIDADE ☐ POR MAIORIA

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

DR. BRUCE WALKER NELSON ______________________
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Marina Anciães
____
(Coordenação PPG-ECO/INPA)

Catalogação na Publicação (CIP-Brasil)

P667e Martins, Maria Pires

Efeito do Clima e Solos na Produção de Serapilheira em Florestas de Terra Firme na Amazônia Central/ Maria Pires Martins; Orientador Carlos Alberto Nobre Quesada; coorientadora Izabela Fonseca Aleixo. - Manaus: [s. l.], 2023.

2.020 KB
60p.: il. color.
Dissertação (Mestrado - Programa de Pós-Graduação em Ecologia) - Coordenação do Programa de Pós-Graduação, INPA, 2023.

1. Produção de serapilheira. 2. Florestas de terra firme. 3. Amazônia Central I. Quesada, Carlos Alberto Nobre. II. Aleixo, Izabela Fonseca.
III. Efeito do clima e solos na produção de serapilheira em florestas de terra firme na Amazônia central

CDD 577 57 811 3

Sinopse:

Neste trabalho investigamos a influência de variáveis climáticas e características do solo na produtividade de serapilheira em diferentes áreas da Amazônia Central.

Palavras-chave: Produção de serapilheira, Floresta de terra firme, Amazônia central.

Dedico aos meus pais “Francisca e Raimundo” e aos meus avós “Maria (*in memoriam*) & Fernandes, Raimundo (*in memoriam*)” que tanto amei e amo, que me deram o mais profundo amor que uma neta pode receber e aos meus amigos que me deram o ombro para chorar.

AGRADECIMENTOS

Aos meus pais, Raimundo e Francisca pelo amor e pela sabedoria, e virtudes a mim repassados.

Aos meus queridos irmãos, Vaninha, Nair, Ronaldo e Denilson pela força e apoio nesta longa caminhada.

Flávio Luizão (*in memoriam*), que possibilitou a realização de todas as coletas.

Aos meus orientadores Dr. Beto Quesada e Dra Izabela Fonseca Aleixo (Iza), por todo apoio e conhecimento transmitido, dedicação, incentivo, paciência, e amor durante a execução do trabalho.

Ao meu parceiro, meu Amor André que está sempre juntinho me fazendo feliz.

Aos amigos do coração, que me acompanharam e que me acompanham até hoje nos diversos momentos da minha vida pessoal e profissional: Nilma França, Adriana Conceição, Gisele de Castro, Fernanda Lima, Crisvaldo Cássio, Ericarlos Rocha, Rodrigo Nunes, Andreza Santos, Cleucilene Ferreira.

À equipe de Team - Agenor Bentes, Antonio Tavares, Claudio Yano, Luciano Castilho, Valdemir Silva, Átila Oliveira, Eveline Ramos, Sheylla Pinto, Jorge Gallardo, Marlon Tavares, Jonas Paz, Pedro Afonso, Francisco Marques e Sr Juscelino.

Grupo Ciclos Biogeoquímicos: Anna Morais, Amanda Damasceno, Sabrina Garcia, Rebeca Santos, Robson, José Carlos, Alessandra, Bruna, Raffaello Di Ponzio, Nathielly Martins, Jéssica Rosa, Laynara Lugli, Yago Santos, Iokanan Salles, Fernanda Luz, Sheila Trierveiler, Flávia Santana, Alacimar Guedes, Cilene Palheta, Gyovanni Ribeiro, Lara, Felipe, Julia, Julyane.

Á equipe de pesquisadores que direta e indiretamente contribuíram para o meu trabalho, Pedro Pequeno, Bruce Nelson, Terezinha Monteiro, Iêda Amaral, Wilson Spironello.

Meus amores de quatro patas: Harry, Amora, Juízo e Dobby.

Ao Projeto Tropical Ecology Assessment Monitoring Network (TEAM) por disponibilizar recurso e parte dos dados utilizados neste estudo e CI (Conservation International).

À equipe de Logística e Colaboradores do LBA - Rubenildo, Ruth, Natan, Zezinho, Nagybe, Júlio, Thiago, Geraldo, Antônio Huxley, Thomé, Ricardo e Jorge.

Aos Projetos LBA, PDBFF Ao Instituto Nacional de Pesquisas da Amazônia (INPA) e ao Programa de Pós-Graduação em Ecologia (PPG/ECO) pela oportunidade do mestrado e por disponibilizar toda a infraestrutura necessária para a realização deste estudo.

O presente trabalho foi realizado com apoio da Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), processo n.º 132317/2020-6.

Ao Projeto Amazon Face e Fundação Humanize

A equipe me micrometeorologia do Projeto LBA)

Ao Professor Dr. Luiz Candido, DICAM/INPA e equipe, que forneceram os dados de precipitação da Estação Climatológica da Reserva Florestal Adolpho Ducke.

Planeta Amazônia

Quando não se conhece, destrói.
A mata se autoalimenta, sobrevive.
O homem, uma selva se pedra constrói,
Mas nesse ambiente, pouco se vive.

A qualidade de vida na cidade,
Que substitui o ambiente natural,
Acaba com a harmonia da sociedade.
O destruidor, esquece que é animal.

Os rios aéreos desembocam no sudeste,
Por isso deveriam preservar aqui.
Cada árvore que cai, alimenta a peste.
O desequilíbrio, pode vir a destruir.

Nossas raízes se alimentam nas superfícies.
Sem a copa, que gera alimento e proteção,
Alimentará a fome, destruindo espécies.
Só não percebe, que tem ganância no coração!

Não adianta, fingir que não está vendo.
Fenômenos naturais estão se multiplicando.
Os efeitos, do El Niño, estão ocorrendo.
Cada vez mais, o aquecimento está aumentando.

Salvar a Amazônia é preservar o planeta.
Um sistema depende do outro sistema.
A vida passa na velocidade do cometa.
Progresso e sobrevivência, nosso dilema.

Manter a mata de pé é salvar vidas.
Milhões de seres nesse microuniverso.
Trator e motosserra abrem feridas.
Entre os animais, somos o mais perverso!

Miguel Rodrigues de Oliveira Filho
Poeta e escritor.
Membro da ALCAMA (Academia de Letras, Ciências e Culturas da Amazônia).

RESUMO

As florestas tropicais possuem cerca de um terço da produtividade primária líquida (PPL) global, das quais aproximadamente 34% (4.8 ± 0.3 Mg C ha $^{-1}$ yr^{-1}) são quantificadas através da biomassa de serapilheira. A serapilheira constitui a camada de matéria orgânica depositada sob a superfície o solo, e representa a principal via de transferência de nutrientes da vegetação para o solo, através da ciclagem de matéria orgânica. Esse processo de deposição e ciclagem são essenciais para manter a fertilidade dos solos altamente intemperizados da Amazônia central, garantindo a manutenção de importantes serviços ecossistêmicos prestados pela floresta. A influência do clima e das características do solo e da vegetação tem forte efeito sobre os padrões de deposição e serapilheira. Eventos climáticos extremos cada vez mais frequentes também afeta os padrões de deposição da serapilheira, alterando, assim, os processos de ciclagem de nutrientes. Para compreender como o clima e as características do solo afetam a produtividade de serapilheira em diferentes áreas, este trabalho teve como objetivo determinar a produção de serapilheira total e por componentes (folhas, materiais lenhosos, flores, frutos e resíduos) ao longo do tempo, relacionando-os às variáveis climáticas locais (precipitação, temperatura máxima, radiação, déficit hídrico cumulativo – CWD e velocidade do vento), índices globais (El Niño Oscilação Sul - ENSO e Índice do Atlântico Tropical - NTA) e fertilidade do solo (Cátions Trocáveis e Concentração de fósforo - P). Investigamos os padrões espaciais e temporais utilizando uma longa série de até 10 anos de produção de serapilheira, coletada quinzenalmente em 150 armadilhas de 0.25m² em 6 parcelas localizados em 3 diferentes áreas de florestas de terra firme na Amazônia central. A produção anual média de serapilheira foi de 7.2 ± 0.8 Mg ha^{-1}ano^{-1}. A produção segue um padrão sazonal, com picos de maior produtividade nos meses mais secos do ano (0.8 ± 0.1 Mg ha^{-1} mês^{-1} entre os meses de junho a outubro), enquanto a produção nos meses mais chuvosos foi praticamente a metade (em média 0.4 ± 0.1 Mg ha^{-1}mês^{-1} novembro a maio). A maior parte da serapilheira foi constituída por folhas (74%), seguido de madeira fina (15%) e flores (3%), frutos (4%) e resíduos (3%). A temperatura máxima, radiação, MCWD, precipitação e velocidade média do vento foram os fatores climáticos que mais influenciaram a produção total de serapilheira. Dentre as variáveis globais, o El Niño 3.4 e NTA, influenciaram na produção total. Nessa escala espacial, a concentração de P também influenciou na produção total de serapilheira, no entanto, houve maior produção de flores em áreas com menor concentração de P. Esses resultados evidenciam os efeitos do clima e do solo para a produtividade da serapilheira, servindo como base para melhoria dos modelos de vegetação e entendimento do efeito das mudanças climáticas para a produtividade da floresta Amazônica.

ABSTRACT

Tropical forests account for about one-third of global net primary productivity (NPP), of which approximately 34% (4.8 ± 0.3 Mg C ha−1 yr−1) is quantified through litter biomass. Litter consists of the layer of organic matter deposited beneath the soil surface and represents the main pathway for nutrient transfer from vegetation to soil through organic matter cycling. This deposition and cycling process is crucial for maintaining the fertility of highly weathered soils in central Amazonia, ensuring the preservation of vital ecosystem services provided by the forest. The influence of climate, soil and vegetation characteristics strongly affects litter deposition and cycling patterns. Increasingly frequent extreme weather events also impact litter deposition patterns, thereby altering nutrient cycling processes. To understand how climate and soil characteristics affect litter productivity in different areas, this study aimed to determine total litter production and its components (leaves, woody materials, flowers, fruits, and residues) over time, relating them to local climatic variables (precipitation, maximum temperature, radiation, cumulative water deficit – CWD, and wind speed), global indices (El Niño Southern Oscillation - ENSO and Tropical Atlantic Index - NTA), and soil fertility (Exchangeable Cations and Phosphorus Concentration - P). We investigated spatial and temporal patterns using a long series of up to 10 years of litter production, collected biweekly in 150 traps of 0.25 m^2 in 6 plots located in 3 different upland forest areas in central Amazonia. The average annual litter production was 7.2 ± 0.8 Mg ha-1yr-1. Production followed a seasonal pattern, with peaks in productivity during the drier months (0.8 ± 0.1 Mg ha-1 month-1 from June to October), while production in the wetter months was nearly half (on average 0.4 ± 0.1 Mg ha-1 month-1 from November to May). Most of the litter consisted of leaves (74%), followed by fine wood (15%), flowers (3%), fruits (4%), and residues (3%). Maximum temperature, radiation, MCWD, precipitation, and average wind speed were the climatic factors that most influenced total litter production. Among global variables, El Niño 3.4 and NTA influenced total production. At this spatial scale, P concentration also influenced total litter production; however, there was higher flower production in areas with lower P concentration. These results highlight the effects of climate and soil on litter productivity, serving as a basis for improving vegetation models and understanding the impact of climate change on Amazonian forest productivity.

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B1	*Km 14* – EEST
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C1	*Base* – RFAD
C2	*Ypiranga* – RFAD
CWD	Cumulative Water Deficit
EEST	Estação experimental de Silvicultura Tropical (Experimental Station for Tropical Silviculture)
ENSO	El Niño-Southern Oscillation
GLS	Generalized Least Squares
INPA	Instituto Nacional de Pesquisas da Amazônia
IOS	Southern Oscillation Index
IUSS	International Union of Soil Science
LTSP	Thematic Laboratory of Soils and Plants
MCWD	Maximum Cumulative Water Deficit
NAO	North Atlantic Oscillation
NPP	Net Primary Productivity
NTA	North Tropical Atlantic
ONI	Oceanic Niño Index
P	Phosphorus
PDBFF	Projeto Dinâmica Biológica de Fragmentos Florestais (Biological Dynamics of Forest Fragments)
RFAD	Reserva Florestal Adolpho Ducke (Adolpho Ducke Forest Reserve)
SI	Supplementary Information
SST	Sea Surface Temperature
SVP	Saturation Vapor Pressure
TEAM	Tropical Ecology, Assessment and Monitoring Network
USDA	United States Department of Agriculture
VPD	Vapor Pressure Deficit
WRB	World Reference Base soil classification

INTRODUÇÃO GERAL

A produção de serapilheira representa uma parte importante da produção primária líquida (PPL) das florestas (Aragão *et al.*, 2009; Malhi; Doughty; Galbraith, 2011; Nakagawa *et al.*, 2019; Zhu *et al.*, 2021) e é essencial para a manutenção de processos ecossistêmicos como a ciclagem de nutrientes (Li e Ye, 2014). A ciclagem se dá através da decomposição da matéria orgânica e liberação de nutrientes que serão absorvidos pelas plantas, ajudando, assim, a manter os estoques de carbono na floresta. Além disso, a serapilheira tem importante papel na manutenção dos ecossistemas terrestres, por atuar como uma camada de proteção dos solos, diminuindo a erosão, regulando a temperatura, umidade e o fluxo de energia (Chakravarty *et al.*, 2020; Li e Ye, 2014).

A serapilheira consiste em todo material orgânico produzido e depositado no solo da floresta. Ela pode ter origem vegetal como folhas, material lenhoso e reprodutivo (flores, frutos e sementes) ou origem animal como insetos, fezes e penas (Luizão, 1989; Malhi, Doughty e Galbraith, 2011; Martinelli, Lins e Dos Santos-Silva, 2017; Vitousek, 1984). Pode ser dividida em serapilheira fina com galhos/gravetos < 2 cm e grossa com galhos/gravetos > que 2 cm. Este material orgânico é constantemente depositado na floresta ao longo do tempo, e existe uma variação entre a quantidade e qualidade de cada material depositado, causando uma diferença na proporção entre eles em diferentes meses ou anos. Dentre os componentes, as folhas contribuem aproximadamente com 75% do total da produção de serapilheira na Amazônia, já a produção de material lenhoso é em torno de 15% do total, enquanto 9%, é composta por material reprodutivo (Chave *et al.*, 2009; Vasconcelos e Luizão, 2004).

Aproximadamente 50% de toda a serapilheira produzida no planeta são provenientes de florestas tropicais (Shen *et al.*, 2019). A produtividade nesses ecossistemas pode variar consideravelmente. Em Bórneu, Ásia, a produção é de aproximadamente 7.0 Mg ha^{-1} yr^{-1} (Nakagawa *et al.*, 2019), enquanto em Camarões, África, é cerca de 7.3 Mg ha^{-1} yr^{-1} (Peh *et al.*, 2012). Já em florestas tropicais antigas da América do Sul, a produção média é de 8.6 Mg ha^{-1} yr^{-1}, (Chave *et al.*, 2010). Na China a produção pode variar entre 9.2 a 14.8 Mg ha^{-1} yr $^{-1}$ (Zhu *et al.*, 2019). Em florestas de platô na Amazônia, a produção de serapilheira pode variar entre 5.2 Mg ha^{-1} yr^{-1} em Gran Sabana, Guayana, Venezuela, (Chave *et al.*, 2009, Vitousek, 1984), a 12.8 Mg ha^{-1} ano $^{-1}$ em Manaus, Amazonas (Moraes, dados não publicados). Essa variação na produtividade em diferentes regiões pode ser determinada por diferentes fatores ambientais, climáticos e das características da vegetação, por exemplo. Entretanto, esperamos que em áreas mais próximas que compartilham características e condições semelhantes, haja uma maior similaridade na produção de serapilheira.

Características do solo como P disponível e cátions trocáveis estão correlacionados à produtividade florestal ao longo da bacia amazônica (Quesada *et al.*, 2012). Em solos mais férteis com maior disponibilidade de P, o investimento em componentes de órgãos reprodutivos (flores, frutos e sementes) pode ser maior (Gentry e Emmons, 1987), enquanto, em regiões de solos mais intemperizados com baixa disponibilidade de P é priorizada a alocação em órgãos fotossintéticos (produção de folhas) (Chave *et al.*, 2010; Wood *et al.*, 2009). Cunha e colaboradores (2022) demonstraram, por meio de um experimento de fertilização na Amazônia Central, que o baixo teor de fósforo no solo limita a produtividade da floresta, incluindo a produção de serapilheira e raízes finas. Observa-se, ainda, que características funcionais das espécies, como o hábito fenológico foliar, apresentam influência sobre a produtividade, como por exemplo a diminuição na deciduidade (estratégia fenológica de perda total ou parcial das folhas em um determinado período do ano), que resulta em menor produção de serapilheira (Ouedraogo *et al.*, 2016).

Ao longo da bacia Amazônica há uma grande diversidade de solos, os mais jovens e férteis possuem maior concentração de P e são encontrados na região oeste da Amazônia, perto da Cordilheira dos Andes (Quesada *et al.*, 2010). Já os solos da Amazônia Central, são mais antigos, intemperizados e passaram por maior perda de nutrientes por lixiviação ao longo do tempo, apresentando menores concentrações de P e cátions trocáveis (Quesada *et al.*, 2009). Florestas que se desenvolvem sob solo com baixa fertilidade conseguem manter uma produtividade alta (Laurance *et al.*, 2010), devido a diversos mecanismos desenvolvidos pelas plantas, como a retranslocação de nutrientes antes da abscisão das folhas (Pires *et al.*, 2022) e reciclagem da matéria orgânica, promovida pela produção e decomposição da serapilheira (Vitousek e Sanford, 1986). A PPL total de uma floresta tende a aumentar com o fósforo do solo e o status do nitrogênio da folha (Aragão *et al.*,2009). Aragão e colaboradores (2009), sugerem ainda, que o tipo de solo não é um determinante principal dos padrões de produção de serapilheira na Amazônia, no entanto, solos de areia branca com baixa fertilidade têm produção de serapilheira significativamente menor do que outros tipos de solo e parecem priorizar a alocação de carbono para os órgãos fotossintéticos em vez da reprodução.

A produção de serapilheira também pode ser influenciada por diversos fatores climáticos. Globalmente, a produção de serapilheira é positivamente correlacionada com a evapotranspiração real (r^2 = 0.41), seguida pela média anual da temperatura (r^2 = 0.37) e precipitação anual ($r^2 = 0.22$) (Shen *et al.*, 2019). Na Amazônia há um aumento na produção nos meses mais secos, influenciado principalmente pela maior troca de folhas que acontece no período de menor precipitação (Chave *et al.*, 2010; Restrepo-Coupe *et al.*, 2013; Wu *et al.*, 2016). Entretanto, apesar de haver um claro padrão sazonal na produtividade da serapilheira, a variação anual dessa produção parece não ser impulsionada pela precipitação anual ou tipo de solo (Chave *et al.*, 2010).

Além das mudanças sazonais ao longo do ano, a produtividade da serapilheira também varia entre anos, podendo aumentar em anos atípicos de maior troca foliar na copa, como aconteceu na seca de 2015/2016 causada pelo ENSO (Gonçalves *et al.*, 2020). Dentre os principais eventos climáticos globais que podem afetar o transporte de umidade para a região amazônica e consequentemente afetar a produtividade da serapilheira, temos o El Niño-Oscilação Sul – ENSO (El Niño, o aquecimento e La Niña, o resfriamento da temperatura da superfície do mar em regiões específicas do Pacífico equatorial). Esse fenômeno é caracterizado pela alteração da temperatura da superfície do mar (TSM) que junto com outros fatores altera o transporte de umidade para diversas regiões do globo, e pode ser determinado por meio do Índice de Oscilação do Sul (IOS), que mede as diferenças de pressão entre duas regiões diferentes do oceano pacífico equatorial (Tahiti e Darwin) (Ropelewski e Jones, 1987).

Os índices que representam alterações no transporte de umidade do Atlântico estão relacionados com variações na temperatura da superfície do mar no Atlântico Tropical Norte - ATN, e com a Oscilação do Atlântico Norte – NAO (representado pela diferença da pressão atmosférica ao nível do mar no Atlântico Norte), causando mudanças no clima em diversas regiões. Na Amazônia, há indícios de que eventos climáticos extremos influenciados por essas oscilações possam induzir variações na produção de serapilheira (Conceição, 2017; Vitousek e Sanford, 1986), porém, existem poucos monitoramentos de longo prazo capazes de captar essas variações sazonais e interanuais, e, desta forma, restam incertezas cruciais sobre como a produtividade da serapilheira está sendo afetada pelas oscilações globais, limitando, por conseguinte, nosso entendimento dos possíveis impactos de mudanças climáticas sobre este importante componente da PPL.

Considerando o relevante papel da produção de serapilheira para a manutenção de processos ecológicos florestais, e sua relação com fatores edafoclimáticos, avaliamos o efeito de variáveis climáticas e da fertilidade do solo na produtividade da serapilheira ao longo de mais de uma década, em três diferentes áreas de floresta madura na Amazônia central. O presente estudo teve como objetivo compreender os efeitos dos eventos climáticos (locais e globais) e da fertilidade do solo na dinâmica da produção de serapilheira (folhas, material lenhoso, reprodutivo e resíduos) ao longo do tempo em diferentes áreas de floresta madura na Amazônia central.

OBJETIVO GERAL

O objetivo deste estudo é investigar o efeito das variáveis climáticas locais, eventos climáticos globais e características do solo sobre a produtividade de serapilheira em diferentes áreas de terra firme na Amazônia central, entre os anos de 2004 e 2014**.**

Objetivos Específicos

- Quantificar e comparar a produtividade de serapilheira em diferentes áreas da Amazônia central;
- Analisar os padrões anuais e sazonais da produtividade da serapilheira;
- Analisar como a produtividade total de serapilheira é distribuída nos diferentes componentes (folhas, material lenhoso, flores, frutos e resíduos);
- Analisar como as variáveis climáticas locais (precipitação, temperatura, umidade, radiação, velocidade do vento e déficit hídrico) e eventos climáticos globais (ENSO e variações do Atlântico) afetam a produtividade de serapilheira ao longo do tempo;
- Analisar como as características do solo (cátions trocáveis, P disponível) podem afetar a produtividade de serapilheira.

Manuscript type: Research Article

Title: Climate and soil effects on litterfall production in Central Amazon Rainforest

Introduction

Litterfall is a layer of organic material deposited and accumulated over time on the top of the forest soil. This organic layer acts as a surface protector of soils, preventing erosion, and regulating the temperature, moisture, and energy flow of forest soils (Chakravarty *et al.*, 2020; Li and Ye, 2014). It plays an essential role in maintaining ecosystem ecological processes through nutrient and carbon cycling, which is the dynamic exchange between soil and vegetation. As litterfall represents a major flux of carbon and nutrients from vegetation to soil, changes in litterfall inputs are likely to have wide-reaching consequences for soil carbon and nutrient dynamics, affecting forest productivity.

The litterfall represents an important part of net primary productivity (NPP), corresponding to about 30% of total production in tropical ecosystems (Aragão *et al.*, 2009; Malhi; Doughty; Galbraith, 2011). Across old-growth tropical rainforests, litterfall production averages 8.6±1.91 Mg ha^{-1}yr^{-1} and is composed of leaves (75%), woody material (15%), and reproductive material (15%) (Chave *et al.*, 2009; Vasconcelos and Luizão, 2004). Both total and litterfall fraction productivity varies in different ecosystems according to climatic (Shen *et al.*, 2019), environmental (Luizão and Schubart, 1987; Souza *et al.*, 2019), and vegetation characteristics (Shen *et al.*, 2019, Souza et al., 2019, Vasconcelos and Luizão, 2004), and varies in the same area over the time, seasonally and between years (Edwards *et al.*, 2018; Zhang *et al.*, 2014).

Globally, the variability of litterfall production was mostly explained by evapotranspiration, increasing when the evapotranspiration is higher in a linear relationship (Shen *et al.*, 2019). In tropical forests, annual litterfall did not significantly vary with total annual rainfall and with soil type (Chave *et al.*, 2009), however, seasonally there is an increase in productivity in the driest months of the year, influenced mainly by the phenological pattern of leaf exchange that occurs in dry months (Chave *et al.*, 2010, Lopes *et al.*, 2016, Restrepo-Coupe *et al.*, 2013, Wu *et al.*, 2016,).

Extreme weather events such as the El Niño-Southern Oscillation – ENSO (El Niño, the warming and La Niña, the cooling of sea surface temperature in the Pacific Ocean) and the Atlantic Ocean anomalies can affect the transport of moisture to the Amazon region, changing the local climate and consequently altering forest dynamics of litterfall productivity (Andrés *et al.*, 2019; Conceição, 2017; Edwards *et al*., 2018; Gonçalves *et al*., 2020; Stenseth *et al.*, 2003; Vitousek and Sanford, 1986, Wright and Calderon, 2006). These events can be determined using indices such as the sea surface temperature (SST) at Niño3.4 region, Oceanic Niño Index (ONI) or Southern Oscillation Index (IOS), which measures pressure differences between two different regions of the Pacific Ocean (Tahiti and Darwin) and indicates ENSO years (Ropelewski and Jones, 1987). For the Atlantic Ocean, SST anomalies in the North Tropical Atlantic (NTA) and the North Atlantic Oscillation (NAO) can express extreme global weather events. Understanding how the global climate variables affect the productivity of this critical component of the NPP is essential to predict the possible effects of climate change in the Amazon. However, there are few long-term monitoring capable of capturing these temporal variations consistently.

Productivity in terrestrial ecosystems is directly related to nutrient cycling and soil fertility (Aragão *et al.*, 2009, Quesada *et al.*, 2012, Wood *et al.*, 2009,). Litterfall is highest in forests growing on fertile soils (Chave et al., 2010), however, herbivory rates are also higher under these conditions (Gentry and Emmons, 1987). The soils of the Amazon are known for their great diversity, with physicochemical variations, according to the paedogenic processes suffered by their source material and time (Quesada *et al*., 2011; Santos *et al.*, 2022,). The youngest and most fertile soils with the highest concentration of P are found in the western region of the Amazon, close to the Andes (Quesada *et al*., 2011). The soils of Central Amazonia, on the other hand, are older and weathered because of nutrient loss by leaching over time, therefore, showing lower concentrations of rock-derived nutrients such as P (Quesada *et al*., 2009). In these highly weathered soils where there is low availability of nutrients, it is through litterfall decomposition that nutrients are transferred to the soil, a fundamental process for the maintenance of tropical forest ecosystems (Silva *et al.,* 2018; Martiuns *et al.,* 2004,). Cunha *et al*., (2022), in a fertilization experiment, showed that litterfall production increases in response to the addition of P to the soil, showing that this nutrient is a limiting resource for productivity in the region. Santos *et al.,* (2022) showed a temporal variation in different fractions of P across the gradients and throughout the months. Additionally, Santos *et al.,* (2022) observed that litterfall production and the corresponding input of P into the litterfall seemed to influence the peaks in individual soil P fractions. However, the mechanism by which this occurs requires further investigation, and there are gaps in understanding the mechanisms by which phosphorus influences litter production.

Studies investigating litter production generally focus only on local climate variables, with few studies examining the combined influence of local climate, global climate events, and soil characteristics. This limitation may be due to the complexity associated with collecting and analysing these variables along a long time series. To improve our understanding of the effects of local climate, global climate events and soil characteristics on litterfall productivity, here we analyse an extensive database collected periodically between 2004 and 2014 in different upland areas in central Amazonia. We evaluated the annual and monthly litterfall productivity in different areas and between the leaf, fine woody, reproductive material, and unidentified material (others) compartments, as well as the relationship with local and global climatic variables, and soil characteristics.

This project explored patterns of litterfall productivity over time in different areas of central Amazonia to understand (i) what is the distribution of litterfall production over months and different years? (ii) what is the amount of biomass produced in each litter fraction (leaves, fine wood, flower, fruit, or others)? (iii) what are the effects of climate (precipitation, temperature, radiation, drought, speed wind and global ENSO and ATN indices) on the amount of litterfall produced and its components? (iv) how does soil fertility affect litter productivity in different areas?

MATERIALS AND METHODS

Study areas

The database used in this study was collected at two different study sites at each of the three Reserves of the Instituto Nacional de Pesquisas da Amazônia – INPA, near the city of Manaus: Adolpho Ducke Forest Reserve (RFAD), Experimental Station for Tropical Silviculture – (EEST), and Project Biological Dynamics of Forest Fragments - PDBFF. The three reserves are in lowland tropical forests, in the central Amazon. The vegetation is a typical tropical humid forest of plateau *terra-firme* (De Oliveira and Mori, 1999), forests with predominantly clayey soils, formed by ancient sediments. The *terra-firme* forests are non-flooded forests, which represent about 65% of the area of the Amazon Basin (Silva *et al.*, 2016). These continuous old-growth evergreen forests have a high-species diversity of tree, shrub, palms, lianas, and herb species, generally distributed in three very distinct vertical strata (understory, sub-canopy, and canopy), where canopy trees can reach up to 35 meters and some emergent trees that can reach 45 meters in height (Nascimento *et al*., 2005; Pereira *et al*., 2019).

The areas have Ferralsols type soils (World Reference Base soil classification – WRB/ Soil Classification) also known as Oxisols (United States Department of Agriculture - USDA Soil Taxonomy), the soils are deep (≥400 cm), with good particle aggregation, friable and with low subsoil bulk density (0.8 – 1.2 g cm^{-3}) (Martins *et al.*, 2015), typically acidic (pH ~ 4.4) and with very low concentrations of nutrients such as Phosphorus (P), calcium (Ca) and potassium K (Quesada *et al.*, 2010, 2011).

The climate of the region is "Am" tropical according to Köppen–Geiger classification, (Peel, Finlayson e McMahon, 2007) with a dry season and a rainy season governed by monsoons. The average annual precipitation varies between 2300 and 3000 mm (Correia *et al.*, 2004) and the average temperature is 26ºC (Andrade Filho *et al.*, 2013) (SI. Table 3). The drier months occur from June to November, with a monthly rainfall of 136 ± 64 mm and a temperature of 26.3 ± 1.3 ºC, while the wetter months, from December to May, had mean monthly rainfall of 288 ± 99 mm and an average temperature of 24.9 ± 1.1 ºC (SI. Figure 9). (Aleixo *et al.*, 2019). Two to three months per year (between July and September) may experience a water deficit, in which evapotranspiration exceeds monthly rainfall (that is, are less than 100 mm $month^{-1}$).

The PDBFF is located 80 km north of Manaus (Figure 1) on the BR-174 road (lat. 02° 25' 50.42" S; long. 59° 48' 2.40" W). The reserve has ~1000 km^2 (Laurance *et al.*, 2018). The two study areas were installed in mature forests without fragmentation, located at *km37*, named **A1**, and at *Cabo Frio*, named **A2**. The EEST Reserve is located 60 km north of Manaus (Figure 1) on the BR-174 road (lat. 2° 36' 32.67 S; long. 60° 12' 33.48 W). The reserve has 22,735 ha and the two sites studied are located at *km 14*, named **B1**, and at *km 34*, named **B2** (Higuchi *et al.*, 2004; Marques Filho, Dallarosa and Pachêco, 2005). The RFAD reserve is located 26 km north of Manaus, Brazil (Figure 1) on AM-010 road (lat. 2° 57' 51, 69" S, long. 59° 56' 27, 26" W). RFAD has 10,000 ha and the two studied sites are named **C1** (near the *Base*), and **C2** (near *Ypiranga*). All monitored plots were installed exclusively in plateau areas, located in the higher and flatter areas where the soil is well drained.

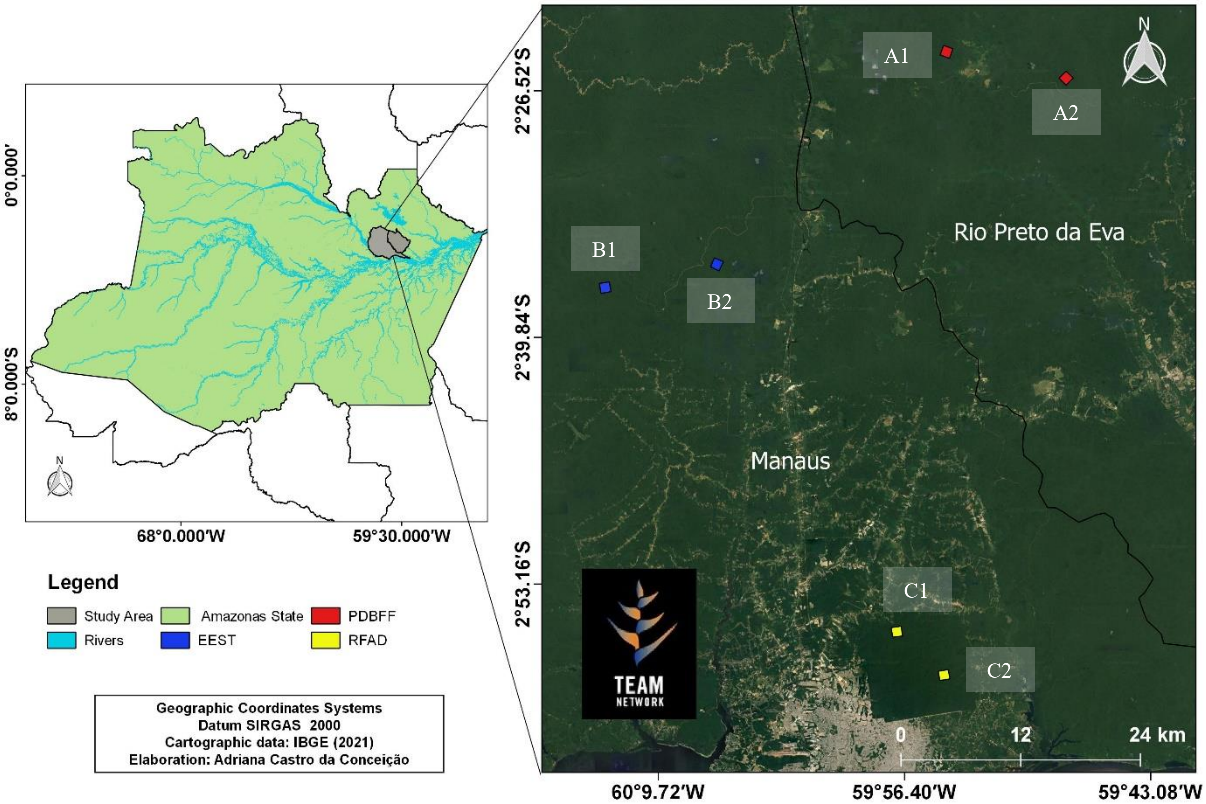

Figure 1. Location map of study areas monitored by the Team project, in Central Amazon. On the left, we have the Map of the state of Amazonas, and in gray colour the location of the study area. All study areas are located in plateau of terra-firme forests. On the right side the location of each plot, with the Adolpho Ducke Forest Reserve (RFAD) in yellow, the Tropical Forestry Experimental Station (EEST) in blue, and the Biological Dynamics of Forest Fragments Project (PDBFF) in red. All reserves belong to the National Institute for Amazonian Research – INPA.

Litterfall data

Litter production was quantified over time by the “Tropical Ecology, Assessment and Monitoring Network” – TEAM Project. Monitoring was carried out with litter traps installed in the two plots in each of the three monitored areas, totalling 150 traps in 6 plots. In each plot, 25 litter traps measuring 50 x 50 cm (area of 0.25 m^2) were installed, suspended 1 m above the ground and distributed every 20 meters in the centre of the 1 ha plot (Figure 2). Every year the litter traps were levelled and replaced whenever there was any deformity.

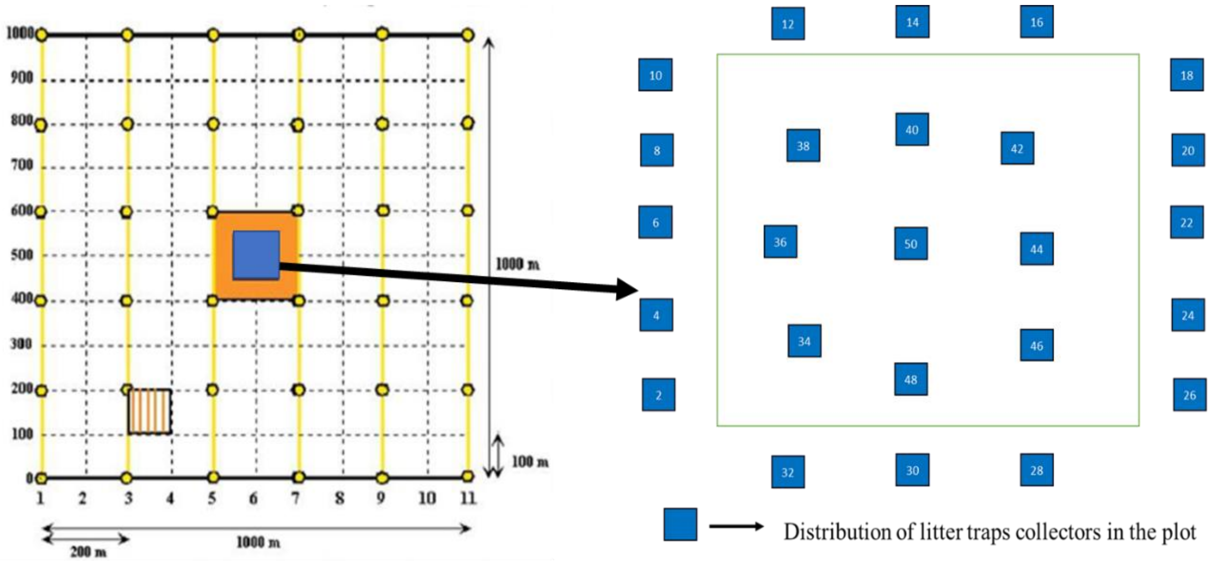

Figure 2. Monitoring grid of 100 ha of the TEAM project, highlighting in blue on the left the location of the central plot of 1 ha, and on the right the distribution of the litter traps of this study (Scheme Source: Vegetation/Litter Protocol of the TEAM Project).

Litterfall was collected every fifteen days from May 2004 to August 2009 in all six plots, totalling 137 collections in each area (totalling 822 samples). The collections became monthly in September 2009 for all sites and ended in May 2011 in PDBFF area in both A1 and A2 plots, and in EEST area B1 plot (totalling 157 samples per plot); ended in May 2014 in EEST area B2 site (194 samples); and September 2012 in RFAD area in both C1 and C2 sites (174 samples per area) (SI. Table 5). Litterfall biomass was quantified periodically from the total amount accumulated in the 25 litter traps of each plot. Between 2004 and 2009, after being retried from the traps, the litterfall was dried in the open air and separated into main fractions: leaf, fine woody (twigs and bark < 2 cm), flower, fruit (seed and fruit) and others (unidentified material). After that, all samples were taken to an oven at 65 ºC for 72 hours, weighed and stored in paper bags. After September 2009, all material retrieved from the traps was dried in the open air and subsequently dried in the laboratory oven at 65 ºC for 72 hours, weighed and stored in paper bags (but not separated in litterfall fractions).

Soil characteristics

Soil phosphorus concentrations and the sum of bases data used in this study were collected and published by the Rainfor project (Quesada *et al.*, 2010). The soil of each study area was classified using the nomenclature of the World Reference Base for Soil Resources ("International Union of Soil Science – IUSS Working Group WRB, 2006) (SI. Table 4). The methods are briefly summarized here, for more details, see (Quesada *et al.*, 2010).

Soil samples were collected at five different profiles using an undisturbed soil sampler (Eijkelkamp Agrisearch Equipment BV, Giesbeek, Netherlands). Sampling depths were 0-5, 5-10, 10-20, 20-30, 30-50, 50-100, 100-150, and 150-200 cm. After collection, all samples were immediately dried in the open air and later taken to the laboratory. In the laboratory, the roots, rocks, and other particles present were separated, then they were sieved using 2 mm sieves and stored for analysis. The analyses were performed at Inpa Thematic Laboratory for Soils and Plants (LTSP) and at the University of Leeds, School of Geography, UK), both laboratories underwent intercalibration exercises using the standard method of determination for soils. Each plot usually had a soil pit dug to a depth of 2.0 m with samples taken from the walls. All samples were analysed individually. In this study, the analysis of available phosphorus concentrations and the sum of the bases was made only in the top soil layer (0-30 cm deep). All sampling was done following a standard protocol (see http://www.geog.leeds.ac.uk/projects/rainfor/pages/manualstodownload.html) to account for spatial variability within the plot.

Local climate data

Climatic variables between the years 2004 to 2014 were obtained in RFAD and EEST climatological stations. Data were managed and provided by the Large-Scale Biosphere-Atmosphere Program, LBA (http://lba2.inpa.gov.br/) and from the climatological station of the Adolpho Ducke Forest Reserve, provided by Dr. Luiz Candido DICAM/INPA. Precipitation (mm) and humidity (%) were collected in a weather station at RFAD site and radiation (W m^{-2}), temperature (°C) and maximum wind speed (m s^{-1}) were obtained in k34 tower at EEST site (SI. Figure 9). Precipitation was calculated monthly by the accumulation of daily rainfall (mm month^{-1}). For humidity and radiation, we used monthly averages from daily measurements. For temperature and wind speed data, we used the maximum values for each month.

To measure the duration and intensity of a drought, we also calculated the monthly cumulative water deficit (CWD) (Aragão *et al.*, 2007). The CWD is an index that assumes negative values when precipitation is lower than the monthly evaporative demand, that is, 100 mm (Malhi *et al.*, 2009; Santos *et al.*, 2018). CWD start with the difference between the recorded precipitation and 100 mm of assumed standard evaporative demand. When precipitation is consecutively less than 100 mm, the CWD becomes increasingly negative, indicating a more severe drought. When monthly precipitation is greater than the monthly evaporative demand (100 mm), the index returns to zero.

The Vapor Pressure Deficit (VPD) indicate how much more capacity there is for humidity (water vapor) in the air, at the current temperature, and was calculated using local temperature and humidity. The conditions represented by VPD variable affect plant transpiration rates, stomata opening, CO_2 and nutrient uptake, and also plant stress, which is important for leaf shedding, affecting the litterfall production over time. This metric was calculated by the following formula (https://pulsegrow.com/blogs/learn/vpd#calculate):

$$SVP = 610.78 \text{ x } e\text{^}(T / (T + 237.3) \text{ x } 17.2694)$$

$$VPD = SVP \text{ x } (1 - RH/100)$$

SVP is saturation vapor pressure in pascals (divided by 1000 to get kPa)
T is the temperature in degrees Celsius
RH in relative humidity in %
e is a mathematical constant called Euler's Number, approximately equal to 2.71828.

Global climate data

To characterize climatic anomalies related to variations in the pattern of the relationship between the atmosphere and the Pacific and Atlantic Oceans, monthly climatic indices of sea surface temperature (SST) and pressure difference at sea level were used. In the Pacific Ocean, we selected three variables to characterize these ENSO events, SST from 5S-5N and 170-120W "ENSO 3.4" – Niño 3.4 Index (http://www.esrl.noaa.gov/psd/gcos_wgsp/Timeseries/Nino34/), "Oceanic Niño Index – ONI (https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php), and sea level press anomaly in tahiti-darwin "Southern Oscillation Index" – IOS (https://www.cpc.ncep.noaa.gov/data/indices/soi). For Central Amazonia, high ENSO or ONI values indicate dry El Niño years and low values indicate wet La Niña years, ONI is based on a threshold of +/- 0.5 ºC 3-month running mean of SST anomalies, based on centered 30-year base periods updated every 5 years (Grimm, Barros e Doyle, 2000). For Atlantic anomalies, we used the SST anomalies averaged over 60W to 20W, 6N to 18N and 20W to 10W, 6N to 10N "North Tropical Atlantic SST Index" – NTA (https://psl.noaa.gov/data/correlation/NTA_ersst.data), and "North Atlantic Oscillation" – NAO (https://www.cpc.ncep.noaa.gov/data/teledoc/nao.shtml), divided into two phases, the positive phase, and the negative phase (NOAA, 2021) The NAO is based on the difference in atmospheric pressure at sea level between the high subtropical (Azores) and the low subpolar, which, in contrast to ENSO, mainly influences the duration and intensity of the dry season in Amazonia.. All available through the NOAA website (https://psl.noaa.gov/data/climateindices/list/).

Data analysis

For each plot in each area, litterfall productivity data were organized on a daily basis, by dividing the accumulated productivity in all 25 litter traps by the time interval between two consecutive surveys (in days). The monthly productivity was then calculated by the sum of the daily production, expressed in Mg ha^{-1} of dry weight. Annual production was obtained by the cumulative of consecutive twelve months, in Mg ha^{-1}, starting in May 2004. As we have five years of material separated into fractions and five years of non-sifted material (SI. Table 5), for the litterfall fraction analysis we use five-year data and for total production data, we use ten years (whole survey time). In the same way, we calculated the daily, monthly, and annual production by litterfall fraction of leaves, fine wood, flowers, fruits, and others.

To access the annual productivity pattern, we calculated the annual total litterfall production using ten years of survey data and five years for each fraction. We conducted ANOVA to assess the differences in productivity between plots for total production and fraction production (Figure 3). To determine where the differences occurred, we performed Tukey's post hoc comparisons ($p < 0.05$) (Souza et al., 2019). When the data did not meet the assumptions required for ANOVA, we used the non-parametric Kruskal-Wallis test ($p < 0.05$), the only case was for fine wood fraction production.

To understand how climate and soil characteristics affect litterfall productivity over time, we use a Generalized Least Squares (GLS) model to account for temporal autocorrelation in residuals, including the "plot" as fixed effects in the model. The temporal autocorrelation of residuals was evaluated through the temporal distance between the observations, using the "acf" function of the "ncf" package. To control the temporal autocorrelation, a numerical variable for time was included, indicating the order of observations and later a moving average temporal autocorrelation structure with two parameters (*p* and *q*) was included in the model (Zuur et al. 2009), with the function "corARMA".

Monthly total litterfall production and monthly production of each compartment (leaves, fine wood, flowers, fruits, and others) were log-transformed to obtain normality and homoscedasticity (Souza *et al*., 2019), scaled to zero mean and unit variance, and used as response variables in separate analyses. All independent covariates, such as local precipitation (mm), maximum temperature (°C), mean humidity (%), cumulative water deficit (CWD), vapor pressure deficit (VPD), maximum wind speed (m s^{-1}), mean radiation (W m^{-2}), Sea Surface Temperature (SST) in Niño3.4 region, oceanic Niño Index (ONI), Southern Oscillation Index (SOI), North Atlantic Oscillation (NAO), North Tropical Atlantic (NTA) and soil characteristics: sum of bases and phosphorus (P) concentration were scaled as before, to obtain standardized model coefficients (ranging from -1 to +1, as partial correlation coefficients). We exclude from the analyses four (4) highly correlated variables (mean temperature (°C), mean humidity (%), oceanic Niño index (ONI), North Atlantic Oscillation (NAO), resulting in a simplified model with eight (8) variables (SI. Fig correlation). A complete model was initially built using all ten (10) variables described above. To arrive at the final model (Table 2) only the significant variables were considered, therefore, cations and VPD were excluded from the construction of the final models. The final model for total litterfall and for each component varies depending on which variables were significant for each dependent variable. All analyses were run with R v.4.2.2, (R Development Core Team 2017), using packages "nlme" and "visreg".

We also tested whether there was a delay between climate conditions and litter production of one, two, or three months, and to our surprise, the best models were always those that used the month-to-month relationship between productivity and climate, without considering a lag time.

RESULTS

Annual litterfall production and differences between study areas and years

During 10 years of monitoring (2004 to 2014), the central Amazon old-growth tropical rainforest litterfall ranges from 5.7 a 9.1 Mg ha $^{-1}$ year $^{-1}$, with an average of 7.2 Mg ha $^{-1}$ year $^{-1}$ and standard deviation ± 0.8 (n=47). Although all plots are in plateau areas (Figure 3), we found significant differences in total and component production (except for fine wood fraction) between some of the plots (Figure 3). The highest average productivity was found in areas C1, A1 and B1 (with no significant difference between them), while the lowest average yields were found in areas B2, A2 and C2 (also with no significant difference between them) (Table 1). Contrary to our expectations, closer plots (located in the same forest reserve) were not more similar in terms of productivity (Figure 3). The highest average total productivity was found in C1 plot at RFAD (mean 8.1 ± 0.7), while the lowest average productivity was observed in B2 at EEST reserve (mean 6.3 ± 0.4), representing a difference of almost 1.8 Mg ha $^{-1}$ year $^{-1}$ between them.

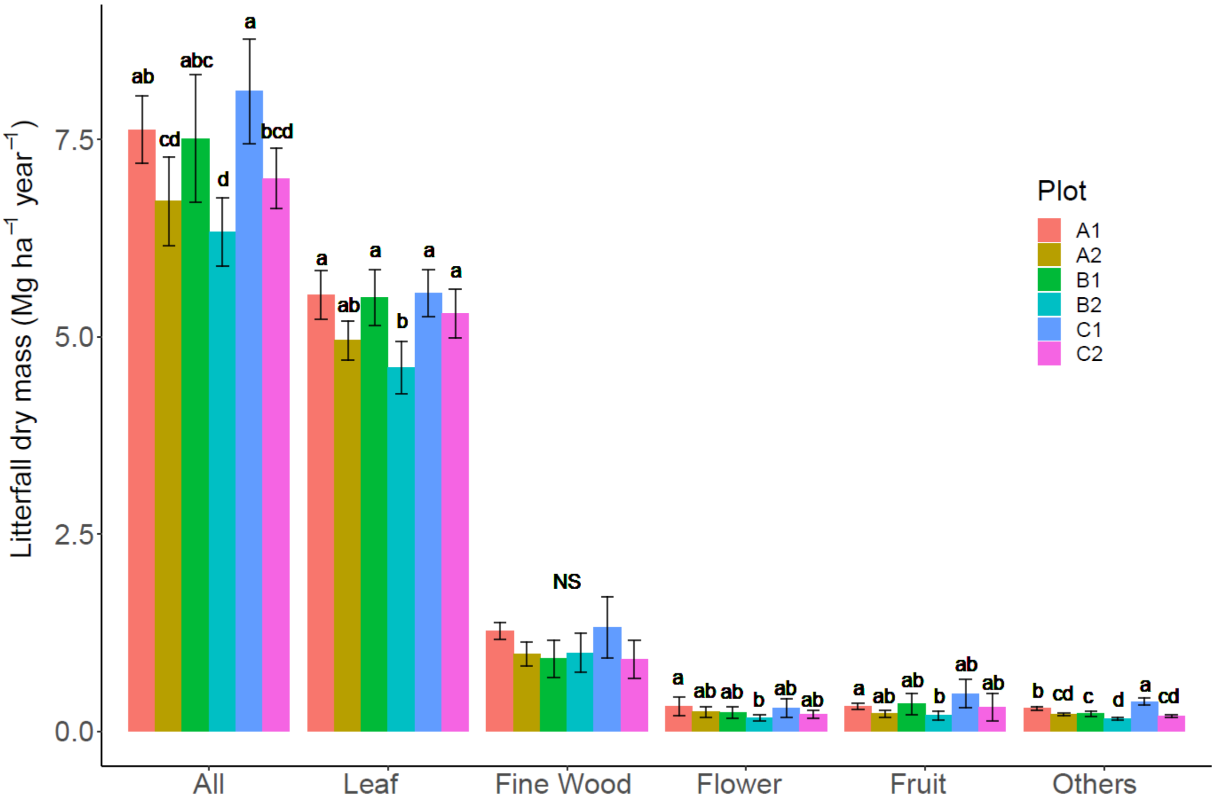

Figure 3. Annual litterfall production in central Amazon Forest. Ten years annual mean and standard deviation of total litterfall production (all components), and five years of leaves, fine wood, flowers, fruits and others production at A1 and A2 (PDFBB), B1 and B2 (EEST), C1 and C2 (RFAD). The letters “a”, “b”, “c”, and “d” above bars indicate significant differences (p < 0.05) within each plot, NS means not significant.

Table 1. Maximum, minimum, and average annual litterfall production for each monitored plot.

	Max	Min	Mean
PDBFF			
A1	8	6.7	7.6 ± 0.4
A2	7.8	6.1	6.7 ± 0.6
EEST			
B1	9	6.4	7.5 ± 0.8
B2	6.9	5.7	6.3 ± 0.4
RD			
C1	9.1	7.3	8.1 ± 0.7
C2	7.5	6.4	7.0 ± 0.4

The highest annual production was recorded in 2009, respectively for C1 and B1, and in 2004 and 2005 for C1 plot, while the lowest value was consistently recorded in the B2 plot. Although there was large variability between years in all studied plots, we observed a consistent increase in the annual production over 2009/2010 (between May 2009 and April 2010), reaching the highest values of 9.1 and 9.0 Mg ha^{-1} year^{-1} (C1 and B1 plots, respectively), followed by a decline in 2010/2011 in all plots (Figure 4, SI. Figure 7).

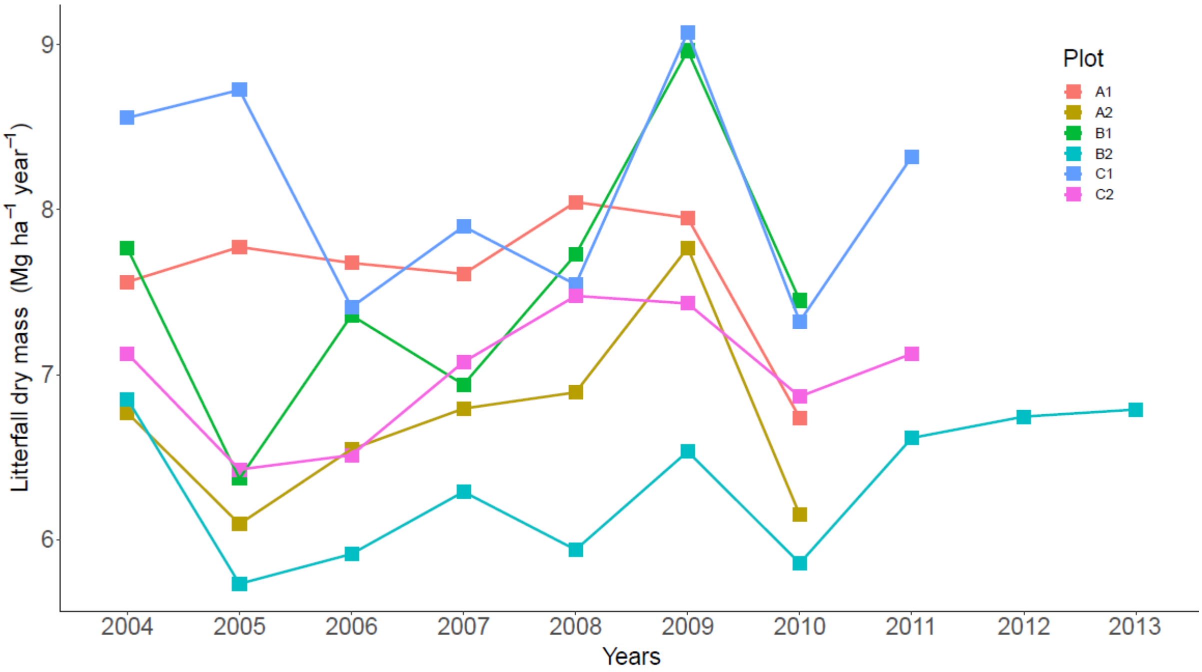

Figure 4. Total annual litterfall productivity over 10 years. Each year was calculated by the sum of the monthly productivity from May to April, in plots A1 and A2 (PDFBB), B1 and B2 (EEST), C1 and C2 (RFAD).

Litterfall seasonality

The monthly litterfall productivity from 2004 to 2014 was on average 0.6 ± 0.2 Mg ha^{-1} (n=575), ranging from the lowest value of 0.2 Mg ha^{-1} month^{-1} in February 2014, to the highest value of 1.6 Mg ha^{-1} monthly^{-1} in August 2004. We found a clear seasonal pattern in litter productivity throughout the year in all studied plots (Figure 5). The lowest production was observed during the wet season (November to May) when litterfall averaged 0.4 ± 0.1 Mg ha^{-1} monthly^{-1}, while peaking in the dry season (June to October) when litterfall averaged 0.8 ± 0.2 Mg ha^{-1} monthly^{-1} (Figure 5). The observed seasonality was mainly driven by the variation in productivity of leaf fraction, flower and others (SI. Figure 8). Fine wood showed two peaks, one during the dry season and another in the wet season (January), while the fruits fraction had little seasonal variation (SI. Figure 8).

We found higher productivity in January 2005 in all areas studied, reaching a 250% increase in litterfall dry mass (Figure 5). This increase in litterfall was caused by an increase in fine wood productivity (SI. Figure 8), which happened in all areas at the same time (January 2005), showing a similar response in forest litterfall productivity to external factor. Other outlier events were also recorded over the 10 years of monitoring, mainly in the driest months, between July and September, but none of them reached levels beyond 200% of mean productivity or had the same effect in all studied areas at the same time (SI. Figure 7).

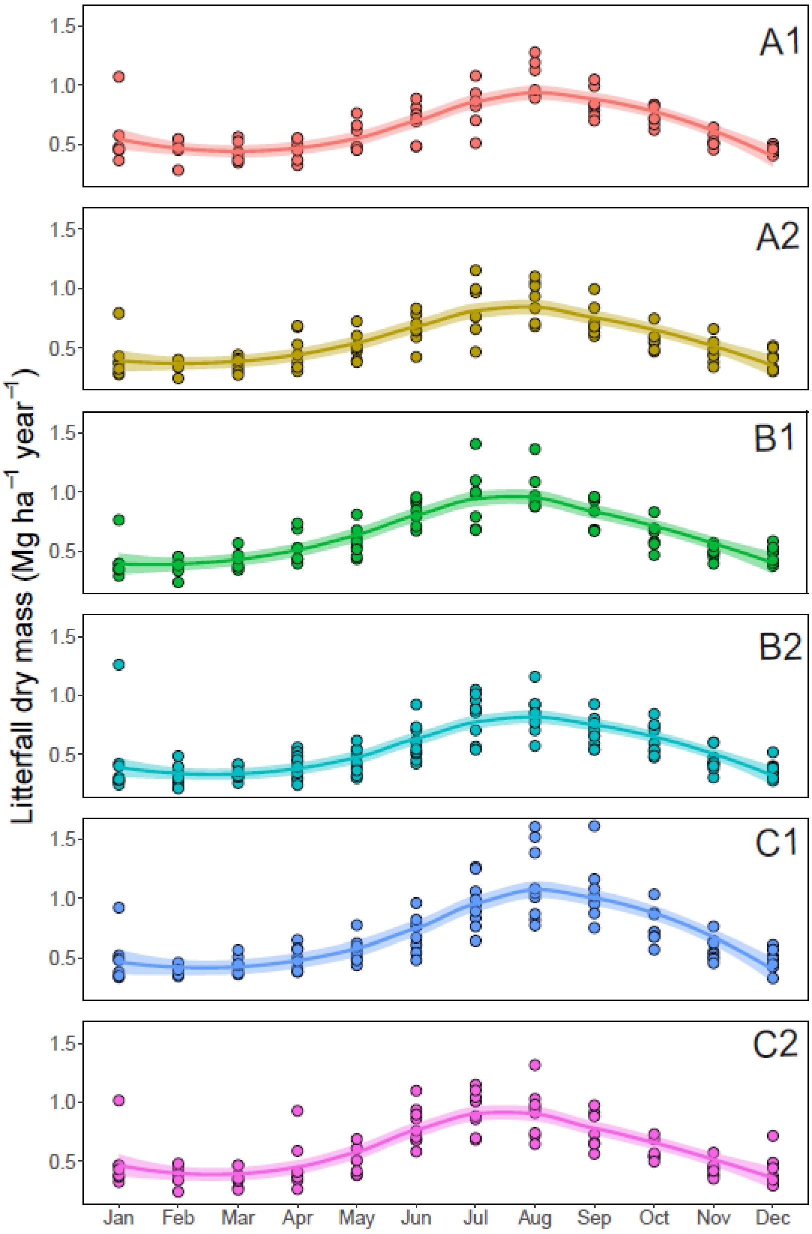

Figure 5. Seasonal variability of the monthly litterfall productivity over 10 years, in the six monitored plots, A1, A2, B1, B2, C1 and C2. Each point represents the monthly productivity in a given year. Averages (lines) and 95% confidence intervals (shaded) over the study period (2004-2014) are shown. Highlights in January (2005), where there was a considerable increase in productivity due to greater fine wood fraction biomass.

Contribution of each litter fraction to total production

The total litterfall production was separated into fractions of leaf, fine wood, flower, fruit and others for 5 years of monitoring. The fraction of leaves contributed with the highest biomass input, with about 74% of the total, producing on average 5.1 ± 0.6 Mg ha^{-1} year^{-1}. Fine wood material was the second component with the highest production, contributing about 15% of the total production, which corresponds, on average, to 1.0 ± 0.3 Mg ha^{-1} year^{-1}. The reproductive material, which includes flowers and fruits (SI. Figure 8), represented about 7.7%

of the total production, with flowers contributing 3.7 %, which is equivalent to 0.3 ± 0.1, while the fruits represented 4.1 % of the total production, totalling 0.3 ± 0.2 Mg ha^{-1} $year^{-1}$. Unidentified material (others) represented 3.4% of total production, which is equivalent to 0.2 ± 0.1 Mg ha^{-1} $year^{-1}$ (Figure 6).

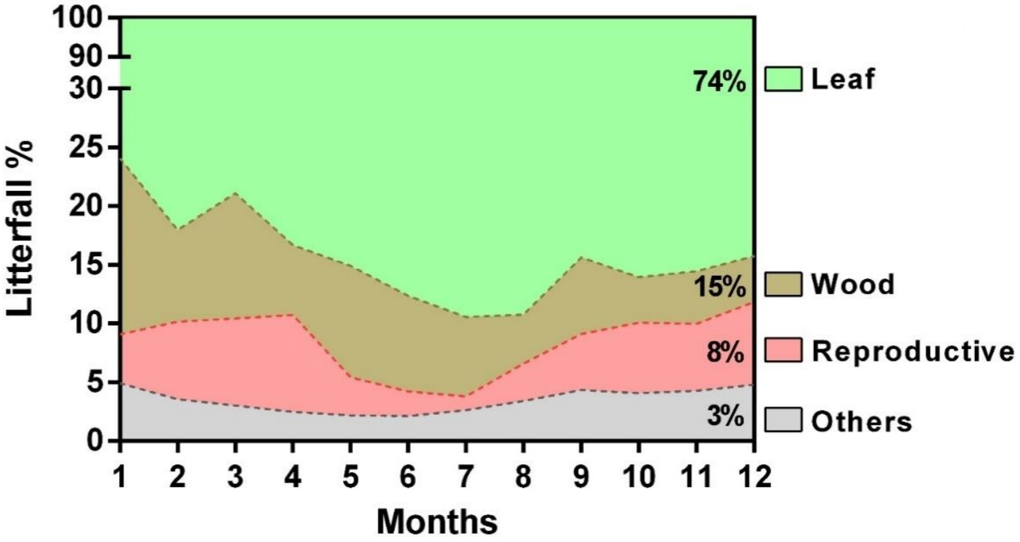

Figure 6. Seasonal variation in litterfall fractions over five years. The monthly proportion of litterfall fractions was calculated relative to the total production collected from the six study plots (A1, A2, B1, B2, C1 and C2) between May 2004 and August 2009. For each month, litterfall was sorted into leaf (green), fine wood (brown), reproductive material including flower and fruit (pink) and others (gray).

Leaf production peaked during the dry season (June to October) while it is lowest during the wet season (November to May). This causes a strong seasonal pattern, with an increase in the proportion of leaves during the dry season, which can reach up to 90% of the total litter production. Regarding fine woody material, we identified two peaks with higher production: one during the rainy season in January and another in the dry season, in September. Fine wood material did not display a clear pattern as leaves. For the reproductive material, we found an irregular pattern throughout the year. However, when separately evaluating flowers and fruits, there is an increase in flower production during the dry season, while the pattern of fruit distribution is more regular during all months of the year (SI. Figure 8). Unidentified remaining material (called others) follows a distribution similar to total productivity, leaf and flower, with an increase during the driest months of the year.

Effect of climate and soil on litter productivity

Total litterfall increased significantly ($p < 0.05$) with increasing radiation, CWD, maximum temperature, wind speed and anomalies in ENSO and NTA index, while decrease with increasing precipitation, P concentration and changes in NTA. Leaf production increased with increasing radiation, CWD, and ENSO, but surprisingly, it was not affected by maximum temperature. Fine wood production increased with wind speed and changes in ENSO and decreased with CWD and NTA. The higher maximum temperature increased flower production as well as changes in ENSO, while flower were negatively influenced by CWD and P concentration. Fruit production was the component least affected by the climatic variables, increasing with precipitation and decreasing with NTA. Production of unidentified material (others) increased with radiation and decreased with NTA and CWD. Partial graphs for each significant variable were presented in the supplementary information (SI, figures 11 to 17).

Table 2. Results for GLS models, fitted with climatic and soil as covariates, are shown for total and litterfall fraction production. To explain litter productivity, we used local climatic variables (precipitation – ppt, radiation – RAD, maximum temperature – Temp-max, cumulative water deficit – CWD, and wind speed – wind), large-scale climatic indices (ENSO – Nino3.4, North Tropical Atlantic – NTA), and soil characteristics (Soil phosphorus concentrations – P). The variance explained by the model is presented at the end of the table for each model.

	Litterfall production		**Leaf**		**Fine Wood**		**Flower**		**Fruit**		**Others**	
Variables	**Estimate**	**Pr(>|t|)**	**Estimate**	**Pr(>|t|)**	**Estimate**	**Pr(>|t|)**	**Estimate**	**Pr(>|t|)**	**Estimate Pr(>|t|)**	**Pr(>|t|)**	**Estimate**	**Pr(>|t|)**
Nino3.4	0.11	0.03	0.11	0.04	0.09	0.03	0.07	0.21				
I(nino3.4^2)	- 0.11	0.00	- 0.13	0.00	- 0.08	0.01	- 0.14	0.00				
NTA	- 0.12	0.01			- 0.24	0.00			- 0.15	0.01	- 0.11	0.03
I(NTA^2)	- 0.09	0.00									- 0.07	0.02
PPT	- 0.21	0.00							0.12	0.00		
CWD	0.14	0.00	0.07	0.00	- 0.14	0.00	- 0.25	0.00			- 0.11	0.00
Temp_Max	0.06	0.04					0.13	0.00				
RAD	0.27	0.00	0.19	0.00							0.14	0.00
I(RAD^2)	0.06	0.03										
WIND	0.06	0.02			0.11	0.00						
P	- 0.19	0.00					- 0.17	0.01				
AIC	**1142.61**		**628.55**		**1309.51**		**1247.15**		**1485.11**		**1107.84**	

DISCUSSION

Annual litterfall production and differences between study areas

This study stands out for using one of the longest time series in old-growth tropical forests to evaluate the production of litterfall, collected fortnightly in central Amazonia. Litterfall was classified by fractions of leaf, fine wood, flower, fruit and other components, and related to the local and global climatic variables and soil characteristics. The average annual production found in this study (7.2 ± 0.8 Mg $ha^{-1}yr^{-1}$) was similar to those found in other tropical forests (range: 5.19 - 12.47 Mg $ha^{-1}yr^{-1}$) and in the Amazon basin (range: 6.6 - 9.4 Mg $ha^{-1}yr^{-1}$) (Chave *et al.*, 2010; Conceição, 2017; Monteiro, 2005), (SI. Table 3).

It is important to emphasize that even considering a small spatial variation within the same region of the Amazon, there are significant variations in the total production of litter and its composition between the studied plots (Figure 3) and over time (Figure 4). This may be related to variations in local dynamics, floristic composition and environmental heterogeneity, or be linked to stochastic events, such as the fall of a large tree or the opening of a forest gap, showing the complexity of factors that can affect litter production in tropical ecosystems and the importance of observing its variation over time and space.

Litterfall seasonality

In the upland tropical forests of central Amazonia, litterfall production occurs throughout the year, but is more intense between the drier months of June to October, causing a strong seasonal effect already described in several previous works (Almeida, Luizão, Rodrigues, 2015; Barlow *et al.*, 2007; Luizão, 1989). Our results show the seasonal pattern of litterfall production in all studied areas (Figure 5), with higher production during the dry season, characterized by low precipitation and higher radiation and temperature (SI. Figure 9). During this period, there is an increase in leaf release and flower production (SI. Figure 8), in addition to the well-known production of new leaves by trees (Alencar *et al.*, 1979; Aleixo *et al.*, 2019; Lopes *et al.*, 2016; Wu *et al.*, 2016). The periodic complete loss of leaves by some trees (deciduousness) and the exchange of leaves during the dry period can be adaptive strategies to deal with water deficit, thus avoiding excessive water loss by leaf transpiration (Reich and Borchert, 1988). Increasing the proportion of mature and more efficient leaves during periods of greater radiation can also improve photosynthetic efficiency, providing greater carbon uptake by the canopy (Menezes *et al.*, 2021). The relationship between litterfall productivity and climate indicates an adaptation of plants in response to seasonal climate variations (SI. Figure 9).

Despite the strong seasonal pattern, atypical events were observed over time in all plots. (Figure 5). These events occurred mainly in the driest months of the year and were related to extreme weather events. However, they also happened in wet months, such as the global Atlantic event in January 2005 (Marengo *et al*., 2008), which simultaneously impacted all plots causing the increase in fine wood production (Figure 7).

Contribution of each component to total litterfall production

Leaves represent most of the litterfall, on average 74% of all plant biomass produced by forests (Figure 6). Nutrient concentrations in leaves may directly reflect soil fertility (Vitousek and Sanford 1986), with great importance for ecosystem processes such as nutrient cycling. In tropical forests growing in poor soils, the maintenance of fertility has long been attributed to the recycling of nutrients through the decomposition of litterfall (Herrera *et al*., 1978; Malhado *et al*., 2009; Vitousek, 1984), and on highly weathered soils in Central Amazon forests, a large proportion of available nutrients is tied up in the living biomass and recycled with the litterfall decomposition.

Fine wood represents an important fraction of biomass input into the soil, about 15% of litterfall production (Figure 6). The highest production peaks occurred both during the dry season, a period in which strong winds are observed (Negrón Juárez *et al*., 2018), and in the rainy season, a period of intense storms that end up breaking down many branches, producing a greater amount of woody material, especially in January (Aleixo *et al*., 2019; Fontes *et al., 2018;* Marra *et al.,* 2014).

The reproductive material such as flowers and fruits represented about 8% of the litterfall and indicated the possible characteristics of the floristic composition of the forest in the future, capturing the diversity of species reproducing in the area. Flowers were more abundant during the dry season, causing a strong seasonal effect on this component, while fruit production was intensified in the rainy season, despite being well distributed throughout the year (Figure 6). These patterns were also observed in long-term phenological studies carried out in the same region (Alencar *et al*., 1979; Aleixo *et al*., 2019; Pinto *et al*., 2005; Barbosa *et al*., 2019). Flowering at the beginning of the dry season can favour pollination (Wright e Calderon 1995) while fruiting during the rainy season can favour seed germination and the development of seedlings that need a more humid environment to grow (Pinto *et al*., 2005).

Unidentified remaining material, often called others, was mostly correlated with leaf and fruit fractions (SI. Figure 11) and accounted for about 3% of the litterfall. Two production peaks were found, one accentuated during the dry season, probably more related to leaf, and another slightly lower in the rainy season. The proportion of fragmented, unidentified material seems to increase with its precursor, thus when leaves and flowers are increasing. There may also be related to continuous decomposition processes that occur faster in the rainy season, when there is greater difficulty in separating some materials that begin to decompose in the litter traps.

Effect of climate and soil on litter productivity

Radiation, precipitation, temperature, CWD, wind speed, ENSO, and NTA were important predictors of litterfall temporal dynamics, although their effects were often distinct among litter fraction. Radiation was the local climate variable that most influenced the production of litterfall, mainly due to the increase in the leaves. Solar radiation may be an important trigger for leaf abscission, leading to concerted leaf fall, and also for new leaves production during the dry season (Borchert *et al.*, 2015; Chave *et al.*, 2010; Wright and Van Schaik, 1994,). Radiation is a primary determinant of photosynthesis; however, when radiation exceeds optimal levels, it can trigger stress responses inducing photoinhibition, damage to plant cells, and promoting leaf senescence. Tropical plants have evolved a suite of mechanisms, including leaf abscission and energy dissipation pathways, to deal with excessive radiation levels, leading to increased litter production under higher radiation. Ourique *et al.*, (2016), showed that leaf change was more influenced by the seasonality of radiation than precipitation. These results also corroborate those found by Zhang *et al.*, (2014), where both temperature and solar radiation modulate the seasonal patterns of litter production worldwide.

Precipitation also played a key role in litter productivity over time (Tonin *et al.*, 2017). Precipitation decreases total litterfall productivity, while increasing fruit productivity, which has a greater chance of seed survival under greater precipitation. Higher litterfall in the driest months has been previously reported for Amazon and other tropical forests (Tonin *et al.*, 2017, Wu *et al.*, 2016), suggesting that leaf resease helps plants reduce water stress during the driest periods. However, cumulative water deficit (CWD) decreased litterfall production by reducing leaf fall, despite increasing production of fine wood, flowers and others. Despite inducing reproduction, lower CWD can cause a break in the water transport column, inducing hydraulic failure, which can cause the death of branches and a consequent increase in fine wood litterfall (Anderegg *et al.*, 2013).

High maximum temperatures increased total production and flower production in litterfall but did not affect the other components. A positive linear relationship between litterfall and temperature was also found worldwide (Zhang *et al.*, 2014), in lowland tropical forests (Wright *et al.*, 2011) and both central and northern Amazon forests (Tonin *et al.*, 2017). We expected that temperature increases evapotranspiration rates, which may lead to temporary water deficits that accelerate the abscission of senescent leaves, but surprisingly the temperature did not affect the fraction of leaves in our analysis.

Strong winds increased total and fine wood production, with important consequences for forest dynamics and carbon storage in the central Amazon Forest (Negrón-Juárez *et al.*, 2018). Winds exert mechanical forces on plants, causing structures and organs to detach. The impact of wind can physically break stems, branches, or attachment points, leading to the immediate shedding of plant organs. This direct physical dislodgment contributes to an abrupt increase in litterfall as wind intensity rises.

Anomalies in global circulation patterns like ENSO e NTA events affect litter dynamics over time in an irregular pattern still little known due to the difficulty in separating the combined influence of different factors on local climate and tree phenology (Andrés *et al.*, 2019). In 2005, an extreme global climate event influenced by SST in the tropical Atlantic (Marengo *et al.*, 2008) affected different regions of the Amazon, causing increased mortality from drought (Phillips *et al.*, 2009) and windthrows (Negrón-Juárez *et al.*, 2010). This period had a significant impact on litter production, especially in January of the same year. During that month, a phenomenon known as Blowdowns, characterized by unusual storms with strong wind gusts, occured around Manaus, Brazil (Marra *et al.*, 2014; Negrón-Juárez *et al.*, 2010; Nelson *et al.*, 1994). This event, or climatic conditions associated to it, caused tree mortality and resulted in increased litter production in all studied plots. Plot B2 lost about 28% of its litter traps, which were damaged by the rupture of tree crowns. This phenomenon coincides with the increase in tree mortality, found by Aleixo *et al.*, (2019) and Marra *et al.*, (2014) in January 2005. Events related to ENSO and ATN anomalies influenced litter production, ENSO affected total productivity, leaf, fine wood and flowers (Wright and Calderon 2006), while ATN influenced total productivity, fine wood, fruits and others. Severe drought events can increase litter production, and extreme rainy years also increase litterfall productivity, such as in the year 2009, during a strong wet La Niña event, we observed a consistent increase in litter production across all plots (Figure 7).

Contrary to our initial hypothesis, in which we expected to find greater litter production in places with higher P availability, our results showed that P available negatively influenced the total litterfall and flower production and that the cations did not affect litterfall in our study scale. These results go against those found by Vitousek (1984) and Cunha *et al*., (2021), who demonstrated that the low availability of P limited the production of fine litter in tropical forests. However, such negative relationship with P could mean higher leaf longevity in P limited systems (Vitousek and Sanford, 1986). Flower fraction was also negatively influenced by P availability, contrary to what was found by Clark *et al.,* (2001), where greater production of reproductive material was found under soils with higher P contents. However, Chave *et al*., 2009, found a tendency for lower P concentration sites to invest more in leaf production and less in reproductive material, while Aragão *et al*., (2009) suggests that the type of soil does not play a determining role in litter production patterns in the Amazon.

CONCLUSIONS

Climate-mediated changes in litterfall can impact forest productivity and nutrient cycling dynamics. The ongoing climate change amplifies the relevance of understanding climate-litterfall relationships. This study highlights the importance of weather events for understanding and modelling the dynamics of forest productivity, as well as highlighting the main factors that cause variations in these patterns over time. The litterfall shows a clear seasonal pattern over the years, mainly determined by the variation in leaf production, which occurred in greater quantity when radiation increased, during the dry season. In addition to seasonal variation, we found that extreme weather events related to changes in global atmospheric circulation patterns affected productivity, impacting different litterfall components. These results provide valuable insights into understanding forest ecosystem productivity and its relationship with local climate and large-scale global events, helping to improve vegetation dynamics models.

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SUPPLEMENTARY INFORMATION

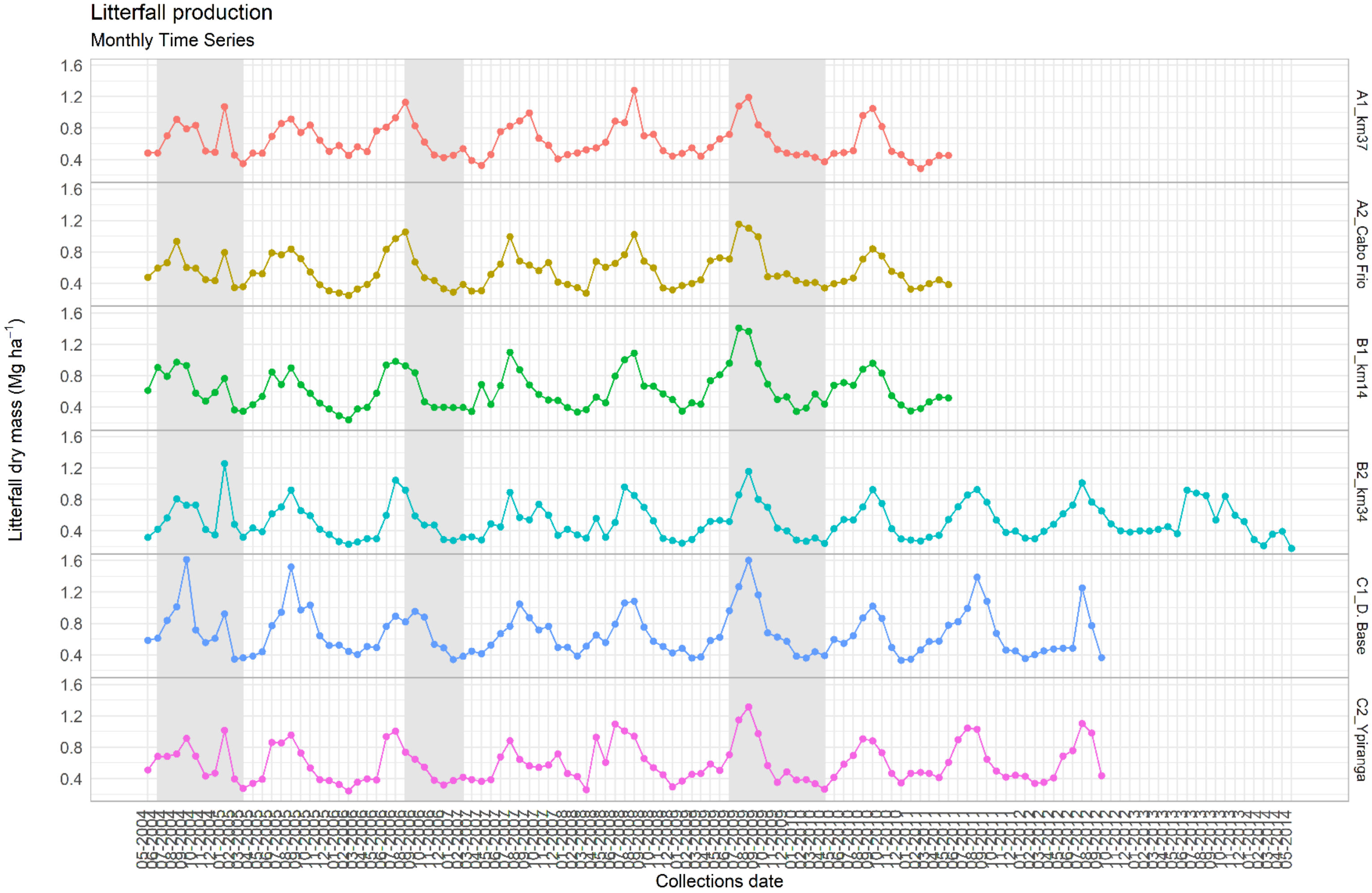
SI. Table 3. Description of study areas and other litter experiments. All studies were carried out in upland forests in plateau areas. We show Forest type, soil classification (World Reference Base Soil Taxonomy System), annual precipitation (mm year^{-1}), average total litter production and for components: leaves, production of reproductive material, woody material, waste production /others, monitoring duration in years, interval of years, number of litter traps used and the size of each collector, reference of the work.

Site	**Forest Type**	**Dominant soil group**	**Rainfall (mm year^{-1})**	**Total litterfall (Mg ha^{-1} ano^{-1})**	**Leaf litterfall (Mg ha^{-1} ano^{-1})**	**Leaf litterfall (g m^{-2})**	**Reprod litterfall (Mg ha^{-1} ano^{-1})**	**Reprod litterfall (g/m^{2})**	**Fine Wood (Mg ha^{-1} ano^{-1})**	**Others (Mg ha^{-1} ano^{-1})**	**Monitoring duration (years)**	**Interval**	**Litter traps**	**Trap Size**	**Reference**
PDBFF	Terra-firme	Ferralsol	2656	8.82	6.63	-	0.6	-	-	0.23	3	1999-2002	140	0.25 m^{2}	Vasconcelos e Luizão, 2004.
PDBFF Dimona	Terra-firme	Ferralsol	2200	8.3	-	-	-	-	-	-	3	1990-1994	18	1 m^{2}	Sizer et al., 2000.
EEST	Terra-firme	Ferralsol	2151	7.79	4.99	-	0.45	-	-	0.74	3	1979-1980	15	80 cm	Luizão, 1989.
EEST	Terra-firme	Ferralsol	2151	8.12	5.48	-	0.31	-	-	0.74	3	1980-1981	15	80 cm	Luizão, 1989.
EEST	Terra-firme	Ferralsol	2151	8.83	4.79	-	0.49	-	-	0.88	3	1981-1982	15	80 cm	Luizão, 1989.
EEST	Terra-firme	Ferralsol	2200	8.9	6.94	-	-	-	-	-	1	2001-2002	10	0.25 m^{2}	Luizão et al., 2004.
EEST	Terra-firme	Ferralsol	3155	7.1	4.89	-	-	-	1.065	1.13	1	2012-2013	60	0.25 m^{2}	Ourique et al., 2016.
EEST	Terra-firme	Ferralsol	2610	-	6.85	-	-	-	-	-	1	2015-2016	30	0.5m^{2}	Valle, 2016.
EEST	Terra-firme	Ferralsol	2151	7.42	4.41	-	-	-	-	-	3	1979-1981	15	80 cm	Luizão e Schubart, 1987.
EEST	Terra-firme	Ferralsol	2286	8.4	6.63	-	-	0.39	1.32	0.11	1	2004-2005	30	0.25m^{2}	Monteiro, 2005.

Continue

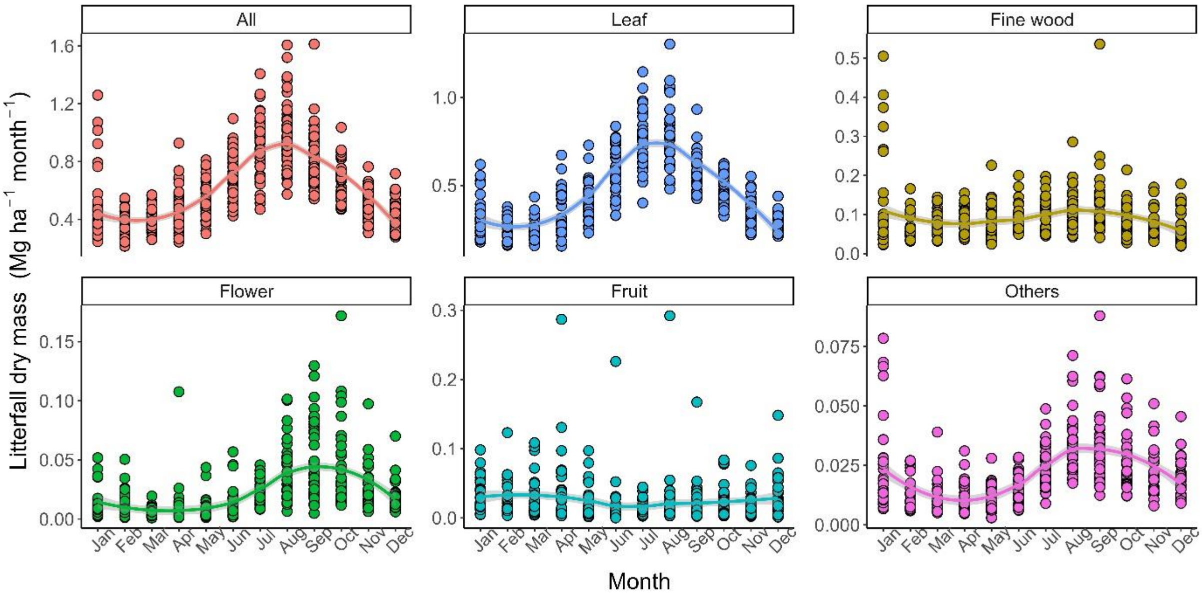
SI. Table 3. Description of the study areas and other litter experiments that took place in the vicinity of these areas. All studies were carried out in upland forests in plateau areas, soil classification (World Reference Base Soil Taxonomy System), annual precipitation (mm year-1), average total litter production, average production of the components: leaves (Mg ha-1 yr-1/g m-2), production of reproductive material (Mg ha-1 yr-1/g m2), production of woody material (Mg ha-1 yr-1), waste production /others (Mg ha-1 year-1), monitoring period in years, range of years of study, number of collectors used and the size of each collector, reference of the work developed.

Site	**Forest Type**	**Dominant soil group**	**Rainfall (mm year^{-1})**	**Total litterfall (Mg ha^{-1} ano^{-1})**	**Leaf litterfall (Mg ha^{-1} ano^{-1})**	**Leaf litterfall (g m^{-2})**	**Reprod litterfall (Mg ha^{-1} ano^{-1})**	**Reprod litterfall (g/m^2)**	**Fine Wood (Mg ha^{-1} ano^{-1})**	**Others (Mg ha^{-1} ano^{-1})**	**Monitoring duration (years)**	**Interval**	**Litter traps**	**Trap Size**	**Reference**
EEST	Terra-firme	Ferralsol	1800-2839	9.4-7.2	5.6	-	2.34	-	1.13	-	10	2005-2015	90	0.25m^2	Conceição, 2017.
PDBFF	Terra-firme	Ferralsol	1900-3500	9.12-10.73	6.66	-	1.21	-	1.85	0.12	1	2017-2018	20	0.25m^2	Moraes, 2018.
Reserve Walter Egler Forest	Terra-firme	Ferralsol	2250	7.9	6.4	-	0.2	-	1.3	0.1	2	1963	10	0.25m^2	Klinge, 1968.
Reserve Walter Egler Forest	Terra-firme	Ferralsol	2250	6.7	4.8	-	0.5	-	1.4	0.009	2	1964	10	0.25m^2	Klinge, 1968.
EEST	Terra-firme	Ferralsol	2130	7.4	-	4.4	-	-	-	-	1	1979-1980	15	80 cm	Luizão, 1982.
ATTO	Terra-firme	Ferralsol	2376	7.03	-	4.39	-	-	-	2.64	1	2016-2017	30	1 m^2	Sanches, 2022.
ATTO	Terra-firme	Ferralsol	2376	8.17	-	4.89	-	-	-	3.28	1	2017-2018	30	1 m^2	Sanches, 2022.
ATTO	Terra-firme	Ferralsol	2376	7.74	-	4.81	-	-	-	2.94	1	2018-2019	30	1 m^2	Sanches, 2022.
EEST	Terra-firme	Ferralsol	2300-3000	6.82	5.06	-	0.24	-	0.96	0.19	10	2004-2014	50	0.25 m^2	this study
PDBFF	Terra-firme	Ferralsol	2300-3000	7.17	5.25	-	0.24	-	1.13	0.25	7	2004-2011	50	0.25 m^2	this study
RFAD	Terra-firme	Ferralsol	2300-3000	7.56	5.44	-	0.32	-	1.11	0.28	8	2004-2012	50	0.25 m^2	this study

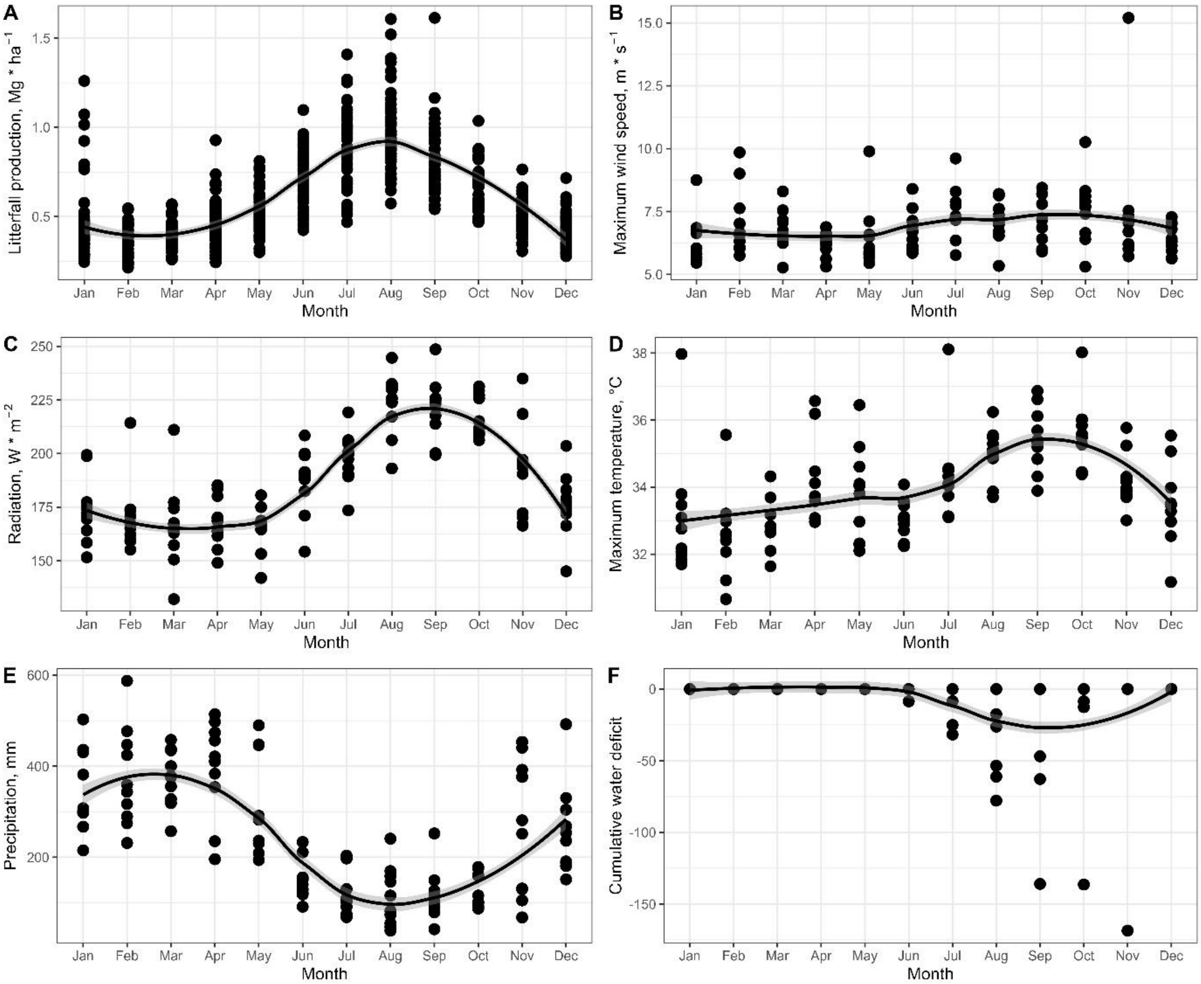


Source: TEAM

SI. Figure 7. Monthly variation of litter production in six plots, during the years 2004 to 2014 in Central Amazonia. The shaded area indicates the major global ENSO weather events that occurred during the study period



SI. Figure 8. Seasonal production of total litterfall and components over 5 years (2004 to 2009). Total production All; Leaves; Fine Wood; Flowers; Fruits; Others in all six areas of tropical forests in the Central Amazon.



SI. Figure 9. Seasonal variation of litter production and local climatic variables. Total litter production (A), maximum wind speed (B), radiation (C), maximum temperature (D), precipitation (E) and cumulative water deficit (F). Monthly values (circles), means (black lines) and 95% confidence intervals (gray lines) during the study period (2004-2014).

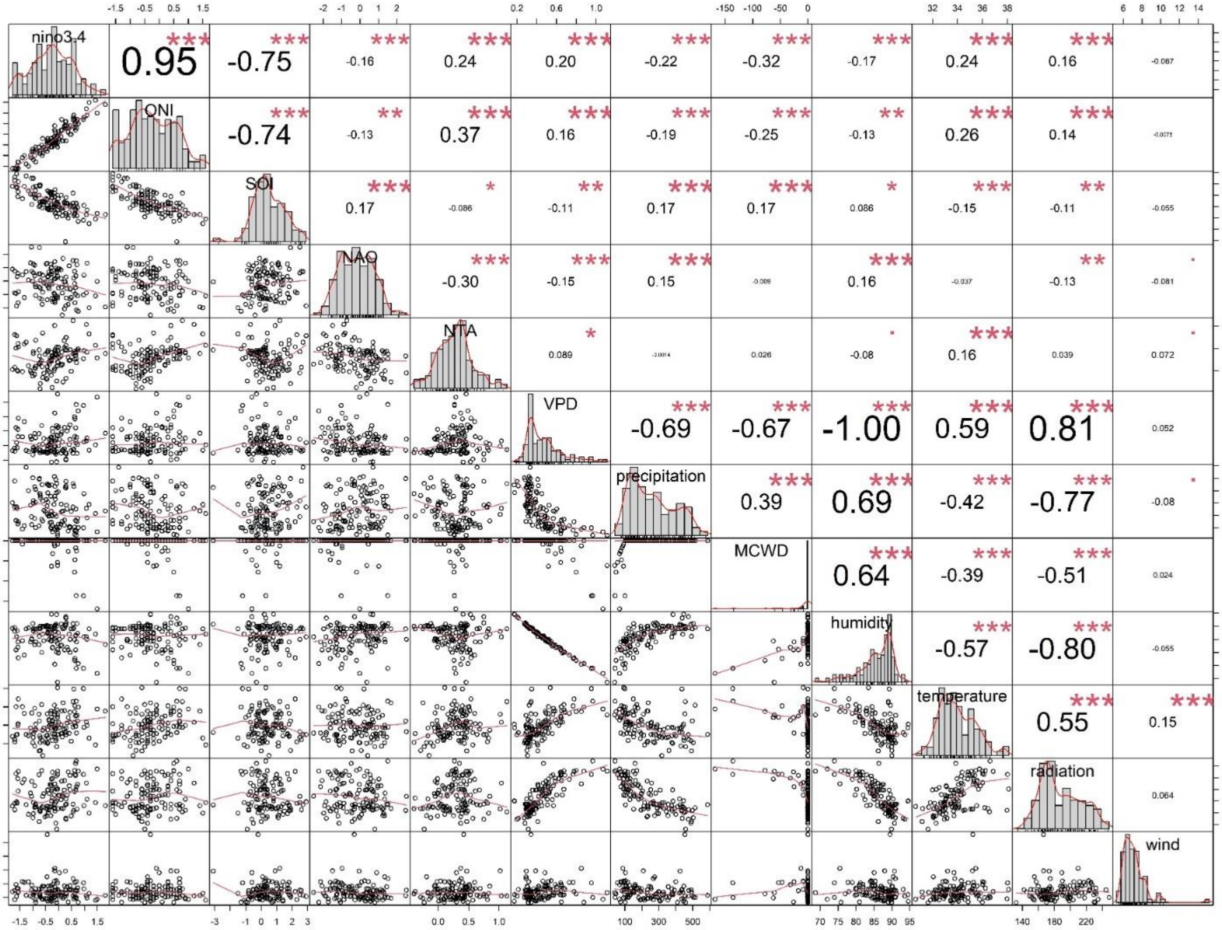
SI. Table 4. Physiographic and edaphic characterization of the six evaluated plots, showing the location of the TEAM/Manaus Project. Adapted from Nascimento *et al*., (2020).

Reservas	**PDBFF**		**EEST**		**RFAD**	
Localização	BR-174, km 37 A1	BR-174, Cabo frio A2	BR-174, km 14 B1	BR-174, km 34 B2	AM-010, Base C1	Ypiranga C2
Coordenadas[2]	lat. 02° 26’ 24”; long. 59° 47’ 51”	lat. 02° 24’ 15”; long. 59° 53’ 32”	lat. 02° 35’ 27"; long. 60° 06’ 53”	lat. 02° 35’ 36"; long. 60° 12’ 42”	lat. 02° 55’ 49”; long. 59° 58’ 32”	lat. 02° 58’ 48”; long. 59° 54’ 25”
Área da Reserva[4 5 6]	3.500 ha	3.500 ha	22.735 ha	22.735 ha	10.072 ha	10.072 ha
Altitude[3]	50 - 100 m	50 - 100 m	100 - 150 m	100 - 150 m	46 - 110 m	46 - 110 m
Cátions Trocáveis (cmolc kg^{-1}) [1]	0.26	0.27	0.19	0.37	0.19	0.10
Conc. de P (mg kg -1) [1]	50.4	62.1	79.5	101.8	55.0	61.0
WRB Soil Classification[1]	Geric Acric Ferralsol (Alumic, Hyperdystric, Clayic)	Geric Acric Ferralsol (Alumic, Hyperdystric, Clayic)	Geric Acric Ferralsol (Alumic, Hyperdystric, Clayic)	Geric Ferralsol (Alumic, Hyperdystric, Clayic)	Geric Acric Ferralsol (Alumic, Hyperdystric, Clayic)	Geric Acric Ferralsol (Alumic, Hyperdystric, Clayic)

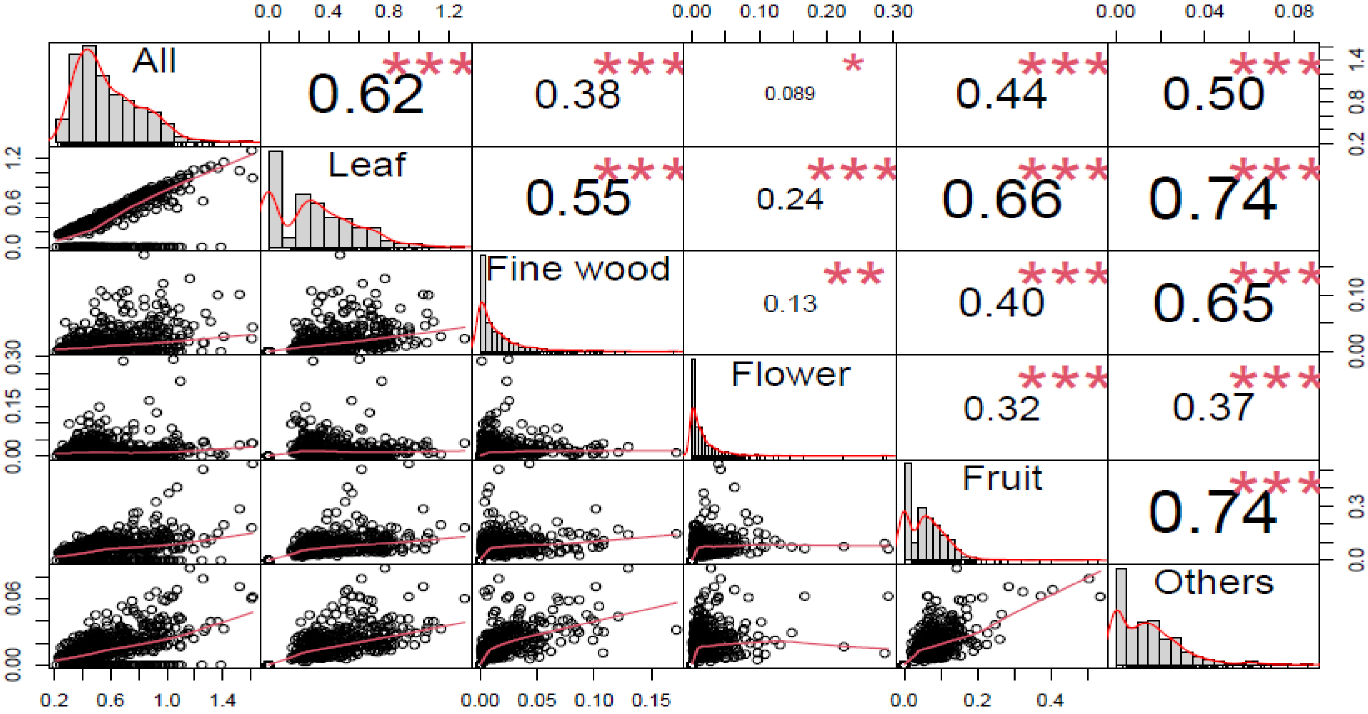
[1] Quesada *et al*., 2010; [2] De Oliveira, 2005; [3] Nascimento *et al*., 2020; [4] Feitosa, 2007; [5] Arana e Artaxo 2014; [6] Pinto *et al*., 2008.

SI. Table 5. Survey summary. Monitoring areas, period and number of sorted and unsorted samples collected, from 2004 to 2014. The collection interval represents the period that the samples were collected monthly or biweekly.

Area/Plot		**Sorted sample**	**No sorted sample**	**Total of sample**	**Interval between survey**	
					Biweekly	**Monthly**
PDBFF	A1-km37	138	19	157	05/2004 a 08/2009	09/2009 a 05/2011
	A2-Cabo Frio	138	19	157	05/2004 a 08/2009	09/2009 a 05/2011
EEST	B1-km 14	137	20	157	05/2004 a 08/2009	09/2009 a 05/2011
	B2-km 34	137	57	194	05/2004 a 08/2009	09/2009 a 05/2014
RFAD	C1-Base	137	37	174	05/2004 a 08/2009	09/2009 a 09/2012
	C2-Ypiranga	137	37	174	05/2004 a 08/2009	09/2009 a 09/2012



SI. Figure 10. Pair-to-pair correlation matrix of climate variables. The bar chart on the lower diagonal shows the correlation of each variable, a histogram of each variable is displayed just above and on the upper diagonal contains the correlation coefficients. The closer to +1 or -1, the stronger the relationship between these variables of the compared pair. The variables ‘nino3.4’, ‘NTA’, ‘precipitation’, ‘CWD’, ‘temperature’, ‘radiation’ and ‘wind’ were selected to perform the final model.



SI. Figure 11. Pair-to-pair correlation matrix of total productivity and litterfall components. The bar chart on the lower diagonal shows the correlation of each variable, a histogram of each variable is displayed just above and on the upper diagonal contains the correlation coefficients. The closer to +1 or -1, the stronger the relationship between these variables of the compared pair.

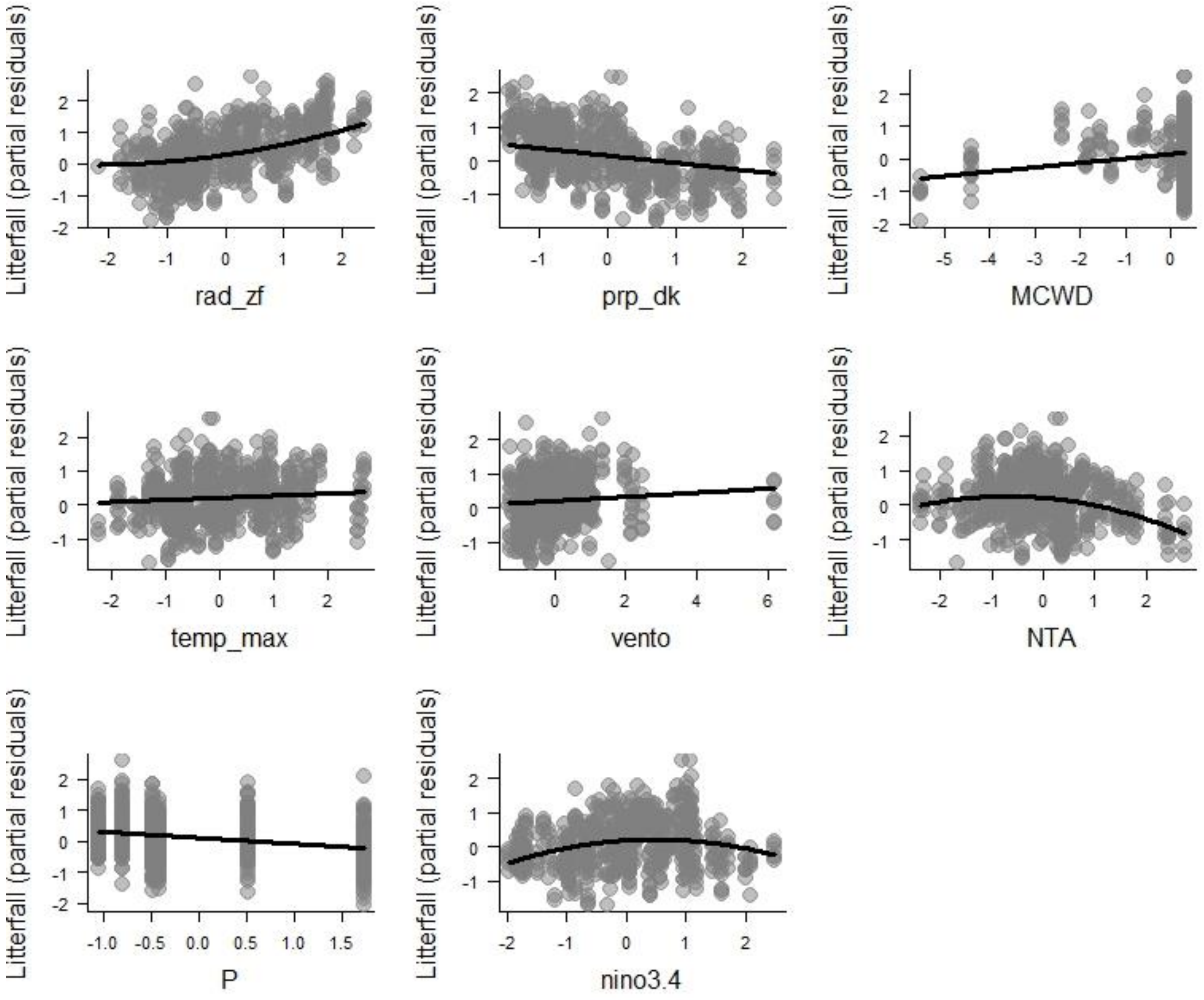


Figure 12. Partial graphs between total litter production and variables that influenced litter production: radiation, precipitation, CWD, maximum temperature, wind, Niño 3.4 and NTA and soil P concentration.

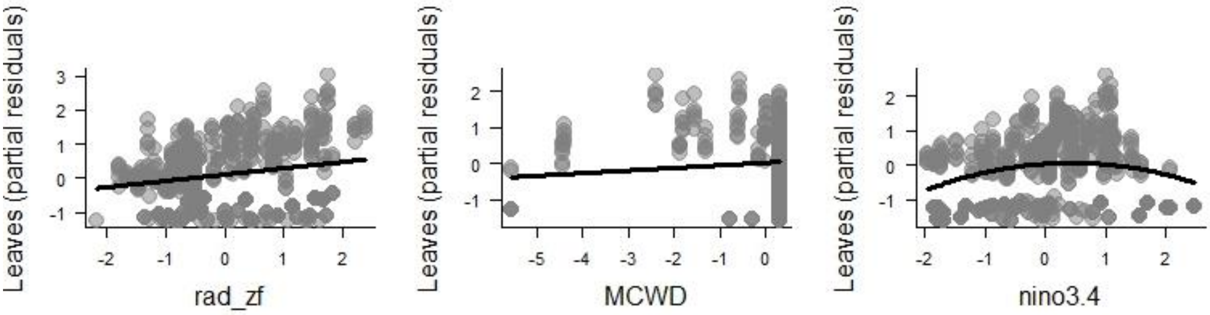


Figure 13. Partial graphs between leaf litter production and variables that influenced leaf litter production: radiation, CWD, and Niño 3.4.

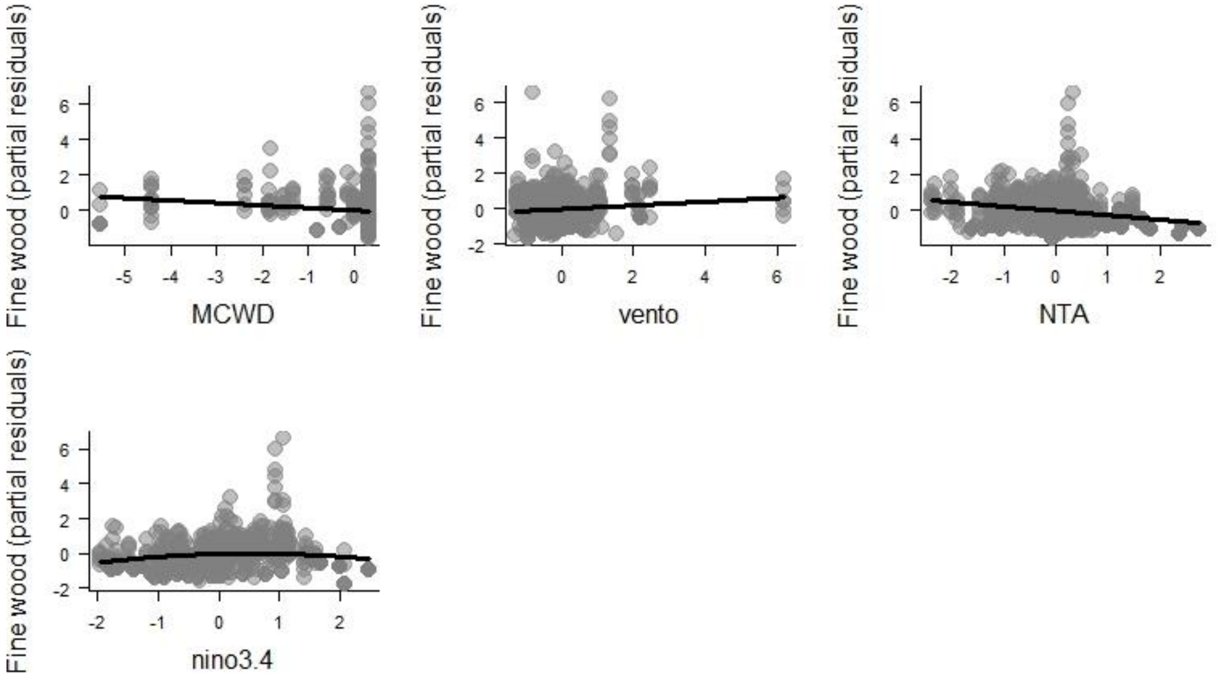


Figure 14. Partial graphs between fine wood litter production and variables that influenced fine wood litter production: CWD, wind, global, Niño 3.4 and NTA.

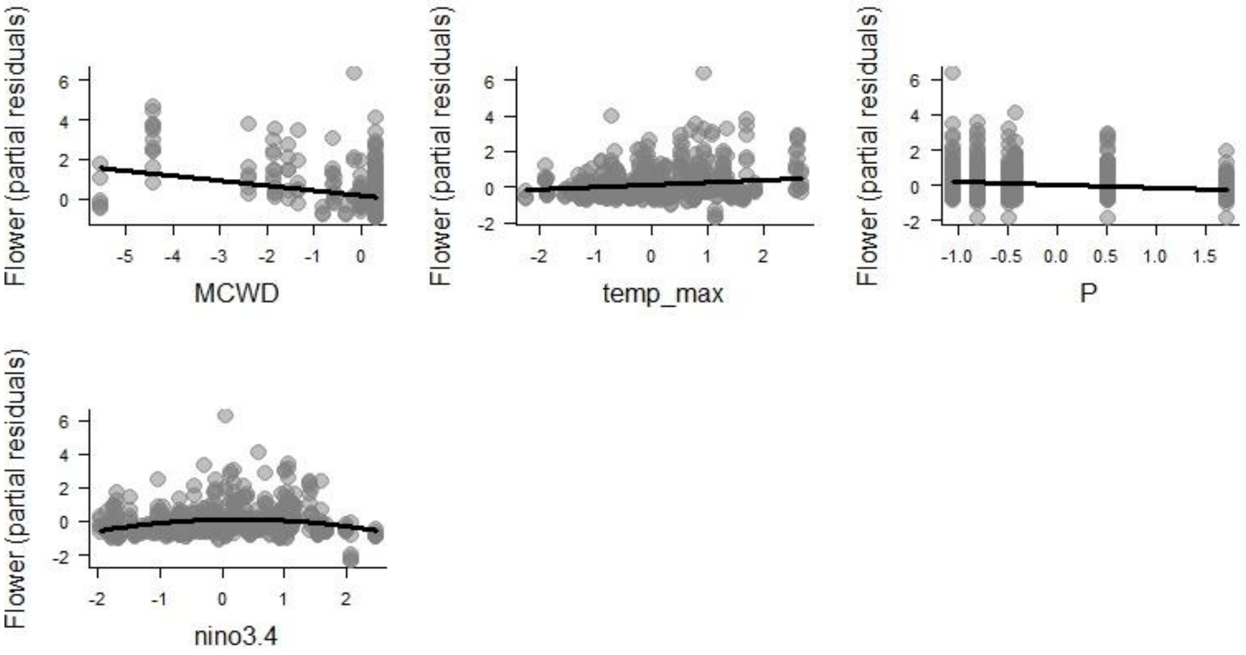


Figure 15. Partial graphs between flower litter production and variables that influenced flower litter production: CWD, maximum temperature, Niño 3.4 and soil P concentration.

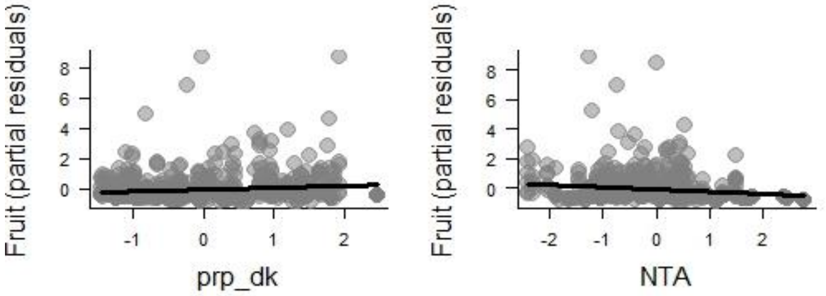


Figure 16. Partial graphs between fruit litter production and variables that influenced fruit litter production: precipitation and NTA.

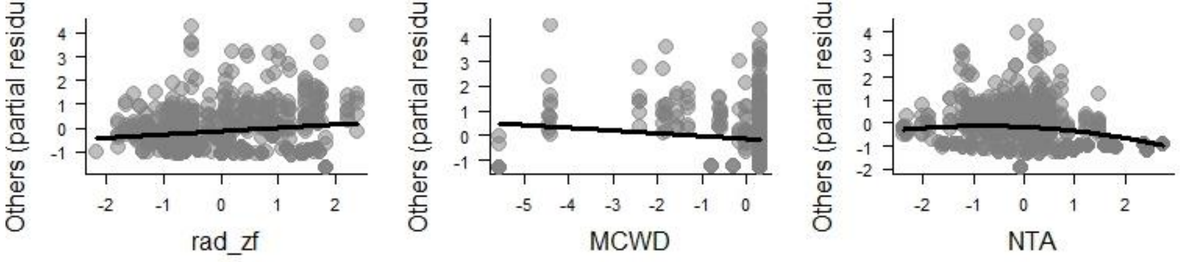


Figure 17. Partial graphs between others litter production and variables that influenced others litter production: radiation, CWD and NTA.