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THE ECOLOGICAL ROLE OF
MAMMAL COMMUNITIES IN
THE BIOGEOCHEMICAL
CARBON CYCLE IN A
TROPICAL ENVIRONMENT

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THE ECOLOGICAL ROLE OF MAMMAL COMMUNITIES IN THE BIOGEOCHEMICAL CARBON CYCLE IN A TROPICAL ENVIRONMENT

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ABSTRACT

Diversity loss can affect the ability of forests to sequester and store carbon from the atmosphere. The capture of atmospheric carbon and its storage in the biomass of organisms and in the ecosystem's soils are key to mitigating the effects of climate change.

Mammals contribute to soil carbon concentration in the northern Amazon, by generating organic remains through trophic interactions with plants and other animals. This thesis investigated whether mammal diversity, interacting with tree diversity and generating such soil organic inputs, affects the content and type of soil organic matter (SOM) and whether these diversity effects on SOM composition differ between mammal and tree communities. The first objective was to test whether both the content and type of SOM accumulated vary with mammal and tree richness because of possible compositional differences between the organic inputs derived from plants versus animals.

Additionally, it is known that some species traits, such as, for example, body size and longevity, determine carbon accumulation in organisms, while others, such as feeding strategies, define which organic remains are incorporated into the soil, affecting the amount and type of organic matter (OM) accumulated in soil. Thus, the diversity of traits in mammal communities – i.e., their functional diversity (FD) – may constitute another mechanism linking biodiversity to SOM accumulation. The second objective was to test whether both the content and type of SOM accumulated vary with functional diversity metrics assessed in mammal communities, and have different effects on the composition of SOM derived from the organic inputs produced by different mammal species, varying in their traits, through their feeding activities.

Besides mammals and trees, microbes are also relevant to the functioning of the carbon cycle. Plant or animal body parts or feces are composed of carbon that can be stored in the soil or released into the atmosphere through microbial mineralization. Yet, the simultaneous effect of trees, mammals and their traits on SOM composition and soil microbial carbon consumption has not been investigated. The third objective was to evaluate whether the effects of the diversity of mammal and tree communities on soil microbial carbon consumption differ, given the possible different effects of mammals and trees on SOM composition.

These questions are relevant because not all carbon forms are equally resistant to microbial mineralization and, thus, relevant to soil organic carbon (SOC) storage.

I analyzed these questions by means of the following methodology: Elemental (by ED-XRF spectrometry and CNH analysis) and molecular (by FTIR-ATR spectroscopy) composition of SOM was analyzed in 401 topsoil samples collected along 83 transects in the northern Amazon (Guyana). I examined the relationships of SOM composition first, with mammal and tree richness, and second, with mammal trait diversity (functional richness, evenness, and divergence) across the 83 transects in the northern Amazon. Third, I analyzed the relationship of soil microbial carbon consumption (assessed by means of Ecoplates) with mammal and tree diversity and SOM composition across 30 sites.

To study these relationships, I considered the environmental variability among transects and combined observational data on mammal and tree diversity and mammal species abundance in the northern Amazon with open-access data on mammal species traits and spectral data on

SOM composition in 83 mammal-tree communities, and additionally, with experimental data on soil microbial carbon consumption assessed at 30 sites.

SOM composition was described by principal component analysis (PCA), and three principal components accounted for 67.9% of the total variance. The first principal component (PC1= 30.7%) described a gradient of variation in clay mineral content (kaolinite and Fe-Al oxides) versus quartz content. The second principal component (PC2=21.9%) reflected the total SOM content, mainly capturing the variance of biophilic elements (C, N and S) and aromatic-nitrogenated SOM. The third principal component (PC3=15.3%) reflected compositional differences in SOM regarding the content of carbonyl groups and aliphatic compounds. Carbonyl (C=O) is a functional group formed by a carbon atom double bonded to an oxygen atom and commonly found in organic compounds, such as organic acids, ketones, aldehydes, esters, among others. Aliphatic compounds (C-H) are linear hydrocarbons formed by chains of carbon atoms (C-C) with hydrogen bonded in lateral positions, such as alkanes (C-C), alkenes (C=C), or alkynes (C≡C), commonly derived from lipids like plant oils and animal fats.

First analysis showed that mammal richness and tree richness had significant but opposite effects on SOM composition. While higher tree richness was related to a higher content of carbonyl groups and aliphatic compounds in SOM, higher mammal richness was related to a lower content of both SOM components and had a positive effect on the total content of N, S, and Fe in the soil.

Second analysis showed that the trait diversity in mammal communities was more relevant for SOM composition than their species richness. In particular, the content of carbonyl groups and aliphatic compounds in SOM decreased with mammal functional richness (when species traits in mammal communities occupied a greater volume of the FD space) but increased with mammal functional divergence (when species traits in mammal communities were more disparately distributed within the FD space). The species number of tree communities was related to the content of carbonyl groups and aliphatic compounds in SOM, while it had an opposite effect to that of mammal functional richness but similar to that of mammal functional divergence.

Third analysis revealed that overall carbon consumption by soil microbes decreased in transects where mammal communities showed higher functional richness (where species traits in mammal communities occupied a greater volume of the FD space) and functional evenness (where species traits in mammal communities were more evenly distributed within the FD space). In addition, the types of carbon consumed by soil microbes decreased with the number of tree species, but increased with the total SOM content. That is, microbial communities consumed a lower variety of carbon sources in topsoils from areas where tree communities exhibited a greater number of species and soils contained lower total SOM.

Thus, it seems that more diverse mammal communities (both in species and their traits) and more diverse tree communities (in species) may promote the accumulation of different types of SOM, and the functional specialization of soil microbial communities in degrading certain carbon sources derived from the type of OM generated by these mammal and tree communities. These results show that not only mammal diversity, but also tree diversity differently affects SOM composition and soil microbial carbon consumption.

In summary, mammal and tree richness have different effects on SOM composition: Mammals promote the accumulation of SOM rich in N, S, and Fe, while trees enhance the accumulation of aliphatic and carboxylic SOM. Also, different mammal functional diversity metrics have opposite effects on SOM composition: Lower mammal functional richness, but higher functional divergence, increases the content of aliphatic and carbonyl-rich SOM, and thus might contribute to recalcitrant SOM. Organic compounds, such as aliphatic compounds,

that are resistant to microbial degradation due to their molecular properties and residually accumulate in SOM, are considered recalcitrant. These results show that not only the number of mammal and tree species, but also mammal trait diversity contribute to variation in SOM composition, with potential effects on recalcitrant SOM, reducing OM decomposition rates and enhancing SOC persistence. Lastly, mammal functional diversity is related to reduced overall microbial carbon consumption, whereas tree richness is associated with a reduced variety of carbon sources consumed by soil microbes.

To conclude, mammals affect the functioning of the carbon cycle, and their effects are complementary, thus not redundant, to those of trees. Mammals and trees promote the accumulation of different components of SOM and have different effects on carbon consumption by soil microbial communities. Additionally, not all species are equally important for the carbon cycle, their traits also matter for its functioning, determining the type of carbon accumulated in the soil and potentially influencing OM degradation by microbes and long-term SOC retention. Given that the current loss of biodiversity is particularly detrimental to large and long-lived animals, such as many mammals, these results indicate that the current extinction crisis might result in a malfunction of the carbon cycle.

RESUMO

O carbono está presente en todos os seres vivos e circula entre a atmosfera, a biosfera e o solo. As plantas son os principais actores biolóxicos do ciclo do carbono, fixando o carbono nos seus tecidos mediante a fotosíntese. Converte o dióxido de carbono (CO_2) atmosférico en hidratos de carbono, que acumulan nas súas raíces, talos e follas. Cando as plantas morren, o carbono dos seus tecidos pasa ao solo, onde pode ser modificado polos microorganismos para incorporarse á materia orgánica do solo (MOS), ou ser liberado á atmosfera en forma de CO_2 . Esta captura do carbono nos organismos e no solo dos ecosistemas reduce os niveis de carbono atmosférico, contribuíndo a mitigar o cambio climático e o quecemento global.

Os bosques tropicais albergan a maior biodiversidade do mundo e son moi sensibles ao cambio climático. As árbores xogan un papel crucial no ciclo do carbono, capturando carbono da atmosfera e regulando o clima. Pero outros organismos forestais como os mamíferos, tamén contribúen ao ciclo do carbono no norte da Amazonía, unha das rexións máis biodiversas do planeta e principal sumidoiro de carbono. A biodiversidade contribúe ao funcionamento dos ecosistemas, facéndoo máis saudable e máis resistente ás perturbacións ambientais. As interaccións entre as especies nos ecosistemas determinan a composición e estrutura das comunidades e inflúen nos fluxos de materia e enerxía. O estudo das relacións entre a biodiversidade e o medio no que viven é crucial para comprender o papel ecolóxico que xogan as especies no funcionamento dos ecosistemas, como o sequestro e almacenamento de carbono no solo.

A perda de biodiversidade está a causar alarma xa que pode dificultar a capacidade das comunidades ecolóxicas para capturar recursos e producir biomasa, afectando directamente ao sequestro de carbono dos ecosistemas. Organismos, como animais, plantas e microbios, inflúen na transferencia de nutrientes e na descomposición e mineralización da MOS. Investigacións previas mostran que os mamíferos, a través dos seus aportes orgánicos, poden afectar á concentración de carbono no solo mediante as interaccións tróficas. Os produtos xerados polos animais, como feces, ouriños ou cadáveres, poden afectar ao contido de carbono e nitróxeno no solo, modificando a actividade das comunidades microbianas do solo. Os animais tamén modifican as comunidades de plantas, transportan e homoxeneizan materiais, afectando á bioxeoquímica do solo. Isto destaca a necesidade de explorar o papel das comunidades de mamíferos no ciclo do carbono no norte da Amazonía.

A diversidade de especies dentro das comunidades ecolóxicas, e das súas características, é dicir, a súa diversidade funcional (FD), pode relacionarse co funcionamento do ciclo do carbono. Características das especies como o tamaño corporal e a lonxevidade relaciónanse co almacenamento de carbono nos organismos, e o tipo de interacción trófica entre as especies relaciónanse coas entradas de carbono no ecosistema. As combinacións de características das especies están asociadas con estratexias de historia de vida (de rápida a lenta) e estratexias de captura e uso de recursos (de conservativas a adquisitivas), que se relacionan cos fluxos e reservas de carbono no solo dos ecosistemas. Daquela, a variación na diversidade de características das especies dentro das comunidades de mamíferos podería influír no funcionamento do ciclo do carbono, afectando á acumulación de carbono no solo. Por exemplo, a variación de características entre as especies dentro dunha comunidade (herbívoras, carnívoras, omnívoras e insectívoras) relaciónase co tipo de interaccións entre as especies e co

contido e tipo de restos orgánicos que incorporan ao solo a través das súas actividades de alimentación. Así mesmo, características como o tamaño corporal e a biomasa dos mamíferos poden relacionarse co seu tipo de dieta, como os grandes herbívoros terrestres que xeran grandes aportes de MOS e afectan á estequiometría dos nutrientes do solo (é dicir, ás proporcións dos nutrientes que se transfiren ao solo, como C e N, entre outros). Entón, o tipo de interaccións tróficas dominantes nas comunidades de mamíferos poderían afectar ao contido e tipo de MOS que se acumula no solo e que logo é procesada polas comunidades microbianas.

Os microorganismos (arqueas, bacterias e fungos) contribúen significativamente ao ciclo do carbono mineralizando a MOS, secuestrando CO₂ no solo e estabilizando o carbono orgánico do solo (COS). Transforman os restos orgánicos en biomasa microbiana e compostos orgánicos complexos e recalcitrantes, que resisten á degradación microbiana e poden interactuar cos compoñentes minerais do solo, formando asociacións organominerais estables. A investigación sobre as interaccións microbio-carbono do solo centrouse principalmente na descomposición microbiana dos restos vexetais e nos cambios nas comunidades microbianas influenciadas pola composición da follaxe. Non obstante, ata agora non se estudaran os efectos simultáneos da diversidade animal e vexetal sobre o consumo de carbono polos microbios do solo. Os microbios son eficientes e rápidos á hora de degradar a MOS lábil (polisacáridos e proteínas), pero son menos eficientes ao degradar a MOS recalcitrante (carbonilos, alifáticos e aromáticos), que se acumula no solo. Os restos animais son unha fonte variable de aminoácidos e amonio (ricos en N) e proteínas (como queratinas ricas en S) na MOS, mentres que os restos vexetais contribúen principalmente con polisacáridos (C lábil) e ligninas (C recalcitrante). Así mesmo, existen procesos fisicoquímicos que estabilizan a MOS, limitando a súa biodegradabilidade. De feito, a composición molecular da MOS inflúe na súa resistencia á descomposición microbiana e ao secuestro do COS a longo prazo. Daquela, a diversidade de especies de mamíferos e das súas características podería contribuír á composición molecular da MOS, afectando á actividade descompoñedora dos microbios do solo e á persistencia do COS. O estudo da composición da MOS axudará a comprender a relación entre a diversidade de mamíferos e o almacenamento de carbono nos solos amazónicos.

Nesta tese investiguei as relacións entre as comunidades de mamíferos e a composición da MOS e o consumo microbiano de carbono do solo no norte da Amazonía (Güiana). Primeiro, examinei o efecto da riqueza de especies das comunidades de mamíferos e de árbores na composición da MOS (obxectivo 1). Segundo, explorei a influencia da diversidade de características nas comunidades de mamíferos sobre a composición da MOS, analizando se diferentes métricas de diversidade funcional poden afectar ao contido e ao tipo de MOS acumulada (obxectivo 2). Terceiro, investiguei a relación entre a diversidade das comunidades de mamíferos e de árbores e o consumo de carbono polos microbios do solo (obxectivo 3). Este estudo pretende mellorar a nosa comprensión do papel da biodiversidade na composición e acumulación da MOS, e as súas implicacións para o funcionamento dos ecosistemas, como o secuestro de carbono no solo, que contribúe a mitigar o cambio climático.

Entre 2007 e 2010 realizouse un proxecto previo no norte da Amazonía, na rexión de Rupununi en Güiana, que abarcou unha superficie de 4,8 millóns de hectáreas de sistema bosque tropical-sabana. A rexión alberga un ecosistema megadiverso con 7.112 especies de plantas e 130 de mamíferos. Os habitantes locais Makushi, Wapishana e Wai-Wai viven en zonas pouco poboadas e practican a caza, a pesca e a agricultura tradicionais. Existe a extracción selectiva de madeira para o uso local. Os solos son principalmente francos e areosos.

Durante tres anos, 345 paratécnicos locais realizaron máis de 4.625 censos de animais ao longo de 83 transectos lineais, tras seren formados para estandarizar o método de censo a distancia. Rexistráronse en total 102.044 individuos pertencentes a 48 especies de mamíferos:

19.347 individuos a través de encontros visuais directos e 82.697 individuos mediante sinais animais (cadáveres, pegadas, feces, restos de alimentos, etc.). Os datos combináronse para estimar a riqueza específica das comunidades de mamíferos a nivel de transecto. Ademais, realizáronse censos das árbores en 72 dos 83 transectos, identificando 24.552 árbores (163 taxóns en total, o 22% a nivel de xénero) de polo menos 25 cm de diámetro á altura do peito (DAP). Tamén se identificaron mensualmente todos os froitos e sementes no solo dos 83 transectos. Estimouse a riqueza arbórea de todos os transectos en función da relación entre a riqueza de froitos e sementes e a riqueza de especies arbóreas. A mostraxe do solo realizouse en 2010 ao longo dos 83 transectos. Recolléronse en total 401 mostras de solo superficial (0-10 cm) para analizar a composición da MOS, das cales 30 mostras foron seleccionadas en 30 sitios de Güiana para analizar tamén o consumo microbiano do carbono do solo.

No laboratorio, primeiro analicei a composición elemental das 401 mostras de solo (83 transectos, 6 ± 2 mostras por transecto) mediante espectrometría de fluorescencia de raios X con dispersión de enerxía (ED-XRF), para determinar a concentración dos principais elementos químicos (S, Fe, Al e Si) en mostras secadas ao aire, peneiradas (< 2 mm), e moídas finamente. Promediei os espectros e compareinos co material de referencia estándar certificado. Determinei as concentracións de C e N (principais elementos na MOS) mediante combustión, despois do secado ao forno (110°C) e o cribado das mostras. Considerei o contido total de Fe, Al, e Si, xa que tenden a acumularse ante a intensa meteorización dos solos tropicais, e tamén de N e S, como principais responsables da estabilización da MOS nos solos tropicais. Segundo, analicei a composición molecular de todas as mostras de solo mediante espectroscopia infravermella con transformada de Fourier (FTIR) combinada con reflectancia total atenuada (ATR), para identificar e cuantificar o contido relativo dos principais compostos orgánicos na MOS xunto cos principais compoñentes minerais da fracción inorgánica do solo. Procesei e estandaricei os espectros de absorbancia, e seleccionei os principais picos usando o paquete de R *{andurinha}*. Identifiquei os principais compoñentes moleculares inorgánicos e orgánicos en 15 bandas espectrais seleccionadas na rexión do infravermello (IR): cuarzo (798 e 777 cm^{-1}), caolinita (3694 , 3620 , 911 cm^{-1}) e óxidos/silicatos de ferro (530 cm^{-1}) na fracción inorgánica; compostos aromáticos e aromáticos-nitroxenados (1630 e 1550 cm^{-1}), ácidos carboxílicos e orgánicos/carboxilatos (1720 , 1710 e 1700 cm^{-1}) e compostos alifáticos (2920 , 2850 cm^{-1}), na fracción da MOS. Tamén incluí vibracións moleculares que poden solaparse con minerais de silicatos e con polisacáridos (1838 and 1823 cm^{-1}). O fraccionamento da súa varianza na análise de compoñentes principais (ACP) permite a discriminación entre os compoñentes orgánicos e inorgánicos do solo así como a solución da ACP non rotada seleccionada. Terceiro, caractericei a utilización microbiana de fontes únicas de carbono mediante ensaios con EcoPlates en 30 mostras de solo recollidas en 30 sitios de Güiana, cubrindo o rango total de carbono. Antes da inoculación, esterilicei o material (121°C , 30 minutos), e mesturei as mostras de solo (2 g) con auga ultrapura (30 mL) para logo axitalas durante 24 horas. Despois, filtrei as mostras e inoculei as microplacas para logo incubalas en escuridade (26°C). Medín os cambios no desenvolvemento da cor dos pociños debido ao consumo microbiano mediante lecturas periódicas de absorbancia a 590 nm cun lector de microplacas. Realicei lecturas dobres inmediatamente despois da inoculación, cada doce horas ata que o consumo comezou a estabilizarse, e cada 24 horas ata que non se observaron cambios en todas as microplacas (ata 332 horas).

En canto á análise de datos, primeiro analicei a composición da MOS incluíndo os principais elementos químicos (C, N, S, Fe, Al, Si) e as 15 bandas IR seleccionadas (polisacáridos, grupos carbonilo, compostos aromáticos e alifáticos, incluíndo tamén os minerais das arxilas e o cuarzo). Identifiquei os principais compoñentes da MOS a partir do

reparto de cargas das puntuacións dos compoñentes principais (CP) obtidos mediante ACP coa función principal() do paquete de R {psych}. Segundo, a partir da base de acceso aberto Amniote Life History Database obtiven tres características (lonxitude e masa corporais, e número de descendentes) para un total de 48 especies de mamíferos censadas, e usando tamén a súa respectiva abundancia por transecto, calculei 3 métricas de diversidade funcional (FD) coa función dbFD() do paquete de R {FD}: i) a riqueza funcional (FRic) que mide o volume do espazo fenotípico FD que ocupan as características das especies en cada comunidade; ii) a uniformidade funcional (FEve) que mide a uniformidade na distribución das características das especies en cada comunidade dentro do espazo fenotípico FD (tendo en conta a abundancia das especies); iii) a diverxencia funcional (FDiv) que cuantifica a disparidade na distribución das características das especies en cada comunidade dentro do espazo fenotípico FD (tendo en conta a abundancia das especies). O cálculo da diversidade funcional (FRic e FDiv) require polo menos tres características comúns para o conxunto das especies en cada comunidade. Deste xeito, non avaliei a diversidade funcional das árbores debido á falta de tres características comúns para o 46% dos taxóns de árbores na base de acceso aberto TRY Plant Trait Database. Determinei a variación no consumo microbiano de 31 fontes de carbono indicado polas Ecoplates, restando o branco (antes da incubación, T0) á cada dobre lectura de absorbancia de cada pociño (valores de densidade óptica, OD590) en cada tempo de lectura (ata 332 horas, T15). Promediei os valores de absorbancia corrixidos polo branco para cada fonte de carbono e para os últimos catro tempos de lectura por microplaca (T12-T15). Con estes datos, cuantifiquei o consumo global de carbono polos microbios do solo calculando o desenvolvemento medio da cor dos pociños (AWCD) de cada microplaca. Calculei o índice de diversidade de Shannon-Wiener (H') para medir a variedade de fontes de carbono consumidas polos microbios do solo en cada microplaca.

Para analizar os efectos das comunidades de mamíferos e de árbores sobre a composición da MOS en 83 transectos (obxectivos 1 e 2), construí tres modelos lineais mixtos (LMM) independentes usando a función lme() do paquete de R {nlme}. As variables resposta foron as puntuacións dos principais compoñentes do solo (CP1 como a variación dos compostos na fracción inorgánica, CP2 como a variación da MOS total, CP3 como a variación da MOS con grupos carbonilo e compostos alifáticos) agregadas pola media a nivel de transecto, e incluí como efectos fixos: i) a riqueza de especies de mamíferos, a riqueza de árbores e a súa interacción, e ii) as métricas de diversidade funcional de mamíferos (FRic, FEve, FDiv). Nos seis modelos incluí a vila orixe do transecto como factor aleatorio. Así mesmo, para controlar a variabilidade ambiental entre transectos incluí como covariables no modelo inicial: a distancia á aldea, á estrada e ao río máis próximos, a lonxitude, a latitude, a temperatura media anual, a precipitación anual; e tamén incluí como factor a litoloxía dominante. Para analizar os efectos das comunidades de mamíferos e de árbores sobre o consumo microbiano de carbono do solo en 30 sitios (obxectivo 3), construí dous modelos lineais xeneralizados (XLM) independentes utilizando a función glm() do paquete de R {stats}, e incluí como variables resposta cada unha das dúas métricas de consumo microbiano de carbono do solo: i) o desenvolvemento medio da cor dos pociños (AWCD) como medida do consumo global de carbono polos microbios do solo, e ii) o índice de diversidade de Shannon-Wiener (H') como indicador da variedade de fontes de carbono consumidas polos microbios do solo. Nos modelos iniciais, incluí como efectos fixos, a riqueza de mamíferos e de árbores xunto coas tres métricas de diversidade funcional de mamíferos (FRic, FEve, FDiv), e como covariables, as variables ambientais (puntuacións dos CP1 e CP2 obtidos da ACP que incluíu precipitación, temperatura, latitude, lonxitude) e a composición do solo (puntuacións do CP1 inorgánico, CP2 da MOS total e CP3 da MOS con carbonilo e alifáticos).

A composición elemental e molecular das 401 mostras de solo superficial dos 83 transectos do norte da Amazonía (Güiana) foi explicada por tres CP obtidos mediante ACP e que representaron o 67,9% da varianza total. O primeiro compoñente principal (CP1= 30,7%) describiu un gradiente de variación no contido dos minerais das arxilas (caolinita e óxidos de Fe-Al) fronte ao contido de cuarzo. O segundo compoñente principal (CP2=21,9%) reflectiu o contido de MOS total, capturando principalmente a varianza dos elementos biofílicos (C, N e S) e da MOS nitroxenada-aromática. O terceiro compoñente principal (CP3=15,3%) reflectiu esencialmente as diferenzas na composición da MOS en relación ao contido de grupos carbonilo e compostos alifáticos. O carbonilo (C=O) é un grupo funcional formado por un átomo de carbono unido dobremente a un átomo de osíxeno e que se atopa habitualmente en compostos orgánicos como ácidos orgánicos, cetonas, aldehídos, ésteres, entre outros. Os compostos alifáticos (C-H) son hidrocarburos lineais formados por cadeas de átomos de carbono (C-C) con hidróxeno unido en posicións laterais, como os alcanos (C-C), alquenos (C=C) ou alquinos (C≡C) comunmente derivados de lípidos, como aceites vexetais e graxas animais.

A primeira análise mostrou que a riqueza de mamíferos e a riqueza das árbores tiveron efectos significativos pero opostos sobre a composición da MOS. Mentres que a maior riqueza arbórea estivo relacionada cun maior contido na MOS de grupos carbonilo e compostos alifáticos, a maior riqueza de mamíferos relacionouse cun menor contido de ambos compoñentes da MOS e tivo un efecto positivo no contido total de N, S, e Fe no solo. Ademais, detectouse un efecto marxinal da distancia á aldea máis próxima e un efecto significativo da lonxitude xeográfica no contido de MOS total. En particular, o contido de MOS total aumentou cara ás áreas occidentais e marxinalmente nos transectos máis remotos de Güiana. Unha maior diversidade nas comunidades de mamíferos podería contribuír non só ao aumento do contido de N e S nos solos amazónicos, senón tamén a unha maior complexación organometálica nos solos con maior contido de Fe e Al, o que implicaría unha maior estabilidade da MOS. Pola contra, unha maior diversidade nas comunidades de árbores podería contribuír ao aumento de compostos recalcitrantes na MOS (como os alifáticos), o que supoñería unha maior retención do COS a longo prazo.

A segunda análise amosou que a diversidade de características nas comunidades de mamíferos foi máis relevante para a composición da MOS que a súa riqueza específica, e diferentes métricas da diversidade funcional dos mamíferos tiveron efectos opostos na composición da MOS. O contido de grupos carbonilos e compostos alifáticos na MOS diminuíu coa riqueza funcional dos mamíferos, pero aumentou coa diverxencia funcional dos mamíferos. O número de especies das comunidades de árbores tamén foi importante para o contido de grupos carbonilo e compostos alifáticos na MOS, e tivo un efecto oposto ao da riqueza funcional dos mamíferos e un efecto similar ao da diverxencia funcional dos mamíferos. A variación nas características das especies está relacionada co seu nivel trófico, e os animais carnívoros, fruxívoros e herbívoros xeran diferente tipo de restos orgánicos que afectan á estequiometría dos nutrientes do solo. A prea e as feces de grandes carnívoros posúen relacións C:N máis baixas, o que favorece unha MOS rica en N, mentres que o esterco dos herbívoros ten relacións C:N máis altas, o que favorece unha MOS máis rica en C. As comunidades de mamíferos nas que as características das especies están distribuídas de forma máis dispar dentro do espazo fenotípico FD, poderían contribuír a unha MOS recalcitrante rica en C (grupos carbonilo e compostos alifáticos), o que reduciría as taxas de descomposición da MOS e favorecería a persistencia do COS. Pola contra, as comunidades de mamíferos nas que as características das especies ocupan un maior volume do espazo fenotípico FD poderían contribuír a unha MOS rica en N, S, Fe, o que favorecería a estabilización da MOS.

A terceira análise revelou unha redución no consumo global de carbono polos microbios do solo coa riqueza funcional e uniformidade funcional nas comunidades de mamíferos. Isto significa que as comunidades microbianas dos solos de áreas onde as características das especies nas comunidades de mamíferos ocupan un maior volume do espazo fenotípico FD (maior riqueza funcional) e están distribuídas de forma máis uniforme no espazo fenotípico FD (maior uniformidade funcional) consomen menos carbono en global. A variedade de fontes de carbono utilizadas polas comunidades microbianas do solo diminuíu co número de especies arbóreas, pero aumentou co contido de MOS total. É dicir, as comunidades microbianas do solo consomen unha menor variedade de tipos de carbono en áreas onde as comunidades de árbores posúen un maior número de especies e onde os solos amosan un baixo contido de MOS total. Os cadáveres e residuos dos vertebrados terrestres poden favorecer a entrada de nutrientes ao solo que afectan ás relacións competitivas entre as especies de microorganismos e á estrutura das comunidades microbianas. As comunidades de mamíferos e de árbores máis diversas acumulan tipos de MOS que poden reducir o consumo global de carbono polos microbios do solo, o que podería relacionarse cunha maior especialización funcional das comunidades microbianas, pero tamén con cambios na diversidade xenética, funcional e filoxenética destas comunidades debido a procesos de adaptación local. O contido de MOS total parece favorecer unha maior variedade de fontes de carbono consumidas polos microbios do solo, o que podería relacionarse cunha menor competencia entre taxóns cando hai máis carbono dispoñible no solo. Porén, non se detectou ningún efecto dos compoñentes da MOS no consumo global de carbono polos microbios do solo, o cal adoita estar ligado á estratexia ecolóxica da comunidade microbiana mediante unha compensación entre a súa taxa de crecemento e a súa eficiencia no uso do carbono.

Para concluír, a riqueza dos mamíferos e das árbores afectan de forma diferente á composición da MOS: os mamíferos relaciónanse coa MOS rica en N, S e Fe mentres que as árbores relaciónanse coa MOS rica en compostos alifáticos e grupos carbonilo. Ademais, diferentes métricas da diversidade funcional dos mamíferos teñen efectos opostos na composición da MOS. A menor riqueza funcional dos mamíferos, e a súa maior diverxencia funcional relaciónanse cun maior contido de grupos carbonilo e compostos alifáticos na MOS, o que podería contribuír á recalcitrancia da MOS. Por último, a diversidade funcional dos mamíferos relaciónase cun reducido consumo global de carbono polos microbios do solo, mentres que a riqueza das árbores relaciónase cunha menor variedade de tipos de carbono consumidos polas comunidades microbianas do solo. Os mamíferos afectan ao funcionamento do ciclo do carbono, e os seus efectos non son redundantes cos das árbores senón, que son complementarios. Ademais, non todas as especies son igualmente importantes para o ciclo do carbono, as súas características tamén importan para o seu funcionamento, determinando os tipos de carbono acumulado no solo, que poden afectar a degradación da materia orgánica polos microbios e o almacenamento do COS a longo prazo. Dado que a actual perda de biodiversidade é particularmente prexudicial para os animais grandes e lonxevos, como moitos mamíferos, estes resultados indican que a actual crise de extinción podería derivar nun mal funcionamento do ciclo do carbono.

1 INTRODUCTION

All living beings are composed of carbon (Bar-On et al., 2018). Carbon is also present in water, soil, and the atmosphere. Carbon circulates constantly between organisms and the environment in the process known as the carbon cycle, which is the movement of carbon between the atmosphere, the biosphere, and the soil (Keenan & Williams, 2018). Plants are the main biological actors in the carbon cycle because they fix carbon from the atmosphere in their tissues. Through photosynthesis, plants grow using sunlight and capture carbon from the atmosphere, absorbing atmospheric carbon dioxide (CO₂) and using the sun's light energy to make carbon-containing molecules known as carbohydrates. Each year, plants transform atmospheric CO₂ into more than 100,000 million tons of carbohydrates (Beer et al., 2010). We find these carbohydrates usually in the roots, stems, and leaves of plants (Kozlowski, 1992). This movement of carbon between the atmosphere and plants is only one part of the carbon cycle. When plants die, carbon from their roots, stems, and leaves goes into the soil. In the soil, part of the carbon from plant materials can be modified by microorganisms to be incorporated into soil organic matter (SOM), while another part returns to the atmosphere in the form of CO₂ through respiration and microbial decomposition. The capture of carbon, which is incorporated into the biomass of organisms and the soil, implies a reduction in the amount of carbon in the atmosphere and constitutes the key role of biodiversity in the terrestrial carbon cycle (Wolters et al., 2000).

CO₂ is one of the gases in the atmosphere that contributes to climate change and the warming of our planet. In the carbon cycle before the Industrial Revolution, only two factors regulated the concentration of atmospheric CO₂: photosynthesis and geological phenomena, such as volcanic eruptions. With the onset of the industrial age, a new factor, human activity, began to disrupt the natural carbon cycle (Steffen et al., 2007). Human activities, such as the burning of wood and fossil fuels or deforestation, have contributed to the increase of carbon in the atmosphere and changed the climate (Kirschbaum, 2003). Therefore, the reduction of carbon from the atmosphere through its incorporation into living organisms and then into the soil can help mitigate climate change (Khan et al., 2021).

Tropical forests host the greatest biodiversity on the planet and are the most sensitive to climate change (Aguirre-Gutiérrez et al., 2022; Raven et al., 2020). Tropical forest trees are fundamental to the carbon cycle as they capture much of the carbon from the atmosphere and regulate the climate (Locatelli et al., 2015; Poorter et al., 2015). But forests are not only made up of plants. Many other forest organisms play an important role in the carbon cycle (Filser et al., 2016; Nielsen et al., 2011; Tanentzap & Coomes, 2012). Indeed, the diversity of mammals in the Amazon influences the carbon cycle (Sobral et al., 2017), and the loss of large vertebrate diversity can affect carbon storage in tropical forests (Bello et al., 2015; Culot et al., 2017). The study of the relationships between biodiversity and the environment in which it lives is key to understanding the ecological role that species play in the functioning of ecosystems. When many different species make up an ecosystem, a greater number of ecological roles or ecosystem functions are developed and, therefore, the ecosystem is healthier and more resistant to environmental disturbances (Eisenhauer et al., 2019). Biodiverse ecosystems can provide important services to humanity, such as carbon sequestration in biomass and soil. Therefore,

biodiversity captures carbon and reduces its concentration in the atmosphere, and this reduction of atmospheric carbon helps mitigate climate change (Lal, 2004).

Global biodiversity loss can threaten the ability of ecological communities to capture resources and produce biomass, which directly affects carbon sequestration in forests (Cardinale et al., 2012; Dirzo et al., 2014; Poorter et al., 2015). Biodiversity also affects soil nutrient transfer and SOM mineralization (Andriuzzi & Wall, 2018; Ayres et al., 2004; Rousk et al., 2016; Roy & Bagchi, 2022). Biodiversity effects on the carbon cycle have been classically investigated on plants, since they primarily capture carbon in their biomass, through photosynthesis, and in the soil, through their plant materials (Butt et al., 2015; De Deyn et al., 2008; Mildrexler et al., 2020; Poorter et al., 2015). However, during the last few years, research has revealed a link between mammal diversity and carbon concentration in tree biomass and soil, mediated by trophic interactions (Bello et al., 2015; Sobral et al., 2017). But not only species diversity, also trait diversity within ecological communities, that is the functional diversity, may influence ecosystem functioning, such as carbon cycling (Sobral et al., 2023; Tilman, 2001). Animal species involved in different trophic interactions can display different combinations of traits and generate different types of organic inputs to the soil when they feed (Andriuzzi & Wall, 2018; Cromsigt et al., 2018; Kristensen et al., 2022). Indeed, animal products (feces, urine, carrion) vary in chemical composition, and this variation can affect soil carbon and nitrogen content and soil microbial diversity and activity (Benbow et al., 2019; Buscardo et al., 2022; Carter et al., 2007; Gharajehdaghpour et al., 2016; Hawlena et al., 2012; Le Roux et al., 2008). Animals also modify the structure and composition of plant communities (Paine et al., 2016; Souza et al., 2022), and transport and homogenize materials (Berzaghi et al., 2018; Nummi et al., 2018; Pringle et al., 2023). As a result, animals can shape soil biogeochemistry (le Roux et al., 2020; Monk & Schmitz, 2022) and promote high nutrient inputs to the soil of ecosystems that can affect SOM (Barton et al., 2019; Lang et al., 2021; Lovich et al., 2018; Macdonald et al., 2014; Nummi et al., 2018). This highlights the need to explore the role of mammal communities in the composition of SOM.

Some molecular components of SOM determine its resistance to microbial decomposition (SOM recalcitrance), such as aliphatic compounds being complex and hardly decomposed, and carbonyl groups being partially decomposed (Gunina & Kuzyakov, 2015; Lorenz et al., 2007; Pérez et al., 2002). Thus, soil organic carbon (SOC) persistence (long-term storage) relies on the molecular complexity and diversity of SOM (Yang, Jansen et al., 2022). The composition of mammal organic inputs, influenced by the diversity of species and their traits, may have consequences on SOM recalcitrance and thus on SOC persistence, which largely depends on SOM stabilization through strong organo-mineral associations, less amenable to microbial attack (Feng et al., 2014; Lehmann & Kleber, 2015; Tamrat et al., 2019). Studying SOM composition improves our understanding of SOC persistence and SOM stabilization and thus, provides more accurate predictions of carbon sequestration and climate change impacts (Heckman et al., 2022; Mikutta et al., 2006; Six et al., 2002). As not all forms of carbon are equally resistant to microbial mineralization, understanding the relationships between the diversity of mammal species and their traits and the type and content of SOM accumulated in the soil will help to understand the mechanisms responsible for the existing relationship between mammal diversity and carbon accumulation in Amazonian soils.

We know that in the northern Amazon, mammals contribute to soil carbon concentration, through their organic inputs from feeding interactions with plants and other animals (Sobral et al., 2017), and that mammal and tree diversity can have complementary effects on ecosystem functioning, but also mammal diversity can interact with tree diversity (Amyntas et al., 2023; Moorhead et al., 2017; Souza et al., 2022; Villar et al., 2020). Clarifying the relationships

between mammal and tree communities, SOM, and soil microbial communities is key to understanding how the carbon cycle works. In this thesis, I investigated the effect of the diversity of mammal communities (considering tree diversity and environmental variability) on SOM composition and soil microbial carbon consumption at landscape scale in the northern Amazon (Guyana). This work will improve the understanding of the role of biodiversity in the carbon cycle (Domeignoz-Horta et al., 2020; Schimel & Schaeffer, 2012) and the possible implications of current changes in biodiversity on ecosystem functioning (Cardinale et al., 2012; Carmona et al., 2021; Forbes et al., 2019; Wardle et al., 2011), such as soil carbon accumulation, which helps to mitigate climate change (Lal, 2004).

1.1 EFFECTS OF MAMMAL AND TREE RICHNESS ON SOM COMPOSITION

Living organisms, such as animals, plants, and microbes, shape soil structure, nutrient transfer, and decomposition and mineralization of SOM (Ayres et al., 2010; Bardgett & Wardle, 2003; Filser et al., 2016; Roy & Bagchi, 2022). SOM is composed of carbon-based molecules. Plants are known to be major contributors to SOM and thus to soil carbon (Fornara & Tilman, 2008; Hooper & Vitousek, 1997; Sun et al., 2021). However, it has been reported that mammals also affect carbon concentration in soils by generating organic remains through trophic interactions (Sobral et al., 2017).

Mammals can influence soil composition in many ways. First, they contribute to SOM through their organic inputs, such as fecal matter, carcasses, and excretory compounds (Benbow et al., 2019). Second, their remains change the diversity (Carter et al., 2007) and activity of soil microbial communities (Le Roux et al., 2008). Third, large mammals transport and homogenize plant materials (Berzaghi et al., 2018; Pringle et al., 2023), but they also heterogenize and increase nutrient inputs to the soil (James et al., 2009; le Roux et al., 2020; Monk & Schmitz, 2022). Last, mammals modify the structure and composition of tree communities (Bello et al., 2015; Souza et al., 2022; Terborgh et al., 2018), which in turn can alter inputs to SOM and thus soil carbon accumulation.

Soil organic carbon accumulates depending on the origin (animal, plant, or microbial), composition and molecular diversity of SOM (Lehmann et al., 2020; Yang, Jansen et al., 2022). Not all carbon forms resist equally to microbial mineralization and thus, are relevant to carbon storage (Castellano et al., 2015; Gunina & Kuzyakov, 2015; Moorhead & Sinsabaugh, 2006). Thus, whether and to what extent mammal diversity, interacting with plant diversity, actually affects SOC will depend on the composition of SOM sourced by animal activities (Kristensen et al., 2022). For example, polysaccharides and proteins are labile SOM components rapidly and easily mineralized by soil microbes into CO₂ (Miltner et al., 2012), while lignin, O-alkyl and aliphatic compounds are slowly and less efficiently degraded by microbes, accumulating as recalcitrant SOM (Lorenz et al., 2007; Mikutta et al., 2006). Plant materials are primarily composed of polysaccharides, i.e., labile C-rich SOM, and lignin, i.e., recalcitrant C-rich SOM (Kögel-Knabner, 2002). In contrast, mammal feces and urine provide N inputs to soil (le Roux et al., 2020; Villar et al., 2021) and their carcasses provide a varying source of amino acids and ammonium (Barton, 2015; Macdonald et al., 2014; Towne, 2000). Moreover, keratin is an S-rich fibrous protein present in hair, nails, horns, and feathers (Marshall et al., 1977) or chitin is an N-rich polysaccharide present in arthropods, and both difficult SOM decomposition by microbes (Fine et al., 2018; Forbes & Carter, 2015; Quaggiotto et al., 2019). Therefore, differences in composition between animal- and plant-derived SOM could have different effects on soil carbon mineralization and sequestration (Christensen, 2020; Lorenz et al., 2007).

I investigated the effects of mammal and tree diversity on SOM composition at a large scale in the northern Amazon, an increasingly threatened megadiverse region that has

historically acted as a carbon sink (Denning, 2021). The diversity of mammal and tree communities may have differing effects on SOM content and type, due to differences in organic inputs derived from plants versus animals. Understanding the relationship between mammal diversity and SOM accumulation in Amazonian soils can enhance our comprehension of the carbon cycle and the consequences of biodiversity loss on ecosystem carbon sequestration, that helps mitigate climate change (Lal, 2004).

1.2 EFFECTS OF MAMMAL FUNCTIONAL DIVERSITY ON SOM COMPOSITION

Functional diversity measures the variation of species traits within an ecological community (Petchey & Gaston, 2006), and links to ecosystem functioning (Krause et al., 2014). Some traits are directly linked to the amount of carbon accumulated (e.g., body size) or the time of accumulation (e.g., longevity) in the organism of species (Luyssaert et al., 2008). Others are related to the type of feeding interactions between species (e.g., herbivory, carnivory, frugivory) that relate to carbon flows in the ecosystem (Ayres et al., 2010; Forbes et al., 2019; Schmitz & Leroux, 2020).

Carbon economics shapes trait combinations that species can display (Blumstein et al., 2022; Castorena et al., 2022). In fact, combinations of traits are associated on the one hand with the life-history of species, from slow to fast strategies, and on the other, with the capture and use of resources, from conservative to acquisitive strategies (Brown et al., 2018; Capdevila et al., 2020; Robert Burger et al., 2021). Both dimensions are related to the reserves and flows of matter and energy –mainly carbon– of ecosystems, such as biomass and productivity (Enquist et al., 2020; Hatton et al., 2015, 2019). In addition, mammal species differ in body size and mass, reproductive strategy, feeding preferences, and daily activity (Capdevila et al., 2020; Flynn et al., 2009; Gorczynski & Beaudrot, 2021; Hempson et al., 2015; Junker et al., 2023). All this diversity of traits within mammal communities, i.e., functional diversity, may constitute another mechanism that would relate mammal diversity to carbon cycling (Sobral et al., 2023).

Variation in traits among species within a community (e.g., among herbivores, carnivores, omnivores, and insectivores) influences the types of trophic interactions and the types of organic remains that animals produce through their feeding activities (Andriuzzi & Wall, 2018; Cromsigt et al., 2018; Kristensen et al., 2022). Thus, the trophic level of the species will be related to the content and type of composition of their organic inputs to the soil. For example, carnivorous animals produce feces with a lower C:N ratio than frugivorous or herbivorous animals. Indeed, herbivore dung has a similar C:N ratio to that of leaves, while carnivore feces have a much more optimal C:N ratio for microbial growth (Benbow et al., 2019). Large mammal herbivores generate large organic inputs that affect soil nutrient stoichiometry (Hempson et al., 2015; le Roux et al., 2020; Pringle et al., 2023). Large mammals are key components of the tropical forest fauna, including felid and canid predators, frugivorous primates and ungulates, folivores and herbivores, among others (Fragoso et al., 2016, 2019). The organic remains collectively generated by these mammal communities can alter carbon inputs to the soil and affect soil organic matter composition.

Thus, trait variation within ecological communities can affect carbon acquisition and retention in the species' organisms, influencing carbon flows and accumulation in soil (Sobral et al., 2023). Furthermore, mammals differ in their ability to digest complex C-rich organic compounds (as aliphatic and carbonyl compounds) that may contribute to SOM recalcitrance, reducing SOM decomposition by microbes and favoring soil organic carbon accumulation (Bardgett & Wardle, 2003; Sitters et al., 2017; Stevens & Hume, 2004). Thus, trait diversity in mammal communities may lead to differences in SOM composition, with potential impacts on microbial decomposition rates and SOC persistence (Lehmann et al., 2020).

I determined whether and to what extent there is a relationship between mammal functional diversity and the content and type of SOM accumulated in Amazonian soils. This relationship would suggest that the functional diversity of mammal communities could affect ecosystem functions, including biogeochemical cycles, nutrient recycling, and soil carbon storage.

1.3 EFFECTS OF MAMMALS AND TREES ON SOIL MICROBIAL CARBON CONSUMPTION

Microorganisms play an essential role in the carbon cycle not only through SOM mineralization, but also through CO₂ sequestration and SOC stabilization (Miltner et al., 2012). Soil microbes — archaea, bacteria, fungi — transform organic remains into microbial biomass (Ludwig et al., 2015), and complex organic compounds, i.e., occluded carbon forms (Faber, 1979; von Lützow et al., 2006). This secondary organic matter (OM) interacts with mineral soil components, leading to the formation of stable organo-mineral associations (Kleber et al., 2015). Microorganisms also contribute to soil aggregation, which promotes physical occlusion and thus OM protection (Six et al., 2002). Both chemical and physical protection provided by microbial activity contribute to SOC accumulation.

Until now, research on microbe-soil carbon interactions has primarily focused on microbial decomposition of plant materials or compositional shifts in microbial communities as influenced by plant chemical composition, such as C:N ratio or labile versus recalcitrant C (Ayres, Steltzer, Berg et al., 2009; Bardgett et al., 1998; Chávez-Vergara et al., 2018; Orwin et al., 2006; Wang et al., 2018; Wardle et al., 2004; Yang et al., 2021). Indeed, the effects of plant diversity on SOC accumulation and soil microbial activity have been extensively studied (Angst et al., 2021; Fujii et al., 2018; Mellado-Vázquez et al., 2016; Smith et al., 2015; Yang, Poorter et al., 2022). This is because plants are the main contributors to SOC and soil microorganisms exhibit high efficacy in breaking down carbon obtained from plants (Cotrufo et al., 2013), mainly carbohydrates that they consume quickly (Gunina & Kuzyakov, 2015). The efficient utilization of carbon by microbes relies on the chemical composition of the organic inputs from plants (Castellano et al., 2015) that varies among plant species (Yang, Poorter et al., 2022). In fact, dominant tree species can favor the dominance of microbial groups specialized in degrading their tissues (Yang et al., 2021), which in turn affects SOM mineralization and stabilization. Recent research suggests that efficient microbial carbon use and diverse plant-fungal associations drive productivity and carbon flows and storage in ecosystems (Gillespie et al., 2021; Hannula & Morriën, 2022; Hawkins et al., 2023; Liu et al., 2023; Tao et al., 2023). Besides, significant evidence is available that vertebrate carcasses dramatically change the soil microbial community around them (Andriuzzi & Wall, 2018; Barton et al., 2013; Carter et al., 2007; Stokes et al., 2009) and that nutrient inputs from large vertebrates can be extremely high in some systems (Barton, 2015; Barton et al., 2019; Lovich et al., 2018; Macdonald et al., 2014). Despite this, the effect of animals and plants on soil microbial carbon consumption and SOM is still poorly understood (Benbow et al., 2019; Forbes & Carter, 2015).

Studying these relationships between mammal and tree communities and soil microbial carbon consumption is key to understanding the role of microorganisms in SOC accumulation and SOM stabilization (Domeignoz-Horta et al., 2020; Schimel & Schaeffer, 2012). Microbial communities can contribute to soil carbon accumulation because i) they are more efficient at degrading labile SOM (e.g., polysaccharides and proteins), so they grow rapidly and microbial necromass exceeds carbon losses through respiration (Miltner et al., 2012); ii) they are less able to degrade more complex SOM (e.g., lignin and aliphatic compounds) (Ludwig et al., 2015) which then accumulates in soils (von Lützow et al., 2006); or because iii) various physicochemical mechanisms that stabilize certain SOM components, limiting their biodegradability (Kleber et al., 2015).

I tested whether variation in mammal and tree communities influences carbon consumption by soil microbial communities in the northern Amazon (Goldfarb et al., 2011; Moorhead et al., 2017) with potential consequences for soil C dynamics (Schimel & Schaeffer, 2012). To this aim, I investigated the simultaneous relationships between mammal and tree diversity and soil microbial activity on the functioning of the carbon cycle.

2 OBJECTIVES

The general objective of this doctoral thesis is to investigate the effects of mammal communities on the composition of soil organic matter and soil microbial carbon consumption at landscape scale in the Amazon biome (Guyana), one of the most megadiverse regions and important carbon sinks on the planet, although increasingly threatened. The general hypothesis is that variation in species richness and trait diversity of mammals influences the content and type of organic matter incorporated into the soil and decomposed by soil microbes, potentially affecting soil carbon mineralization and sequestration.

In this thesis, I investigated the following **specific objectives**:

The **first specific objective** is to analyze the relationship between species richness in mammal communities and SOM composition. I investigated whether and how mammal richness (considering tree richness and environmental variability) influences the molecular and elemental composition of SOM across 83 transects in the northern Amazon. The hypotheses formulated for this first objective are: i) SOM content varies according to the number of species within mammal and tree communities, ii) mammal and tree richness also affect the type of SOM accumulated, iii) the effects of mammal and tree richness on SOM composition are different from each other.

The **second specific objective** is to assess whether the functional diversity, i.e., the diversity of species traits, within mammal communities is also relevant for SOM composition in these Amazonian soils. For this aim, I analyzed the effects of different metrics of functional diversity (functional richness, functional evenness, and functional divergence) within mammal communities (considering mammal and tree richness and their respective interaction) on the content and type of SOM accumulated across 83 communities in the northern Amazon. The hypotheses evaluated in this second objective are: i) functional diversity in mammal communities affects the content and type of SOM, and ii) different metrics of functional diversity in mammal communities affect SOM composition differently.

The **third specific objective** is to investigate the relationship between mammal communities (considering tree communities and environmental variability) and carbon consumption by soil microbial communities. In particular, I analyzed experimental data of soil microbial carbon consumption (indicated by Biolog Ecoplates) and SOM composition (assessed by soil molecular and elemental analyses) combined with observational data on mammal and tree diversity (mammal and tree richness, mammal species abundance) and open-access data on mammal traits across 30 communities in the northern Amazon. The hypotheses tested in the third objective are: diversity of mammal and tree communities influences i) overall microbial carbon consumption, and ii) the variety of carbon sources consumed by soil microbial communities.

3 METHODOLOGY

3.1 STUDY AREA

The fieldwork was conducted between 2007 and 2010 in the context of a previous international citizen science project in the northern Amazon, in the Rupununi region of Guyana (Figure 1) (Sobral et al., 2017). The study covers an area of 4.8 million ha of forest-savanna system, with a humid tropical climate (Hijmans et al., 2005), and an environmental range of elevation (71-798 m.a.s.l.), temperature (23-27 °C), precipitation (1,205-2,416 mm), and 8 types of lithology: i) continental sands and silts under thin Tertiary cover, ii) gabbro-norite sills and large dikes, iii) granitoids, including diorite, Makarapan riebeckite granite, pyroxene granite, iv) granulites and charnockites, v) greenstone belts, mainly intermediate metavolcanics, vi) high-grade gneisses, vii) subvolcanic granites, viii) acid or intermediate volcanics (Guyana Geology and Mines Commission, 2010). The study area is located in one of the most biodiverse regions on the planet, which is home to 7,112 species of vascular plants, the Guyana Shield (Funk et al., 2007), and up to 130 species of mammals, the Iwokrama Forest (Lim & Engstrom, 2005; Pickles et al., 2011). Likewise, this is home to the Makushi, Wapishana and Wai-Wai people (Luzar et al., 2012), who live in sparsely populated areas (from 122 to 1,192 people per village, Luzar et al., 2011) and practice traditional hunting, fishing and agriculture (Iwamura et al., 2014; Read et al., 2010). Selective timber extraction exists only for local use and most habitats within the study area are well preserved (Cummings et al., 2015, 2018). Soils are mainly loam (21.77% clay - 44.34% sand - 33.87% silt) and sandy (3.5% clay - 90.5% sand - 6.2% silt) in the study area (Jiménez Espinosa et al., 2022).

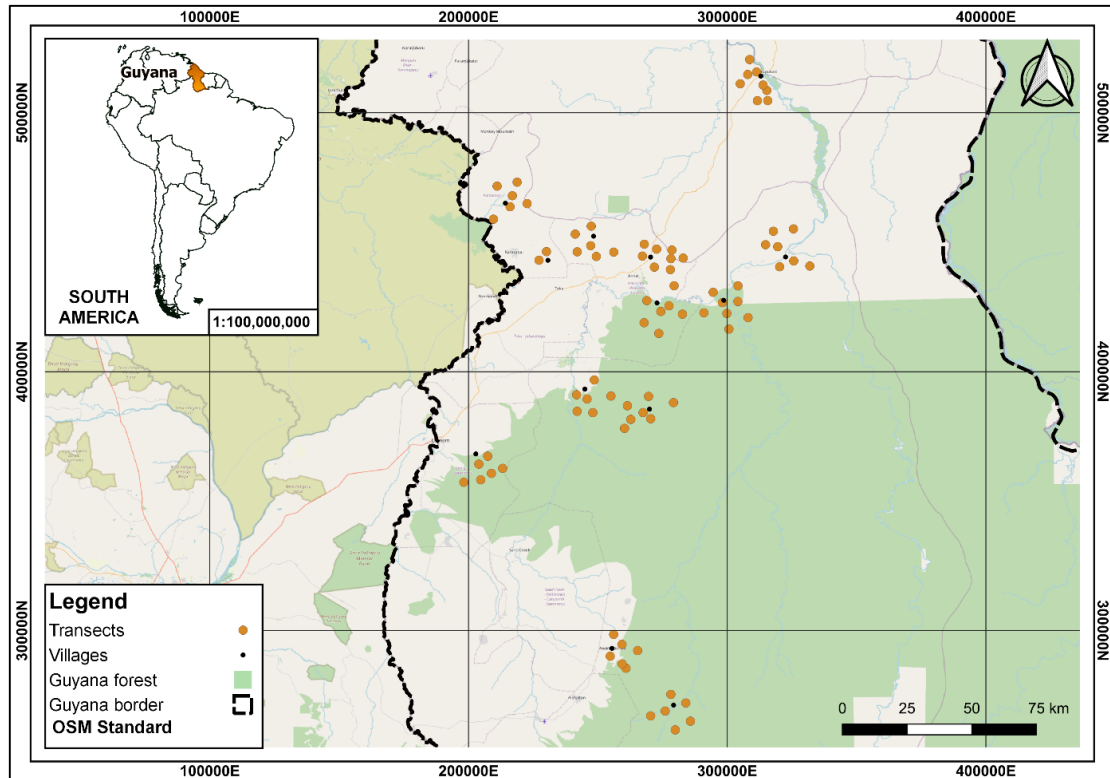


Figure 1. Map of the study area in Guyana (WGS84/UTM zone 21N), with the geographic location of the 83 transects surveyed for mammal and tree communities and soil characteristics (orange dots), by trained local paratechnicians from 13 villages (black dots) in a forest-savanna system (layer: <https://www.openstreetmap.org>, OpenStreetMap, CC-BY-SA), created with QGIS Desktop version 3.22.0 for Windows (QGIS Development Team, 2022).

3.2 FIELD PROCEDURES

3.2.1 Soil sampling

Soil sampling was carried out in 2010 along 83 linear transects of 4 km length, separated by at least 3 km from each other, and arranged around 13 villages, with an average of 6 ± 1 transects per village (83 transects were included in this thesis out of the 215 from the initial project; see Sobral et al., 2017). In total, 401 topsoil samples (from the 825 soil samples initially collected at 0-10 cm depth in 20 cm diameter excavated pits, after clearing the leaf litter from the surface) were used in this work and collected along 83 transects (6 ± 2 samples per transect), as shown in Figure 1. A total of 30 topsoil samples collected at 30 sites in the study area were selected (Figure S1, Annex A) covering the geographic and soil carbon concentration (0.2-7% C) ranges of all samples included in this thesis, to analyze soil microbial carbon consumption.

3.2.2 Mammal surveys

Over three years (2007-2010), local paratechnicians previously trained in the standard distance sampling method (Anderson et al., 1979) conducted over 4,625 animal surveys along the 83 transects, once a month by animal signs (fresh tracks, feces, hair, food remains, carcasses, burrows, diggings, etc.) and once a month by direct visual encounters during the day (Fragoso et al., 2016, 2019). To standardize the survey method, 345 indigenous people were trained in five classroom sessions and several practical field sessions (Luzar et al., 2011). A total of 102,044 individuals belonging to 48 mammal species (41 genera, 23 families, 8 orders, excluding volant and small terrestrial mammals due to the difficulty of detection; see Table S1,

Annex A) were recorded in a 1-m wide strip by direct visual encounters (19,347 individuals) and by animal signs (82,697 individuals). Both datasets were combined to estimate the species richness of the 83 mammal communities at the transect level (Sobral et al., 2017), as this provides more complete information on the ecology of the species, considering both diurnal and nocturnal, arboreal and terrestrial (Fragoso et al., 2016). At 30 sites selected to assess soil microbial carbon consumption, a total of 38,630 individuals belonging to 45 mammal species from 38 genera (Table S2, Annex A) were recorded in 1,705 animal surveys conducted biweekly over 3 years by direct visual encounters (7,252 individuals) and by animal signs (31,378 individuals).

3.2.3 Tree surveys

Local paratechnicians previously trained in tree surveys and supervised by an expert botanist (Luzar et al., 2011) recorded 24,552 trees with at least 25 cm of diameter at breast height (DBH) and belonging to 163 taxa identified at species or genus level (127 species, 109 genera, 37 families, 15 orders, see Table S3, Annex A) in 72 of the 83 transects within a 10 m band (Cummings, 2013; Cummings et al., 2018; Cummings & Read, 2016). 22% of the 163 taxa surveyed were identified only to the genus level. In addition, all the fruits and seeds on the ground in 83 transects were identified in a 1-m-wide strip monthly (May 2007 - June 2010). Tree richness of the 11 transects without direct identification of all tree species was estimated based on the relationship found between fruit and seed richness and tree species richness for all the transects (see Sobral et al., 2017). At the 30 sites selected for the assessment of soil microbial carbon consumption, 8,320 trees with DBH > 25 cm were identified (25% of the tree taxa were surveyed only at the genus level, i.e., 32 out of 144 tree taxa surveyed in total, see Table S4, Annex A). Fruits and seeds on the ground were also identified on the 30 transects once a month for 3 years along a 1-m-wide strip. Both datasets were used to estimate tree richness in all transects.

3.3 LABORATORY PROCEDURES

3.3.1 Soil geochemical analysis: Elemental composition

The quantitative elemental composition of 401 soil samples from the 83 transects was analyzed by energy dispersive X-ray fluorescence spectrometry (ED-XRF), using a XEPOS spectrometer (Ametek Corporation). Spectrometer detects fluorescent X-rays emitted from a sample surface, first excited by X-rays, differentiates the emissions with an analytical crystal, and determines the concentration of the main chemical elements (such as S, Fe, Al, Si considered for this work). This technique allows the identification and quantification of the elemental composition of the soil samples. First, each sample was air-dried, sieved (<2 mm), finely ground (1.00-3.00 g), and compressed with a plunger (250-260 gm force) into a Teflon cup with a prolene membrane at the bottom (Illustration 1). The ED-XRF spectra obtained from 4 points in each cup were averaged and compared with the values obtained when measuring the certified standard reference material (NBS-1572; Gaithersburg MD). Only the total content of S, Fe, Al, and Si obtained by ED-XRF spectrometry was considered for this work: Fe, Al, and Si are elements that tend to accumulate under the intense weathering of tropical soils, both as resistant primary minerals (Si in quartz) and secondary phases (oxy-hydroxides of Fe and Al) (Souza et al., 2017); but also N and S are elements present in mineralized soil organic matter (SOM) of tropical soils and that can interfere with C accumulation during SOM formation (Tipping et al., 2016). In addition, the concentrations of C and N (major bioelements in SOM) were determined in all samples, after oven drying (110°C), sieving (<2 mm), and weighing with a microbalance (+0.0005 mg) by combustion using a CNH analyzer type Carlo Erba NA-1500

(see Sobral et al., 2017). The concentrations of these six main elements (C, N, S, Fe, Al, Si) were centered log-ratio (CLR) transformed prior to principal component analysis (PCA) to facilitate the interpretation of the distribution of factor loadings (Aitchison, 1984).

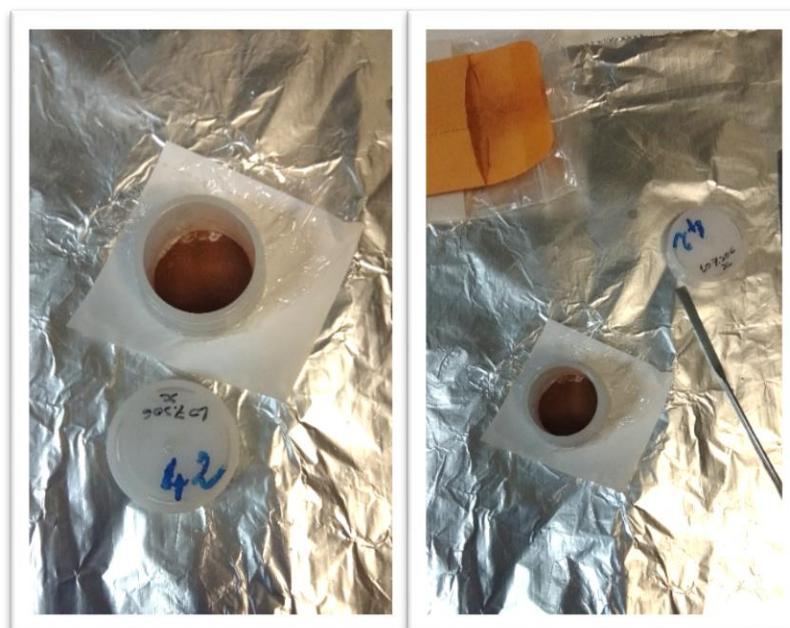


Illustration 1. Elemental composition analysis. Cup with a prolene membrane on the bottom used for analyzing the soil samples by ED-XRF spectrometry.

3.3.2 Soil spectroscopic analysis: Molecular composition

The absorbance spectra of the 401 soil samples were obtained by Fourier transform infrared (FTIR) spectroscopy combined with attenuated total reflectance (ATR), using an AGILENT CARY 630 FTIR spectrometer (Agilent Technologies Inc., Illustration 2a) and the MicroLab FTIR software provided with the equipment (Illustration 2b). This technique allows the identification of soil molecular composition from the characteristic molecular infrared (IR) vibrations that are detected when a soil sample is exposed to mid-infrared radiation, and also quantifies the relative content of the main functional groups and organic compounds in SOM along with the mineral components of the soil inorganic fraction (Martínez Cortizas et al., 2021). A total of 100 scans per sample were performed between a wavelength range of 4000-400 cm^{-1} (mid-infrared region) with a spectral band resolution of $\pm 4 \text{ cm}^{-1}$. The absorbance spectra of all the samples were standardized (standardization of the z-scores by subtracting the mean and dividing by the standard deviation; $Z=(\mu - n)/\sigma$; see Figure 2a) and the main absorbance peaks were selected (using the sum of the second derivative spectra; see Figure 2b) with the {*andurinha*} R package developed specifically for it (Álvarez-Fernández & Martínez Cortizas, 2020). This simple and fast routine determines the wavenumbers of the main absorbance peaks and provides the standardized values for each IR band/peak and sample, as well as the average and standard deviation spectra for all the samples (see Figure 2c).

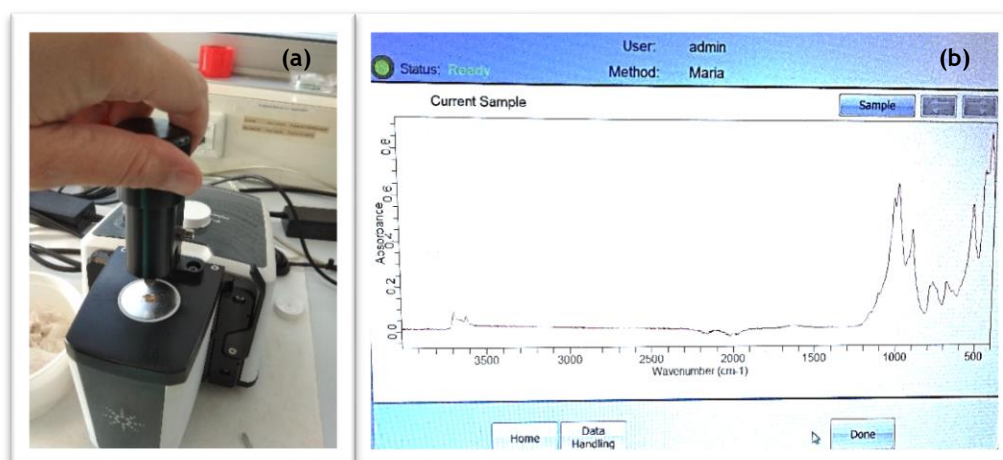


Illustration 2. Molecular composition analysis. AGILENT CARY 630 FTIR spectrometer to analyze the soil samples by FTIR-ATR spectroscopy (a) and soil absorbance spectrum after measuring with the MicroLab FTIR software provided with the equipment (b).

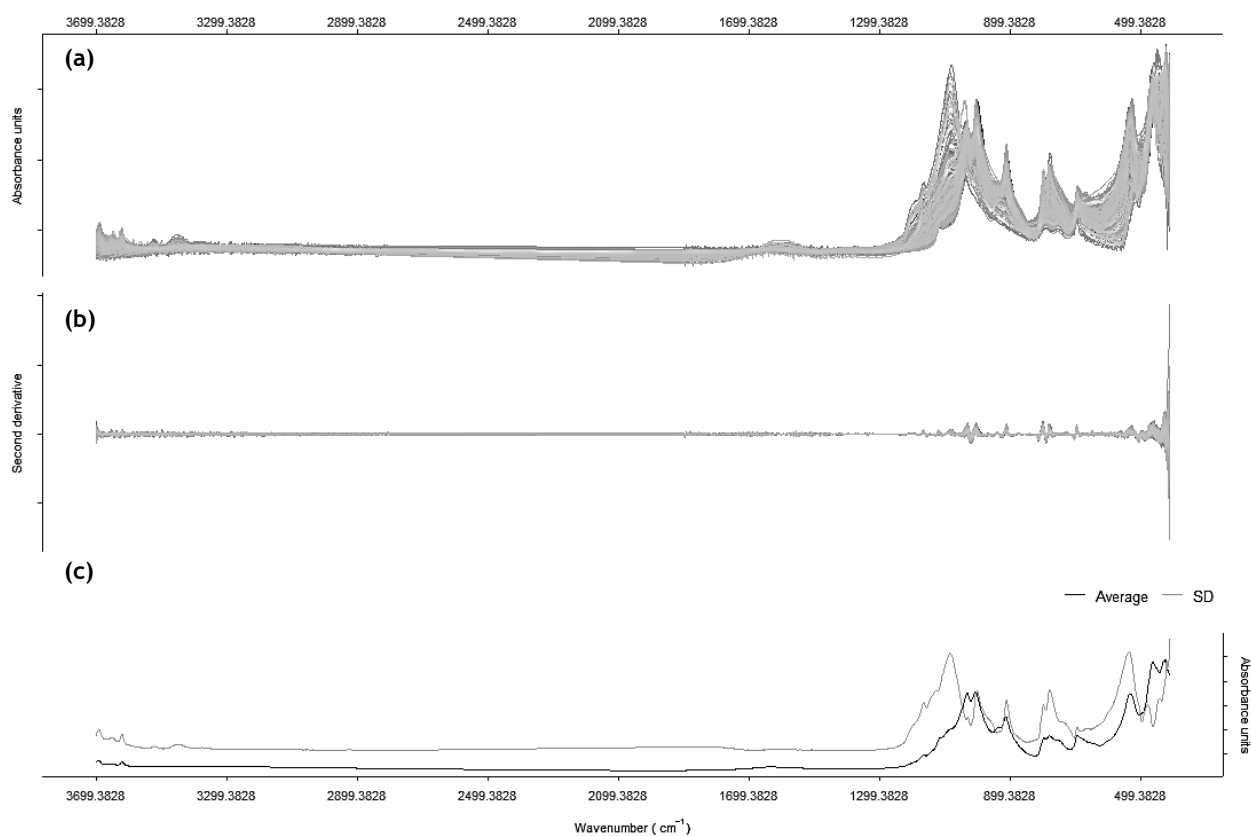


Figure 2. Molecular composition analysis. Standardized (a), second derivative (b), average and standard deviation (c) spectra obtained using the *{andurinha}* R package, for all soil samples analyzed by FTIR-ATR spectroscopy.

To characterize the main inorganic and organic molecular components of the soil samples, 15 spectral bands in the mid-infrared region were selected after identification from the existing literature: quartz (798 and 777 cm^{-1}), kaolinite (3694, 3620, 911 cm^{-1}) and iron oxides/silicates (530 cm^{-1}) as dominant primary and secondary minerals in the inorganic fraction (Müller et al., 2014); while aromatic and aromatic-nitrogenated compounds (1630 and 1550 cm^{-1}), carboxylic acids/carboxylates (1720, 1710 and 1700 cm^{-1}) and aliphatic compounds (2920, 2850 cm^{-1}) as the main molecular components of SOM (Coates, 2006; Larkin, 2011; Socrates, 2001). Therefore, we can determine not only the content of SOM in these soils (total SOM represented by the total content of C, N and S), but also the type of SOM that accumulates rich in C (aliphatic, carbonyl, and aromatic SOM) or N (amides from proteins). Molecular vibrations at 1838 and 1823 cm^{-1} were also included because they can result from the overlap of both, silicate minerals (Si-O vibrations) and polysaccharides (C-O vibrations), a typical plant-derived and labile SOM component that is not easy to identify in mineral soils (Tinti et al., 2015) and is usually depleted in tropical soils due to intense SOM transformation by microbes (Hoyos-Santillan et al., 2015; Nacro et al., 2005). However, the fractionation of their variance in the principal component analysis (PCA) enables to discriminate between both soil components as well as the selected unrotated PCA solution.

3.3.3 Microbial substrate utilization

Microbial substrate utilization was assessed in 30 topsoil samples collected at 30 sites in the study area (Figure S1, Annex A), and selected covering the range of soil carbon content in all the samples included in this thesis ($n=401$). The 30 samples were also air-dried, sieved, and finely ground for analysis of elemental composition (by ED-XRF spectrometry and CNH analysis) and molecular composition of SOM (by FTIR-ATR spectroscopy). Soil sample preparation followed standard protocols (Anderson & Ingram, 1993; Kohler et al., 2005) but the microbial communities analyzed in this study may differ from those we would find in situ, as the soil samples analyzed were stored in air-dried conditions for years. Although soil desiccation may reduce microbial activity (Erich & Hoskins, 2011), this would affect all samples equally and is less likely to affect microbial community structure (Wang et al., 2021).

The carbon substrate utilization profile (Garland & Mills, 1991; Insam, 1997; Insam & Goberna, 2008) of the microbial communities present in 30 soil samples was assessed by using Biolog® EcoPlates™ (Biolog Inc.). This is a redox-based technique that allows the characterization of microbial consumption of 31 sole carbon sources replicated in three wells and belonging to six carbon guilds (Dobranic & Zak, 1999). Changes in well color development over time were measured by periodic readings of absorbance at a wavelength of 590 nm (optical density, OD590 values) as an indicator of microbial consumption of the carbon sources per microplate. Three wells for water were also included (i.e., 96 wells per microplate, see Figure S2, Annex A) as a control for chemical degradation (Lagomarsino et al., 2007). Each well contains tetrazolium dye which, when reduced due to microbial consumption of the carbon source, turns violet (Garland & Mills, 1991; Insam, 1997).

Before inoculation, all material was autoclaved at 121°C for 30 minutes (Pérez-Rodríguez & Martínez Cortizas, 2014), and 2g of soil samples were suspended in 30 mL of miliQ water in 50 mL Falcon tubes (Preston-Mafham et al., 2002), shaken for 24 hours at room temperature to activate microbes and homogenize samples (Piñeiro-Juncal et al., 2018), and then filtered with FILTER-LAB® 1240 paper (Filtros Anoia, S.A.) to avoid differences in absorbance values due to inoculum density (not assessed before inoculation to better reproduce the environmental conditions of the soils analyzed). The 30 microplates were inoculated using a multichannel pipette (see Illustration 3a): 93 wells with 100 μL of sample and 3 control wells with 100 μL of

miliQ water (Dobranic & Zak, 1999; Grzesiak et al., 2021; Pérez-Rodríguez & Martínez Cortizas, 2014; Piñeiro-Juncal et al., 2018), and were incubated in the dark at a constant temperature (26°C). Changes in well color development due to microbial consumption of carbon sources were measured with periodic double absorbance readings at 590 nm (Preston-Mafham et al., 2002) using a Biochrom™ model EZ Read 400 microplate reader (Biochrom Ltd.) and Galapagos for EZ Read software version 1.0.0 provided with the equipment (Illustration 3b). Readings were taken immediately after inoculation (blank, T0), at 67 hours of incubation when color development was detected in at least one of the microplates (T1), and then every 12 hours until consumption began to stabilize in most of the microplates (at 174 hours, T10), and then every 24 hours until no changes were observed in all of the microplates (at 332 hours, T15, Illustration 3c).



Illustration 3. Biolog EcoPlates assays. First, an inoculated microplate at the start of the experiment (T0) before reading the blank (a), followed by the microplate reader used for periodic absorbance readings at 590nm over the experiment (b), and the same microplate at 332h of incubation (T15), with well color development due to microbial consumption of different carbon sources (c).

3.4 DATA ANALYSIS

3.4.1 Characterization of soil composition

Chemical elements and IR bands were selected to reflect the main chemical constituents of the soils studied in terms of total content (% C, N, S) and composition of SOM (molecular organic compounds). Under the intense weathering of the tropics, primary minerals (i.e., quartz) and secondary minerals (i.e., clay minerals) accumulate. Therefore, I included the total content of Fe, Al, and Si and the IR band absorbances (kaolinite, Fe-Al oxides, and quartz) as proxies for the main inorganic components of the studied soils. The concentrations of C, N, S, Fe, Si, Al with CLR transformation (by ED-XRF and CNH analysis) and the standardized absorbance of the 15 selected IR bands (by FTIR-ATR) for all the soil samples were analyzed by PCA (Estracanholti et al., 2012) using the principal() function of the {psych} R package (Revelle, 2021). First three principal components (PCs) explained ~68% of the total variance, and the main compositional signal of each PC was identified using the distribution of factor loadings (Table S5, Annex A): PC1 (30.7%) represented the variation in the inorganic signal; PC2 (21.9%) reflected the total SOM content; and PC3 (15.3%) reflected the compositional differences in SOM with respect to the content of N, S, and Fe or carbonyl groups and aliphatic compounds. The PC scores obtained for all the soil samples (Figure S3, Annex A) were averaged at the transect level (n=83), after standardization of the IR spectra and peak selection with the {andurinha} routine, and then analyzed the effect of mammal and tree diversity on the different types of SOM and major inorganic composition obtained.

3.4.2 Assessment of functional diversity (FD)

Mammal trait data were obtained from the open-access [Amniote Life History Database](#) (Myhrvold et al., 2015), which provides a single value for each trait and species and averaged across all values collected from different authors' sources. For a total of 48 mammal species surveyed in all transects (see Tables S1, Annex A), only three continuous traits were obtained and used to assess functional diversity (Laliberté et al., 2014; Villéger et al., 2008): body length (as the body length of an adult individual in cm, from snout to tail base including head, see "adult_svl_cm": 20-60.28 cm; 2.08 ± 0.69 records), body mass (as the body mass of an adult individual in g, see "adult_body_mass_g": 175-950.000 g; 4.44 ± 2.43 records); offspring number (as the number of offspring born per litter, see "litter_or_clutch_size_n": 1-10 individuals; 3.40 ± 1.77 records). A potential limitation in this step was that the FD calculation required trait data for all species within the entire community, thus compromising the number of traits available for all mammal species surveyed. Although there is no limit on the number of traits for functional evenness (FEve), functional richness (FRic) and functional divergence (FDiv) indices rely on finding the minimum convex hull that includes all species within a community (Villéger et al., 2008).

Functional diversity (FD) was assessed in 83 mammal communities using two matrices, one with the sum of species counts per transect ($n = 102,044$ individuals) recorded in 4,625 surveys (Fragoso et al., 2016, 2019), and the other with the standardized mean values of three traits per species (body length, body mass, and offspring number) obtained from the cited open-access *Amniote* database (Myhrvold et al., 2015), for a total of 48 mammal species in all transects (41 genera, 23 families, 8 orders, Table S1, Annex A). For each mammal community, the FD space was defined as a theoretical multidimensional phenotypic space delimited by the traits of all the species within each community (Villéger et al., 2008), and three metrics of FD were calculated (Figure 3) using the function `dbFD()` of the `{FD}` R package (Laliberté et al., 2014; Laliberté & Legendre, 2010): i) the functional richness (FRic), which quantifies the volume of the multidimensional FD space occupied by the species traits of each community; ii) the functional evenness (FEve), which quantifies the uniformity of the distribution of species traits of each community within the FD space (considering the species abundances), being higher when the species traits are more uniformly distributed in the FD space; and iii) the functional divergence (FDiv), which quantifies the disparity in the distribution of species traits of each community within the FD space (considering the species abundances), being higher when more species have more extreme trait values relative to the community mean (Villéger et al., 2008). A limitation of this section was that I needed trait data for all species within each community to calculate functional diversity, which compromised the number of traits available for all species. Even so, I secured three common traits for all the species in the dataset, which are commonly used in mammal functional diversity studies (Flynn et al., 2009; Gorczynski & Beaudrot, 2021; Hempson et al., 2015) and are related to the resource use strategy (slow versus fast metabolic rate) and the longevity (short versus long lifespan) of the species, which may shape their ability to acquire and store carbon (Sobral et al., 2023). Despite having tree abundance data ($n = 24,552$ trees), I did not assess functional diversity in the 83 tree communities due to the lack of at least three traits in the open-access database [TRY Plant Trait Database](#) (Kattge et al., 2020), for 46% of tree taxa surveyed in all the transects ($n = 163$, Table S3, Annex A).

At the 30 sites selected for analysis of soil microbial carbon consumption, three metrics of FD (FRic, FEve, FDiv) were also calculated for 30 mammal communities using two matrices, one with the sum of species counts ($n= 38,630$ individuals) per transect recorded in 1,705 animal surveys conducted biweekly for 3 years (Sobral et al., 2017), and the other with the averaged species values of three continuous traits (body length, body mass, and offspring number) common to a total of 45 species surveyed in 30 mammal communities (Table S2, Annex A) and obtained from the same open-access database for mammal traits (Myhrvold et al., 2015). Despite the availability of tree abundance data ($n= 8,320$ trees), I did not assess the FD in the 30 tree communities because trait data were not available for 50% of the tree taxa surveyed ($n=144$, Table S4, Annex A) in the same open-access database for plant traits (Kattge et al., 2020).

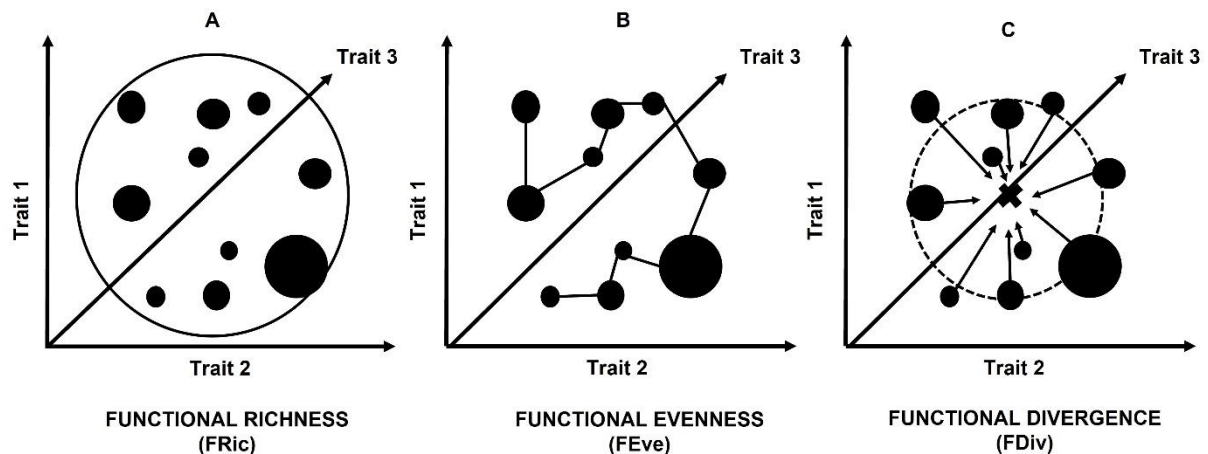


Figure 3. Conceptual explanation of each of the three metrics of Functional Diversity (FD) assessed in this study: A) Functional Richness (FRic), which measures the volume of the multidimensional FD space occupied by the species traits within each community; B) Functional Evenness (FEve), which measures the uniformity of the distribution of the species traits of a community within the FD space (considering branch distances and species abundances); and C) Functional Divergence (FDiv), which measures the degree of disparity among the species traits of each community within the FD space (considering the community mean regarding the centroid of the hypervolume occupied by species traits within each community).

3.4.3 Assessment of soil microbial carbon consumption

To obtain the variation due to microbial carbon consumption (OD590 values) during the incubation experiment (up to 332 hours, T15), the blank (before incubation, T0) was first subtracted from each absorbance reading of each well (A1-H12) at each reading time (T1-T15). Next, the blank-corrected absorbance of 2 readings from 3 wells (i.e., 6 measurements per carbon source and reading time) corresponding to the 31 carbon sources and water as control (A1, A5, A9) was aggregated by the mean. Finally, the blank-corrected mean absorbance values per carbon source were averaged for the last four reading points (T12-T15) per microplate ($n=30$). This allows for a reduction in measurement error, due to time differences in the stabilization of well color development between samples at the end of the experiment (Pierce et al., 2014). To quantify the overall carbon utilization potential per microbial community, i.e., overall microbial carbon consumption, I calculated the average well color development (AWCD) of each microplate, using the blank-corrected absorbance values of 31 carbon sources averaged for the last four reading points of the experiment (T12-T15) in the following equation (Garland & Mills, 1991; Preston-Mafham et al., 2002):

$$AWCD = \sum (R_i - C) / N \quad (1)$$

where R_i is the average absorbance per carbon source at time i (OD590 mean values after blank subtraction), C is the average absorbance of the control wells (OD590 mean values of the water after blank subtraction) and N is the number of carbon sources per microplate (31).

The Shannon-Wiener diversity index (H') was calculated as a parameter of the diversity of microbial carbon consumption, i.e. the variety of carbon sources that a microbial community can consume, as follows (Piñeiro-Juncal et al., 2018; Preston-Mafham et al., 2002; Stefanowicz, 2006; Weber & Legge, 2010):

$$H' = - \sum p_i * (\ln p_i) \quad (2)$$

where p_i is the average absorbance per carbon source i (OD590 mean values after blank correction and water values subtraction) divided by the sum of the average absorbance of all carbon sources (blank corrected and water subtracted) consumed in the microplate.

3.4.4 Statistical analysis

For all the analyses described below, the best minimum adequate model fitted by the maximum likelihood (ML) method was selected starting with an initial model (including all covariates and factors considered in the following subsections) and then using the stepAIC() function of the {MASS} R package (Venables & Ripley, 2002) for (“backward”, “forward”) stepwise selection to eliminate non-significant terms according to the AICc criterion (Burnham & Anderson, 2004), and the final model was fitted by the restricted maximum likelihood (REML) method. Before building the independent models, multicollinearity was checked using the function vif() ($VIF < 10$) of the {car} R package (Fox & Weisberg, 2019). Potential outliers were also assessed using the dixon.test() function of the {outliers} R package (Komsta, 2022). For generalized linear models (GLMs), goodness of fit and model predictive quality were evaluated by the R^2 and R^2 -adjusted, calculated using the rsq() function of the {rsq} R package (Zhang, 2021). For linear mixed models (LMMs), the marginal coefficient of multiple determination (R^2_m), which determines the amount of variation in each soil component (PC scores) explained by the fixed factors, was calculated using the r.squaredGLMM() function of the {MuMIn} R package (Bartoń, 2023). Data analysis and statistical modeling were performed in the RStudio environment (R Studio Team, 2020) for R version 4.2.1 for Windows (R Core Team, 2021). For data visualization, maps were created using the open-access program QGIS Desktop version 3.22.0 for Windows (QGIS Development Team, 2022). Other figures were generated using the ggplot() function of the {ggplot2} R package (Wickham, 2016), except for Figure S3 (Annex A), which was generated using the plot() function of the {base} R package (R Core Team, 2021).

3.4.4.1 Effects of mammal and tree richness on SOM composition

Three independent LMMs were constructed using the lme() function of the {nlme} R package (Pinheiro et al., 2023; Pinheiro & Bates, 2000), where the response variables were the mean scores of each of the three main soil components (PC1, PC2, PC3, see Table S5, Annex A) aggregated at the transect level ($n=83$), with normal error distribution and identity link function, and the village of the transect as a random factor. Species richness of mammal and tree communities and the respective interaction mammal richness * tree richness (objective 1) were included as fixed factors to separate the effects of mammal species richness from tree species richness, and their interaction. To control for environmental heterogeneity among

transects on soil composition variation, the following covariates were also included in the initial models: distance to the nearest village, the nearest road and the nearest river (m), longitude and latitude (WGS84/UTM zone 21N), mean annual temperature (°C), annual precipitation (mm). The dominant lithology in each transect (8 lithology classes) was included as a factor. All continuous variables were standardized (mean = 0; SD = 1; by subtracting the mean from the raw values and dividing by the standard deviation) to improve model convergence and to compare the relative effect sizes of continuous predictors.

3.4.4.2 *Effects of mammal functional diversity on SOM composition*

Three independent LMMs were constructed using the `lme()` function of the `{nlme}` R package (Pinheiro et al., 2023; Pinheiro & Bates, 2000) where the response variables were the mean scores of each of the three main soil components (PC1, PC2, and PC3, Table S5, Annex A) aggregated at the transect level (n=83), with normal error distribution and identity link function, and the village of the transect as a random factor. The three metrics of mammal functional diversity (FD): functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv) (objective 2), as well as mammal and tree species richness per transect and the respective interaction mammal richness * tree richness were included as fixed factors to separate the effects of mammal functional diversity from mammal and tree species richness, and their interaction. To control for environmental heterogeneity among transects on soil composition variation, the following covariates were also included in the initial models: distance to the nearest village, the nearest road, and the nearest river (m), longitude and latitude (WGS84/UTM zone 21N), mean annual temperature (°C), annual precipitation (mm). Dominant lithology (8 lithology classes) was also included as a factor. All continuous variables were standardized (mean = 0; SD = 1; by subtracting the mean from the raw values and dividing by the standard deviation) to improve model convergence and to compare the relative effect sizes of continuous predictors.

3.4.4.3 *Effects of mammals and trees on soil microbial carbon consumption*

To control for environmental variation among sites, and given the reduced number of parameters to include in the models due to sample size reasons (n=30), a principal component analysis (PCA) of the environmental variables, including longitude and latitude (WGS84/UTM zone 21N), mean annual temperature and annual precipitation, was performed using the `principal()` function of the `{psych}` R package (Revelle, 2021). The first two principal components (PCs), which explained ~80% of the total variance, were identified as the main environmental components using the factor loadings (Table S6, Annex A).

To account for the effect of SOM composition on soil microbial carbon consumption, CLR-transformed concentrations of C, N, S, Fe, Si, and Al (by ED-XRF and CNH analysis), and standardized absorbance of 15 IR bands selected as main soil molecular components (by FTIR-ATR) were included in another PCA (Estracanholli et al., 2012), using the `principal()` function of the `{psych}` R package (Revelle, 2021). The first three PCs were extracted (~68% of the total variance) and the main soil PC signals were identified by factor loadings (Table S5, Annex A).

Two independent GLMs were constructed using the `glm()` function of the `{stats}` R package (R Core Team, 2013), including as response variables: i) the average well color development (AWCD) as the overall microbial carbon consumption (n=28, 2 outliers excluded); and ii) the Shannon-Wiener diversity index (H') as the variety of carbon sources

consumed by soil microbes ($n = 30$), both with normal error distribution and identity link function (objective 3). The species richness of mammals and trees (number of species) and the interaction mammal richness*tree richness together with the three metrics of mammal FD (FRic, FEve, FDiv) were included as fixed factors in the initial models. The two main environmental components (PC1 and PC2 scores from the environment PCA) and the three main soil components (PC1, PC2 and PC3 scores from the soil PCA) were also included as covariates in the initial models. All continuous variables were standardized (mean = 0; SD = 1; by subtracting the mean from the raw values and dividing by the standard deviation) to improve model convergence and to compare the relative effect sizes of continuous predictors.

4 RESULTS

4.1 SOIL COMPOSITION

The elemental and molecular composition of the 401 soil samples was explained by three principal components, which accounted for 67.9% of the total variance (Table S5, Figure S3, Annex A). The first component was related to inorganic matter composition, while the second and third were related to soil organic matter (SOM) composition, as follows: The first component (PC1=30.7%) showed large positive loadings for infrared (IR) vibrations of secondary minerals (i.e., kaolinite and iron-aluminum oxides). Large negative loadings in PC1 were found for quartz vibrations. Thus, this component described a gradient of variation in the content of clay minerals versus quartz (PC1, Table S5, Annex A). The second component (PC2=21.9%) was related to total SOM content. This component showed large positive loadings for carbon (C), nitrogen (N) and sulfur (S) concentrations, and positive loadings for aromatic and nitrogenated-aromatic, carboxylated and aliphatic SOM, and total iron (Fe), aluminum (Al) and silicon (Si). Negative loadings were found for carbohydrates/silicates (PC2, Table S5, Annex A). The third component (PC3=15.3%) essentially reflected differences in the content of SOM rich in carbonyl groups and aliphatic compounds versus SOM rich in N, S, and Fe. This component showed large positive loadings related to carboxylic acids/carboxylates and aliphatic compounds. Positive loadings were also found for aromatic compounds and carbohydrates. Negative loadings were obtained for the total content of N, S, Fe, Al and Si (PC3, Table S5, Annex A).

4.2 EFFECTS OF MAMMAL AND TREE RICHNESS ON SOM COMPOSITION

Linear Mixed Models (LMMs) were built for the three principal components reflecting inorganic components in PC1, total SOM content in PC2, and different types of SOM composition in PC3 (Table 1). The LMM of the PC1 scores indicated that higher quartz content was associated with areas of higher precipitation, while higher clay mineral content (i.e., kaolinite and Fe-Al oxides) was associated with areas where tree richness was high (Table 1a). The LMM of PC2 scores showed that total SOM content increased towards western areas of Guyana and in more remote transects (longitude and distance to the nearest village effects, the latter was marginal, Table 1b). The LMM of PC3 scores showed that mammal richness and tree richness had opposite effects on SOM composition (Table 1c, Figure 4). Carbonyl-rich and aliphatic compounds covaried negatively with total N, S, and Fe in these soils, and the effects of trees and mammals on this covariation were opposite to each other. The content of N, S, and Fe in SOM increased with mammal diversity and decreased with tree diversity (Figure 4A, 4B). The content of carbonyl-rich SOM and aliphatic SOM increased with tree diversity and decreased with mammal diversity (Figure 4C, 4D).

Table 1: Results of Linear Mixed Models (LMMs) after reduction by minimum adequate model performed to analyze the effect of mammal and tree richness on the covariation of soil elemental and molecular composition: a) PC1, b) PC2 and c) PC3 (PC scores mean of topsoil samples aggregated per original transect) among 83 transects from 13 different villages (as random) in the northern Amazon (Guyana). In bold, all significant statistical effects ($p < 0.05$), and in italics, the marginal effects ($0.05 < p\text{-value} < 0.10$). Marginal coefficient of multiple determination (R^2_m) explains the amount of variation in each soil component (PC scores) explained by the fixed factors.

Response variable	Effects	Variance	SD	Estimate	s.e.	d.f.	Wald Chi-square	p-value
(a) Clay vs quartz content (PC1= 30.71%) <i>n</i> = 83 R^2_m = 0.313	Precipitation			-0.468	0.101	1	21.601	<0.001
	Tree richness			0.170	0.076	1	4.999	0.025
	Village (random)	0.057	0.240					
(b) Total SOM content (PC2 = 21.87%) <i>n</i> = 83 R^2_m = 0.220	<i>Distance nearest village</i>			0.107	0.062	1	2.945	<i>0.086</i>
	Longitude			0.386	0.150	1	6.669	0.010
	Village (random)	0.270	0.519					
(c) Carbonyl and aliphatic vs N-, S-, Fe-rich SOM content (PC3 =15.32%) <i>n</i> =83 R^2_m = 0.116	Mammal richness			-0.192	0.069	1	7.619	0.006
	Tree richness			0.148	0.069	1	4.527	0.033
	Village (random)	5.198E-10	2.280E-05					

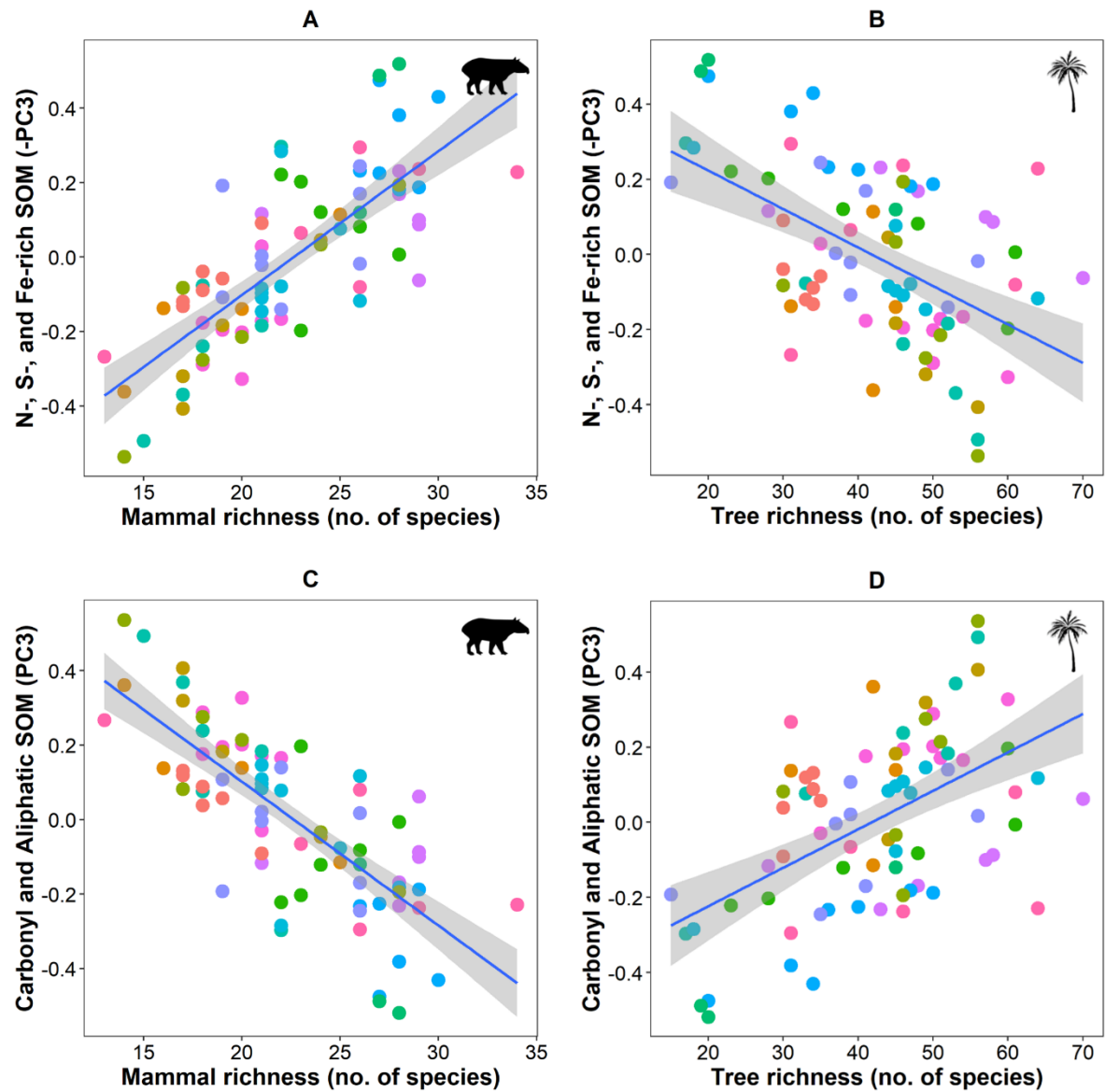


Figure 4. LMM predicted values of N-, S-, Fe-rich SOM content (-PC3) and carbonyl and aliphatic SOM content (PC3) as a function of mammal richness (A and C) and tree richness (B and D) among 83 transects in the northern Amazon (transect arrays for each village are represented by different colored dots).

4.3 EFFECTS OF MAMMAL FUNCTIONAL DIVERSITY ON SOM COMPOSITION

Total SOM content (PC2, Table 2b) increased with geographic longitude (towards western Guyana) and marginally with distance to the nearest village (towards remote areas). Carbonyl-rich and aliphatic SOM decreased with mammal functional richness (PC3, Table 2c, Figure 5A) and increased with mammal functional divergence (Figure 5B) and with tree species richness (Figure 5C). Thus, mammal trait diversity was more relevant for the content of this type of SOM composition than mammal species richness (not retained in the selected models). The number of species in tree communities had the opposite effect to that of mammal functional richness but similar to that of mammal functional divergence on PC3 (Table 2c).

Although the inorganic component in Amazonian topsoils was not the objective of this study, the LMM of PC1 was reported as well (Table 2a). A negative relationship was detected between mammal functional evenness (FEve) and the variation in the content of clay minerals (i.e., kaolinite and iron-aluminum oxides) versus quartz (PC1): topsoils had more clay minerals in transects where mammal communities showed lower functional evenness (Table 2a).

Table 2: Results of Linear Mixed Models (LMMs) after reduction by minimum adequate model performed to analyze the effect of functional diversity metrics (FRic, FEve, FDiv) calculated in mammal communities on the variation of soil elemental and molecular composition: a) PC1, b) PC2 and c) PC3 (PC scores mean of topsoil samples aggregated per original transect) among 83 communities from 13 different villages (as random) in the northern Amazon (Guyana). In bold, all significant statistical effects ($p < 0.05$), and in italics, the marginal effects ($0.05 < p\text{-value} < 0.10$). Marginal coefficient of multiple determination (R^2_m) explains the amount of variation in each soil component (PC scores) explained by the fixed factors.

Response variable	Effects	Variance	SD	Estimate	s.e.	d.f.	Wald Chi-square	<i>p</i> -value
(a) Clays vs quartz content (PC1) <i>n</i> = 83 $R^2_m = 0.330$	Precipitation			-0.410	0.094	1	19.193	<0.001
	FEve mammals			-0.195	0.075	1	6.779	0.009
	Village (random)	0.046	0.215					
(b) Total SOM content (PC2) <i>n</i> = 83 $R^2_m = 0.220$	<i>Distance nearest village</i>			0.107	0.062	1	2.945	<i>0.086</i>
	Longitude			0.386	0.150	1	6.669	0.010
	Village (random)	0.270	0.520					
(c) Carbonyl and aliphatic SOM content (PC3) <i>n</i> =83 $R^2_m = 0.184$	Tree richness			0.147	0.067	1	4.841	0.028
	FRic mammals			-0.237	0.067	1	12.587	<0.001
	FDiv mammals			0.135	0.067	1	4.035	0.045
	Village (random)	2.555E-09	5.055E-05					

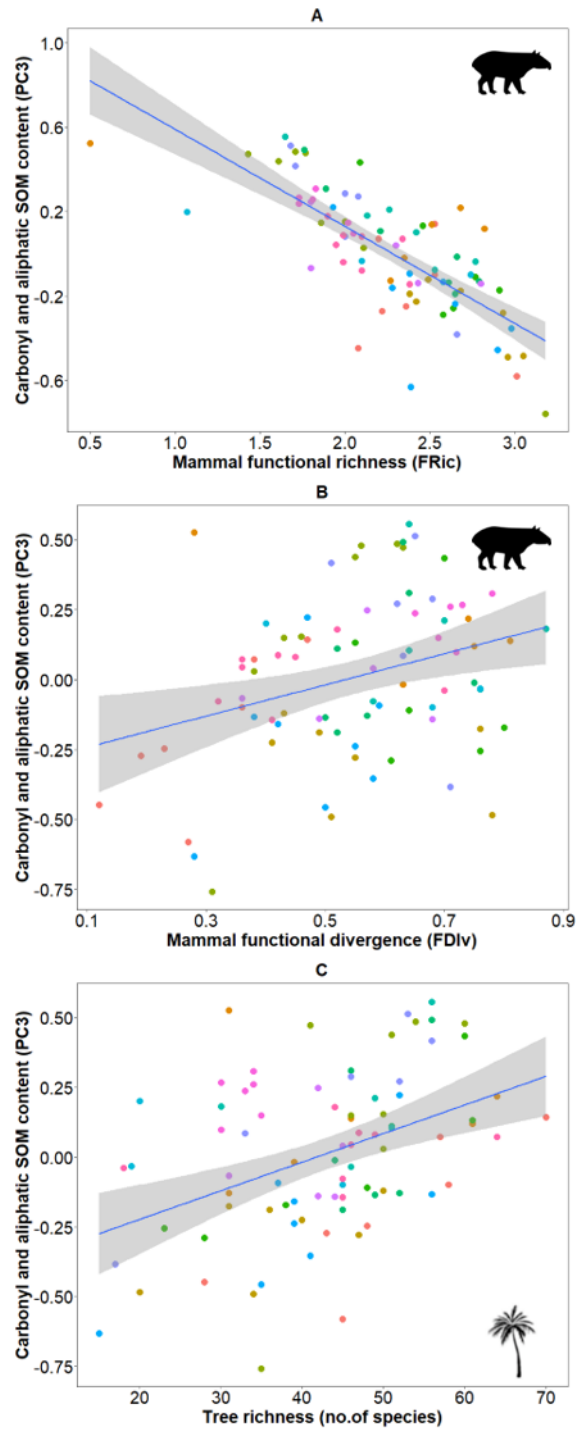


Figure 5. LMM predicted values of the carbonyl and aliphatic SOM content (PC3 scores mean per transect) in response to (A) mammal functional richness (FRic), (B) mammal functional divergence (FDiv), and (C) tree richness (no. of species) among 83 transects in the northern Amazon (transect arrays for each village represented by different colored dots).

4.4 EFFECTS OF MAMMALS AND TREES ON SOIL MICROBIAL CARBON CONSUMPTION

Overall carbon consumption by soil microbes (measured as the average well color development, AWCD, i.e., the overall carbon utilization potential) decreased in areas with higher mammal functional richness and evenness (FRic and FEve values; Table 3a, Figure 6). Lower average well color development (AWCD values) indicates lower overall microbial carbon consumption per Ecoplate. Soil microbial communities in areas with higher mammal functional richness and evenness (where species traits of mammal communities occupied a greater volume of the FD space and were more uniformly distributed within the FD space) consumed less carbon overall. A marginal and negative effect of tree richness on overall carbon consumption by soil microbes was detected (Table 3a, Figure S4, Annex A).

Variety of carbon sources consumed by soil microbes (measured as the Shannon-Wiener diversity index, H' , i.e., the diversity of microbial consumption of 31 carbon sources) decreased with tree richness (number of species) but increased with total SOM content (higher PC2 scores values; Table 3b, Figure 7). That is, soil microbial communities consumed a lower variety of carbon sources in areas where tree communities had a greater number of species and where soils contained less SOM. A marginal and negative effect of mammal functional evenness (FEve values) and soil quartz content (PC1 scores) on the variety of carbon sources consumed by soil microbes was found (Table 3b, Figure S5, Annex A). In summary, the variety of carbon sources consumed by soil microbes was lower in areas with higher tree richness, while overall carbon consumption by soil microbes was lower in areas with higher mammal functional diversity.

Of the three principal components (PCs) that explained ~68% of the variation in soil composition among samples, only the second component (PC2=22%), representing the variation in total SOM content, clearly influenced the variety of carbon sources consumed by soil microbes (Table 3b, Figure 7B). The first component (PC1=31%), describing a gradient of variation in the content of clay minerals versus quartz, was marginally related to a decreased variety of carbon sources consumed by soil microbes (Table 3b, Figure S5B, Annex A). However, no effect of organic or inorganic soil components on overall microbial carbon consumption was detected in the studied soils (Table 3a).

Table 3: Results of Generalized Linear Models (GLMs) after reduction by minimum adequate model performed to analyze the effect of tree richness and mammal functional diversity (FRic, FEve, FDiv metrics) on: (a) overall microbial carbon consumption (n=28, 2 outliers excluded), as the average well color development (AWCD), and (b) variety of carbon sources consumed by soil microbes (n=30), as the Shannon-Wiener diversity index (H'). In bold, significant statistical effects (p -value<0.05), and in italics, the marginal effects ($0.05 < p$ -value < 0.10). For minimum adequate model selection, I started from the initial models that also accounted for environmental variability (PC1: Longitude + Precipitation; PC2: Latitude vs Temperature), soil composition (PC1: Clays vs quartz, PC2: Total SOM, PC3: Carbonyl and aliphatic SOM), and mammal richness (no. of species) and the corresponding interaction with tree richness. Only the effects on both metrics of soil microbial carbon consumption that were selected by minimum adequate model are shown below.

Response variable	Effects	Estimate	s.e.	d.f.	Wald Chi-square	p -value
(a) Overall microbial carbon consumption (AWCD) <i>n</i> = 28 <i>R</i> ² = 0.359/ <i>R</i> ² -adjusted= 0.278	<i>Tree richness</i>	-0.009	0.005	1	3.376	0.066
	FRic mammals	-0.010	0.005	1	4.474	0.034
	FEve mammals	-0.012	0.005	1	6.581	0.010
(b) Variety of carbon sources consumed by soil microbes (H') <i>n</i> = 30 <i>R</i> ² = 0.290/ <i>R</i> ² -adjusted= 0.177	<i>Tree richness</i>	-0.353	0.172	1	4.193	0.041
	<i>FEve mammals</i>	-0.305	0.177	1	2.983	0.084
	<i>Clays vs. quartz content (PC1)</i>	-0.316	0.176	1	3.219	0.073
	Total SOM content (PC2)	0.371	0.172	1	4.660	0.031

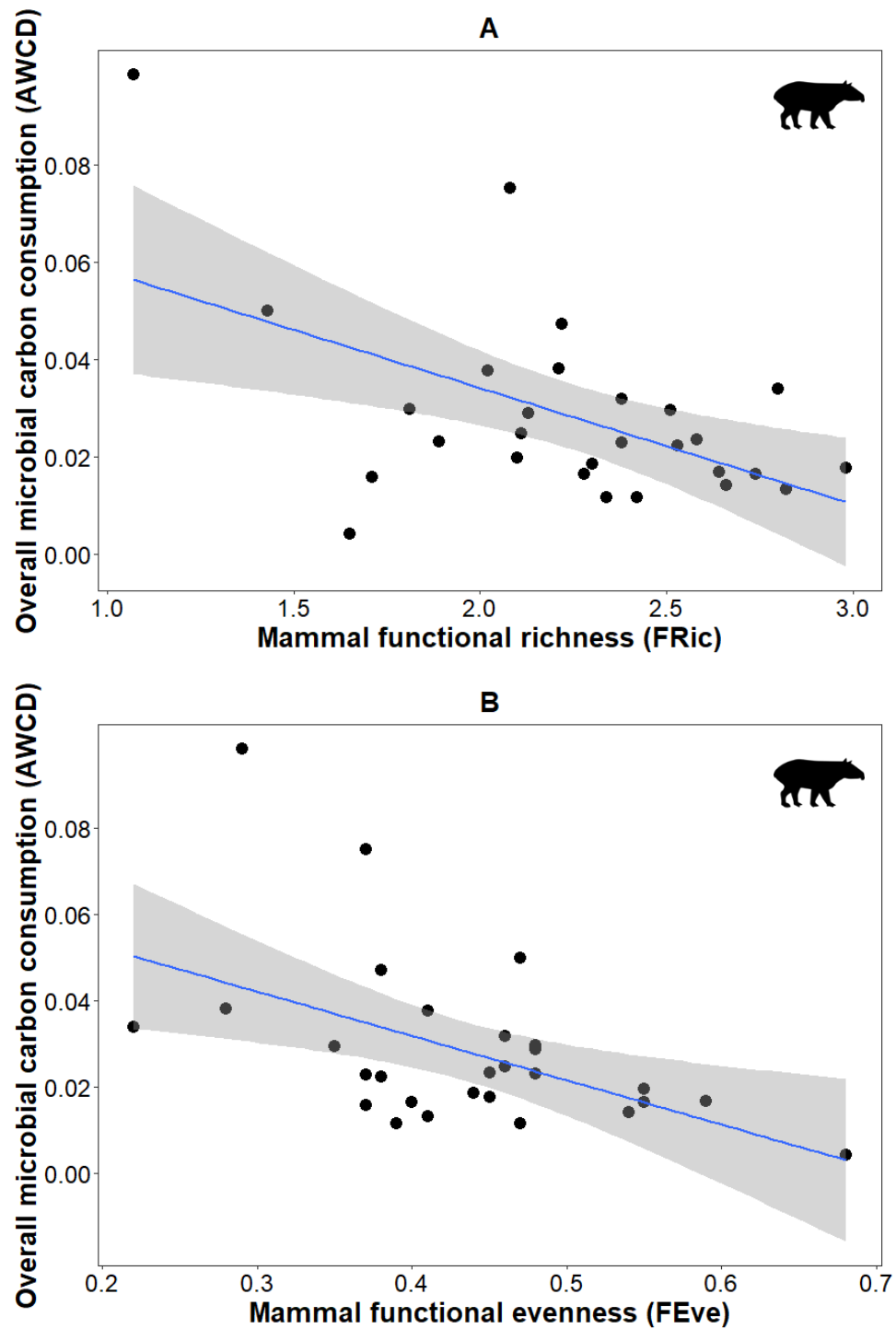


Figure 6. GLM predicted effects of (A) mammal functional richness (FRic) and (B) mammal functional evenness (FEve) on the overall carbon consumption by soil microbial communities (average well color development, AWCD).

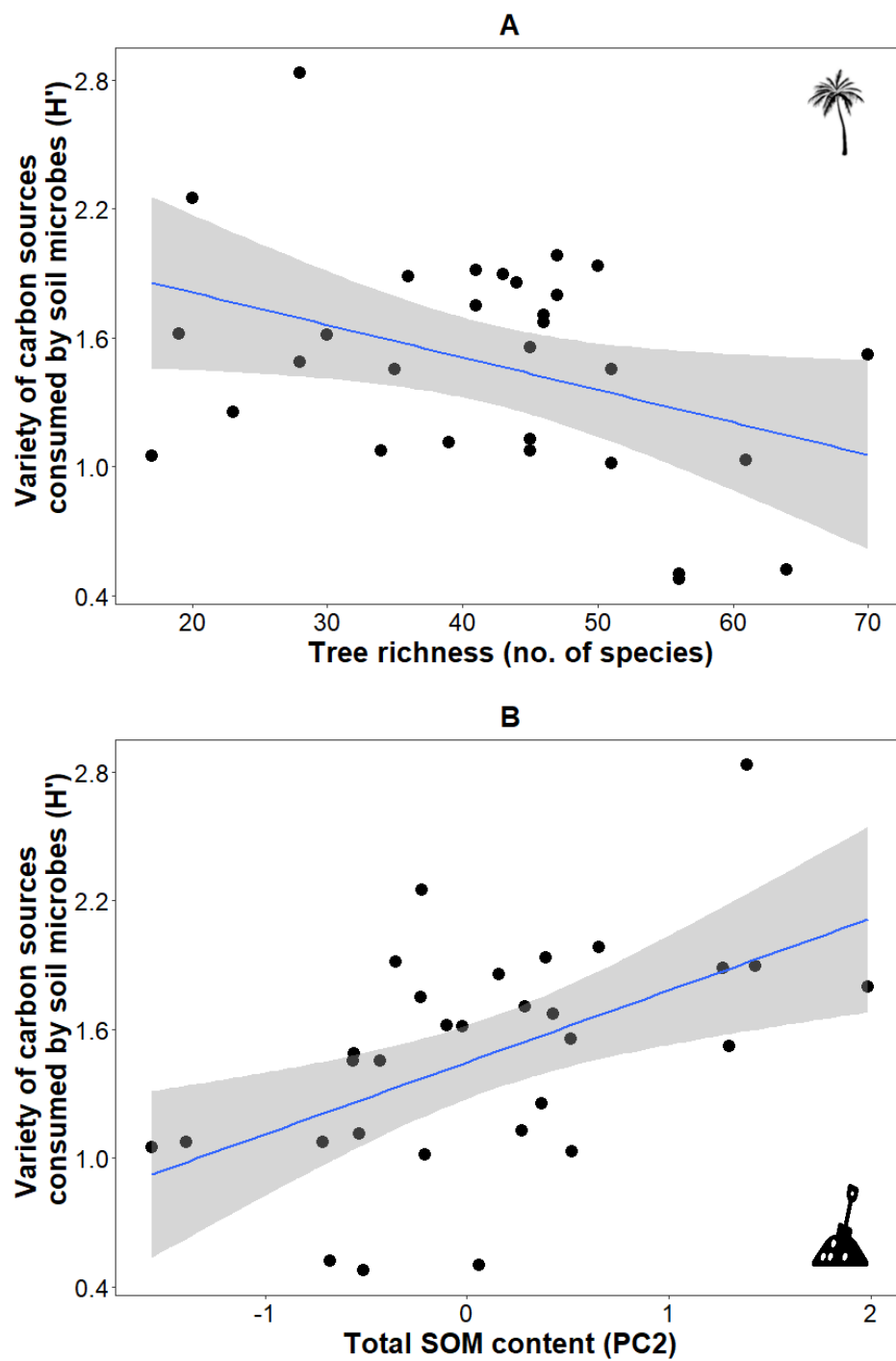


Figure 7. GLM predicted effects of (A) tree richness and (B) total SOM content on the variety of carbon sources consumed by soil microbial communities (Shannon-Wiener diversity index, H').

5 DISCUSSION

5.1 EFFECTS OF MAMMAL AND TREE RICHNESS ON SOM COMPOSITION

Mammal and tree diversity have been shown to influence key ecosystem functions, such as nutrient cycling (Estes et al., 2011; Fornara & Tilman, 2008; Furey & Tilman, 2021; Leroux et al., 2020; Schneider et al., 2016; Sobral et al., 2017). Biodiversity influences carbon (C) sequestration through several mechanisms, including the increased species productivity and resource use (Aarssen, 1997; Cardinale et al., 2011; Tilman et al., 1997). For instance, plant diversity enhances biomass production, favoring carbon capture in both biomass and soil organic matter – SOM (Cardinale et al., 2011; Cong et al., 2014; Fornara & Tilman, 2008; Poorter et al., 2015). The first results of this thesis are aligned with these findings and with recent work providing evidence that mammals, and eventually interacting with plants, impact on soil C at landscape scale (Naidu et al., 2022; Nummi et al., 2018; Roy & Bagchi, 2022; Schmitz et al., 2018). However, while mammal and tree richness are positively linked to the soil C concentration in the northern Amazon (Sobral et al., 2017), my results show that the diversity of mammal and tree communities have opposite effects on SOM composition.

Previous research had shown that this positive effect of both mammals and trees on soil C is mediated by the organic inputs generated through mammal feeding interactions with plants (Sobral et al., 2017), but now mammal and tree diversity seem to favor the accumulation of different types of SOM. On the first hand, the content of carbonyl (C=O bonds) and aliphatic (C-H bonds) compounds in SOM (PC3) increased with species number in tree communities, while it decreased with species richness in mammal communities. On the second hand, nitrogen (N)-, sulfur(S)-, and iron (Fe)-rich SOM (-PC3) increased with the diversity in mammal communities. Mammal diversity was also positively correlated with soil content of iron (Fe) and aluminum (Al), which may be related to higher organo-metal (Fe) complexation in these soils (Souza et al., 2017). Therefore, tree and mammal diversity promote the accumulation of different SOM components, thus their effects are not redundant, but rather they are complementary. That is, more diverse mammal communities contribute to an increase in N-, S-, Fe-rich SOM (likely stabilized by organo-metal complexation), while species-rich tree communities contribute to an increase in recalcitrant C-rich SOM (likely reducing SOM mineralization by microbes), both favoring soil organic carbon (SOC) accumulation.

This mammal-mediated accumulation of N and S in soils is likely related to animal organic inputs, such as carrion, hair, feces and urine (Carter et al., 2007; Kasper et al., 2012; Macdonald et al., 2014; Marshall et al., 1977). Animal tissues decompose faster than plant materials (Parmenter & MacMahon, 2009) and represent a variable source of N (Barton et al., 2019), mostly proteins and amino acids (Macdonald et al., 2014) or ammonium (Towne, 2000), which may be related to high soil N content in areas with high mammal diversity. Moreover, S-rich proteins, such as keratin from hair, nails, horns, feathers (Marshall et al., 1977), and N-rich polysaccharides, such as chitin from arthropods, contribute to more stable SOM, since they are hardly degraded by soil microbes (Fine et al., 2018; Forbes & Carter, 2015; Quaggiotto et al., 2019).

Besides, mammal diversity was also associated with higher soil Fe and Al content, which could be due to organo-mineral associations formed by co-precipitation of Al and Fe with organic compounds of dissolved SOM (Tamrat et al., 2019). Higher mammal diversity may

contribute not only to higher total N and S contents in Amazonian soils, but also to greater organo-metal complexation in soils with higher total Fe and Al contents (Singh et al., 2017; Souza et al., 2017), favoring a more stabilized SOM that enhances SOC retention, rather than being released to the atmosphere (Kleber et al., 2015; Naidu et al., 2022). In contrast, tree richness was associated with the accumulation of SOM rich in carbonyl groups and aliphatic compounds that are resistant to microbial decomposition (i.e., recalcitrant SOM). Plant diversity is known to influence nutrient transfer and soil fertility (Fujii et al., 2018; Furey & Tilman, 2021; Hooper et al., 2005), depending on the chemical composition of the organic remains derived from plant species (Lin et al., 2021). SOC accumulation is highly dependent on these plant contributions to recalcitrant SOM, which reduces SOM mineralization by microbes and enhances atmospheric C retention in soils (Lehmann & Kleber, 2015; Lorenz et al., 2007).

In the studied system, organic remains are the main contributors to soil C concentration, and they are generated through feeding interactions with plants, such as frugivory, and other animals, such as carnivory (Sobral et al., 2017). Large herbivores favor soil C by mediating N-stabilization of SOM in many systems (Naidu et al., 2022; Roy & Bagchi, 2022; Tanentzap & Coomes, 2012) and regions of high plant diversity (Maestre et al., 2022). Large frugivores concentrate ammonium and nitrates in the soil (Villar et al., 2021). Feces and urine of large mammals can generate large N inputs to soil that vary with their diet, such as frugivory or herbivory (le Roux et al., 2020; Villar et al., 2021). In contrast, carrion accumulated by large carnivores promotes rapid microbial consumption, favoring animal inputs to SOM (Gutiérrez-Cánovas et al., 2020), and their feces contain more N than those of frugivorous or herbivorous mammals (Benbow et al., 2019). Thus, the type of SOM that accumulates in the soil may also be related to the dominant trophic interactions in mammal communities (Bodmer & Ward, 2006; Forbes & Carter, 2015). This may also influence microbial activity and SOM decomposition (Benbow et al., 2019), and thus SOC accumulation.

Soil organic carbon can be retained in the soil or mineralized by microbes and released to the atmosphere as CO₂, depending on the origin (animal, plant or microbial), composition and molecular diversity of the SOM (Yang, Jansen et al., 2022). This helps to understand that different organic matter (OM) produced by mammal and tree communities contributes to different types of accumulated SOM (PC3). Higher content of carbonyl groups (C=O) and aliphatic compounds (C-H) in SOM was observed in areas with higher tree richness. Plant remains vary in content and type of carbohydrates and lipids within and between species, and polysaccharides and lignins are their major C-rich molecular constituents (Blumstein et al., 2022; Kögel-Knabner, 2002; Schoonmaker et al., 2021). Plant tissues also vary in the content and type of chemical compounds in response to the feeding activity of large herbivores (Ayres et al., 2004; Wang et al., 2018; Wardle et al., 2002). For example, plant parts avoided by herbivores concentrate more lignin, which contributes to recalcitrant SOM and makes it more resistant to microbial degradation (Wardle et al., 2002).

Likewise, tree diversity was also positively related to soil content of kaolinite and Fe-Al oxides (clay minerals, PC1), contrary to the absence or negative correlations previously found in tropical systems (de la Peña et al., 2016; Medinski et al., 2010; Mills et al., 2009). However, plants can promote clay stabilization at the soil surface by translocating nutrients they use for growth (Barré et al., 2009). In tropical forests, some tree species associated with mycorrhizal fungi in their roots can release organic acid ligands and enzymes for nutrient uptake (Fujii, 2014). If plants can increase the content of free organic acids in SOM (e.g., carbonyl groups, PC3), they may contribute to soil acidification (van Breemen et al., 1983), which favors a higher relative degree of mineral weathering, and thus greater formation of clay minerals (i.e., kaolinite

and Fe-Al oxides). Although soil inorganic composition was not the objective of the study, elements and clay minerals dominant in the studied soils were considered because they play a regulatory role in the accumulation and stabilization of SOM in tropical soils (Feller & Beare, 1997). For example, OH groups from Fe-Al hydroxides contribute to the retention of organic molecules by forming strong metal–O–C bonds (Borer & Hug, 2014; Singh et al., 2018). In this way, tree diversity may enhance the accumulation of clay minerals that could favor stabilized SOM, such as that accumulated by more diverse mammal communities.

However, animal and plant diversity did not affect SOM content (PC2). Total SOM was concentrated in soils from transects in the western part of Guyana and marginally in those furthest from human settlements. Furthermore, total SOM (% C, N, S) appears to have little influence on the variation in the content of carbonyl groups and aliphatic compounds in SOM (PC3), suggesting that SOM accumulation may depend on other processes that vary with longitude and human presence. Indeed, the density of tree biomass (wood and seeds) increases towards the center of Guyana compared to the rest of the Amazon (ter Steege et al., 2006). This could be related to higher SOM accumulation in the transects further west. Likewise, the intensity of mammal hunting decreases with the distance from the center of the villages in the study area (Read et al., 2010). This could favor the accumulation of mammal biomass (carcasses and waste products) as we move away from the villages, and more SOM accumulates overall.

5.2 EFFECTS OF MAMMAL FUNCTIONAL DIVERSITY ON SOM COMPOSITION

The analysis of functional diversity in mammal communities revealed an inverse relationship between different metrics of mammal trait diversity and the presence of carbonyl-rich and aliphatic SOM in Amazonian soils. Lower functional richness (FRic) but higher functional divergence (FDiv) in mammal communities were associated with higher carbonyl and aliphatic content in SOM. Furthermore, mammal species richness was not retained in the second models, suggesting that species traits are better predictors of variation in this type of SOM than species number in mammal communities. Consistently, trait-based measures often better predict the effects of animal communities on ecosystem functioning than species richness, such as nutrient cycling, dung removal and seed burial (Gagic et al., 2015). Likewise, mammal species richness and functional diversity are decoupled in many regions of the world. Species-rich regions harbor many trait-redundant species because species richness is more dependent on environmental factors such as available resources, while functional diversity is more dependent on evolutionary history such as evolutionary time and niche diversification (Oliveira et al., 2016). In summary, not only species diversity but also their traits influence the type and content of SOM that accumulates in these soils. This is relevant because the current loss of biodiversity due to human activities affects the largest and longest-lived species with low reproductive rates, such as many mammals (Carmona et al., 2021; Tomiya, 2013), which could lead to losses in the functional diversity of communities worldwide (Carmona et al., 2021; Toussaint et al., 2021), with consequences for the operation of the carbon cycle.

Mammal functional diversity is linked to C cycling because mammal traits, such as body size, body mass and reproductive rate, are related to ecological strategies followed by species, such as slow-fast life history and conservative-acquisitive resources use, which in turn are related to ecosystem C reserves and fluxes (Capdevila et al., 2020; Junker et al., 2023; Sobral et al., 2023). Second results also showed that mammal communities with more diverse traits (high functional richness) are positively related to SOM rich in nitrogen (N), sulfur (S), and iron (Fe), probably stabilized by strong organo-metal (Fe) associations that promote SOC persistence (Feng et al., 2014; Mikutta et al., 2006). On the contrary, mammal communities with more extreme traits (high functional divergence) contributed to recalcitrant SOM rich in

carbonyl groups and aliphatic compounds, which could reduce OM decomposition rates in favor of SOC persistence (Kristensen et al., 2022; Lehmann & Kleber, 2015). Therefore, combinations of more diverse and disparate traits within mammal communities might lead to stabilized and recalcitrant SOM that enhances long-term SOC storage (Kristensen et al., 2022; Lehmann & Kleber, 2015). This depends on the microbial response to recalcitrant SOM and its molecular complexity (Lehmann et al., 2020).

To study the mechanistic relationships between biodiversity and ecosystem functioning, it is increasingly necessary to incorporate trophic variation between species (Barnes et al., 2018; Eisenhauer et al., 2019). Heterogeneous systems show stronger positive relationships between species richness and ecosystem function, where species make a more complex use of resources and show greater variation in their traits (Barry et al., 2019; Hodapp et al., 2016). Thus, functional diversity appears to influence ecosystem function and stability (de Bello et al., 2021; Hoehn et al., 2008). At least in aquatic systems, species richness has emerged as a key measure of biodiversity related to landscape-scale C levels, and with stronger effects than functional diversity (Allgeier et al., 2015), whereas in terrestrial systems, C accumulation appears to be strongly related to functional and phylogenetic diversity (Finegan et al., 2015; Huang et al., 2018). Indeed, the results of this thesis indicate differences in the role of different mammal species in SOM accumulation at the landscape scale in the northern Amazon, such as large herbivores (tapirs, deers), large frugivores (peccaries, primates), large rodents (agoutis, squirrels; see Table S1, Annex A).

Large frugivores ingest, digest, and defecate large amounts of pulp and seeds from the fruits they consume, as well as grasses and leaves that they uproot and remove in search of food (Fragoso & Huffman, 2000; Stevenson & Guzmán-Caro, 2010). Plant materials transported by these animals are secondarily buried by beetles (Nichols et al., 2008), dispersed by rodents (Moorhead et al., 2017) or rammed and crushed by ungulates, with consequences for the soil biota (Ramirez et al., 2021). Large herbivores contribute to soil C with their dung inputs and the distribution of plant materials (Holter, 2016; Kristensen et al., 2022; Roy & Bagchi, 2022), while large frugivores increase soil N with their ammonium and nitrate inputs (Villar et al., 2021). Indeed, some models and experimental tests had shown that mammal herbivory affects soil C in grasslands (Frank et al., 2011; McSherry & Ritchie, 2013; Ritchie, 2014), depending on the intensity of herbivory (Ritchie, 2014) or the composition of the plant community (McSherry & Ritchie, 2013). In contrast, large carnivores favor a rapid accumulation of OM derived from their prey (Gutiérrez-Cánovas et al., 2020), and indirectly a rapid N mineralization by microbes (Cayuela et al., 2009). In short, large mammals transport plant and animal materials across the landscape and process them in different ways so that they can be consumed by a diversity of soil invertebrates, fungi and microbes. Then, the type of SOM accumulated by mammal communities with more diverse species (rich in N and S and poor in carbonyls and aliphatics) could also be related to the dominant trophic groups in these Amazonian communities.

Species from different trophic groups differ in their traits, and their feeding remains vary in the chemical composition, which affects C fluxes and inputs to the soil (Andriuzzi & Wall, 2018; Kristensen et al., 2022; Monk & Schmitz, 2022). Indeed, body size and body mass are associated with mammal feeding strategies that affect soil nutrient stoichiometry, such as C:N:P ratios (Hempson et al., 2015; le Roux et al., 2020). For example, carrion and feces from large carnivores have lower C:N ratios (i.e., N-rich OM), which promotes a rapid OM decomposition by microbes (Benbow et al., 2019; Hilderbrand et al., 1999), whereas dung from large herbivores has higher C:N ratios (i.e., C-rich OM), which can enhance C storage (Kristensen et al., 2022). Large herbivore dung also favors high soil N:P ratios, which can limit the availability

of soil nutrients to plants (le Roux et al., 2020; Sitters & Olde Venterink, 2021). In the studied system, the mammal communities are composed of ungulates, primates, rodents, and predators with different biomass, and across transects, the biomass of herbivores exceeds that of carnivores (Table S1, Annex A, Fragoso et al., 2016). The dominance of herbivore biomass may lead to long-term SOC persistence (Kristensen et al., 2022; Naidu et al., 2022; Schmitz & Leroux, 2020), by potentially contributing to recalcitrant (C-rich) SOM, such as that accumulated in mammal communities with more disparate traits. Furthermore, carnivory and frugivory interactions are the largest contributors to soil C concentrations in the studied system (Sobral et al., 2017), which may be related to the type of SOM (N-rich) accumulated by more trait-diverse mammal communities (Peziol et al., 2023; Villar et al., 2021). Thus, functional richness and divergence in mammal communities may differently affect SOM recalcitrance in this system, with potential consequences for microbial OM decomposition rates and SOC persistence (Lehmann et al., 2020; Lehmann & Kleber, 2015).

On the other hand, the diversity of tree traits may influence the decomposition rate of plant remains (Chávez-Vergara et al., 2018). However, the functional diversity of tree communities was not assessed in this study due to the lack of species-level traits available for the whole community. Nevertheless, tree richness was positively associated with recalcitrant SOM, which is rich in aliphatic and carbonyl compounds that are more resistant and less efficiently degraded by soil microbes (Cotrufo et al., 2013). The recalcitrant organic compounds are poorly digested by the bacterial communities in the stomach of large herbivores, and their levels in plant tissues can alter the dietary preferences of these mammals (Freeland & Janzen, 1974; Jung & Allen, 1995), thereby altering the composition of their inputs to SOM (Risch et al., 2015). The chemical composition of plants can influence the amount and composition (cellulose:lignin) of plant biomass that accumulates in the soil, thus modifying the activity of microbial communities that subsequently process this biomass (Moorhead & Sinsabaugh, 2006). In this system, carbonyl-rich and aliphatic SOM appears to be enhanced in areas with high tree richness but also high mammal functional divergence. Thus, different patterns of SOM accumulation associated with mammal and tree communities and the species traits within mammal communities can explain the inverse effect detected between mammal functional richness and tree richness on the content of carbonyl groups and aliphatic compounds in SOM. This result is also consistent with the first finding of this thesis on the complementary effects of mammals and trees on SOM composition: mammal richness is related to SOM rich in N, S, and Fe, while tree richness is related to SOM rich in carbonyl groups and aliphatic compounds.

The clay fraction of the studied soils negatively covaried with functional evenness in mammal communities. That is, the soil content of clay minerals (PC1) was higher in areas with lower mammal functional evenness, i.e., lower uniformity in the distribution of species traits in mammal communities within the FD space. Given the positive relationship found between the tree richness and soil clay content in the first analysis of this thesis, mammal communities with low functional evenness associated with tree communities with high species richness may indirectly promote the formation/accumulation of clay minerals in these soils. These clay minerals with Fe/Al oxides can potentially stabilize SOM, such as that accumulated by more diverse mammals, through organo-mineral associations that are known to be less susceptible to microbial attack (Feng et al., 2014; Singh et al., 2018).

Alternatively, environmental factors such as soil mineralogy and vegetation type may influence habitat selection by mammal species, the composition of mammal communities and thus, their trait diversity. In tropical forests, soil nutrient availability has trophic cascading effects on mammal communities, influencing mammal biomass through induced changes in tree diversity and chemical composition (Peres, 2008). Indeed, clay-rich soils are real

biodiversity hotspots in tropical forests, such as the Amazon (Blake et al., 2011; Molina et al., 2018), often used by herbivorous and frugivorous mammals as licking points to obtain minerals to complete their diet or to detoxify secondary compounds from plants (Klaus et al., 1998; Mahaney et al., 1996; Voigt et al., 2008). However, functional diversity of mammals in the tropics appears to be primarily influenced by habitat productivity and anthropogenic disturbance, rather than other factors related to tree diversity and soil clay content (Boron et al., 2019; de Oliveira et al., 2019; Gorczynski et al., 2021). Even so, the trait composition of mammal communities influences the type of SOM accumulated, which may be also related to soil clay minerals (kaolinite and Fe-Al oxides), given their stabilizing role on SOM through the OM-metal complexation with soil Fe (Singh et al., 2018).

5.3 EFFECTS OF MAMMALS AND TREES ON SOIL MICROBIAL CARBON CONSUMPTION

Traditionally, microorganisms, invertebrates, and plants have been recognized as key players in the carbon cycle (Angst et al., 2021; Ayres, Steltzer, Berg et al., 2009; Brussaard, 1997; Filser et al., 2016; Miltner et al., 2012). The relationship between biodiversity and carbon cycling is intricated due to the multiple processes and trophic levels involved in carbon fluxes and storage in soils. The third finding of this thesis was that mammal communities in the northern Amazon also influence soil microbial carbon consumption, and in a complementary manner to tree communities. This suggests that soil microbes respond differently to mammal and plant diversity. Specifically, higher functional richness and evenness in mammal communities were associated with lower overall microbial carbon consumption (lower AWCD values), while higher tree richness was associated with a lower variety of carbon sources consumed by soil microbes (lower H' values). Thus, more diverse mammal and tree communities accumulate specific types of soil organic matter (SOM) that may reduce soil microbial carbon consumption, possibly due to a higher microbial functional specialization.

With respect to mammal impacts on soil microbes, evidence is accumulating that terrestrial vertebrates produce carcasses and waste products that alter soil nutrient stoichiometry (Barton et al., 2013; Dos Santos Neves et al., 2009; Parmenter & MacMahon, 2009; Sitters et al., 2014) and modify the soil microbial community below and around them (Andriuzzi & Wall, 2018; Barton et al., 2013; Carter et al., 2007; Stokes et al., 2009). In particular, vertebrate inputs with their C:N ratios and their release of other limiting nutrients, such as Ca and P (from bones, feathers, and chitin) could affect competitive relationships among microbes and alter microbial community structure, including fungal:bacterial ratios, copiotroph:oligotroph bacteria or symbiotroph:saprotroph fungi (Benbow et al., 2019; Bhunia et al., 2021; Bödeker et al., 2016). In Amazonian Dark Earth (ADE) — anthropogenic, pre-Columbian soils that are hyper-rich in OM — there are significant differences in several components of microbial diversity compared to adjacent soils with lower SOM content (Grossman et al., 2010; Kim et al., 2007; Lucheta et al., 2016, 2017). In my study, mammal functional diversity appears to be associated with reduced overall carbon consumption (AWCD) and a reduced variety of carbon sources consumed by soil microbes (H' , this latter effect was marginal). It is therefore possible that SOM accumulated by more species-rich and trait-diverse mammal communities (e.g., rich in N and S and poor in aliphatic and carbonyl-rich compounds) alters soil microbial carbon consumption through changes in the trophic structure of microbial communities that promote higher functional specialization in the degradation of specific carbon sources (Kim et al., 2021). Thus, the diversity of SOM incorporated by animal communities could influence the trophic structure of microbial communities present in the northern Amazon, thereby affecting SOM

degradation by microbes (Carter et al., 2007; Fierer et al., 2013; Hawlena et al., 2012) and ultimately carbon sequestration in ecosystems (Lehmann & Kleber, 2015).

However, no direct effect of both SOM components (PC2 and PC3) on overall microbial carbon consumption was detected. Conversely, the total SOM content (PC2) seems to promote the diversity of carbon sources consumed by soil microbes, as it could favor less competition between microbial taxa when more carbon is available. Although studies of functional diversity on ecosystem services such as carbon storage mostly focus on animal and plant diversity (Finegan et al., 2015; Flynn et al., 2009; Gagic et al., 2015), these results suggest the need to include the functional diversity of soil microbiota in this approach (Krause et al., 2014), as in the case of SOM accumulation (Douglas, 2018). The effect of mammal functional diversity on microbial diversity has been detected mainly in gut microbiomes (Gaulke et al., 2018; Kohl et al., 2016; McKenzie et al., 2017), but here a relationship between mammal functional diversity and overall microbial carbon consumption in Amazonian soils was revealed. This result is relevant because it suggests that mammal communities with more diverse species traits and more evenly distributed in the FD space may favor microbial communities that are more specialized in degrading specific carbon compounds, which could reduce soil microbial carbon consumption.

Conversely, the variety of carbon sources consumed by soil microbes (H') was lower in areas with higher tree richness. In contrast, other studies have found that soil microbial communities can consume less carbon and a lower variety of carbon compounds in forests with fewer plant species (Klimek et al., 2016), which negatively affects leaf litter decomposition rates (Lin et al., 2021). This result suggests that more species-rich tree communities may also promote functional specialization of soil microbial communities in the degradation of specific carbon compounds derived from the type of organic remains they incorporate into the soil (C-rich SOM). In fact, plant richness may favor microbial communities that are more specialized in consuming C-rich SOM due to higher C:N ratios in the foliage (Chávez-Vergara et al., 2018), and higher levels of root exudation that facilitate carbon consumption by gram-negative bacteria and arbuscular mycorrhizal fungi (Mellado-Vázquez et al., 2016). Thus, leaf composition and root exudates in more diverse tree communities may limit microbial diversity, favoring only certain bacterial and fungal species that decompose plant biomass (Sridhar et al., 2022). Indeed, the diversity of carbon types consumed by soil microbes increased in soils with higher SOM content (total C, N, S, and aromatic-nitrogenated and carboxylated SOM). This may indicate that microbial communities can only diversify their consumption preferences when more carbon is available in the soil (Fierer et al., 2007; Goldfarb et al., 2011). Carbon availability may be also related not only to the number of species, but also to the abundance of the plant species present in tree communities, which may determine the amount of SOM accumulated and then available to microbes.

The influence of mammal functional diversity and tree richness on soil microbial carbon consumption may also be related to changes in the genetic, functional, and phylogenetic diversity of microbial communities due to processes of local adaptation (Ayres, Steltzer, Simmons et al., 2009; Rúa et al., 2016). Microbial evolutionary processes may be related to carbon fluxes and storage in soil (Anthony et al., 2020; Wilpiseski et al., 2019), depending on the metabolic strategy followed by microorganisms to allocate carbon uptake (Schimel & Schaeffer, 2012). The efficiency of carbon use by soil microbes, i.e., the fraction of organic matter consumed by microbes that is converted into microbial biomass versus that which is respired as CO₂, can exert an important control on the C balance of ecosystems (Lipson et al., 2009; Lipson & Xu, 2019; Manzoni et al., 2012; Sinsabaugh et al., 2016; Wieder et al., 2013). Carbon consumption by soil microbes is often linked to the ecological strategy of the microbial

community through a trade-off between growth rate and carbon use efficiency, such that fast-growing species (copiotrophs) are less efficient at carbon consumption than slow-growing species (oligotrophs) (Kreft & Bonhoeffer, 2005; Lipson, 2015; Lipson et al., 2009). Furthermore, the effects of SOM on microbial activity can be both short-term (acclimation/change in community structure) and long-term (adaptation). Thus, phylogenetic and taxonomic characterization of soil microbial communities would complement current research, and improve the interpretation of the relationships found between mammal and tree diversity and soil microbial carbon consumption in the northern Amazon.

Other factors, such as reduced microbial biomass, taxonomic and phylogenetic differences between microbial communities, or dominant slow-growing species, could slow down carbon consumption by microbial communities, which may result in a decrease in overall carbon consumption. It is then necessary to quantify the microbial biomass after carbon consumption (Miltner et al., 2012), and to consider the taxonomic, phylogenetic and functional structure of microbial communities (Buscardo et al., 2018; Chávez-Vergara et al., 2014; Lipson, 2015). This would allow us to know the real impact of these mammal and tree communities on carbon consumption by soil microbial communities. Another potential limitation is that the observed overall amount and diversity of carbon sources consumed by soil microbes cannot be related to actual rates of soil carbon turnover. Therefore, future research should evaluate microbial carbon use efficiency (CUE) (Domeignoz-Horta et al., 2020; Tao et al., 2023), microbial biomass carbon (Cmic) (Chávez-Vergara et al., 2018) and quantify actual microbial carbon uptake using stable isotope techniques (Mellado-Vázquez et al., 2016; Steffan et al., 2015).

5.4 SOME METHODOLOGICAL CONSIDERATIONS

Importance of taking environmental covariation into account: Total SOM content was related to environmental factors, such as geographic longitude and remoteness (marginal effect of distance to the nearest village). This suggests that different underlying processes follow a longitudinal gradient and are related to human presence, such as possible restricted movements of vertebrates due to human settlements (Doherty et al., 2021) or the hunting habits of local communities already reported in this region (Iwamura et al., 2014; Luzar et al., 2011; Read et al., 2010), could affect the abundance of mammals and the spatial distribution of preys, limiting the amount of vertebrate carcasses accumulated at a site (Benítez-López et al., 2019; Morant et al., 2023; Roopsind et al., 2017). Fewer animal carcasses in the soil can slow microbial SOM decomposition and reduce N inputs to the soil (Macdonald et al., 2014; Quaggiotto et al., 2019). A reduction in microbial decomposition could result in a decrease in accumulated SOM (Carter et al., 2007), which may be dominated by aliphatic compounds and carbonyl groups that contribute to SOM recalcitrance (Six et al., 2001). Although the dominant lithology appears to be irrelevant for both, soil organic and inorganic variation, the mineralogy of phyllosilicates could influence SOM stabilization through the physical OM protection provided by clay minerals such as kaolinite and Fe-Al oxides (Barré et al., 2014).

Importance of considering the complexity of soil organic matter (SOM): Soil molecular analysis provides information on the content and type of SOM rich in C (carbohydrates, aliphatics, carbonyl-rich OM, and aromatics) or N (proteins), with opposite effects on SOM recalcitrance (resistance to microbial degradation). Polysaccharides, mainly derived from plants, contribute to labile SOM that is easily and efficiently degraded by microbes (Kögel-Knabner, 2002). In contrast, aliphatic, carbonyl, and aromatic compounds contribute to recalcitrant SOM, which tends to accumulate because it resists microbial degradation (Six et al., 2001). Moreover, elemental concentrations (C, N, S, Fe, Si, and Al) were included to improve our interpretation of the molecular composition of SOM (Table S5, Annex A): C as a

major constituent of SOM, N and S as major elements of mineralized SOM in tropical soils (Tipping et al., 2016), and Fe, Al, and Si, which concentrate due to intense mineral weathering in tropical soils. Si is an essential component of primary minerals, such as quartz that resists mineral weathering, while Fe and Al are present in secondary minerals, such as clays and oxihydroxides that contribute to SOM stabilization (Souza et al., 2017). All these components can coexist and interact with each other in SOM, so studying their relationships together is necessary to understand the complexity of soil C dynamics in nature.

Some caveats: First, despite the evidence found, the nature of this study is observational and does not explicitly test for causality. However, correlative studies are widely used to understand the effects of biodiversity on ecosystem functioning (Cardinale et al., 2012; de Vries et al., 2013; Hoehn et al., 2008) and are often used to understand complex processes that depend on multiple environmental variables occurring at large spatial scales, as in the case of C and N cycling (Feeley & Terborgh, 2005; Sobral et al., 2017). In addition, long-term experimental exclosures would have improved this study (Naidu et al., 2022; Roy & Bagchi, 2022; Villar et al., 2021), as they would allow testing the causality of the effects of mammal and tree contributions to SOM, and then, to SOC storage. Second, estimating C stocks would require sampling soil at greater depths and assessing soil bulk density as well as the C content in different soil layers. Although most recent research on the effects of biodiversity on soil C and N stocks has focused on soils up to 30 cm deep (Naidu et al., 2022; Sheil et al., 2016), C accumulation and persistence also vary with soil depth (Heckman et al., 2022). Soil C typically declines in deeper soils (Kramer et al., 2017), but SOC pools remain larger, even up to 2 m deep (Jackson et al., 2017). Therefore, estimating bulk density and C content at different soil depths would help to know the real impact of these mammal and tree communities on soil C storage.

5.5 POTENTIAL IMPLICATIONS FOR RESTORATION AND CONSERVATION

My findings have potential implications for ecosystem conservation and restoration. Ecological conservation and restoration, to reduce the loss of diversity and functions in already degraded areas, are global priorities according to the Convention on Biological Diversity, the Convention on Climate Change, the United Nations Framework Convention on Desertification, and the International Union for Nature Conservation (Aronson & Alexander, 2013). Restoration efforts in impacted ecosystems attempt to reestablish the structure and function of ecosystems prior to the impact. However, restoration today only partially recovers biodiversity and ecosystem functions, even after many decades (Moreno-Mateos et al., 2012).

So far, efforts to conserve and restore biodiversity have traditionally focused on conserving species as independent entities (Tylianakis et al., 2010). However, biotic communities are composed of species that interact with each other, forming complex ecological networks with both mutualistic (e.g., seed dispersal) and antagonistic (e.g., predator-prey) interactions. We know that human activities alter the structure of these interaction networks (Albrecht et al., 2007; Lopezaiza-Mikel et al., 2007), and that this structure affects ecosystem functions (Tylianakis et al., 2010) and contributes to the maintenance of biodiversity (Bascompte et al., 2006; Bastolla et al., 2009). Despite this, the incorporation of trophic networks and their trait diversity in ecosystem restoration has yet to be explored, and to date there are few restoration studies that measure network properties (Forup et al., 2007; Ribeiro da Silva et al., 2015). The success of conservation and restoration in terms of functional diversity and structure of ecological networks, and their impact on the conservation and restoration of ecosystem functions, especially key ecosystem services such as ecosystem carbon sequestration and accumulation, is still unknown. The evaluation of conservation and restoration measures should

be based on quantifiable properties that describe the community in terms of structure and function and not just its specific composition (Albrecht et al., 2007). The study of network structure has already demonstrated its usefulness in the fields of computer science, medicine, and conservation ecology, among others (Albert & Barabási, 2000; Barabási & Bonabeau, 2003), and promises to be equally useful as a tool to be used in carbon cycle conservation and restoration strategies (Montoya et al., 2015).

My results suggest that restoring the functional diversity and structural complexity of ecological networks could contribute to restoring the functionality of the carbon cycle. To improve the effectiveness of restoration efforts in recovering the functionality of natural ecosystems, restoration actions should include quantitative measures that describe the diversity of traits and the structure of interactions among species beyond the community-level assessments of species composition that have been used to date.

To test the idea that animals and plants influence the carbon cycle, direct observations of animals and plants living in a highly biodiverse system such as the Amazon were needed. Large amounts of data were needed and required the participation of 345 Makushi, Wapishana and Wai-Wai indigenous and local people from Guyana, an example of a collaborative citizen science project that supports the relevant role of indigenous and local people in biodiversity data collection (Copete et al., 2023). Their traditional ecological knowledge was essential in gathering the quantity and quality of information needed for this study. These indigenous and local communities have accumulated expert knowledge about plants and animals through hundreds of years of direct contact with their environment. This study highlights the importance of indigenous peoples' knowledge of their natural systems, and shows that actions to protect biodiversity and the services it provides can also benefit humans.

Given that current biodiversity loss is particularly detrimental to large and long-lived animals, such as many mammals, my results suggest, first, that the extinction crisis may lead to changes in the functioning of the carbon cycle. Second, my results also suggest that managing mammal diversity can provide carbon sequestration benefits that are additive to those provided by tree conservation. By simultaneously managing and protecting mammal and tree diversity, humanity can help secure a key service of nature, such as carbon storage, and thereby mitigate climate change.

6 CONCLUSIONS

1. Tree and mammal richness contributed to the accumulation of distinct types of soil organic matter (SOM). More species-rich mammal communities were related to soils with SOM rich in N, S, and Fe, whereas more species-rich tree communities were related to soils with SOM rich in carbonyl groups and aliphatic compounds.
2. Functional diversity in mammal communities was more relevant for SOM composition than their species richness. Thus, trait diversity seems to better predict variation in the type of SOM accumulated than species number.
3. Different metrics of trait diversity in mammal communities (functional richness and functional divergence) inversely affected the accumulation of carbonyl groups and aliphatic compounds in SOM. Thus, not all species are equally important for the carbon cycle, species traits also influence the functioning of the carbon cycle.
4. Functional diversity of mammals was related to a decrease in overall carbon consumption by soil microbes, while species richness of trees was related to a decrease in the variety of carbon sources consumed by soil microbes.

The overall conclusion is that the effects of mammals and trees on SOM composition are not redundant but rather complementary, since they promote the accumulation of different organic compounds and have different effects on carbon consumption by soil microbial communities.

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<i>Species</i> Order - Family ¹	<u>Common name</u> (body mass; body length) and other traits ^{2,3} Habitat, ecology, and diet ^{1,2}	IUCN Red List ¹	Photo ⁴
<i>Alouatta seniculus</i> Primates - Atelidae	<u>Red howler monkey</u> (6.4kg; 0.74m), reddish fur with prehensile tail. Emit loud howls. Arboreal, social (groups of 2-3) and herbivorous.	LC	
<i>Ateles paniscus</i> Primates - Atelidae	<u>Black spider monkey</u> (7.8kg; 0.6m), black fur. Diurnal, social (groups of 30), and omnivorous.	VU	
<i>Bassaricyon gabbii</i> Carnivora - Procyonidae	<u>Northern olingo</u> (1.2kg; 0.4m), with reddish fur and long tail. Arboreal, nocturnal, solitary, and omnivorous.	LC	
<i>Bradypus tridactylus</i> Pilosa - Bradypodidae	<u>Pale-throated three-toed sloth</u> (4kg; 0.5m), dark fur, males with a yellow dorsal spot. Diurnal, solitary, and herbivorous.	LC	
<i>Cabassous unicinctus</i> Cingulata - Clamyphoridae	<u>Southern naked-tailed armadillo</u> (3.9kg; 0.45m), hard carapace and long, sticky tongue. Nocturnal, solitary, and insectivorous.	LC	
<i>Cebus apella</i> * Primates - Cebidae	<u>Brown capuchin</u> (2.6kg; 0.49m), brown hair, black at the crown, prehensile tail. Arboreal, diurnal, social (groups of 6-30), and omnivorous (*currently: <i>Sapajus apella</i>).	LC	
<i>Cebus olivaceus</i> Primates - Cebidae	<u>Wedge-capped capuchin</u> (2.5kg; 0.48m), brown coat, black crown, light face, prehensile tail. Arboreal, diurnal, social (groups of 12), and omnivorous.	LC	
<i>Cerdocyon thous</i> Carnivora - Canidae	<u>Crab-eating fox</u> (5.7kg; 0.67m), short, strong legs and variable reddish-brown fur. Nocturnal, monogamous, and carnivorous.	LC	
<i>Chiropotes satanas</i> Primates - Pitheciidae	<u>Black bearded saki</u> (8.6kg; 0.63m) black hair, beards, and shaggy tail. Diurnal, social (groups of 40), and omnivorous.	EN	
<i>Choloepus didactylus</i> Pilosa - Megalonychidae	<u>Linnaeus' two-toed sloth</u> (2.3kg; 0.8m), brown or greenish fur (mutualism with algae), and two strong claws. Arboreal, diurnal, solitary, and herbivorous.	LC	
<i>Coendou melanurus</i> Rodentia - Erethizontidae	<u>Black-tailed hairy dwarf porcupine</u> (1.4kg; 0.5m) covered with strong grayish quills. Arboreal, nocturnal, solitary, and herbivorous.	LC	
<i>Coendou prehensilis</i> Rodentia - Erethizontidae	<u>Brazilian porcupine</u> (3.9kg; 0.5m), covered with gray quills, prehensile tail. Arboreal, nocturnal, solitary, and herbivorous.	LC	

¹ IUCN. (2023, January 20). *The IUCN Red List of Threatened Species, Version 2022-2*. <https://www.iucnredlist.org>

² Martín Brañas, M., Gagliardi Urrutia, G., Álvarez Alonso, J., Díaz Alván, J., García Dávila, C., Ruiz Tafur, M., Vásquez Bardales, J., Vásquez Mora, W., Mejía Carhuana, K., Dávila Cardozo, N., Zárate Gómez, R., Rengifo Salgado, E., Pérez Peña, P., & Bellido Collahuacho, J. J. (2022). *Amazônia: Guía ilustrada de flora y fauna*. Instituto de Investigaciones de la Amazonía Peruana. ISBN 978-612-4372-47-6. <https://hdl.handle.net/20.500.12921/680>

³ Myers, P., Espinosa, R., Parr, C. S., Jones, T., Hammond, G. S., & Dewey, T. A. (2023, January 20). *The Animal Diversity Web*. <http://animaldiversity.org>

⁴ Openverse media library. (n.d.). Openverse: Openly Licensed Images, Audio and More. Retrieved January 20, 2023, from: <https://openverse.org>

<i>Cuniculus paca</i> Rodentia - Cuniculidae	<u>Lowland paca</u> (9kg; 0.6m), reddish-brown fur with white spots on the sides. Living in forests near water, nocturnal, and herbivorous.	LC	
<i>Dasyprocta leporina</i> Rodentia - Dasyproctidae	<u>Red-rumped agouti</u> (3kg; 0.6m), reddish fur and short, naked tail. Living in forests, diurnal, and herbivorous.	LC	
<i>Dasyus kappleri</i> Cingulata - Dasypodidae	<u>Greater long-nosed armadillo</u> (9.9kg; 0.6m), gray bony carapace and elongated snout. Living in forests, diurnal, solitary and omnivorous.	LC	
<i>Dasyus novemcinctus</i> Cingulata - Dasypodidae	<u>Nine-banded armadillo</u> (4kg; 0.5m), bony carapace, elongated tail and snout. Wide range of habitats, nocturnal, and omnivorous.	LC	
<i>Didelphis marsupialis</i> Didelphimorphia - Didelphidae	<u>Common opossum</u> (1kg; 0.4m), gray fur with a black mask. Terrestrial-arboreal, nocturnal, solitary, and omnivorous.	LC	
<i>Eira barbara</i> Carnivora - Mustelidae	<u>Tayra</u> (4.1kg; 0.6m), dark fur, light head. Living in forests, terrestrial-arboreal, diurnal-crepuscular, and omnivorous.	LC	
<i>Galictis vittata</i> Carnivora - Mustelidae	<u>Greater grison</u> (2.3 kg; 0.5 m), slender and elongated body, with short limbs. Terrestrial, crepuscular, and omnivorous.	LC	
<i>Herpailurus yagouaroundi</i> Carnivora - Felidae	<u>Jaguarundi</u> (7kg; 0.7m) slender body with short legs, gray or reddish fur without spots. Terrestrial, diurnal, solitary, and carnivorous.	LC	
<i>Hydrochoerus hydrochaeris</i> Rodentia - Caviidae	<u>Capybara</u> (51kg; 1.2m), robust body with brown fur. Living in riparian forests, in groups (8-10), diurnal, and herbivorous.	LC	
<i>Leopardus pardalis</i> Carnivora - Felidae	<u>Ocelot</u> (10.5kg; 0.9m), yellow fur with brown-black spots. Terrestrial, nocturnal-crepuscular, solitary, and carnivorous.	LC	
<i>Leopardus tigrinus</i> Carnivora - Felidae	<u>Oncilla</u> (2.3kg; 0.5m), brown fur with dark spots. Living in forests, terrestrial, nocturnal-crepuscular, solitary, and carnivorous.	VU	
<i>Leopardus wiedii</i> Carnivora - Felidae	<u>Margay</u> (3.6kg; 0.7m), yellow fur with dark spots. Living in forests, terrestrial, nocturnal-crepuscular, solitary, and carnivorous.	NT	
<i>Lontra longicaudis</i> Carnivora - Mustelidae	<u>Neotropical otter</u> (7kg; 0.7m), elongated, with brown waterproof fur and long tail. Living in riversides, terrestrial-aquatic, solitary, and carnivorous.	NT	
<i>Mazama americana</i> Artiodactyla - Cervidae	<u>Red brocket</u> (23.0kg; 1.3m), reddish fur, males with short and straight antlers. Living in forests, nocturnal, solitary, and herbivorous.	DD	
<i>Mazama gouazoubira</i> Artiodactyla - Cervidae	<u>Gray brocket</u> (16.6kg; 1.1m), grayish fur, juveniles with white spots and males with unbranched antlers. Nocturnal, solitary, and herbivorous.	LC	
<i>Mesomys hispidus</i> Rodentia - Echimyidae	<u>Ferreira's spiny tree rat</u> (0.2kg; 0.2m), brown fur. Living in forests, nocturnal, solitary, and omnivorous.	LC	
<i>Myoprocta acouchy</i> Rodentia - Dasyproctidae	<u>Red acouchi</u> (0.84kg; 0.4m), reddish-brown fur with a lighter head. Living in forests, in groups (7), diurnal, and herbivorous.	LC	
<i>Myrmecophaga tridactyla</i> Pilosa - Myrmecophagidae	<u>Giant anteater</u> (30kg; 1.5m), gray and black fur from chest to back, long trunk with extensible and sticky tongue. Diurnal, solitary, and insectivorous.	VU	

<i>Nasua nasua</i> Carnivora - Procyonidae	South American coati (4kg; 0.6m), brown fur, cream rings on the tail. Living in forests, terrestrial-arboreal, diurnal, solitary, and omnivorous.	LC	
<i>Odocoileus virginianus</i> Artiodactyla - Cervidae	White-tailed deer (65.3kg; 0.2m), grey fur with white spots on face and tail, and males with antlers. Crepuscular, solitary, and herbivorous.	LC	
<i>Panthera onca</i> Carnivora - Felidae	Jaguar (81.1kg; 0.6m), yellow fur with black spots. Crepuscular, solitary, and carnivorous.	NT	
<i>Philander opossum</i> Didelphimorphia - Didelphidae	Gray four-eyed opossum (0.5kg; 0.3m), grey fur, a white mole over the eyes, long and prehensile tail. Arboreal-terrestrial, nocturnal, and omnivorous.	LC	
<i>Pithecia pithecia</i> Primates - Pitheciidae	Guianan saki (1.5kg; 0.5m), black males with white face with grey strands. Living in groups (2-9), and omnivorous.	LC	
<i>Potos flavus</i> Carnivora - Procyonidae	Kinkajou (2.4kg; 0.6m), brown fur, long and prehensile tail. Living in forests, arboreal, nocturnal, solitary, and omnivorous.	LC	
<i>Priodontes maximus</i> Cingulata - Clamphoridae	Giant armadillo (45kg; 1m), with a bony carapace and a large front claw. Nocturnal, terrestrial, solitary, and insectivorous.	VU	
<i>Procyon cancrivorus</i> Carnivora - Procyonidae	Crab-eating raccoon (6.3kg; 0.6m), brown fur, with a black mask. Living in riparian forests, solitary, and omnivorous.	LC	
<i>Pteronura brasiliensis</i> Carnivora - Mustelidae	Giant otter (24kg; 1.3m), dark brown fur with white spots on throat and tail. Living in groups (10-15), and carnivorous.	EN	
<i>Puma concolor</i> Carnivora - Felidae	Cougar (48kg; 1.7m), yellow-brown fur. Nocturnal, solitary, and carnivorous.	LC	
<i>Saguinus midas</i> Primates - Callitrichidae	Golden-handed tamarin (0.5kg; 0.3m), black fur with yellow feet. Arboreal, diurnal, social (groups of 4-15) and omnivorous.	LC	
<i>Saimiri sciureus</i> Primates - Cebidae	Common squirrel monkey (0.8kg; 0.3m), short gray fur with yellow legs and a non-prehensile tail. Living in groups (300), and omnivorous.	LC	
<i>Sciurus aestuans</i> Rodentia - Scuridae	Guianan squirrel (0.2kg; 0.2m), reddish-gray fur and long, shaggy tail. Diurnal, solitary, and omnivorous.	LC	
<i>Speothos venaticus</i> Carnivores - Canidae	Bush dog (6kg; 0.7m), brown fur, lighter on the head and with a small tail. Diurnal and carnivorous.	NT	
<i>Tamandua tetradactyla</i> Pilosa - Myrmecophagidae	Southern tamandua (4.5kg; 0.7m), yellow and black fur, prehensile tail, and long trunk. Nocturnal, solitary, and insectivorous.	LC	
<i>Tapirus terrestris</i> Perissodactyla - Tapiridae	Lowland tapir (225kg; 2.2m), short grayish-brown fur with an elongated mane and snout. Terrestrial, nocturnal, solitary, and herbivorous.	VU	
<i>Tayassu pecari</i> Artiodactyla - Tayassuidae	White-lipped peccary (32kg; 1m), dark fur, white in mouth and cheeks, long snout, large and sharp canines. Terrestrial, diurnal, social (herds of 400) and herbivorous.	VU	
<i>Tayassu tajacu</i> Artiodactyla - Tayassuidae	Collared peccary (20.5kg; 1m), dark fur with a light fur collar. Diurnal-crepuscular, social (herds of 6-30), and omnivorous.	LC	

Table S2: List of mammal species surveyed (n=45) at 30 sites selected to analyze soil microbial carbon consumption in the northern Amazon (Guyana), and their corresponding trait values extracted from open access [Amniote Life History Database](#): 1) body length (as the body length of an adult individual in cm, from snout to tail base including head, see “adult_svl_cm”), 2) body mass (as the body mass of an adult individual in kg, see “adult_body_mass_kg”), and 3) offspring number (as the number of offspring born per litter, see “litter_or_clutch_size_n”).

Scientific name	Common name	Body length (cm)	Body mass (kg)	Offspring n° (indiv.)
<i>Alouatta seniculus</i>	Red howler monkey	74	6	1
<i>Ateles paniscus</i>	Black spider monkey	61	8	1
<i>Bassaricyon gabbii</i>	Northern olingo	44	1	1
<i>Bradypus tridactylus</i>	Pale-throated three-toed sloth	55	4	1
<i>Cabassous unicinctus</i>	Southern naked-tailed armadillo	45	4	1
<i>Cebus apella</i>	Brown capuchin	49	3	1
<i>Cebus olivaceus</i>	Wedge-capped capuchin	48	3	1
<i>Cerdocyon thous</i>	Crab-eating fox	67	6	4
<i>Chiropotes satanas</i>	Black bearded saki	63	9	1
<i>Choloepus didactylus</i>	Linnaeus' two-toed sloth	77	6	1
<i>Coendou melanura</i>	Black-tailed dwarf porcupine	39	1	1
<i>Coendou prehensilis</i>	Brazilian porcupine	53	4	1
<i>Cuniculus paca</i>	Lowland paca	72	9	1
<i>Dasyprocta leporina</i>	Red-rumped agouti	60	3	2
<i>Dasytus kappleri</i>	Greater long-nosed armadillo	57	10	3
<i>Dasytus novemcinctus</i>	Nine-banded armadillo	51	4	4
<i>Eira barbara</i>	Tayra	65	4	2
<i>Galictis vittata</i>	Greater grison	55	2	2
<i>Hydrochoerus hydrochaeris</i>	Capybara	125	52	3
<i>Leopardus pardalis</i>	Ocelot	87	11	2
<i>Leopardus tigrinus</i>	Oncilla	55	2	2
<i>Leopardus wiedii</i>	Margay	69	4	2
<i>Lontra longicaudis</i>	Neotropical otter	71	7	3
<i>Mazama americana</i>	Red brocket	135	23	1
<i>Mazama gouazoubira</i>	Gray brocket	113	17	1
<i>Myoprocta acouchy</i>	Red acouchi	37	1	2
<i>Myrmecophaga tridactyla</i>	Giant anteater	151	30	1
<i>Nasua nasua</i>	South American coati	60	4	4
<i>Odocoileus virginianus</i>	White-tailed deer	181	65	2
<i>Panthera onca</i>	Jaguar	159	81	2
<i>Philander opossum</i>	Gray four-eyed opossum	28	1	5
<i>Pithecia pithecia</i>	Guianan saki	53	1	1
<i>Potos flavus</i>	Kinkajou	63	2	1
<i>Priodontes maximus</i>	Giant armadillo	94	45	2
<i>Procyon cancrivorus</i>	Crab-eating raccoon	60	6	3
<i>Pteronura brasiliensis</i>	Giant otter	127	24	2
<i>Puma concolor</i>	Cougar	168	48	3
<i>Saguinus midas</i>	Golden-handed tamarin	29	1	2
<i>Saimiri sciureus</i>	Common squirrel monkey	34	1	1
<i>Sciurus aestuans</i>	Guianan squirrel	24	0	2
<i>Speothos venaticus</i>	Bush dog	69	6	4
<i>Tamandua tetradactyla</i>	Southern tamandua	72	5	1
<i>Tapirus terrestris</i>	Lowland tapir	225	225	1
<i>Tayassu pecari</i>	White-lipped peccary	106	32	2
<i>Tayassu tajacu</i>	Collared peccary	91	21	2

Table S3: Tree taxa description. 163 taxa, 127 species of 109 genera, 37 families, 15 orders were identified by direct observations (n=24,552 trees) in 72 communities in the northern Amazon (Guyana).

Family - Order	Description (Genus: <i>species</i>) ^{5,6,7}	Photo ⁸
Amaranthaceae Caryophyllales	Simple, whole-leaved herbaceous plants or shrubs with inconspicuous flowers in a variety of inflorescences and pyxidium (Amaranthus: <i>A. viridis</i>)	
Anacardiaceae Sapindales	Trees with resinous, compound, or simple leaves with an axillary or terminal panicle of many flowers. Drupe fruit with bark or samara (Anacardium: <i>A. giganteum</i> ; Loxopterygium : <i>L. sagotii</i> ; Mangifera : <i>M. indica</i> ; Spondias: <i>S. mombin</i> ; Tapirira : <i>T. obtusa</i> ; Thyrsoodium : <i>T. spruceanum</i>)	
Annonaceae Magnoliales	Lianas, trees or shrubs with hard bark and simple alternate leaves. Solitary or grouped flowers. Syncarpic or apocarpic fruit with elongated seeds (Bocageopsis: <i>B. multiflora</i> ; Duguetia: <i>Duguetia spp.</i> ; Guatteria: <i>Guatteria spp.</i> ; Unonopsis: <i>U. glaucopetala</i> ; Xylopia: <i>Xylopia spp.</i>)	
Apocynaceae Gentianales	Latex-producing trees, shrubs or lianas, with simple, alternate leaves. Panicles, fascicles or solitary flowers and berry or seed capsule fruit (Aspidosperma: <i>A. excelsum</i> ; Geissospermum: <i>G. seriocum</i> ; Parahancornia: <i>P. amapa</i>)	
Aquifoliaceae Aquifoliales	Evergreen shrubs with simple alternate leaves. Inflorescences in axillary cymes, and reddish globose drupe fruit (Ilex: <i>I. martiniana</i>)	
Araliaceae Apiales	Trees with alternate, simple leaves and panicle of racemes, spikes or umbels of flowers and drupe or berry fruit (Schefflera: <i>Sclerobium morototoni</i>)	
Arecaceae Arecales	Trees, shrubs or pinnate flowering vines with panicles or flower spikes and drupe fruit with one seed (Astrocaryum: <i>A. aculeatum</i> , <i>A. jauari</i> , <i>A. vulgare</i> ; Attalea: <i>A. maripa</i> , <i>A. speciosa</i> ; Euterpe: <i>E. oleracea</i> ; Manicaria: <i>M. saccifera</i> ; Mauritia: <i>M. flexuosa</i> ; Oenocarpus: <i>O. bacaba</i> , <i>O. batua</i>)	 
Bignoniaceae Lamiales	Trees, shrubs or lianas with simple, pinnate leaves and large flowers in inflorescences. Siliqua, drupe or berry fruit with winged seeds (Arrabidaea: <i>A. tuberculata</i> ; Jacaranda: <i>J. coupaia</i> ; <i>J. obusifolia</i> ; Tabebuia: <i>T. capitata</i> ; <i>T. insignis</i> ; <i>T. serratifolia</i> ; <i>T. stenocalyx</i>)	
Boraginaceae Boraginales	Trees, shrubs or herbs with simple, alternate leaves, flowers in panicles or cymes, and berry or nut fruit (Cordia: <i>C. alliodora</i> ; <i>C. tetrandra</i>)	
Burseraceae Sapindales	Trees with resin, pinnate leaves and unisexual flowers, drupe or seed capsule fruit (Protium: <i>P. decandrum</i>)	

⁵ Walter, P. (2016). *Árboles del Ecuador: Familias y Géneros* (1st ed.). Universidad Técnica del Norte. ISBN 978-9942-8590-5-1.

⁶ Pirani, J. R. (1993). Burseraceae – 21. In G. F. Bocquet, & M. R. Crosby (Eds.), *Flora de Paraguay* (pp. 1–12). Conservatoire et Jardin Botaniques de la Ville de Genève & Missouri Botanical Garden. <https://www.tropicos.org/reference/45786>

⁷ Milliken, W., Klitgard, B., & Barakat, A. (2010). *Neotropikey - Interactive key and information resources for flowering plants of the Neotropics*. Royal Botanic Gardens. <http://www.kew.org/science/tropamerica/neotropikey.htm>

⁸ Openverse media library. (n.d.). Openverse: Openly Licensed Images, Audio and More. Retrieved January 20, 2023, from: <https://openverse.org>

Caryocaraceae Malpighiales	Trees or shrubs with terminal racemes of showy flowers and drupe fruit with 1-4 seeds (Caryocar: <i>C. microcarpum</i> ; <i>C. nuciform</i>)	
Chrysobalanaceae Malpighiales	Woody trees, simple, alternate leaves, with flowers in panicles or racemes, and drupe fruit with one seed (Chrysobalanus: <i>C. icaco</i> ; Couepia: <i>C. comosa</i> ; Licania: <i>L. alba</i> , <i>L. buxifolia</i> , <i>L. heteromorpha</i> , <i>L. laxiflora</i> , <i>L. majuscula</i> ; Parinari: <i>P. campestris</i>)	
Clusiaceae Malpighiales	Latex-producing trees or hemiepiphytes with opposite leaves, flowers in panicles, racemes or fascicles, and capsule fruit with several seeds or drupe fruit with few seeds (Calophyllum: <i>C. lucidum</i> ; Clusia: <i>C. grandiflora</i> ; Platonina: <i>P. insignis</i> ; Rheedea: <i>Rheedea spp.</i> ; Symphonia: <i>S. globulifera</i> ; Tovomita: <i>Tovomita spp.</i>)	
Ebenaceae Ericales	Shrubs or trees with alternate, simple leaves with solitary or crested flowers, fleshy or fibrous berry fruit with oily seeds (Diospyros: <i>Diospyros spp.</i>)	
Euphorbiaceae Malpighiales	Latex-producing trees or shrubs with simple or compound leaves. Flower in spikes or racemes, drupe or nut fruit (Sapium: <i>S. paucinervium</i>)	
Goupiaceae Malpighiales	Evergreen alternate-leaved trees with inflorescences in umbel and drupe fruit with 1-5 seeds (Goupia: <i>G. glabra</i>)	
Humiriaceae Malpighiales	Trees of simple and alternate leaves, drupe fruit (Humiria: <i>H. balsamifera</i> ; Sacoglottis: <i>S. guianensis</i>)	
Hypericaceae Malpighiales	Trees, shrubs, lianas or perennial herbs with oils and resins, simple leaves, flowers in opposite inflorescences in umbels, panicles or cymes. Capsule, berry or drupe fruit with several seeds (Vismia: <i>V. macrophylla</i>)	
Lamiaceae Lamiales	Shrubs and trees with opposite, entire leaves, and hermaphrodite flower cymes. Nucellar fruit (Aegiphila: <i>A. longifolia</i> ; Vitex: <i>Vitex spp.</i>)	
Lauraceae Laurales	Trees with hard bark and drupes with 1 oily seed (Aniba: <i>A. excelsa</i> , <i>A. guianensis</i> , <i>A. ovalfolia</i> ; Chlorocardium: <i>C. rodiei</i> ; Ocotea: <i>O. acutangula</i> , <i>O. canaliculata</i> , <i>O. rubra</i>)	
Lecythidaceae Ericales	Trees with hard bark, simple, alternate and pinnate leaves, panicles or racemes of large flowers and pixidium (Bertholletia: <i>B. excelsa</i> ; Eschweilera: <i>E. alata</i> ; <i>E. decolorans</i> ; <i>E. sagotiana</i> ; <i>E. wachenheimi</i> ; Lecythis: <i>L. confertiflora</i> ; <i>L. corrugata</i> ; <i>L. davisii</i>)	
Leguminosae Fables	Highly variable and third-large family of species of trees and shrubs, with compound, stipulate leaves and the fruit is a legume (Abarema: <i>A. jupumba</i> ; Balizia: <i>Balizia spp.</i> ; Campisandra: <i>C. comosa</i> ; Cassia: <i>C. apoucoutia</i> ; Centrolobium: <i>C. paraense</i> ; Clathrotropis: <i>C. brachypetala</i> , <i>C. macrocarpa</i> ; Dimorphandra: <i>D. conjugata</i> ; Diplotropis: <i>D. purpurea</i> ; Dipteryx: <i>D. odorata</i> ; Elizabetha: <i>E. macrostachya</i> ; Eperua: <i>E. falcata</i> ; Hymeneia: <i>H. courbaril</i> , <i>H. davisii</i> , <i>H. oblongifolia</i> ; Hymenolobium: <i>Hymenolobium spp.</i> ; Inga: <i>I. alba</i> ; Mora: <i>M. excelsa</i> ; <i>M. gonggrippii</i> ; Muellera: <i>M. urens</i> ; Myroxylon: <i>M. peruiferum</i> ; Ormosia: <i>Ormosia spp.</i> ; Peltogyne: <i>P. venosa</i> ; Pentaclethra: <i>P. macroloba</i> ; Pterocarpus: <i>P. officinalis</i> ; Sclerolobium: <i>S. guianense</i> ; Swartzia: <i>S. leiocalycina</i> ; Sweetia: <i>S. praclara</i>)	  
Linaceae Malpighiales	Shrubs with simple, entire leaves with stipules; cymes, panicles or corymbs of flowers and fruit in capsule or drupe (Hebepetalum: <i>H. humiriifolium</i>)	

Malpighiaceae Malpighiales	Lianas, shrubs or trees with simple leaves, small flowers and variable fruit (Byrsonima: <i>B. aerugo</i> ; <i>B. crassifolia</i> ; <i>B. stipulacea</i>)	
Malvaceae Malvales	Shrubs or trees with alternate, simple leaves with stipules. Flowers solitary or in cymes. Berries, capsules or nuts (Apeiba: <i>A. glabra</i> , <i>A. petoumo</i> ; Bombax: <i>B. surinamensis</i> ; Catostemma: <i>C. commune</i> , <i>C. fragrans</i> ; Ceiba: <i>C. pentandra</i> ; Pachira: <i>Pachira spp.</i> ; Sterculia: <i>S. guianensis</i>)	
Meliaceae Sapindales	Trees or shrubs with compound and pinnate leaves, with flowers in panicles or racemes, and capsule or drupe (Carapa: <i>C. guianensis</i> , <i>C. procera</i> ; Cedrela: <i>C. odorata</i> ; Guarea: <i>G. guidonia</i>)	
Moraceae Rosales	Trees producing white latex or hemiepiphytes with simple and alternate leaves, flowers in spikes or racemes (Bagassa: <i>B. tilifolia</i> ; Brosimum: <i>Brosimum spp.</i> ; Ficus: <i>Ficus spp.</i> ; Piratinera: <i>P. guianensis</i>)	
Myristicaceae Magnoliales	Trees with latex and simple, alternate leaves, flowers in inflorescences, and drupes (Iryanthera: <i>I. juruensis</i> ; Virola: <i>V. melinonii</i> ; <i>V. sebifera</i> ; <i>V. surinamensis</i>)	
Myrtaceae Myrtales	Trees or shrubs with simple, opposite leaves, fascicles, racemes or panicles of solitary flowers, and drupes (Myrciaria: <i>M. vismiifolia</i>)	
Polygonaceae Caryophyllales	Trees, shrubs, or lianas with alternate and entire leaves, flowers in spikes or axillary racemes, dried fruits (Triplaris: <i>T. weigeltiana</i>)	
Rubiaceae Gentianales	Trees and shrubs with simple and opposite leaves, flowers in panicles, racemes or spikes, and drupes or berries (Cinchona: <i>Cinchona spp.</i> ; Genipa: <i>G. americana</i> ; Posoqueria: <i>P. longiflora</i>)	
Salicaceae Malpighiales	Trees or shrubs with simple, alternate, stipulate leaves, small flowers in erect catkins, and capsule, berry or drupe fruit with woody seeds (Laetia: <i>L. procera</i>)	
Sapindaceae Sapindales	Trees, shrubs or lianas with pinnate leaves, flowers in panicles and very variable fruits (Talisia: <i>Talisia spp.</i> ; Toulicia: <i>T. guianensis</i>)	
Sapotaceae Ericales	Trees or shrubs producing white latex, with simple and alternating leaves, flowers in fascicles or racemes, and drupes with 1-5 seeds (Chrysophyllum: <i>C. beardii</i> ; Ecclinusa: <i>E. guianensis</i> ; Manilkara: <i>M. bidentata</i> ; Pouteria: <i>P. caimito</i> , <i>P. cuspidata</i> ; <i>P. guianensis</i> ; <i>P. speciosa</i> ; Pradosia: <i>P. schomburgkiana</i>)	
Simaroubaceae Sapindales	Sap-producing trees or shrubs with alternate, pinnate or simple leaves, drupe or samara (Quassia: <i>Q. simarouba</i> ; Simarouba: <i>S. amara</i>)	
Urticaceae Rosales	Trees with alternate or opposite leaves with flowers in racemes and umbels, drupes or achenes with oily seeds (Cecropia: <i>C. juranyiana</i> ; Pourouma: <i>P. tomentosa</i>)	
Violaceae Malpighiales	Evergreen shrubs with simple and alternate leaves, solitary flowers or in racemes, capsule or berry fruit with oily seeds (Paypayrola: <i>P. longifolia</i>)	
Vochysiaceae Myrtales	Trees with simple, opposite and pinnate leaves. Flowers in panicle of erect racemes, and capsules with several winged seeds or samara with 3-4 seeds (Vochysia: <i>V. surinamensis</i>)	

Table S4: List of all tree taxa surveyed at 30 sites selected to analyze soil microbial carbon consumption in the northern Amazon (Guyana). Note that 25% of the tree taxa were surveyed at the genus level (32 out of 144 tree taxa in total).

Scientific name	Genus name	Family name
<i>Abarema jupunba</i>	Abarema	Leguminosae
<i>Aegiphila longifolia</i>	Aegiphila	Lamiaceae
<i>Amaranthus viridis</i>	Amaranthus	Amaranthaceae
<i>Anacardium giganteum</i>	Anacardium	Anacardiaceae
<i>Aniba excelsa</i>	Aniba	Lauraceae
<i>Aniba ovalifolia</i>	Aniba	Lauraceae
<i>Aniba spp.</i>	Aniba	Lauraceae
<i>Apeiba glabra</i>	Apeiba	Malvaceae
<i>Apeiba petoumo</i>	Apeiba	Malvaceae
<i>Arrabidaea tuberculata</i>	Arrabidaea	Bignoniaceae
<i>Aspidosperma excelsum</i>	Aspidosperma	Apocynaceae
<i>Aspidosperma spp.</i>	Aspidosperma	Apocynaceae
<i>Astrocaryum aculeatum</i>	Astrocaryum	Arecaceae
<i>Astrocaryum jauari</i>	Astrocaryum	Arecaceae
<i>Astrocaryum spp.</i>	Astrocaryum	Arecaceae
<i>Attalea maripa</i>	Attalea	Arecaceae
<i>Attalea speciosa</i>	Attalea	Arecaceae
<i>Bagassa tilifolia</i>	Bagassa	Moraceae
<i>Balizia spp.</i>	Balizia	Leguminosae
<i>Bocageopsis multiflora</i>	Bocageopsis	Annonaceae
<i>Bombax surinamense</i>	Bombax	Malvaceae
<i>Brosimum spp.</i>	Brosimum	Moraceae
<i>Byrsonima crassifolia</i>	Byrsonima	Malpighiaceae
<i>Byrsonima stipulacea</i>	Byrsonima	Malpighiaceae
<i>Calophyllum lucidum</i>	Calophyllum	Clusiaceae
<i>Carapa guianensis</i>	Carapa	Meliaceae
<i>Carapa procera</i>	Carapa	Meliaceae
<i>Caryocar microcarpum</i>	Caryocar	Caryocaraceae
<i>Cassia apoucutia</i>	Cassia	Leguminosae
<i>Catostemma commune</i>	Catostemma	Malvaceae
<i>Catostemma fragrans</i>	Catostemma	Malvaceae
<i>Cecropia juranyiana</i>	Cecropia	Urticaceae
<i>Cecropia spp.</i>	Cecropia	Urticaceae
<i>Cedrela odorata</i>	Cedrela	Meliaceae
<i>Cedrela spp.</i>	Cedrela	Meliaceae
<i>Ceiba pentandra</i>	Ceiba	Malvaceae
<i>Ceiba spp.</i>	Ceiba	Malvaceae
<i>Centrolobium paraense</i>	Centrolobium	Leguminosae
<i>Chlorocardium rodiei</i>	Chlorocardium	Lauraceae
<i>Chrysophyllum beardii</i>	Chrysophyllum	Sapotaceae
<i>Cinchona spp.</i>	Cinchona	Rubiaceae
<i>Clathrotropis macrocarpa</i>	Clathrotropis	Leguminosae
<i>Clusia grandiflora</i>	Clusia	Clusiaceae
<i>Cordia alliodora</i>	Cordia	Boraginaceae
<i>Cordia spp.</i>	Cordia	Boraginaceae
<i>Dimorphandra conjugata</i>	Dimorphandra	Leguminosae
<i>Diospyros spp.</i>	Diospyros	Ebenaceae
<i>Diploptropis purpurea</i>	Diploptropis	Leguminosae
<i>Dipteryx odorata</i>	Dipteryx	Leguminosae
<i>Duguetia spp.</i>	Duguetia	Annonaceae
<i>Ecclinusa guianensis</i>	Ecclinusa	Sapotaceae
<i>Eperua falcata</i>	Eperua	Leguminosae
<i>Eperua spp.</i>	Eperua	Leguminosae
<i>Eschweilera alata</i>	Eschweilera	Lecythidaceae
<i>Eschweilera decolorans</i>	Eschweilera	Lecythidaceae

<i>Eschweilera sagotiana</i>	Eschweilera	Lecythidaceae
<i>Eschweilera</i> spp.	Eschweilera	Lecythidaceae
<i>Euterpe oleracea</i>	Euterpe	Arecaceae
<i>Ficus</i> spp.	Ficus	Moraceae
<i>Geissospermum sericeum</i>	Geissospermum	Apocynaceae
<i>Genipa americana</i>	Genipa	Rubiaceae
<i>Goupia glabra</i>	Goupia	Goupiaceae
<i>Guarea guidonia</i>	Guarea	Meliaceae
<i>Guatteria</i> spp.	Guatteria	Annonaceae
<i>Hebepetalum humiriifolium</i>	Hebepetalum	Linaceae
<i>Humiria balsamifera</i>	Humiria	Humiriaceae
<i>Hymenaea courbaril</i>	Hymenaea	Leguminosae
<i>Hymenaea davisii</i>	Hymenaea	Leguminosae
<i>Hymenolobium</i> spp.	Hymenolobium	Leguminosae
<i>Ilex martiniana</i>	Ilex	Aquifoliaceae
<i>Inga alba</i>	Inga	Leguminosae
<i>Inga</i> spp.	Inga	Leguminosae
<i>Iryanthera juruensis</i>	Iryanthera	Myristicaceae
<i>Iryanthera</i> spp.	Iryanthera	Myristicaceae
<i>Jacaranda copaia</i>	Jacaranda	Bignoniaceae
<i>Laetia procera</i>	Laetia	Salicaceae
<i>Lecythis corrugata</i>	Lecythis	Lecythidaceae
<i>Lecythis davisii</i>	Lecythis	Lecythidaceae
<i>Lecythis</i> spp.	Lecythis	Lecythidaceae
<i>Licania alba</i>	Licania	Chrysobalanaceae
<i>Licania buxifolia</i>	Licania	Chrysobalanaceae
<i>Licania heteromorpha</i>	Licania	Chrysobalanaceae
<i>Licania laxiflora</i>	Licania	Chrysobalanaceae
<i>Licania majuscula</i>	Licania	Chrysobalanaceae
<i>Licania</i> spp.	Licania	Chrysobalanaceae
<i>Loxopterygium sagotii</i>	Loxopterygium	Anacardiaceae
<i>Manicaria saccifera</i>	Manicaria	Arecaceae
<i>Manilkara bidentata</i>	Manilkara	Sapotaceae
<i>Mauritia flexuosa</i>	Mauritia	Arecaceae
<i>Mauritia</i> spp.	Mauritia	Arecaceae
<i>Mora excelsa</i>	Mora	Leguminosae
<i>Mora</i> spp.	Mora	Leguminosae
<i>Muelleria urens</i>	Muelleria	Leguminosae
<i>Myrciaria vismiifolia</i>	Myrciaria	Myrtaceae
<i>Myroxylon peruiferum</i>	Myroxylon	Leguminosae
<i>Ocotea acutangula</i>	Ocotea	Lauraceae
<i>Ocotea rubra</i>	Ocotea	Lauraceae
<i>Ocotea</i> spp.	Ocotea	Lauraceae
<i>Oenocarpus bacaba</i>	Oenocarpus	Arecaceae
<i>Oenocarpus bataua</i>	Oenocarpus	Arecaceae
<i>Ormosia</i> spp.	Ormosia	Leguminosae
<i>Pachira</i> spp.	Pachira	Malvaceae
<i>Parahancornia amapa</i>	Parahancornia	Apocynaceae
<i>Parinari campestris</i>	Parinari	Chrysobalanaceae
<i>Paypayrola longifolia</i>	Paypayrola	Violaceae
<i>Peltogyne venosa</i>	Peltogyne	Leguminosae
<i>Pentaclethra macroloba</i>	Pentaclethra	Leguminosae
<i>Platonia insignis</i>	Platonia	Clusiaceae
<i>Posoqueria longiflora</i>	Posoqueria	Rubiaceae
<i>Pourouma tomentosa</i>	Pourouma	Urticaceae
<i>Pouteria caimito</i>	Pouteria	Sapotaceae
<i>Pouteria cuspidata</i>	Pouteria	Sapotaceae
<i>Pouteria guianensis</i>	Pouteria	Sapotaceae
<i>Pouteria speciosa</i>	Pouteria	Sapotaceae

<i>Pradosia schomburgkiana</i>	Pradosia	Sapotaceae
<i>Protium decandrum</i>	Protium	Burseraceae
<i>Protium spp.</i>	Protium	Burseraceae
<i>Pterocarpus officinalis</i>	Pterocarpus	Leguminosae
<i>Quassia simarouba</i>	Quassia	Simaroubaceae
<i>Sacoglottis guianensis</i>	Sacoglottis	Humiriaceae
<i>Sapium paucinervium</i>	Sapium	Euphorbiaceae
<i>Sclerolobium guianense</i>	Sclerolobium	Leguminosae
<i>Simarouba amara</i>	Simarouba	Simaroubaceae
<i>Spondias mombin</i>	Spondias	Anacardiaceae
<i>Sterculia spp.</i>	Sterculia	Malvaceae
<i>Swartzia leiocalycina</i>	Swartzia	Leguminosae
<i>Symphonia globulifera</i>	Symphonia	Clusiaceae
<i>Tabebuia capitata</i>	Tabebuia	Bignoniaceae
<i>Tabebuia insignis</i>	Tabebuia	Bignoniaceae
<i>Tabebuia serratifolia</i>	Tabebuia	Bignoniaceae
<i>Tabebuia stenocalyx</i>	Tabebuia	Bignoniaceae
<i>Tapirira obtusa</i>	Tapirira	Anacardiaceae
<i>Thyrsodium spruceanum</i>	Thyrsodium	Anacardiaceae
<i>Toulicia guianensis</i>	Toulicia	Sapindaceae
<i>Tovomita spp.</i>	Tovomita	Clusiaceae
<i>Triplaris weigeltiana</i>	Triplaris	Polygonaceae
<i>Unonopsis glaucopetala</i>	Unonopsis	Annonaceae
<i>Virola melinonii</i>	Virola	Myristicaceae
<i>Virola sebifera</i>	Virola	Myristicaceae
<i>Virola spp.</i>	Virola	Myristicaceae
<i>Virola surinamensis</i>	Virola	Myristicaceae
<i>Vitex spp.</i>	Vitex	Lamiaceae
<i>Vochysia surinamensis</i>	Vochysia	Vochysiaceae
<i>Xylopia spp.</i>	Xylopia	Annonaceae

Table S5: Factor loadings of the three first principal components (PC) extracted from PCA of soil elemental composition (total content of C, N, S, Si, Al, Fe with CLR transformation) and molecular composition (standardized mean absorbance of 15 IR bands selected as main inorganic and organic constituents, by their wavenumber - WN) variables, which explained a 67.91% of total variance (% explained by each PC in table) among 401 soil samples from 83 transects in Guyana.

Soil composition	PC1 ^a (30.71%)	PC2 ^b (21.87%)	PC3 ^c (15.32%)
silicon (Si)	-0.38	0.50	-0.36
aluminum (Al)	0.32	0.67	-0.38
iron (Fe)	0.69	0.37	-0.25
iron-aluminum oxides/silicates (WN530)	0.93	0.11	-0.02
clay (kaolinite; WN911)	0.89	0.10	-0.04
clay (kaolinite; WN3620)	0.89	0.06	-0.12
clay (kaolinite; WN3694)	0.91	0.07	-0.06
quartz (WN777)	-0.94	-0.15	-0.07
quartz (WN798)	-0.92	-0.13	-0.03
carbon (C)	-0.07	0.89	-0.23
nitrogen (N)	0.07	0.86	-0.29
sulphur (S)	-0.36	0.80	-0.31
aromatic SOM (WN1550)	-0.13	0.60	0.36
aromatic-N SOM (WN1630)	-0.11	0.63	0.29
carbonyl SOM (carboxylates; WN1700)	-0.01	0.36	0.71
carbonyl SOM (organic acids; WN1710)	0.02	0.26	0.69
carbonyl SOM (carboxylic acids; WN1720)	0.14	0.17	0.72
aliphatic SOM (WN2850)	-0.17	0.35	0.65
aliphatic SOM (WN2920)	-0.1	0.43	0.54
carbohydrates/silicates (WN1823)	0.52	-0.31	0.30
carbohydrates/silicates (WN1838)	0.49	-0.34	0.31

Footnote1. Each PC represents different elemental-molecular soil composition, as follows:

^a Clay vs quartz content (kaolinite + iron-aluminum oxides versus quartz)

^b Total SOM content (C, N, S concentrations + aromatic-nitrogenated, carboxylated and aliphatic SOM)

^c Carbonyl and aliphatic SOM vs N-, S-, Fe-rich SOM content (carbonyl groups + aliphaticity versus total N, S, Fe).

Table S6: Factor loadings of the two first principal components (PC) extracted from PCA of environmental variables (longitude, latitude, temperature and precipitation), which explained a 79.97% of total variance (% explained by each PC in table) among 30 sites in Guyana.

Variables	PC1 (51.86%) ^a	PC2 (28.12%) ^b
Longitude (m)	0.93	-0.19
Latitude (m)	0.42	0.73
Temperature (°C)	0.60	-0.67
Precipitation (mm)	0.81	0.33

Footnote1. Each PC represents different environmental conditions, as follows:

^a Environment PC1 (Longitude + Precipitation variation)

^b Environment PC2 (Latitude vs Temperature variation)

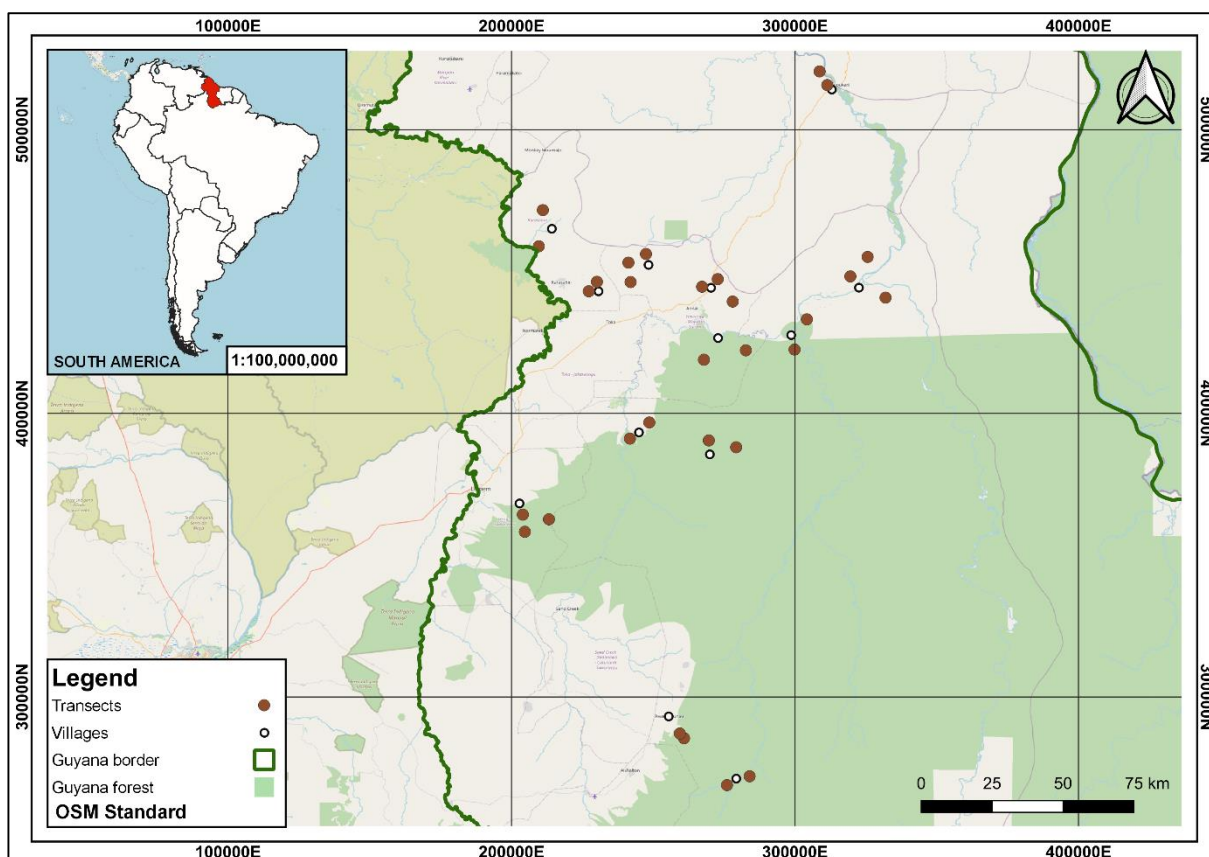


Figure S1. Map of the 30 sites selected to analyze soil microbial carbon consumption in Guyana (WGS84/UTM zone 21N), where mammal, tree and soil data (brown dots) were surveyed by indigenous people from local villages (white dots) in a forest-savanna system (layer: <https://www.openstreetmap.org>, OpenStreetMap, CC-BY-SA). This map was created with QGIS Desktop version 3.22.0 for Windows (QGIS Development Team, 2022).

A1 Water	A2 β -Methyl-D-Glucoside	A3 D-Galactonic Acid γ -Lactone	A4 L-Arginine
B1 Pyruvic Acid Methyl Ester	B2 D-Xylose	B3 D-Galacturonic Acid	B4 L-Asparagine
C1 Tween 40	C2 i-Erythritol	C3 2-Hydroxy-Benzoic Acid	C4 L-Phenylalanine
D1 Tween 80	D2 D-Mannitol	D3 4-Hydroxy-Benzoic Acid	D4 L-Serine
E1 α -Cyclodextrin	E2 N-Acetyl-D-Glucosamine	E3 γ -Hydroxy-Butyric Acid	E4 L-Threonine
F1 Glycogen	F2 D-Glucosaminic Acid	F3 Itaconic Acid	F4 Glycyl-L-Glutamic Acid
G1 D-Cellobiose	G2 Glucose-1-Phosphate	G3 α -Keto-Butyric Acid	G4 Phenylethylamine
H1 α -D-Lactose	H2 D,L- α -Glycerol-Phosphate	H3 D-Malic Acid	H4 Putrescine

Figure S2. Biolog Ecoplate simplified design. One set of 31 sole carbon sources assessed by Ecoplate and classified in six carbon guilds by different colored wells: polymers (fucsia), carbohydrates (sea green), carboxylic acids (light red), miscellaneous compounds (light blue), amino acids (green), amines (olive green). Modified from the Biolog® technical documentation (<https://www.biolog.com/products-portfolio-overview/microbial-community-analysis-with-ecoplates/>).

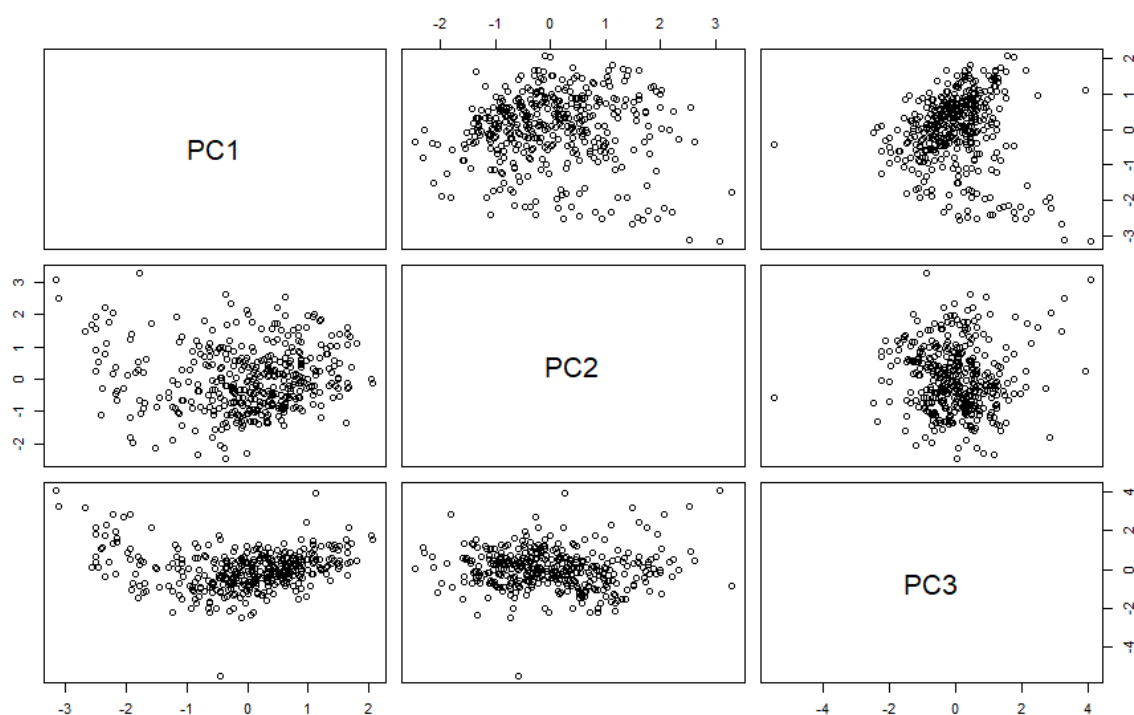


Figure S3. Biplots of the scores of three first principal components (PC) obtained by principal component analysis (67.9% of total variance) of soil composition (n=401 samples). PC1 (30.71%) represents variation in clay minerals vs quartz content, PC2 (21.87%) reflects the variation in total SOM content, and PC3 (15.32%) represents the variation in the content of N-, S-, Fe- rich SOM versus carbonyl and aliphatic SOM.

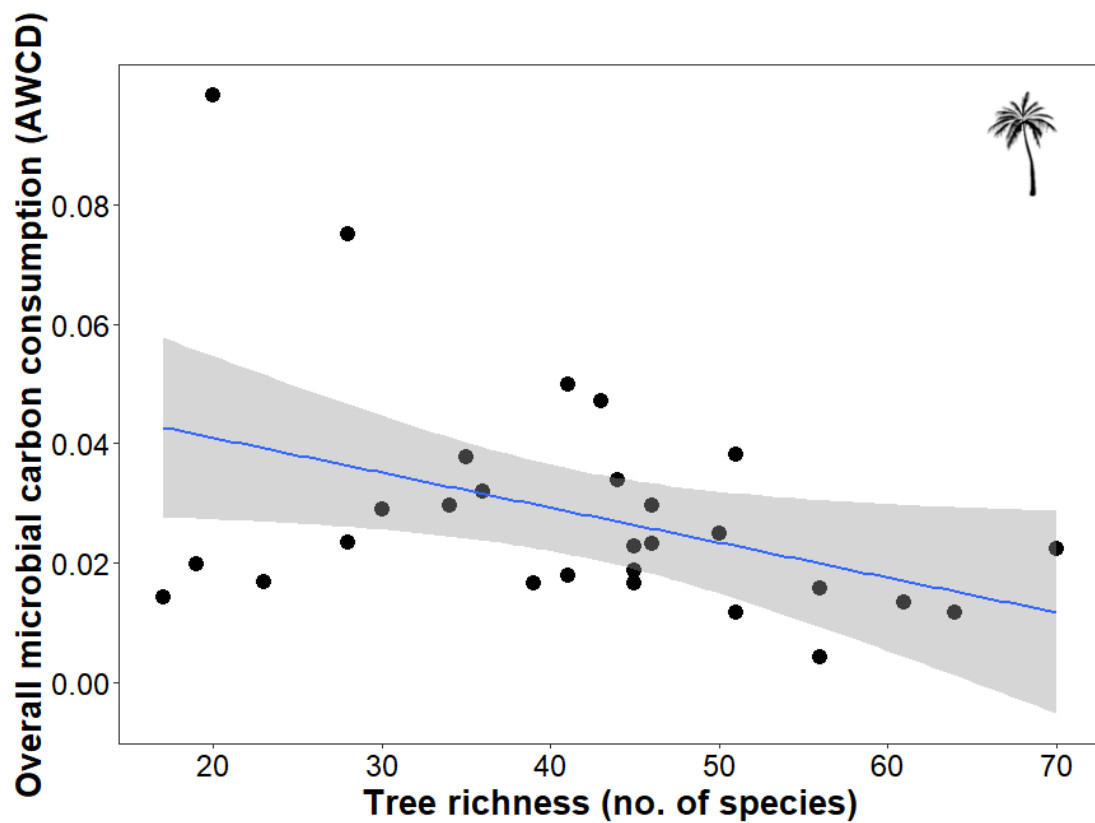


Figure S4. GLM predicted relationship between tree richness (no. of species) and overall carbon consumption by soil microbes (average well color development, AWCD). This effect was marginally significant ($0.05 < p\text{-value} < 0.10$).

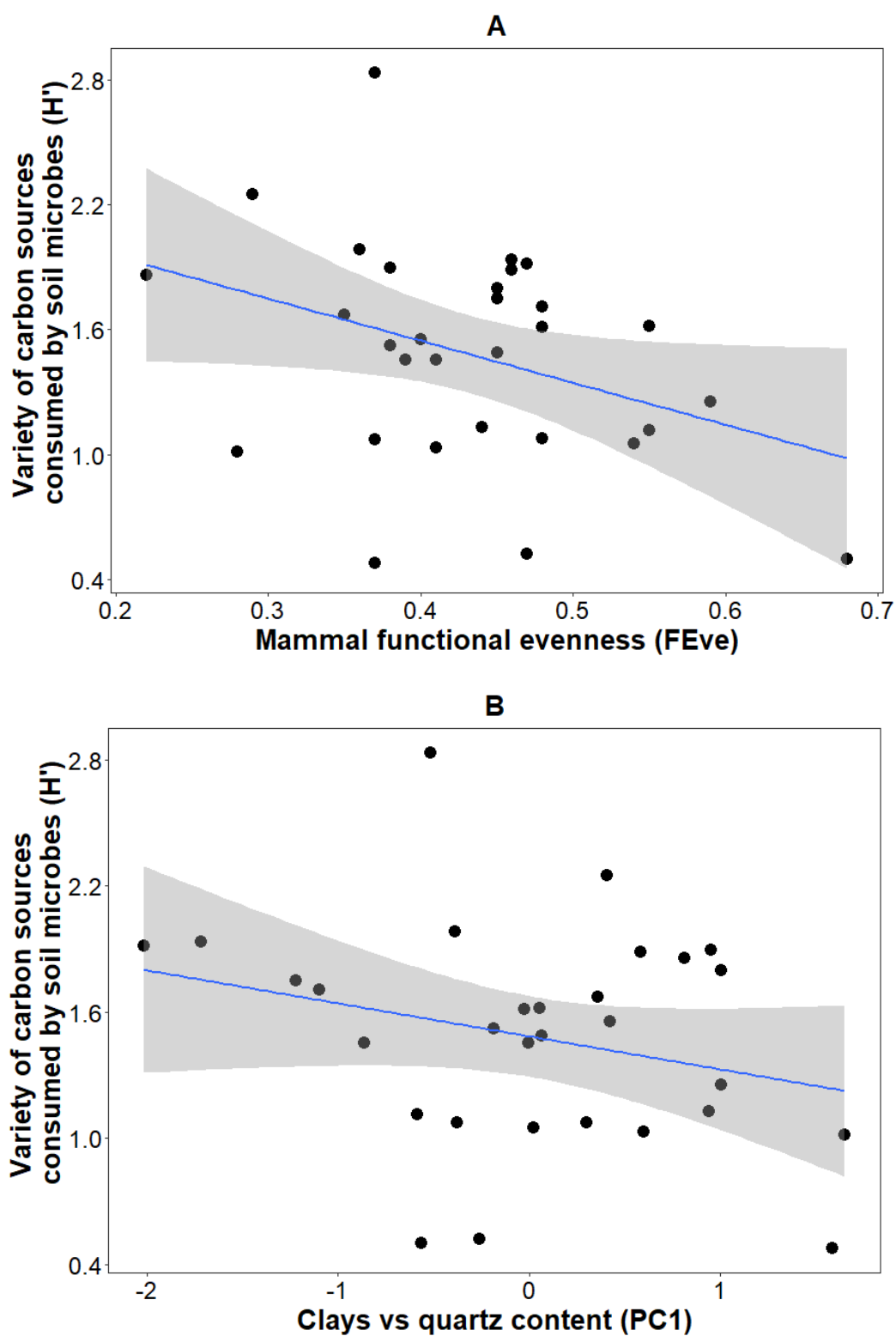


Figure S5. GLM predicted relationships between (A) mammal functional evenness (FEve), (B) soil clay vs quartz content (soil PC1 scores), and the variety of carbon sources consumed by soil microbes (Shannon-Wiener diversity index, H'). Both effects were marginally significant ($0.05 < p\text{-value} < 0.10$).

ANNEX B: LIST OF PUBLICATIONS

Publication 1.

a. Losada M.¹, Martínez Cortizas, A. M.^{1,2}, Silvius, K. M.³, Varela, S.⁴, Raab, T. K.⁵, and Fragoso, J. M. V.^{6,7}, & Sobral, M.¹ (2023). Mammal and tree diversity accumulate different types of soil organic matter in the northern Amazon. *iScience*, 26(3), 106088. DOI: <https://doi.org/10.1016/j.isci.2023.106088>. **JCR IF (2022): 5.8, CiteScore: 6.9, Quartil: Q1 (Multidisciplinary Sciences)**

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Mammal and tree diversity accumulate different types of soil organic matter in the northern Amazon

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c. Contribution of the PhD student: Hypothesis design, laboratory analysis, statistical analysis, visualization, data interpretation, and manuscript writing and revision.

Publication 2.

a. Losada, M.¹, Sobral, M.¹, Silvius, K. M.², Varela, S.³, Martínez Cortizas, A. M.⁴, & Fragoso, J. M. V.^{5,6} (2023). Mammal traits and soil biogeochemistry: Functional diversity relates to composition of soil organic matter. *Ecology and Evolution*, 13(8), e10392. DOI: <https://doi.org/10.1002/ece3.10392>. JCR IF (2022): 2.6, CiteScore: 4.6, Quartil: Q1 (Ecology) / Q1 (Ecology, Evolution, Behavior and Systematics)

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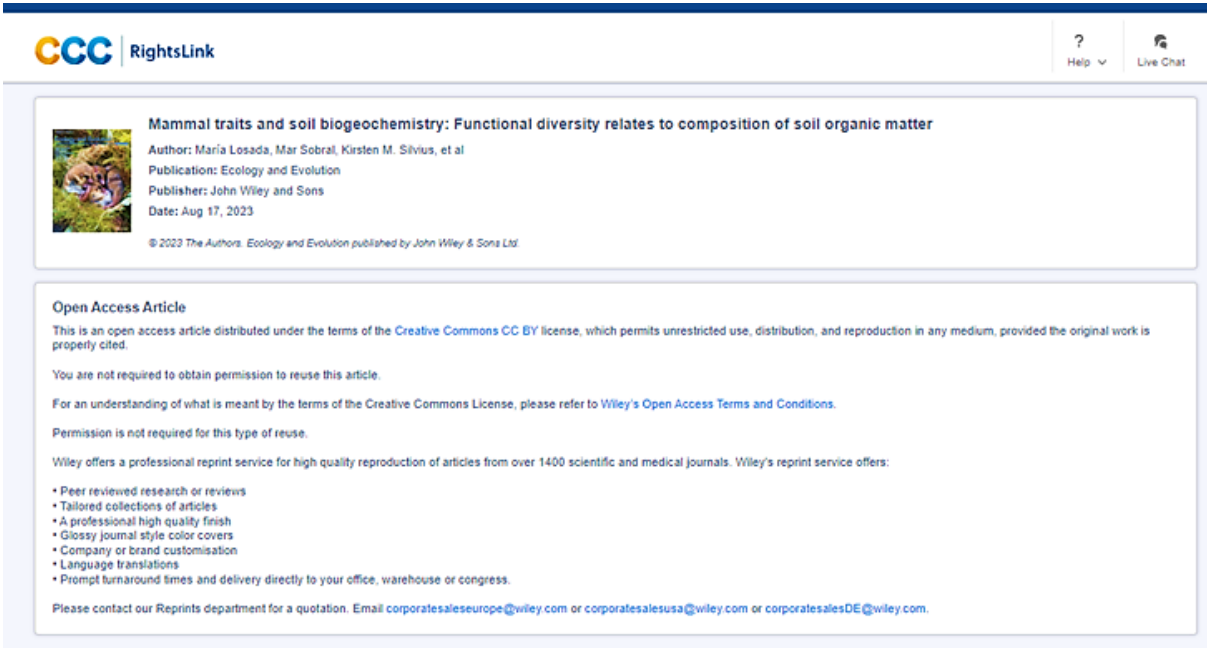
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c. Contribution of the PhD student: Hypothesis design, laboratory analysis, statistical analysis, visualization, data interpretation, and manuscript writing and revision.

ANNEX C: FUNDING INFORMATION

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This Ph.D. thesis explores the impact of mammal communities on the carbon cycle in the northern Amazon, focusing on the species and trait diversity' effects on soil organic matter (SOM) and microbial carbon consumption. The study reveals that high mammal richness reduces carbon-rich SOM while it increases soil nitrogen, sulfur, and iron content, which favors SOM stabilization. Functional diversity (FD) within mammal communities has a more relevant influence on SOM composition than species richness, and different FD metrics affect carbon-rich SOM accumulation, reducing soil microbial carbon consumption. This research highlights the critical importance of considering not only species richness but also trait diversity in animal communities to understand their impacts on the intricate carbon dynamics and SOM accumulation.