Forest Diversity and Environmental Factors Shape Contrasting Soil-Litter BVOC and Methane Fluxes in Three Central Amazonian Ecosystems

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Abstract

Biogenic volatile organic compounds (BVOCs) play a crucial role in biosphere-atmosphere interactions and the global carbon cycle. While vegetation is recognized as the primary source of BVOC fluxes in forest ecosystems, recent studies suggest that the carbon-rich soil-litter compartment ~~contributes~~ plays a significant~~ly~~ role in gas fluxes. However, the~~se fluxes, their underlying~~ drivers, ~~and their~~ variability, and magnitude of these fluxes across different forest types remain poorly understood~~,~~. ~~with measurements still scarce~~ — This is particularly notable in the Amazon rainforest, the world's largest source of BVOCs, where measurements ~~still~~remain scarce. In this study, we investigated the net soil-litter gas exchange of BVOCs and methane ~~fluxes and~~, along with their potential drivers — ~~including~~ - soil and litter nutrient content, soil and litter microbial biomass, soil temperature, and soil moisture — - across three forest types in central

Amazonia: ~~w~~White ~~s~~Sand ~~f~~Forest (WS), ~~u~~Upland ~~f~~Forest (~~UP~~Up), and ~~a~~Ancient ~~r~~River ~~t~~Terrace ~~f~~Forest (AR). Our results showed distinct ~~flux~~soil-litter gas exchange patterns ~~among~~across the forest types. WS exhibited both high emissions and consumption of gases, notably high acetaldehyde and methane emissions, ~~and strong isoprene and~~along with a uptake of monoterpene~~s uptake~~. ~~UP~~Up showed lower overall fluxes, with moderate emissions and consumption of dimethyl sulfide (DMS), isoprene, and acetaldehyde. In contrast, AR presented no significant fluxes. ~~Linear models identified~~ Among the variables tested, models indicated that soil moisture and temperature ~~as~~were the ~~primary~~strongest drivers of fluxes in WS, ~~while~~whereas microbial biomass was the main driver in ~~UP~~Up. Our measurements suggest that, despite covering a relatively small area in the Amazon basin, WS can be a significant ecosystem for BVOC and methane fluxes, ~~regulated~~where these fluxes are influenced by soil moisture and temperature. Our findings underscore the need to account for forest-type-specific fluxes when modeling BVOC and methane emissions in the Amazon, particularly under changing climate conditions.

Key words

Amazon rainforest; Biogenic ~~v~~Volatile ~~o~~Organic ~~c~~Compounds (BVOC); Methane (CH_4); rain-induced emissions; Soil-litter fluxes; Forest heterogeneity; Soil-litter microorganism~~-~~s

1. Introduction

Biogenic Volatile Organic Compounds (BVOCs) play critical roles across scales, from cellular processes to global climate regulation. While primarily emitted by plants, BVOCs can also be produced and consumed by soils, litter and microorganisms. Once released into the atmosphere, they actively participate in atmospheric chemistry and physics, influencing climate dynamics. BVOCs react with key atmospheric oxidants - including hydroxyl radicals (OH), ozone (O_3), and nitrate radicals (NO_3) - to form secondary organic aerosols (SOAs) (Artaxo et al., 2022; Yáñez-Serrano et al., 2020). SOAs, in turn, have a major influence on cloud properties, enhancing cloud condensation nuclei (CCN) concentrations, which impacts precipitation patterns and alters cloud lifecycles (Liu and Matsui, 2022). Depending on their chemical composition, SOAs can also influence the Earth's radiation budget by scattering incoming solar radiation (resulting in a cooling effect) or absorbing outgoing longwave radiation. Additionally, depending on the concentration of NO_x, BVOCs contribute to the formation of tropospheric ozone - an important greenhouse gas and

a major air pollutant (Vella et al., 2025). Given these large-scale impacts, accurately quantifying BVOC fluxes in terrestrial ecosystems is essential for advancing our understanding of forest–atmosphere interactions and for improving Earth system models, thereby improving climate predictions.

Global emissions of BVOCs from terrestrial vegetation are estimated at approximately 760 Tg C yr^{-1}, with isoprene (C_5H_8) and monoterpenes ($C_{10}H_{16}$) accounting for around 70% and 11% of these emissions, respectively (Guenther et al., 2012, Sindelarova et al., 2014). Isoprene is a simple building block compound emitted in large quantities, particularly by tropical forests. Monoterpenes (e.g., α-pinene, β-pinene, limonene) are structurally more complex (Guenther et al., 2012; Alves et al., 2016) with (-)α-pinene being the second most emitted compound (Zannoni et al., 2020; Yanez-Serrano et al., 2018). The Amazon rainforest alone contributes about 40% of global BVOC emissions, playing a critical role in the global carbon cycle (Guenther et al., 2012; Wang et al., 2024; Tripathi et al., 2025). However, these global estimates primarily consider emissions from plants, neglecting potential contributions from soil and litter, which might also include a large variety of BVOC chemical species.~~Soil and litter constitute an ecological~~ This gap is particularly significant given recent evidence that the soil–litter together is a compartment that can also play~~s~~ a crucial role in ~~gas fluxes of biogenic volatile organic compounds (BVOCs) (~~BVOC emissions (Bourtsoukidis et al., 2018; Drewer et al., 2021; Fan et al., 2020, 2024; Peñuelas et al., 2014; Tang et al., 2019). ~~and greenhouse gases (GHGs) (Fan et al., 2020, 2024).~~ Within this compartment, multiple ~~B~~biological and physical processes ~~are essential in soil and litter BVOC and GHG fluxes.~~influence BVOC dynamics. ~~In terms of biological processes, roots release BVOCs for~~These include plant-related processes such as intra- and inter-organism communication, ~~defense against~~ herbivor~~y~~e defense, and symbiotic ~~relationships~~interactions (Gfeller et al., 2013; Lin et al., 2007; Rasheed et al., 2021; Steeghs et al., 2004; Tang et al., 2019; Trowbridge et al., 2020)~~,~~. ~~and~~Additionally, soil microorganisms produce and consume BVOCs for communication and ecological interactions (e.g., defense and competition), with these compounds also being released as residual metabolic products (Isidorov & Jdanova, 2002; Leff & Fierer, 2008; Liu et al., 2024; Monard et al., 2021). ~~GHGs, such as methane (CH_4) and carbon dioxide (CO_2), are produced by microorganisms in the soil. Methane fluxes are primarily driven by methanogenic (archaea) and methanotrophic microorganisms in anaerobic and aerobic environments, contributing to the global methane budget (Conrad, 2009; Hofmann et al., 2016). The~~

~~decomposition of litter also influences BVOC and GHG fluxes; particularly physical factors, such as temperature and soil moisture, greatly impact litter decomposition by influencing the activity of microorganisms, a process that also releases BVOCs and GHGs (Greenberg et al., 2012; Tang et al., 2019; Mäki et al., 2017; Asensio et al., 2008). Temperature directly affects gas production and consumption (Conrad, 2009), the evaporation of stored compounds (Aaltonen et al., 2011), and the desorption from leaf litter tissue and soil organic matter (Bachy et al., 2018; Schade & Goldstein, 2001; Tang et al., 2019, Warneke et al., 1999). Soil moisture affects microbial activity (Abis et al., 2020; Liu et al., 2024) and BVOC adsorption (Jiao et al., 2023), thereby directly affecting the magnitude of soil gas fluxes (Conrad, 2009; Liu et al., 2024; Pugliese et al., 2023; Shah et al., 2024; Svendsen et al., 2016). In addition to changes in soil moisture, precipitation events can induce BVOC emissions, e.g., by pushing stored soil BVOC gases out of the soil pore space (Miyama et al., 2020).~~

~~Soil type can also influence gas fluxes, with sandy soils facilitating BVOC volatilization and retention due to larger pore spaces that promote water movement and faster evaporation under higher temperatures (Onwuka, 2018). For example, soil texture influences the relationship between methane and soil moisture, with methane emission fluxes being generally higher in sandy soils than in clay soils (Cai et al., 1999), probably due to their larger pore size, which facilitates gas diffusion (Rosace et al., 2020). Additionally, changes in vegetation cover also impacts gas fluxes (Gomes Alves et al., 2022). Plant species composition influences BVOC emissions in terms of chemical composition and emission rates (Bao et al., 2023; Mu et al., 2022; Zhang et al., 2024), and since different soil types often support distinct vegetation (Rodrigues et al., 2018), soil-litter gas fluxes are expected to vary across forest types (Wachiye et al., 2020).~~

~~The Amazon basin is the largest source of BVOCs to the global atmosphere (Guenther et al., 2012). BVOCs are crucial for understanding climate dynamics due to their role in atmospheric chemistry. They contribute to the formation of secondary organic aerosols (SOAs) and influence cloud properties, which in turn affect global climate patterns (Fuentes et al., 2000; Jimenez et al., 2009). Although vegetation is considered the main source of these compounds, with large effects on the above-mentioned atmospheric processes, some studies have shown that soils are as important as plants for BVOC emissions (Penuelas et al., 2014).~~

~~The Amazon basin has different soil types (Quesada et al., 2011), which determine forest structure (Quesada et al., 2012) and plant species composition (Ter Steege et al., 2013), resulting in a mosaic of different forest types throughout the basin (Oliveira-Filho et al., 2020). These different forest and soil types have been little - or not at all investigated for soil-litter BVOC and GHG fluxes and, therefore, are not included in model estimates. In this sense, studies integrating biological and physical measurements are essential to understand the processes controlling soil-litter BVOC and GHG fluxes across Amazonian forest types. Quantifying BVOC emissions from soil is essential for accurately modeling these processes and predicting their effect on climate, as soil can be a significant source of BVOCs.~~

Greenhouse gases (GHGs), such as methane (CH_4), carbon dioxide (CO_2) and nitrous oxide (N_2O), are also produced and consumed by soil microorganisms through key metabolic processes, including methanogenesis, methanotrophy, and respiration (Conrad, 2009,2020; Hofmann et al., 2016). While CO_2 and methane are not classified as BVOCs, they play a crucial role in overall gas exchange processes and provide a broader perspective of soil-litter gas (carbon) fluxes. Moreover, environmental factors such as soil moisture, temperature, and nutrient availability influence both BVOC and GHG fluxes, albeit through distinct-but interconnected-biological and physical mechanisms (Greenberg et al., 2012; Tang et al., 2019; Asensio et al., 2007). These interconnected processes drive net ecosystem gas exchange between the soil-litter compartment and the atmosphere, making methane and CO_2 key components for understanding processes driving BVOC flux dynamics.

Fluxes of GHGs and BVOCs can also be linked to litter decomposition. This process is influenced by various physical factors, including soil moisture, temperature, and nutrient availability, which collectively can enhance microbial activity—one of the main drivers of these fluxes (Greenberg et al., 2012; Tang et al., 2019; Mäki et al., 2017; Asensio et al., 2007). Specifically, microbial processes such as nitrification and denitrification can result in the production and consumption of N_2O in soils (Butterbach-Bahl et al., 2013; Snyder et al., 2009). Together, these processes drive the net ecosystem exchange of BVOCs and GHGs between the soil-litter compartment and the atmosphere, and the magnitude and direction of this exchange may vary across different ecosystem types.

The Amazon Basin is a mosaic of diverse forest types (Oliveira-Filho et al., 2021), each with distinct plant species composition (Ter Steege et al., 2013), shaped by the region's highly variable soil properties (Quesada et al., 2011; Quesada et al., 2012). Although Amazonian heterogeneity is known to play a critical role in regulating biogeochemical cycles, comparative studies across forest types, especially at the soil–litter interface, are still scarce. Distinct interactions between vegetation and soil can lead to highly variable patterns of BVOC and GHG exchange. This lack of representation underscores the urgent need for studies that account for the region's ecological diversity to better capture the unique contributions of each forest type to biogeochemical processes. Quantifying this variability is key to improving both regional and global models, as gas fluxes are unlikely to be uniform within the Amazon.

~~With a unique set of measurements~~To address these gaps, we investigated soil-litter fluxes of BVOCs (acetaldehyde, methanol, m/z 42, dimethyl sulfide, isoprene and monoterpenes) and GHGs (CH_4 and CO_2)~~ fluxes~~, soil and litter nutrient content and microbial biomass, and soil temperature and moisture from three forest types in central Amazonia: (i) ~~a~~Ancient ~~r~~River ~~t~~Terrace ~~f~~Forest - a forest that was flooded in the past and is no longer flooded due to changes in the river course (paleoigapó); (ii) ~~w~~White ~~s~~Sand ~~f~~Forest (locally called campinarana) - a less common forest type that occupies about 5% of the Amazon basin (Adeney et al., 2016); and (iii) ~~u~~Upland ~~f~~Forest (locally called terra-firme) - the most common forest in Amazonia, with the highest plant species richness (Emidio et al., 2016; Luize et al., 2018). We aimed to answer the following questions: (i) what is the emission/consumption of ~~gases (~~BVOCs, CO_2, and CH_4~~)~~ in magnitude and chemical diversity, and~~?~~; ~~and~~ (ii) what are the main drivers of soil-litter gas ~~fluxes~~exchanges across these three forest types in central Amazonia~~?~~ (specifically, soil moisture, soil temperature, nutrient content and microbial biomass from soil and litter)?

2. Material and Methods

2.1 Site Description

This study was conducted in the MAUA–PELD experimental plots (PELD is the abbreviation in Portuguese for long-term ecological research) (Fig. 1) at the Amazon Tall Tower Observatory (ATTO) experimental site. This site is located 150 km northeast of Manaus and is part of the Uatumã Sustainable Reserve (USDR), which covers an area of 424,430 hectares

(Andreae et al., 2015). The climate is tropical humid, with average annual rainfall of 2,376 mm and a temperature of 28°C (Botía et al., 2022). There are two distinct seasons, the wet season from December to May and the dry season from July to October, with transition seasons in between. The ATTO site contains three dominant non-flooded ecosystems: a dense ~~u~~Upland ~~f~~Forest (Up) on the plateau, with an elevation close to 100 m (*terra-firme*); a ~~w~~White ~~s~~Sand ~~f~~Forest (WS) (*campinarana*); and another type of *terra-firme* vegetation that developed on the lower-laying ancient river terraces (~~a~~Ancient ~~r~~River ~~t~~Terrace ~~f~~Forests (AR)) (Fig. 1) (Andreae et al., 2015).

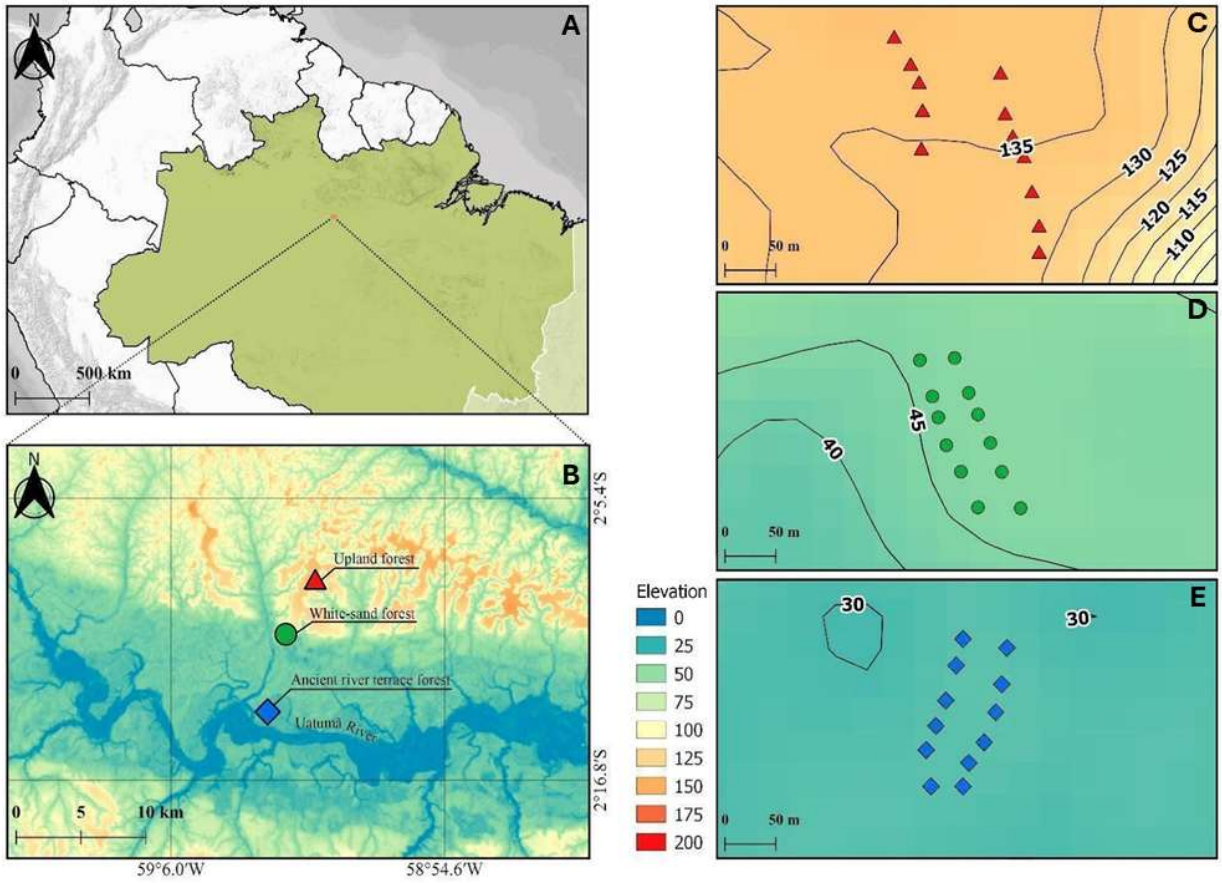


Figure 1. (A) Location of the ATTO site. (B) A map illustrating the locations of the different forest types evaluated in this study: ~~u~~Upland ~~f~~Forest, ~~w~~White ~~s~~Sand ~~f~~Forest, and ~~a~~Ancient ~~r~~River ~~t~~Terrace ~~f~~Forest; and showing the Uatumã River, a tributary of the Amazon River. (C), (D) and (E): The distribution of sampling points along the ~~t~~Transects in each forest type (~~u~~Upland ~~f~~Forest - top, ~~w~~White ~~s~~Sand ~~f~~Forest - middle, and ~~a~~Ancient ~~r~~River ~~t~~Terrace ~~f~~Forest - bottom); black lines and numbers indicate the elevation (above sea level – a.s.l.).

Topography is critical to soil formation in the central Amazon region (Quesada et al., 2009). At the ATTO site, a clear topographic gradient is associated with different soil characteristics (Fig. 1). In the ~~a~~Ancient ~~r~~River ~~t~~Terrace ~~f~~Forest, soil contains more silt and clay (39% sand, 37% silt, 23% clay) in comparison to the adjacent sandy ~~w~~White ~~s~~Sand ~~f~~Forest soils (57% sand, 40% silt, 1.50% clay). Upland ~~f~~Forest soils are more clayey and contain very little sand (13% total sand, 34% silt, 52% clay) (data from this study; supplementary material, Section 1; Table S1). Upland ~~f~~Forest soils, which are predominantly ferrasols, are known to hold more water than other tropical soils, benefiting forest activity during the dry season (Quesada et al., 2009). Ancient ~~r~~River ~~t~~Terrace ~~f~~Forest soils are typically allisols, younger and richer in nutrients compared to upland ferralsols (Andreae et al., 2015). White ~~s~~Sand ~~f~~Forest soils are arenosols, characterized by high permeability and low water retention, with low specific heat capacity and often nutrient-poor organic layers (Quesada et al., 2011). The study area in the ~~w~~White ~~s~~Sand ~~f~~Forest has high water table variability, with a hard subsoil layer that restricts drainage and can flood the root system during the wet season (Demarchi et al., 2022).

2.2 Sampling Design

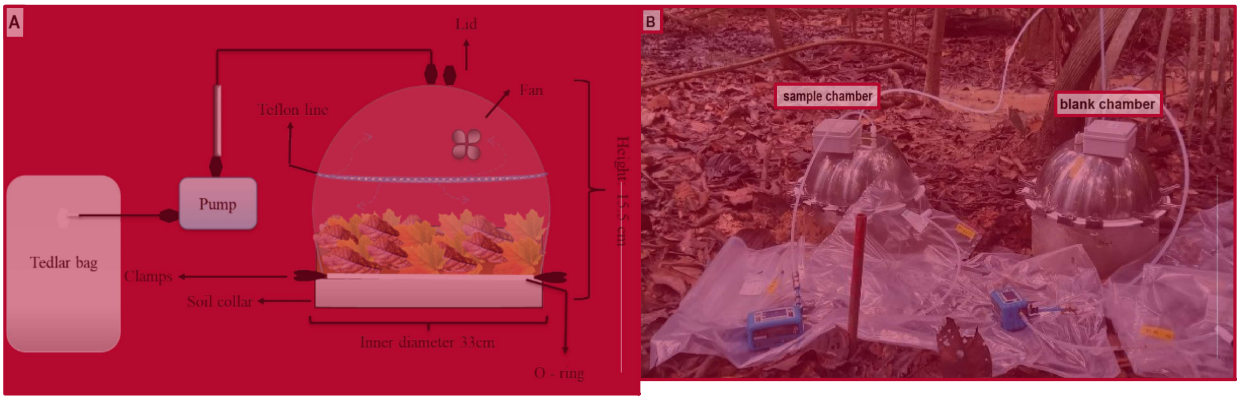
For each forest type, a PELD-MAUA plot (~1 hectare) ~~was selected, wherein two 150 m transects were marked.~~(https://peld-maua.inpa.gov.br) was selected. ~~Six collection points, approximately 30 m apart, were determined for each transect~~, ~~resulting in a total of 36 soil chamber measurements (Fig. 1). Additionally, three blank chambers per transect were measured, which consisted of chambers with the same volume but with a completely bottom-sealed collar.~~Within each plot, two 150 m Transects were established (Fig. 1) in homogeneous areas characterized by consistent vegetation structure, soil characteristics, and topography, to minimize spatial variability and avoid pseudo replication. Along each Transect, six sampling points were marked at ~30 m intervals, resulting in a total of 36 soil chamber measurements conducted on consecutive days; although this design was necessary for logistical reasons, it also allowed us to examine the influence of external factors beyond forest-type differences. Chamber-based methods (Section 2.3; Fig. 1) were employed for the in-situ quantification of CO_2, CH_4, and BVOC fluxes from the soil–litter compartment. These chambers were installed directly in the field with minimal disturbance to the surrounding environment. ~~These blank chambers were measured simultaneously and under the same conditions as the sample chambers covering soil and litter.~~ To account for potential

background signals and chamber interferences, three blank chambers, each featuring completely bottom-sealed collars, were deployed per Transect and measured simultaneously alongside the sample chambers (Fig. 2b).

Tedlar bags (CEL Scientific, Cerritos, CA, USA) were used to collect gas samples directly from the outlet of the pump connected to the chambers, capturing the air for subsequent analysis of BVOCs, CO_2 and CH_4. After each gas flux measurement, soil temperature (T, ºC) (TP-101, Delhi, India) and soil volumetric water content (VWC, %) ~~(AT-SMT150, Cambridge, UK)~~ were measured around the collar five times using a probe (AT SMT150, Cambridge, UK), and the averages ~~was~~ were calculated. Surface soil samples were collected from the organic layer, approximately within the upper 5 cm of the soil. Samples from the litter and surface soil layers were collected inside the chamber and stored for analysis of chemical and physical characteristics and microbial biomass. Due to expected low variation and limited possibility for laboratory analyses, nutrient samples from soil and litter (excluding carbon and nitrogen) and ~~soil~~ granulometry were collected as mixed samples pooled and homogenized from two collars. To minimize diurnal variation, each ~~t~~Transect was measured between 8:00 and 10:00 (local time), after which collected ~~bag~~ samples were processed and analyzed for BVOC and GHG concentrations. During the measurements, no precipitation was observed, but one large rain event occurred just before the measurement of ~~t~~Transect 2 of the ~~w~~White ~~s~~Sand ~~f~~Forest.

2.3 Flux Chamber Measurements

The flux chambers used in this study were produced by the Max Planck Institute for Biogeochemistry ~~and were made~~. The soil chamber, consisting of a lid and a soil collar (Fig. 2a), was made entirely of 100% stainless steel ~~(Fig. 2)~~, with a total volume of 21 L and a surface area of 855 cm^{2}~~^{2}~~ (0.0855 ~~m^{2}~~m^{2}). Two Teflon inlets were connected to the top of the chamber, and inside the chamber was a fan that ~~provided air mixing of~~mixed the gases ~~-~~in the chamber headspace. A PTFE-coated Viton O-ring was positioned at the edge of the collar over which the chamber was placed~~.~~, ~~The collar and~~ensuring a tight seal between the chamber ~~were sealed together with multiple clamps to prevent outside air from entering the chamber.~~and the collar.



~~**Figure 2**. (A) Schematic of the flux chamber. (B) Photo of the measurement setup of the sample and the blank chambers.~~

Before gas sampling, each ~~soil~~ collar was carefully installed in a non-invasive manner by gently pressing ~~the collar~~its edge into the ~~soil to avoid damage~~litter and surface soil to minimize disturbance to plant shoots and roots~~,~~. ~~and then sealed with~~To further ensure a tight seal preventing any potential leakage, the surrounding soil was carefully pressed against the outer edges of the collar (Aaltonen et al., 2011). This method ensured that the chamber system was effectively isolated from external gas exchange. The chamber and collar were sealed together with multiple clamps to prevent outside air from entering the chamber during measurements. The collars were installed approximately 24 hours ~~before the measurements.~~prior to sampling to allow the surrounding environment to stabilize.

~~2.4 Field gas measurements~~

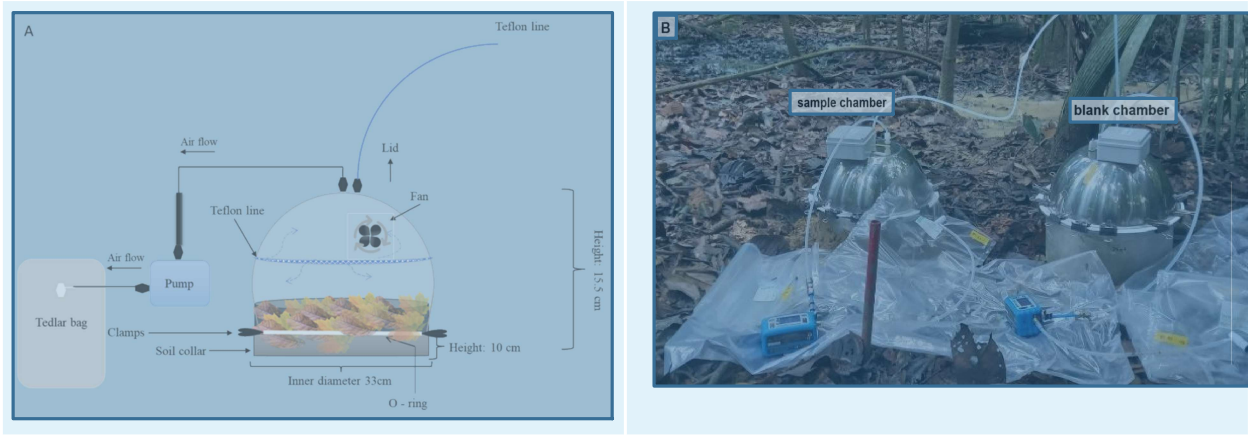


Figure 2. (A) Schematic of the flux chamber. (B) Photo of the measurement setup of the sample and the blank chambers.

The gGas collection took place in December 2021, atduring the dry-to-wet season transition. Tedlar bags (CEL Scientific, Cerritos, CA, USA) were used to sample soil-litter gas fluxes (BVOCs, CO_2, CH_4)Before placing the lid on the collar, the chamber was manually ventilated to minimize collar-induced CO_2gas accumulation caused by the collar. Once the chamber was closed and sealed with clamps, the internal fan was turned on to ensure mixing. An air sampling pump (GilAir® Plus, Levitt Safety, Ottawa, ON), operateding at a flow rate of 500 sccm, ensuringinitiated continuous flow atfrom the chamber outlet. immediately after closure to maintain constant conditions throughout the measurement.

After 20 minutes of chamber closure with continuous flow, a sampling bag was connected to the outlet of the Teflon pump, and a 5 L sample was collected over 10 minutes.air circulation, a Tedlar bag was connected to the outlet of the Teflon pump, and a 5 L air sample was collected over the next 10 minutes. By the end of the 30-minute measurement process, a total of 15 L of air had flowned through the chamber, of whichand the last 5 L waswere used for subsequent analyses. The sample volumes collected were determined by the specific requirements of each analytical instrument. Measurements of BVOCs were performed using proton-transfer-reaction quadrupole mass spectrometry (PTR-QMS,; IONICON Analytik, Innsbruck, Austria), prioritizing sufficient ion counts per second (CPS) and integration cycles for reliable detection of BVOC concentrations with the required precision, especially considering their typically trace levels. Greenhouse gases (GHGs) were measured using a Los Gatos Ultra-Portable Gas Analyzer (California, USA), hereafter referred to as the Los Gatos analyzer. Finally, for the offline measurements with cartridges and for specific compound identification and qualitative analysis with thermal-desorption gas chromatography time-of-flight mass spectrometry (TD-GC-TOF-MS; Bench ToF Tandem Ionisation, Markes International, Bridgend, UK), at least 2 L of sample air was required to effectively load the adsorbent cartridges. These analyses are further detailed in the Supplementary Materials, Section 3.2.

~~At the end of the 30-minute process, a total of 15 L of air had flown through the chamber, of which the last 5 L was used for analysis by the PTR-QMS, the Los Gatos analyzer, and for collecting a cartridge sample (see below)~~The same procedure was followed for a blank chamber, which was measured under identical conditions to account for gas contributions unrelated to soil and litter processes. For logistical reasons, measurements were conducted with three chambers ~~at a time~~simultaneously, pairing two sample chambers with one blank chamber, followed by two additional sets, resulting in the measurement~~s~~ of six samples and three blank chambers per day.

~~Before placing the lid on the collar, the chamber was manually ventilated to minimize collar-induced CO_2 accumulation. The chamber was then closed, the internal fan was turned on, and the lid was sealed with clamps.~~ Because air was continuously extracted from the chamber headspace~~, both (blank and sample) chambers had an attached~~ by the pump, ambient air entered the chamber through one additional inlet, which consisted of a 2 m long open Teflon tube, fixed approximately 2 m above the ground and positioned at the same location~~, which~~for both sample and blank chambers. The setup ensured that both chambers (sample and blank) were diluted or affected by ambient air to the same degree~~.~~, minimizing potential biases. ~~After collection, the bags were stored in a dark box for transport to the laboratory. Gas concentration analyses were conducted on the same day; first, the bags were measured using proton-transfer-reaction quadrupole mass spectrometry (PTR-QMS, IONICON Analytik, Innsbruck, Austria), followed by a Los Gatos Analyzer (see section 2.5). Subsequently, each bag was sampled using a cartridge (stainless steel tubes filled with Tenax TA and Carbograph 5 TD adsorbents) to be later qualitatively analyzed through thermal-desorption gas chromatography time-of-flight mass spectrometry (TD-GC-TOF-MS; Bench ToF Tandem Ionisation, Markes International, Bridgend, UK). To maintain conciseness and ensure clarity of our main findings, detailed descriptions of the analyses and results are presented in the supplementary material, sections 3 and 3.1. The Tedlar bags were analyzed or sampled within 10 hours of analysis, as recommended by Beauchamp et al. (2024).~~

After sampling, bags were handled carefully to prevent leakage. Potential compound losses due to adsorption onto the inner walls or diffusion through the bag material were minimized by storing all samples in a dark, stainless-steel box to avoid light exposure, and keeping them in air-conditioned lab containers at low temperatures until analysis. All samples were analyzed on the

same day, within a maximum of 8 hours post-collection, following the recommended~~ed~~ations ~~by~~of Beauchamp et al. (2008). Gas analysis began with the quantification of BVOCs using a PTR-QMS. Subsequent analyses of CO_2 and CH_4 concentrations were conducted using a Los Gatos analyzer. Each sample bag was then used to fill stainless steel ~~tubes filled with~~cartridges (containing Tenax TA and Carbograph 5 TD adsorbents), ~~to be~~which were later ~~qualitatively~~ analyzed via TD-GC-TOF-MS. Detailed descriptions of the ~~analyses~~analytical procedures and results are in Sections 3 and 3.1. of the Supplementary Material.

2.~~5~~4 PTR-QMS measurements and Los Gatos analyzer measurements

Tedlar bags were connected to the PTR-QMS ~~(Ionicon Analitik, Austria)~~ for analysis of BVOCs (Lindinger et al., 1998). The PTR-QMS H3O+ mode was used for chemical ionization, which is extremely sensitive to all BVOCs that have a higher proton affinity than water, covering most volatile organic compounds (Edtbauer et al., 2021). ~~Seven~~Six compounds were analyzed (Table 1). The PTR-QMS was operated under standard conditions at 2.3 mbar, and E/N 120, with 60°C, with a drift tube voltage of 600 V. During each PTR-QMS measurement cycle, the following specific protonated mass-to-charge ratios (m/z) were measured, 21 (H_3O^{18}+), 32 (O_2+), and 37 (H_2O-H_3O+), with a dwell time of 500 ms each; and Methanol (33), compound not identified (m/z 42), Acetaldehyde (45), Dimethyl sulfide - DMS (63), Isoprene (69) and Monoterpenes (137), with a dwell time of 1 second. We measured approximately 17 cycles for each bag. Mass identifications were based on the available literature (Warneke et al., 2015), and were consistent with a PTR-MS mass library database - GLOVOC (Yañez-Serrano et al., 2021) and gas calibration with certified standards.

Table 1. Compounds analyzed by the PTR-QMS

BVOC	Chemical formula (H+)	m/z	Group
Methanol	CH_4O+	33	Alcohol
not identified		42	N-compound
Acetaldehyde	C_2H_4O+	45	Aldehyde
Isoprene	C_5H_8+	69	Alkenes
Dimethyl sulfide (DMS)	C_2H_6S+	63	Organosulfides
Monoterpenes	$C_{15}H_{16}$+	137	Alkenes

Calibrations were performed before the experiment using a multi-component calibration mix containing various gases of known concentrations ~~(supplementary material; Table S2)~~ (Apel-Riemer Environmental, Inc.) (supplementary material; Section 2; Table S2). Four-point calibration curves were generated by diluting the multicomponent with synthetic air, humidifying the air stream with a water bubbler filled with distilled water, and controlling the flow with mass flow controllers ~~(0, 1, 3, and 5 ppb)~~ (supplementary material; Section 2; Fig. S1). Curves were calculated considering the normalized counts per second as a function of the mixing ratio. Previously, some compounds important for soil-litter processes (Peñuelas et al., 2014)~~,~~ - such as acetone, ethanol, and formaldehyde - were considered for this study, but as they did not show a good fit, they were excluded from this work. The error of PTR-QMS concentration measurements of the six presented compounds is expected to consist of a systematic part and a statistical part. The systematic error consists of the uncertainty of the calibration gas standard (+-5%), the error of the flow measurements (+-5%), and the error of the calibration slope (14.8%, 52.4%, 12.5%, 18.4%, 18.2%, 20.4% for methanol, m/z42, acetaldehyde, DMS, monoterpenes and sesquiterpenes, respectively). The statistical error is based on the repeatability of the concentration measurement during the calibration routine, and was found to be 14.4%, 26.2%, 14.8%, 13.7%, 6.0%, 8.5% for methanol, m/z42, acetaldehyde, DMS, monoterpenes and sesquiterpenes, respectively. The systematic error affects both bags in the same direction, whereas the statistical error can differ between the two bags in a pair. Therefore, to evaluate the uncertainty of the fluxes, we focused on the propagated statistical uncertainty, as described in Section 2.5.

~~The mass m/z 42 can be attributed to acetonitrile; however, acetonitrile is usually considered a biomass-burning tracer/or, more generally, a compound of anthropogenic origin (Huangfu et al., 2021). Acetonitrile can be produced in the oceans (Sanhueza et al., 2004) and can also be consumed by these ecosystems. It can be produced by microorganisms (Raio et al., 2020), but there is a lack of evidence to support its emission from the soil. When using the PTR-QMS to measure m/z 42, it is essential to consider the possibility of interference from fragments and side reactions (Dunne et al., 2012). Consequently, it remains uncertain whether the signal at m/z 42 was due to acetonitrile since the instrument cannot distinguish between isobaric compounds. However, we decided to present this mass in our results (section 3), as our measurements showed substantial amounts of it. In addition, the mass 63 is attributable to DMS. However, earlier studies in the humid Amazon have found that acetaldehyde (mass 45) can form an agglomerate with water,~~

~~resulting in the same mass (63). Thus, results for mass 63 attributed to DMS can be strongly influenced by acetaldehyde. We have studied the relation of the masses 63 and 45, and found a correlation coefficient of 0.51, indicating that a part of the observed 63 could indeed be acetaldehyde. Since we expect that a considerable part of the mass 63 is still originating from DMS, we focus our discussion of the mass 63 on the possible sources and sinks of DMS.~~

After PTR-QMS analysis, the bags were connected to a Los Gatos ~~Ultraportable~~ analyzer to measure the mixing ratios of ~~CH_4~~methane and CO_2. The Los Gatos analyzer is an instrument based on laser absorption spectroscopy specifically Off-axis Integrated Cavity Output Spectroscopy (OA-ICOS), enabling ultra-sensitive, precise, and real-time measurements of trace gases in gas samples (Pohlman et al., 2021; van Asperen et al., 2024). The instrument operates at a relatively low sample flow rate (~0.1 L min^{-1}), and a minimum gas volume of 0.3 L was used as a precaution to ensure measurement stability and accurate determination of CH_4 and CO_2 concentrations; air from the sample bags~~ air~~ was ~~measured~~analyzed for 3 minutes~~ with an airflow of ~ 0.1 LPM, and an average was taken~~, and mean concentrations were calculated from the ~~last~~final 2 minutes of ~~the~~ measurement.

2.~~6~~5 BVOC & GHG flux calculation

To calculate BVOC and GHG fluxes, the Volumetric Mixing Ratios of the blank chamber bags (VMRb) were subtracted from the sample chamber bags (VMR):

$$dVMR = VMR - VMRb \quad (1)$$

in which VMR is expressed in pptv or ppbv. By subtracting the mixing ratios of a blank chamber, dVMR represents the concentration difference attributable solely to soil and litter fluxes, corrected for potential chamber effects or the influence of ambient air entering the system. ~~A dilution effect due to the constant sample flow is expected to exist but, at most, may lead to a slight underestimation of our fluxes~~To ensure data reliability, bag pairs for which the concentration difference (dVMR) was less than or equal to the combined statistical uncertainty (calculated using the Root-Sum-Square method from the individual bag uncertainties) were assigned a value of zero. This approach ensures that only reliably detected fluxes are considered, while retaining the full sample size for modeling purposes. To convert dVMR to fluxes, we used:

$$F = dVMR * N * (V / A) * (1/T) \quad (2)$$

where N is the value of fixed molar volume at 25 °C (24.8 L mol^{-1}; 40.3 mol m^{-3}), V is the chamber volume (0.021 m^3), A is the chamber area (0.0855 m^2), and T is the average sampling time (25 min)~~.~~. ~~giving fluxes~~Flux values in nmol m^{-2} min^{-1}~~, then~~were converted to ng m^{-2} h^{-1}.

2.~~7~~6 Soil and Litter Analyses

The Thematic Laboratory of Soils and Plants (LTSP, at the National Institute for Amazonian Research - INPA) analyzed soil and litter nutrient content according to adapted protocols (EMBRAPA, 1999). The nutrients - iron (Fe^{+2}), calcium (Ca^{+2}), magnesium (Mg^{+2}), zinc (Zn^{+2}), potassium (K^{+}), manganese (Mn^{+}), phosphorus (P), and aluminum (Al) - were determined by digestion with a nitro-perchloric acid solution (Malavolta et al., 1989). Total phosphorus (P) was quantified using colorimetry (Murphy & Riley, 1962; Olsen & Sommers, 1982) and measured using a UV spectrophotometer (Model 1240, Shimadzu, Kyoto, Japan). Potassium (K), calcium (Ca), and magnesium (Mg) concentrations were determined by atomic absorption spectrophotometry (AAS, 1100 B, 250 Perkin Elmer, Ueberlingen, Germany), as described by Anderson and Ingram (1993). Soil carbon and nitrogen content was determined by the Routine Measurements & Analyses Lab (RoMA, MPI-BGC) with the elemental analyzer "varioEL" (Elementar Analysensysteme GmbH, Elementar-Straße 1, D-63505 Langenselbold, Germany). Soil porosity was analyzed using the pycnometer method described in Flint & Flint (2002). The amount of water was corrected for soil density.

For analysis of soil and litter microbial Carbon, Nitrogen, and Phosphorus (C, N, and P) contents, 2g of fresh litter and 5g of fresh soil were used from each sample chamber. These were separated into fumigated and non-fumigated samples. The fumigated samples were left with chloroform for 24 hours and then divided into two sub-samples. For first, 50 mL of KCl (Potassium Chloride) was added, and total C and N were extracted, and for the second, 50 mL of $NaHCO_3$ (Sodium Bicarbonate) was added for total P extraction. Following the same extraction protocol, the non-fumigated samples were prepared for direct extraction without going through the 24-hour fumigation period. Microbial C, N, and P content was estimated in fumigated and non-fumigated extracts from the difference in organic C, N, and total P measured by a TOC/TN analyzer (Jenkinson et al., 2004). The extraction of the microbial biomass was performed at INPA, and the analyses were done by the Routine Measurements & Analyses Lab (RoMA, MPI-BGC).

2.~~8~~7 Statistical analyses

A total of 36 samples were evaluated (n = 12 per forest type). Gas fluxes were first correlated with potential predictors (soil and litter characteristics, Table 2), revealing variations between forest types. Separate regression models were built for each forest type to maximize predictive ability, with variable selection based on the following criteria: 1) given the statistical power limitation of models (n = 12), the maximum number of independent variables possible to include was two; thus, 2) we tested all models with one or two independent variable combinations; ~~3)~~ finally, 3) we chose the models which showed no multicollinearity and had the highest adjusted R-squared and lowest Akaike's information criterion (AIC). The "ols_step_all_possible" function from the "olsrr" package (Hebbali, 2024) was used, and multicollinearity was assessed via VIF (<2.5; Hair et al., 2009). Principal Component Analysis (PCA) and Pearson's correlation (Hmisc package; Harrell, 2018) were performed to explore variable interactions. Variations within forest types (e.g., between ~~t~~Transects) were analyzed using t-tests for normal data and Kruskal-Wallis tests for non-normal data, with a significance level of 0.05. All analyses were conducted in R (v4.3.0; R Core Team, 2023).

Table 2. Variables, their respective codes, and units.

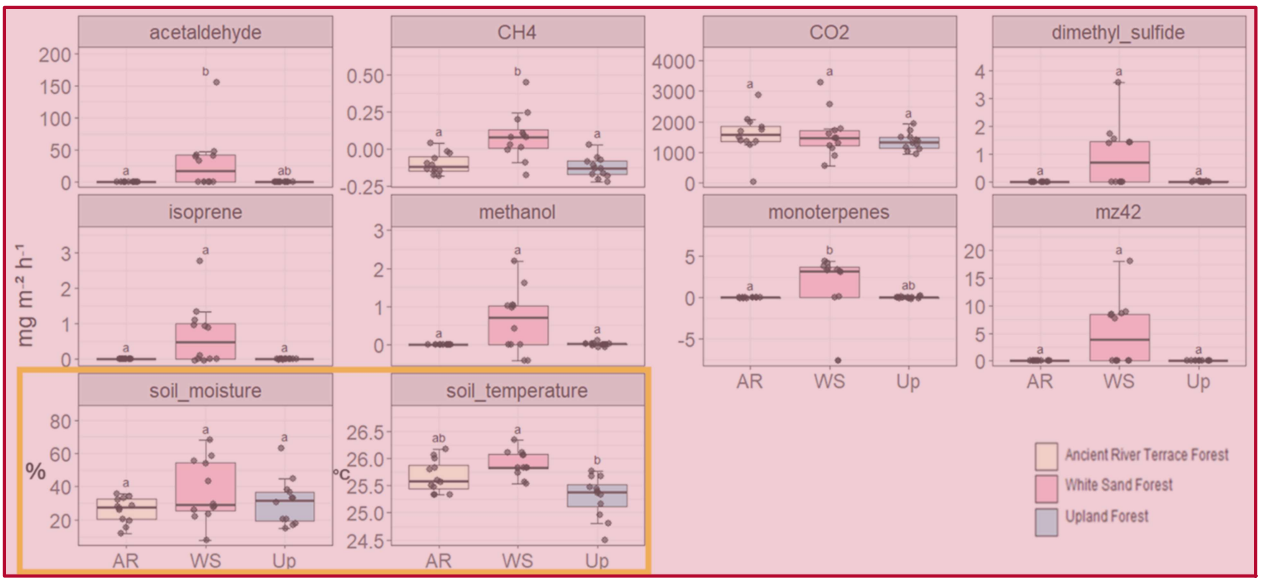
Variable	Code	Unit
Soil carbon	c_soil	%
Soil nitrogen	n_soil	%
Soil phosphorus	p_soil	P mg/kg
Soil potassium	k_soil	K^{+} mg/kg
Soil calcium	ca_soil	Ca^{+2} mg/kg
Soil magnesium	mg_soil	Mg^{+2} mg/kg
Soil aluminum	al_soil	Al^{+3} mg/kg
Soil iron	fe_soil	Fe^{+2} mg/kg
Soil zinc	zn_soil	Zn^{+2} mg/kg
Soil manganese	mn_soil	Mn^{+2} mg/kg
Soil ph	ph_soil	pH
Soil temperature	soil_temp	Celsius
Soil moisture	soil_moisture	%
Litter carbon	c_litter	%
Litter nitrogen	n_litter	%
Litter calcium	ca_litter	Ca^{+2} mg/kg
Litter magnesium	mg_litter	Mg^{+2} mg/kg

Litter potassium	k_litter	K^{+}mg/kg
Litter iron	fe_litter	Fe^{+2} mg/kg
Litter zinc	zn_litter	Zn^{+2} mg/kg
Litter manganese	mn_litter	Mn^{+2} mg/kg
Microbial biomass soil carbon	c_mic_soil	g/kg
Microbial biomass soil nitrogen	n_mic_soil	g/kg
Microbial biomass soil phosphorus	p_mic_soil	g/kg
Microbial biomass litter carbon	c_mic_litter	g/kg
Microbial biomass litter nitrogen	n_mic_litter	g/kg
Microbial biomass soil phosphorus	p_mic_litter	g/kg

3. Results

3.1 Comparison between forest types

The three forest types showed very different gas fluxes for BVOCs and GHGs (Fig. 3), with the highest fluxes observed in the ~~w~~White ~~s~~Sand ~~f~~Forest. Fluxes were very low in the ~~u~~Upland ~~f~~Forest, and almost no gas fluxes were observed in the ~~a~~Ancient ~~r~~River ~~t~~Terrace ~~f~~Forest. Acetaldehyde emissions showed the most significant differences between forest types, with ~~emission~~flux averages of ~~29.911~~35.87 ± 46.86 mg m^{-2} h^{-1} ~~and 0.0885 mg m^{-2} h^{-1}~~ (mean ± SD) for the ~~w~~White ~~s~~Sand ~~f~~Forest, ~~and upland forest respectively, and low consumption~~ -0.09 ± 0.02 (mean ± SD) mg m^{-2} h^{-1} for the Upland Forest, and -0.02 ± 0.008 (mean ± SD) mg m^{-2} h^{-1} for the ~~a~~Ancient ~~r~~River ~~t~~Terrace ~~f~~Forest ~~(-0.0140 mg m^{-2} h^{-1})~~. Isoprenoid (isoprene and monoterpenes) ~~emissions~~fluxes were also high in the ~~w~~White ~~s~~Sand ~~f~~Forest, and clear differences were found between forest types concerning the speciation of monoterpenes (supplementary material; Fig. S2).


acetaldehyde
CH4
CO2
dimethyl_sulfide
isoprene
methanol
monoterpenes
mz42
soil_moisture
soil_temperature
mg m⁻² h⁻¹
%
°C
AR
WS
Up
Ancient River Terrace Forest
White Sand Forest
Upland Forest

469

Figure 3. Biogenic Volatile Organic Compounds (BVOC) and Greenhouse Gas (GHG) fluxes from soil and litter across ~~the~~ three forest types: ~~a~~Ancient ~~r~~River ~~t~~Terrace ~~f~~Forest (AR), ~~w~~White ~~s~~Sand ~~f~~Forest (WS), and ~~u~~Upland ~~f~~Forest (Up). ~~Letters indicate s~~Statistically significant differences ~~in fluxes~~ between forest types ~~at~~ are indicated by lowercase letters (*p < 0.05*, N=36 ~~(~~), "ns" is not significant. Differences were assessed using the Kruskal-Wallis test for non-normal data ~~- BVOC and GHG).~~and ANOVA for normally distributed data, followed by Dunn's post hoc test with Bonferroni. The left axis represents BVOC and GHG fluxes (mg m^{-2} h^{-1}) for AR and Up, while the right axis represents flux values for WS (mg m^{-2} h^{-1}). Boxes represent the median

(horizontal line) and the interquartile range (IQR, first and third quartiles). Whiskers extend up to 1.5 times the IQR, and points beyond whiskers represent statistical outliers.

In the ~~w~~White ~~s~~Sand ~~f~~Forest, ~~in addition to the~~ high isoprenoid emissions were observed, with isoprene fluxes averaging 0.66 ± 0.84 mg m^{-2} h^{-1}, and monoterpene fluxes averaging 1.12 ± 4.31 mg m^{-2} h^{-1}, details on the monoterpene and sesqueterpene speciation can be found in Supplementary Material, Section 3.2. Conversely, very low (negative) values were recorded in the Upland Forest (Isoprene, -0.005 ± 0.003 mg m^{-2} h^{-1} and monoterpenes -0.02 ± 0.08 mg m^{-2} h^{-1}) and Ancient River Terrace Forest (Isoprene, -0.002 ± - 0.001 mg m^{-2} h^{-1} and monoterpenes -0.011 ± 0.015 mg m^{-2} h^{-1}). In the WS we also observed the consumption of monoterpenes (with -7.6~~2~~83 mg m^{-2} h^{-1}, highlighted as an outlier in Fig. 3) and high emissions of DMS (1.10 ± 1.14 mg m^{-2} h^{-1}), whereas aconsumption of the latter was observed in the Upland Forest (-0.001 ± 0.005 mg m^{-2} h^{-1}) and Ancient River Terrace Forest (-0.0003 ± 0.001 mg m^{-2} h^{-1}). CH_4 fluxes showed substantial~~ly varied~~variation in the ~~w~~White ~~s~~Sand ~~f~~Forest, with ~~large~~both uptake (-0.09 ± 0.16 mg m^{-2} h^{-1}) and emission (0.08 ± 0.07 mg m^{-2} h^{-1}). In contrast, the Upland Forest and Ancient River Terrace Forest showed primarily methane uptake, with average fluxes of -0.14 ± 0.05 mg m^{-2} h^{-1} and -0.13 ± 0.03 mg m^{-2} h^{-1}, respectively.

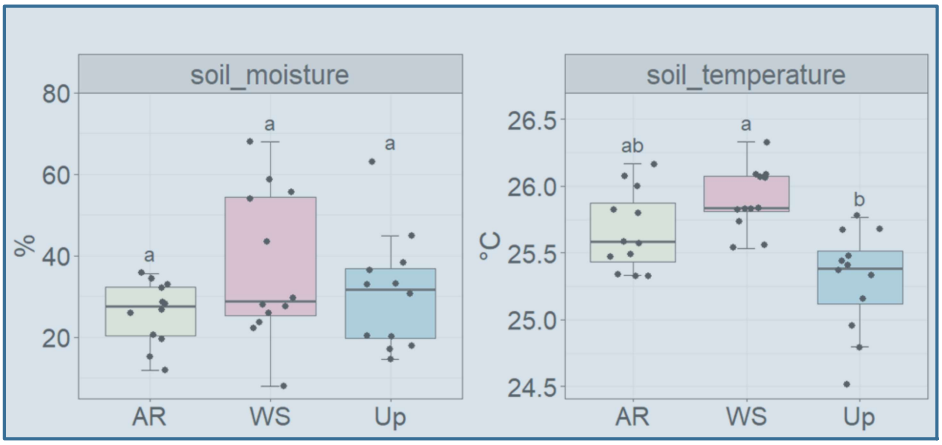


Figure 4. ~~The yellow rectangle represents soil moisture (soil moisture expressed as %~~Soil moisture and soil temperature (expressed ~~as °C), and soil~~% for moisture °C for temperature) across the three forest types: Ancient River Terrace Forest (AR), White Sand Forest (WS), and Upland Forest (Up). Letters indicate statistically significant differences in fluxes between forest types at $p < 0.05$, N=36 (ANOVA test for normal distribution). Boxes show median and first and third quartiles, with whiskers and points distinguished at 1.5 times the interquartile range.

~~In the white sand forest, in addition to the high isoprenoid emissions, we also observed the consumption of monoterpenes (-7.628 mg $m^{-2} h^{-1}$, outlier in Fig. 3) and high emission of dimethyl sulfide (DMS) (0.924 mg $m^{-2} h^{-1}$, on average). Upland and ancient river terrace forests exhibited a small amount of DMS consumption. CH_4 fluxes substantially varied in the white sand forest, with large uptake and emission fluxes, while ancient river terrace and upland forests both showed mainly CH_4 uptake.~~

There were no statistically significant differences in soil moisture ~~between the~~across forest types (Fig. ~~3~~4); however, the ~~w~~White ~~s~~Sand ~~f~~Forest showed the highest and the lowest soil moisture values. ~~Differences in soil moisture and temperature were found between transects (Fig. 8). The large difference in soil texture (see supplementary material, table S1) between the sites will affect how soil moisture translates to the amount of soil moisture available for plants and microbes. Still, since individual transects were measured on different (consecutive) days, it is difficult to distinguish temporal from spatial effects.~~

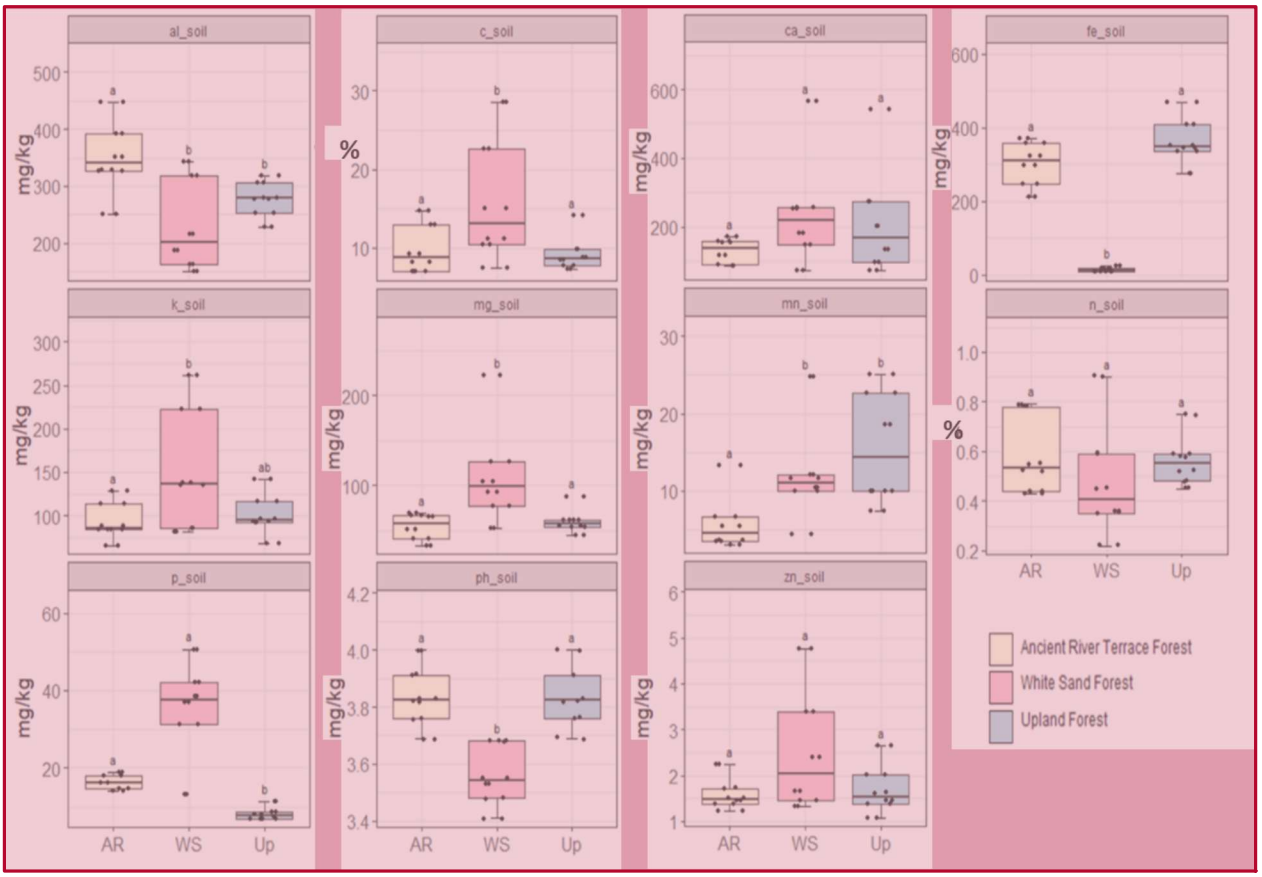
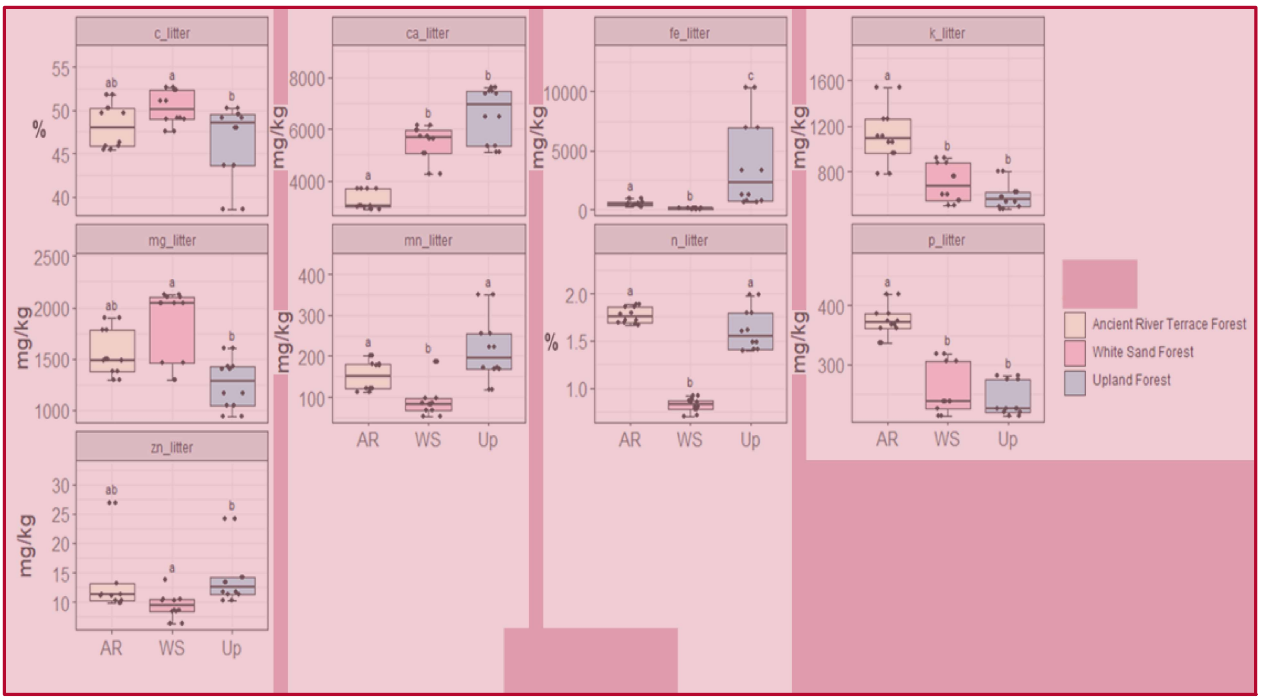


Figure 45. Concentrations of soil micro- and macronutrients in the three forest types: ~~a~~Ancient ~~r~~River ~~t~~Terrace ~~f~~Forest (AR), ~~w~~White ~~s~~Sand ~~f~~Forest (WS), and ~~u~~Upland ~~f~~Forest (Up). Letters indicate statistically significant differences in nutrients between forest types at $p < 0.05$, N=36. (ANOVA test for normal data (aluminum) and Kruskal-Wallis test for non-normal data (carbon, calcium, iron, potassium, magnesium, manganese, nitrogen, phosphorus, pH, and zinc). Boxes show median and first and third quartiles, with whiskers and points distinguished at 1.5 times the interquartile range.

Soil macro- and micronutrients varied considerably between the forest types, with statistically significant differences in carbon, magnesium, phosphorus, and iron for the ~~w~~White ~~s~~Sand ~~f~~Forest. Phosphorus content was the highest in the ~~w~~White ~~s~~Sand ~~f~~Forest compared to other forest types (Fig. 45). All litter nutrients exhibited significant differences between forest types: ~~u~~Upland ~~f~~Forest showed the highest average concentrations of calcium, iron, manganese, and zinc,

while the ~~a~~Ancient ~~r~~River ~~t~~Terrace ~~f~~Forest had the highest nitrogen, potassium, and phosphorus concentrations, and the ~~w~~White ~~s~~Sand ~~f~~Forest had slightly higher carbon concentrations (Fig. ~~5~~6).


c_litter
ca_litter
fe_litter
k_litter
mg_litter
mn_litter
n_litter
p_litter
zn_litter
%
mg/kg
AR
WS
Up
Ancient River Terrace Forest
White Sand Forest
Upland Forest

531

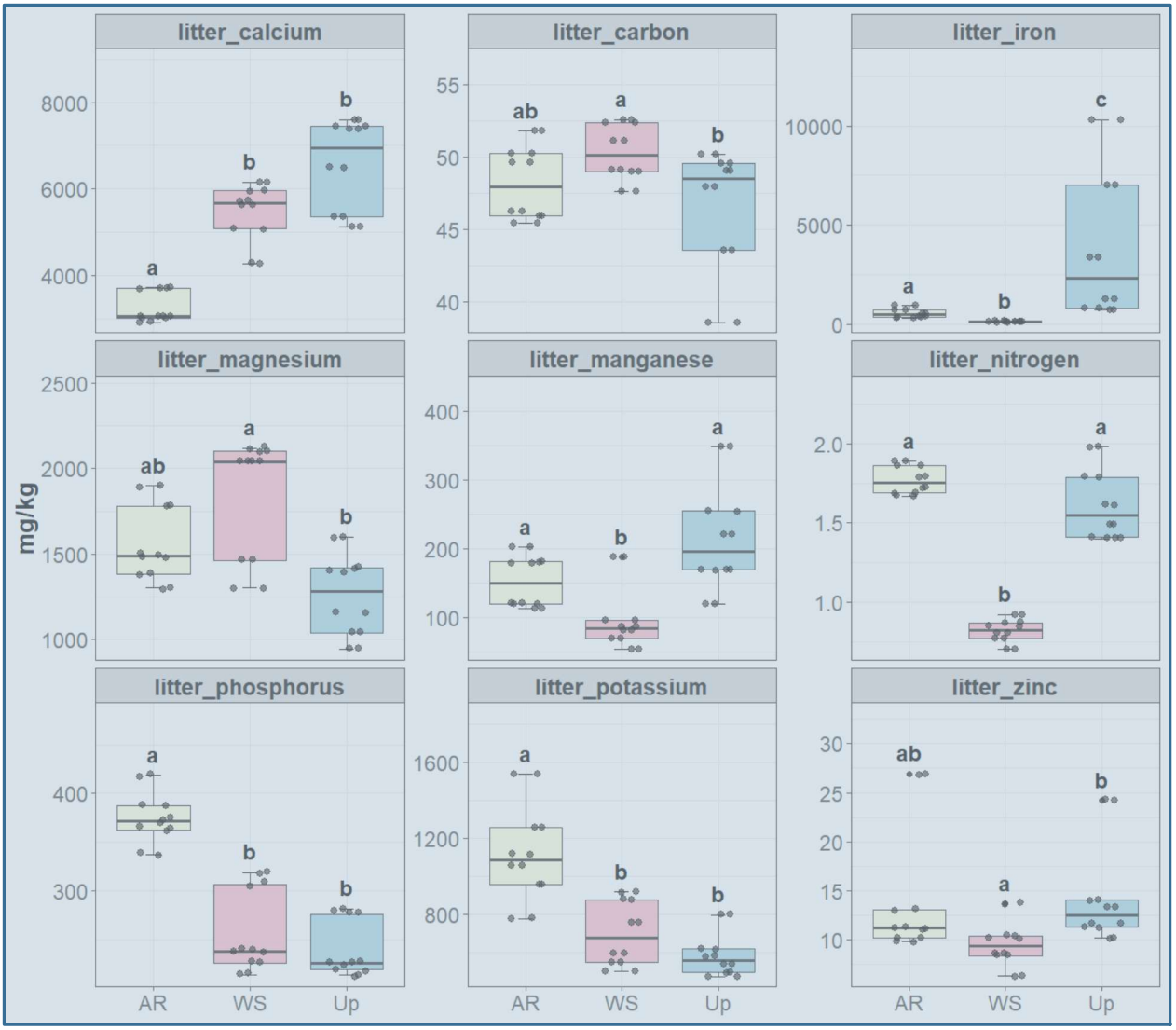
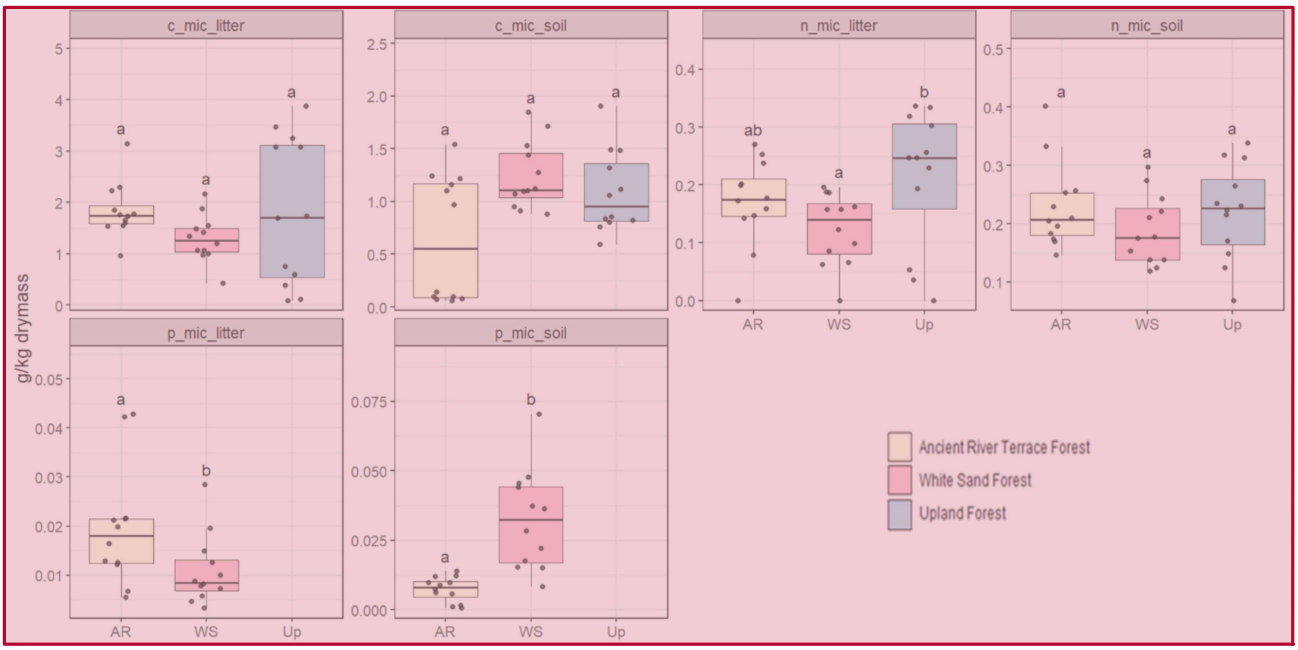
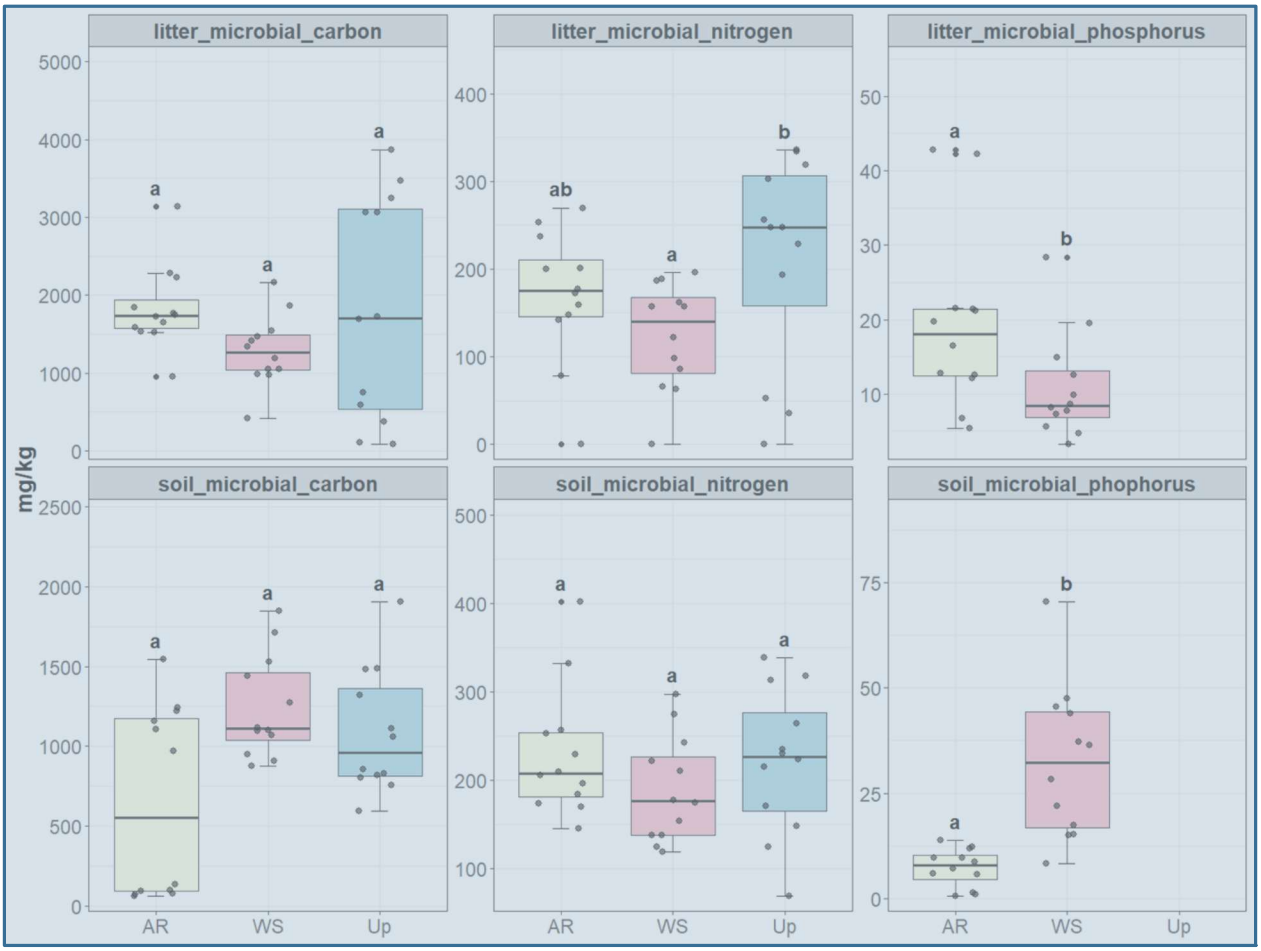


Figure ~~5~~6. Concentrations of litter micro- and macronutrients in the three forest types: ~~a~~Ancient ~~r~~River ~~t~~Terrace ~~f~~Forest (AR), ~~w~~White ~~s~~Sand ~~f~~Forest (WS), and ~~u~~Upland ~~f~~Forest (Up). Letters indicate statistically significant differences in nutrients between forest types at $p < 0.05$, N=36. (ANOVA test for normal data - potassium and nitrogen, and Kruskal-Wallis test for non-normal data - carbon, calcium, iron, magnesium, manganese, phosphorus, and zinc). Boxes show median and first and third quartiles, with whiskers and points distinguished at 1.5 times the interquartile range.


c_mic_litter
c_mic_soil
n_mic_litter
n_mic_soil
p_mic_litter
p_mic_soil
g/kg drymass
AR
WS
Up
Ancient River Terrace Forest
White Sand Forest
Upland Forest

540


litter_microbial_carbon
litter_microbial_nitrogen
litter_microbial_phosphorus
soil_microbial_carbon
soil_microbial_nitrogen
soil_microbial_phophorus
mg/kg
AR
WS
Up

541

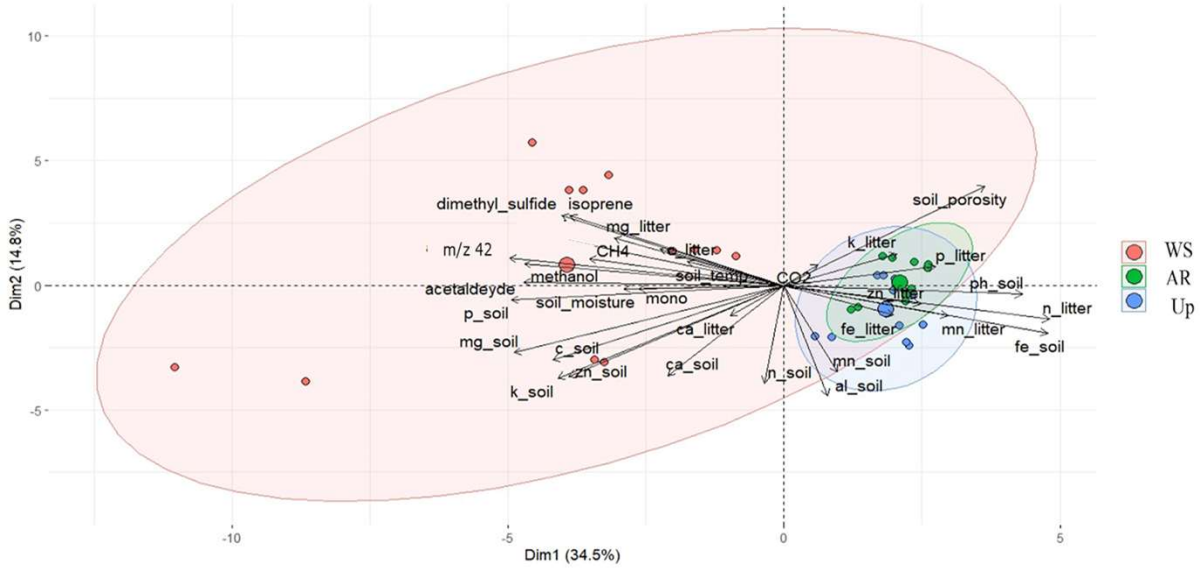
Figure ~~6~~7. Concentrations of C, N, and P microbial biomass (µg g^{-1} dry mass) of soil and litter in the three forest types: the ~~a~~Ancient ~~r~~River ~~t~~Terrace ~~f~~Forest (AR), the ~~w~~White ~~s~~Sand ~~f~~Forest (WS), and the ~~u~~Upland ~~f~~Forest (Up). Letters indicate statistically significant differences in microbial biomass between forest types at $p < 0.05$, N=36. ANOVA test for normal data (litter microbial carbon, soil microbial phosphorus, and nitrogen) and Kruskal-Wallis test for non-normal data (soil microbial carbon, litter microbial nitrogen, and litter microbial phosphorus). Boxes show median and first and third quartiles, with whiskers and points distinguished at 1.5 times the interquartile range.

Microbial biomass (soil and litter), ~~- measured as a potential~~ used here as a proxy for microbial activity~~–~~, showed significant differences between forest types~~. Soil microbial~~only for soil phosphorus, which was ~~significantly~~ higher in the ~~w~~White ~~s~~Sand ~~f~~Forest ~~than in~~compared to the ~~a~~Ancient ~~r~~River ~~t~~Terrace ~~f~~Forest (no data available for the ~~u~~Upland ~~f~~Forest). ~~In contrast,~~For carbon and nitrogen, significant differences were observed only in litter microbial biomass ~~(carbon and nitrogen) was the highest in~~, with the upland forest ~~and the lowest in~~exhibiting the highest values and the white sand forest ~~(carbon, nitrogen, phosphorus)~~the lowest. However, for most microbial biomass parameters measured across soil and litter, differences between forest types were not statistically significant (Fig. ~~6~~7).

3.2 Identification of drivers of BVOC and GHG fluxes

3.2.1 Principal Component Analysis

A ~~Principal Component Analysis (~~PCA~~)~~ of soil and litter characteristics and microbial biomass, and gas fluxes (BVOC and GHG) indicated that PC1 and PC2 axes accounted for 48.5% of the data variation (Fig. ~~7~~8). The first axis explained 31.6% and the second 12.6% (Table 3). The PCA grouped forest types into two distinct groups: ~~a~~Ancient ~~r~~River ~~t~~Terrace and ~~u~~Upland ~~f~~Forests showed considerable overlap, with lower fluxes linked to litter characteristics, soil and litter microbial biomass, CO_2, and soil pH~~;~~. ~~in~~In contrast, the ~~w~~White ~~s~~Sand ~~f~~Forest formed a separate group with higher fluxes associated with soil temperature, moisture, and elevated levels of phosphorus, magnesium, and potassium.



569

570 **Figure ~~7~~8.** ~~Principal Component Analysis (~~PCA~~),~~ wherein the vectors reflect their correlation with
571 the variables, and the colored circles represent the average PCA score related to each ambient. The
572 analyzed variables are BVOCs (methanol, m/z 42, acetaldehyde, ~~dimethyl sulfide~~DMS, isoprene
573 and monoterpenes), greenhouse gases (~~CH_4~~methane and CO_2), soil characteristics (carbon,
574 nitrogen, phosphorus, potassium, calcium, magnesium, aluminum, iron, zinc, manganese, pH,
575 temperature, and soil moisture), litter characteristics (carbon, nitrogen, calcium, magnesium,
576 potassium, iron, zinc, manganese), and soil and litter microorganism dynamics (soil microbial
577 nitrogen, soil microbial phosphorus, soil microbial carbon, litter microbial nitrogen, litter
578 microbial phosphorus and litter microbial carbon). AR = Ancient River Terrace Forest, Up =
579 Upland Forest, WS = White Sand Forest

580 **Table 3.** Percentage correlation values extracted from ~~Principal Component Analysis (~~PCA; Fig.
581 ~~7)~~8.

	PC1		PC2
Soil iron	83.480	Isoprene	52.345
Litter nitrogen	83.440	Dimethyl sulfide	51.718
Litter manganese	52.649	Litter Iron	21.662
Litter phosphorus	46.040	Soil moisture	20.658
Soil magnesium	-79.524	Soil carbon	-63.818
Methanol	-80.097	Soil zinc	-64.436
Soil phosphorus	-83.184	Soil aluminum	-71.054
m/z 42	-84.917	Soil nitrogen	-71.553

3.2.2 Linear regression models for different forest types

We used linear regression models (referred to as linear models) to better understand the relationships between predictor variables and fluxes, as identified by the PCA analyses. Flux predictors showed substantial variation between the forest types (Fig. S3a, b, S4a, b, and S5a, b, in Section 4; supplementary material). Model comparisons for each forest type revealed similarities between aAncient rRiver tTerrace ~~(Table 4)~~Forest and uUpland fForests (Table ~~5~~4). In contrast, the ~~w~~White sSand fForest ~~(Table 6)~~ was distinct (Table 4), as also shown by the PCA analysis.

In the aAncient rRiver tTerrace fForest, linear models for gas fluxes and predictor variables showed coefficients of determination (R^2) above 0.8 for methanol, acetaldehyde, isoprene, and monoterpenes (Table 4). The most important nutrients for predicting gas fluxes from ~~the ancient river terrace~~this forest type were potassium, manganese, magnesium, iron, carbon, and phosphorus. The linear models for monoterpenes had ~~the~~ soil microbial biomass carbon and litter potassium as predictors. The ~~GHG~~linear models for GHG had soil temperature, soil moisture, and litter nutrients as predictors.

Table 4. Multiple linear regression models with soil and litter characteristics and microbial biomass as predictors of gas fluxes in the three forest types – aAncient rRiver tTerrace fForest (AR), Upland Forest (Up), and White Sand Forest (WS). B = unstandardized coefficients. CI = confidence interval. f^2 = Cohen's f^2 effect size. R^2 = R-squared value. R^2_{adj} = Adjusted R-squared value. N = ~~12~~36.

Forest Type	Gas	R^2/R^2adj	Predictor Variable	B	95% CI	P	f^2
AR	Methanol	0.839/0.803	Soil potassium	0.034	0.02~~1~~; 0.047	≤ .001	1.92
			Litter ~~manganese~~nitrogen	0.02	~~0.000~~0.01; 0.0~~00~~3	≤ .001	2.31

	Acetaldehyde	0.8629/0.791547	Soil iron	0.000	-0.001; 0.000	0.059	0.127
			Soil manganese	0.004	0.003; 0.005	0.004	1.58
	Dimethyl sulfide	0.574/0.479	Soil magnesium	0.006	0.001; 0.0100.00	0.2	0.059
			Litter magnesium	-0.004	-0.006; -1;0.002	0.00413	1.0679
	Isoprene	0.9690/0.9635 1	Soil IronPhophorus	0.000	0.000; 0.000	≤ .001	15.03
			Litter Phophorus	0.0016	0.0004; 0.0017	≤ .001	9.38
	Monoterpenes	0.811/0.769	Soil microbial carbon	0.000	0.000; 0.000	0.084	4.26
			Soil Moisture	0.03	0.000; 0.05	< .001	0.05
	Methane	0.276/0.203	Soil moisture	0.00	0.00; 0.00	0.0824	0.50
			0.4520.330Litter carbon	0.00	0.00;0.00	0.024	0.32
	CO_2	0.685/0.615	Soil temperature	9.054	3.101; 15.007	0.007	1.232
			Litter phosphorus	-87.940	-156.215; -19.666	0.017	0.943
	Methanol	0.617/0.532	Soil potassium	0.61	0.418; 1.10	0.0010	0.17
Up			Soil microbial nitrogen	0.00	0.00; 0.00	0.0026	1.44
	m/z 42	0.6789/0.6082	Soil potassium	0.000	0.000; 0.001	0.002	0.68773

			Soil microbial nitrogen	0.000	0.000; 0.000	0.006	1.50
	Acetaldehyde	0.608/0.521	Soil iron	0.00	0.00; 0.00	0.14	0.17
			Litter microbial carbon	0.02	0.00; 0.00	0.006	1.38
	Dimethyl sulfide	0.747/0.690	Litter microbial carbon	0.00	0.00; 0.00	<0.001	1.10
			Litter microbial nitrogen	0.00	0.00; 0.00	0.003	1.85
	Isoprene	0.774/0.724	Soil carbon	0.00	0.00; 0.00	0.007	1.25e-03
			Liter mangnesium	0.00	0.00; 0.00	< .001	5.94
	Monoterpenes	0.792/0.746	Soil potassium	1.6	1.30.94;2.3	< .001	0.96
			Litter microbial nitrogen	0.00	0.00;0.00	< .001	2.86
	Methane	0.888/0.863	Soil carbon	0.231	0.00; 0.00	0.043	0.06
			Soil moisture	0.00	0.00; 0.00	< .001	7.91
	CO_2	0.626/0.543	Litter microbial nitrogen	0.00	0.01; 0.06	0.025	0.25
			Litter microbial carbon	0.00	0.00;0.00	0.006	1.43
WS	Methanol	0.8258/0.790	Soil temperature	-0.0643.0	-34.4, -0.461.5	≤ 0.0015	2.60
			Litter phosphorus	--8.4	-16,-0.37	< 0.042	0.62

m/z 42	0.866/0.837	Soil moisture	0.187	0.099; 0.276	≤ .001	2.938
		Litter nitrogen	-54.196	-75.901; -32.491	≤ .001	3.545
Acetaldehyde	0.653/0.576	Soil moisture	1.368	0.284; 2.452	0.019	1.022
		Litter nitrogen	-327.465	-593.333; -61.596	0.021	0.863
Dimethyl sulfide	0.78463/0.73611	Soil temperature	-0.320.06	-4.9; -1.40.09; -0.03	0.003	1.87
		Soil phosphorus	-0.06	-0.09,-0.03	0.003	1.36
Isoprene	0.764/0.712	Soil temperature	-1.9882.3	-3.6; -0.96	0.0034	1.70
		Soil phosphorus	-0.05	-0.007; -0.02	0.0043	1.54
Monoterpene	0.857/0.825	Soil moisture	0.13	0.06; 0.20	0.003	0.36
		Litter nitrogen	2.1	1.5; 2.8	≤ 0.001	5.66
Methane	0.508/0.399	Soil moisture	0.00	0.0; 0.0	0.027	0.35
		Litter zinc	0.00	0.0; 0.0	0.035	0.69
CO_2	0.742/0. 685	Soil microbial carbon	0.02	0.0; 0.03	0.029	1.07
-	-	Litter zinc	3.5	1.6; 5,5	0 .003	1.81

603

Variable	B	95% CI	P	f^2	R^2	R^2_{adj}
Methanol					0.839	0.803
Soil potassium	0.034	0.021; 0.047	<.001	2.222		
Litter manganese	0.000	0.000; 0.000	<.001	2.972		
Acetaldehyde					0.829	0.791
Soil iron	0.000	-0.001; 0.000	<.001	0.127		
Soil manganese	0.004	0.003; 0.005	<.001	4.711		
Dimethyl sulfide					0.635	0.554
Soil magnesium	0.006	0.001; 0.010	0.016	0.059		
Litter magnesium	-0.004	-0.006; -0.002	0.004	1.679		
Isoprene					0.969	0.963
Soil Iron	0.000	0.000; 0.000	<.001	4.452		
Soil Manganese	0.001	0.000; 0.001	<.001	27.279		
Monoterpenes					0.920	0.902
Soil microbial carbon	0.000	0.000; 0.000	<.001	10.81		
Litter potassium	0.03	0.000; 0.05	-0.026	0.78		
CH_4					0.276	0.203
Soil moisture	0.00	0.00; 0.00	0.0824	0.50	0.452	0.330
Litter carbon	0.00	0.00;0.00	0.024	0.32		
CO_2					0.685	0.615
Soil temperature	9.054	3.101; 15.007	0.007	1.232		
Litter phosphorus	-87.940	-156.215; -19.666	0.017	0.943		

For the ~~u~~Upland ~~f~~Forest, linear models for gas fluxes ~~models~~ showed R^2 higher than 0.8 for isoprene and ~~CH_4~~methane (Table ~~5~~4)~~.~~, and ~~K~~key nutrients for predicting gas fluxes included potassium, iron, manganese, and carbon. Microbial biomass was significant in predicting gases like methanol and ~~dimethyl sulfide~~DMS. Acetaldehyde and isoprene shared soil iron and manganese as predictors, while ~~dimethyl sulfide~~DMS and CO_2 were linked to litter carbon and microbial nitrogen.

~~**Table 5.** Multiple linear regression models with soil and litter characteristics as predictors of gas fluxes in the upland forest. B = unstandardized coefficients. CI = confidence interval. f^2 = Cohen's f^2 effect size. R^2 = R-squared value. R^2_{adj} = Adjusted R-squared value. N = 12.~~

~~Variable~~	~~B~~	~~95% CI~~	~~p~~	~~f^2~~	~~R^2~~	~~R^2_{adj}~~
~~**Methanol**~~					~~0.735~~	~~0.676~~
~~Soil potassium~~	~~0.77~~	~~0.41; 1.1~~	~~0.001~~	~~0.82~~		
~~Soil microbial nitrogen~~	~~0.00~~	~~0.00; 0.00~~	~~0.002~~	~~1.96~~		
~~**m/z 42**~~					~~0.679~~	~~0.608~~
~~Soil potassium~~	~~0.000~~	~~0.000; 0.001~~	~~0.002~~	~~0.687~~		
~~Soil microbial nitrogen~~	~~0.000~~	~~0.000; 0.000~~	~~0.006~~	~~1.417~~		
~~**Acetaldehyde**~~					~~0.793~~	~~0.748~~
~~Soil iron~~	~~0.00~~	~~0.00; 0.00~~	~~<.001~~	~~0.05~~		
~~Soil manganese~~	~~0.02~~	~~0.1; 0.02~~	~~0.02~~	~~3.80~~		
~~**Dimethyl sulfide**~~					~~0.775~~	~~0.725~~
~~Litter microbial carbon~~	~~0.00~~	~~0.00; 0.00~~	~~<0.001~~	~~1.44~~		
~~Litter microbial nitrogen~~	~~0.00~~	~~0.00; 0.00~~	~~0.002~~	~~2.01~~		
~~**Isoprene**~~					~~0.899~~	~~0.877~~

Variable	B	95% CI	p	f^2	R^2	R^2_{adj}
Soil iron	0.00	0.00; 0.00	< .001	5.48e-03		
Soil manganese	0.00	0.00; 0.00	< .001	5.94		
Monoterpenes					0.695	0.627
Soil potassium	1.18	1.3;2.3	< .001	2.94		
Litter microbial nitrogen	0.00	0.00;0.00	< .001	4.63		
CH_4					0.888	0.863
Soil carbon	0.231	0.00; 0.00	0.043	0.06		
Soil moisture	0.00	0.00; 0.00	< .001	7.91		
CO_2					0.626	0.543
Litter microbial nitrogen	0.00	0.01; 0.06	0.025	0.25		
Litter microbial carbon	0.00	0.00;0.00	0.006	1.43		

In the white sand forest, models

In the White Sand Forest, linear models showed R^2 higher than 0.8 for methanol, m/z 42 and monoterpenes showed high R^2 values, explaining over 80% of emission variation (tTable 64). Key nutrient predictors included phosphorus, nitrogen, and zinc. All emitted gases (except CO_2) were influenced by soil temperature or moisture. Soil temperature was inversely related to fluxes of methanol, DMS, and isoprene, while emissions of m/z 42, acetaldehyde, monoterpenes and CH_4methane increased with soil moisture.

Table 6. Multiple linear regression models with soil and litter characteristics as predictors of gas fluxes in the white sand forest. B = unstandardized coefficients. CI = confidence interval. f^2 = Cohen's f^2 effect size. R^2 = R-squared value. R^2_{adj} = Adjusted R-squared value. N = 12.

Variable	B	95% CI	p	f^2	R^2	R^2_{adj}
Methanol					0.825	0.790
Soil temperature	-0.064	-3.4, -0.46	< 0.015	4.21		
Litter phosphorus	-8.4	-16, -0.37	< 0.042	0.62		
Acetonitrile					0.866	0.837
Soil moisture	0.187	0.099; 0.276	<.001	2.938		
Litter nitrogen	-54.196	-75.901; -32.491	<.001	3.545		
Acetaldehyde					0.653	0.576
Soil moisture	1.368	0.284; 2.452	0.019	1.022		
Litter nitrogen	-327.465	-593.333; -61.596	0.021	0.863		
Dimethyl sulfide					0.784	0.736
Soil temperature	-0.32	-4.9; -1.4	0.003	1.87		
Soil phosphorus	-0.06	-0.09, -0.03	0.003	1.36		
Isoprene					0.764	0.712
Soil temperature	-1.988	-3.6; -0.96	0.003	1.70		
Soil phosphorus	-0.05	-0.007; -0.02	0.004	1.54		
Monoterpene					0.857	0.825
Soil moisture	0.13	0.06; 0.20	0.003	0.36		
Litter nitrogen	2.1	1.5; 2.8	< 0.001	5.66		
Sesquiterpene					0.888	0.863
Soil moisture	1.1	0.52;1.7	0.002	2.50		
Litter nitrogen	-435	-5.75; -294	< 0.001	5.43		

Variable	B	95% CI	p	f^2	R^2	R^2_{adj}
CH_4					0.508	0.399
Soil moisture	0.0	0.0; 0.0	0.027	0.35		
Litter zinc	0.0	0.0; 0.0	0.035	0.69		
CO_2					0.742	0. 685
Soil microbial carbon	0.02	0.0; 0.03	0.029	1.07		
Litter zinc	3.5	1.6; 5,5	0 .003	1.81		

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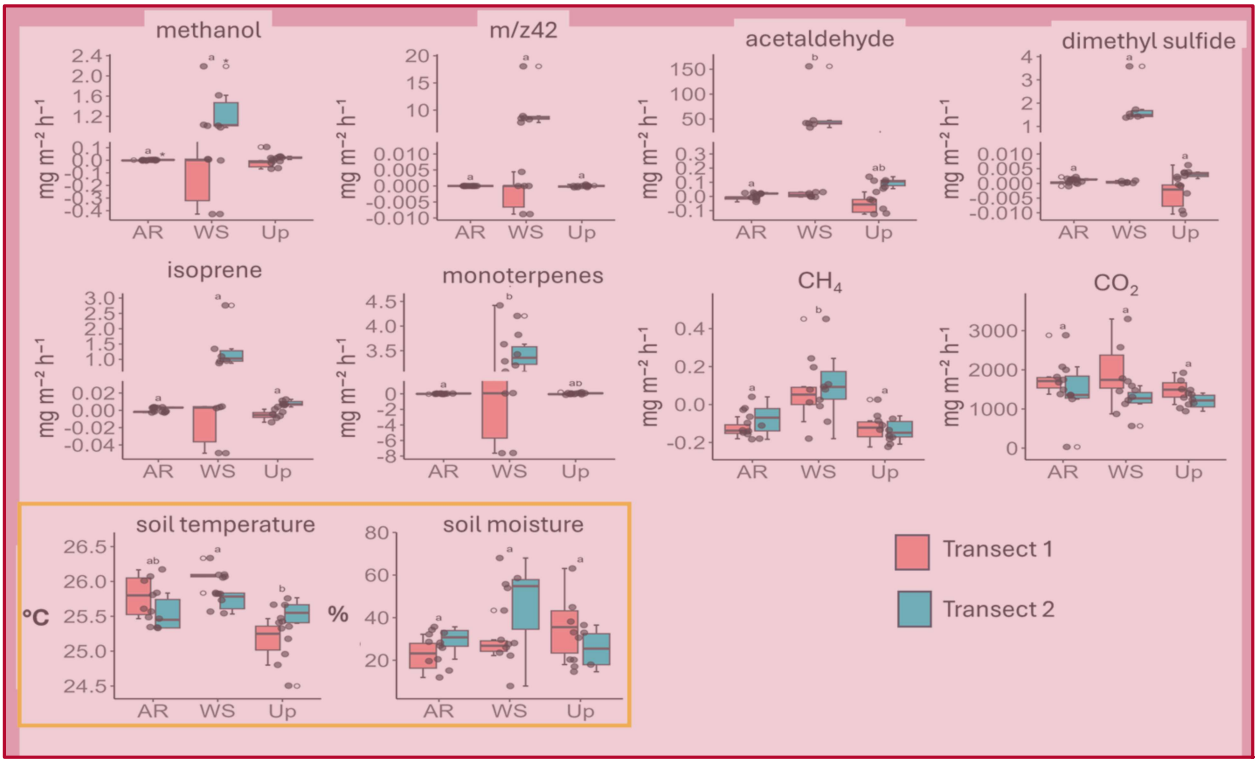
626

627 **3.3 Spatial variability within forest types**

628 Figure 89 shows BVOC and GHG fluxes of each Transect, Figure 10 shows soil
629 temperature and soil moisture of each tTransect, and Figure 911 illustrates the spatial variability
630 within and between tTransects ofor isoprene and monoterpenes (see supplementary material,
631 Section 8; Fig. S8, S9, and S10 for other gases). In the aAncient rRiver tTerrace fForest, BVOC
632 fluxes were generally lower in tTransect 1, while GHG fluxes were similar between tTransects
633 (Fig. 89).:; The soil temperature was higher in tTransect 1, while tTransect 2 was slightly wetter
634 (although not statistically significant). (Fig.10). The wWhite sSand fForest exhibited the greatest
635 variation between tTransects, with the highest BVOC emissions in tTransect 2, and significant
636 variations in acetaldehyde, m/z 42, dimethyl sulfideDMS, isoprene, and methanol.:; In addition,
637 monoterpene fluxes showed high variation in emissions and consumption in tTransect 1, while
638 tTransect 2 had low variation and high emissions.:; Furthermore,and methanol was emitted in
639 tTransect 1 and consumed in tTransect 2. In the uUpland fForest, significant differences between
640 tTransects were noted for acetaldehyde, m/z 42, dimethyl sulfideDMS, and isoprene. For the
641 ancient river terrace forest, the gas fluxes between transects were similar with only few variations
642 in GHG fluxes, however significant differences in isoprene fluxes were observed.

643


methanol
m/z42
acetaldehyde
dimethyl sulfide
isoprene
monoterpenes
CH4
CO2
soil temperature
soil moisture
mg m−2 h−1
°C
%
AR
WS
Up
Transect 1
Transect 2

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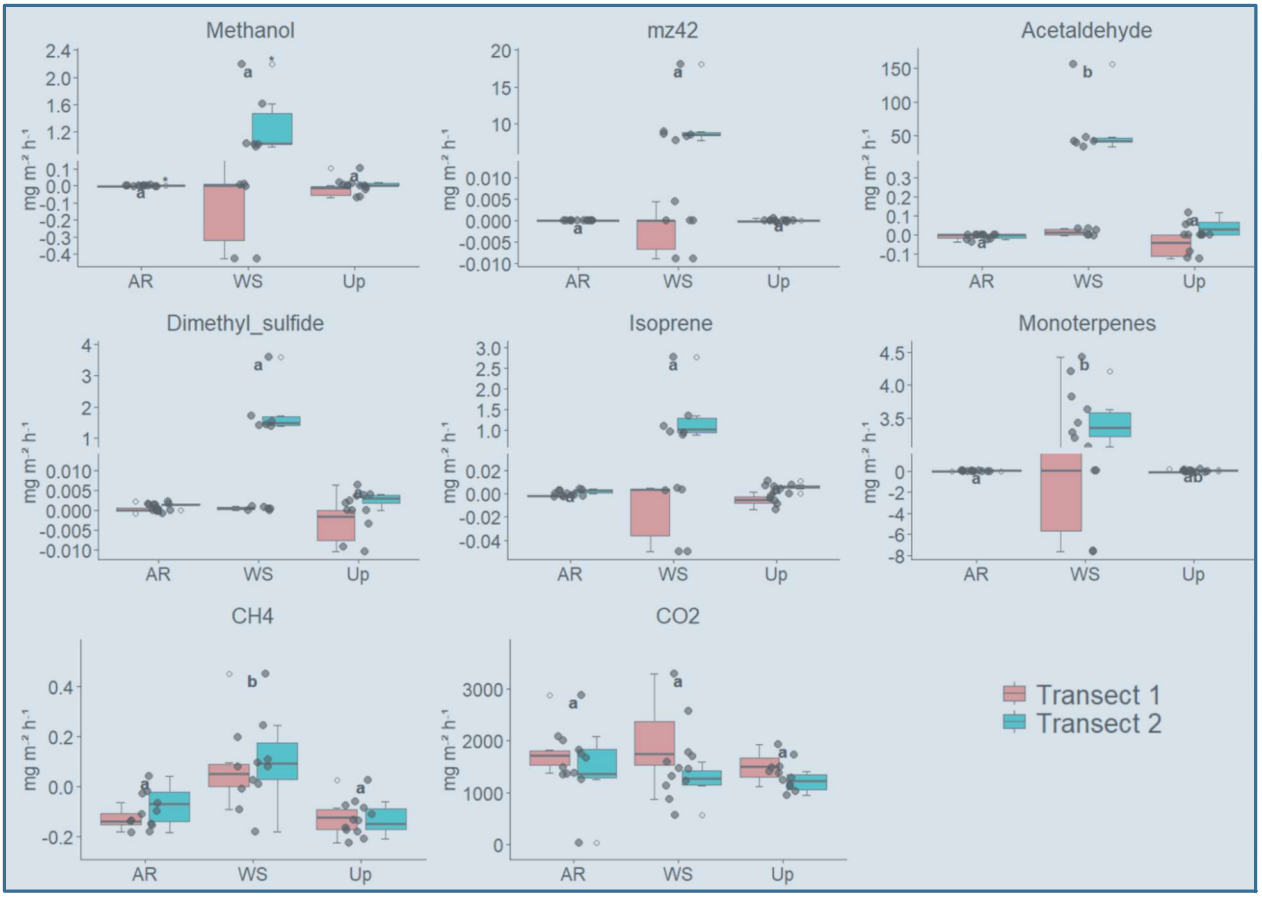
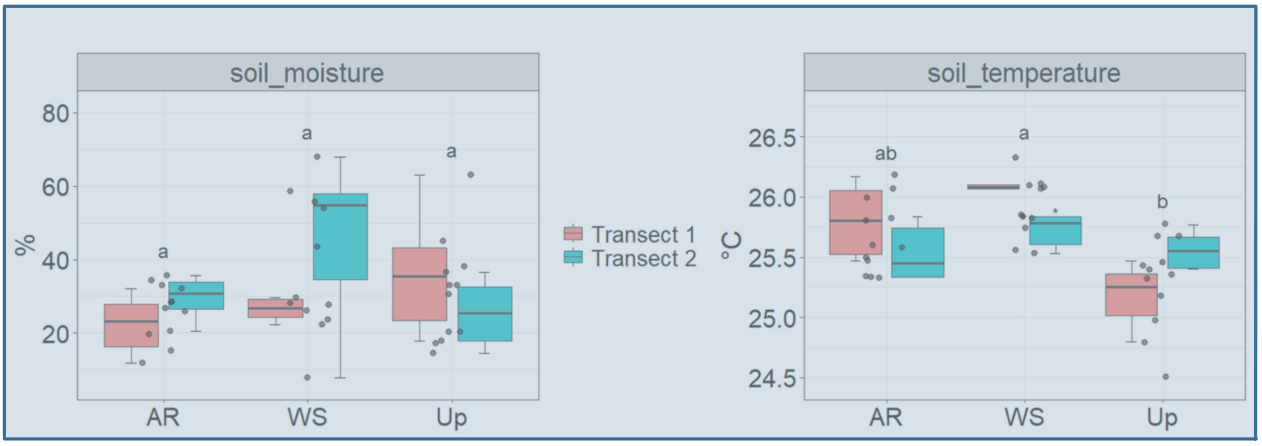


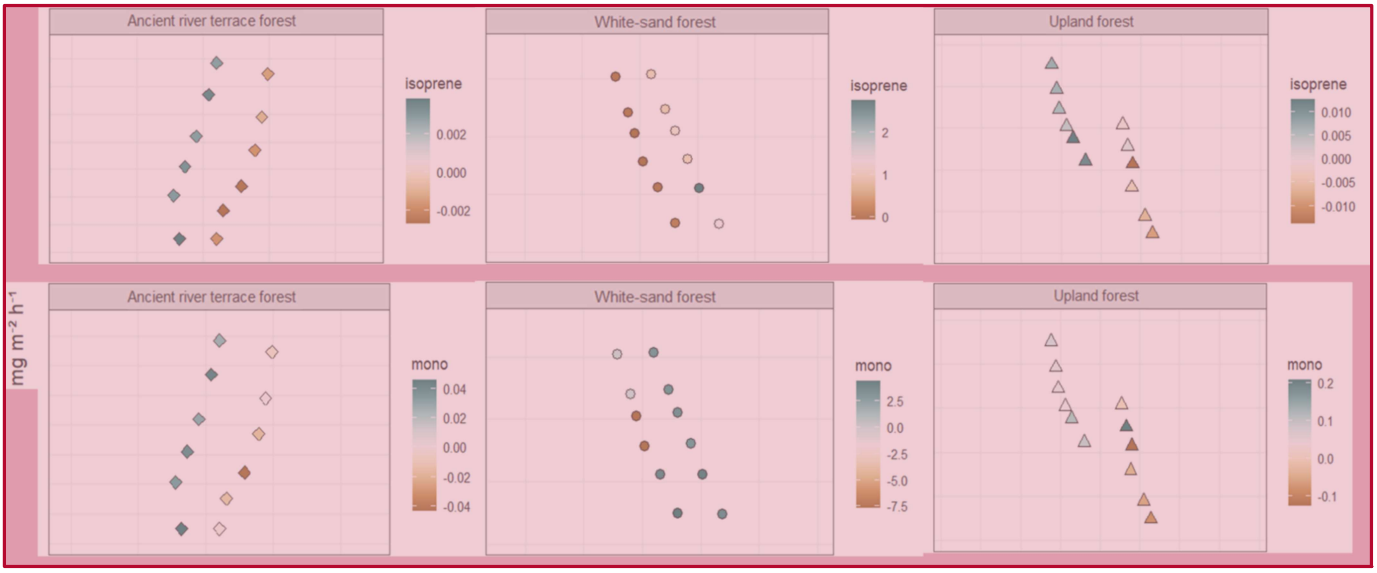
646

647 **Figure 89.** Soil and litter BVOC and GHG fluxes in each forest type - ~~a~~Ancient ~~r~~River ~~t~~Terrace
648 ~~f~~Forest (AR), ~~w~~White ~~s~~Sand ~~f~~Forest (WS), ~~u~~Upland ~~f~~Forest (Up), and ~~t~~Transects within forest
649 types. Letters indicate statistically significant differences in fluxes between the forest types at $p <$
650 0.05, N=36 (Kruskal-Wallis test for non-normal data - BVOC and GHG). Boxes show median and
651 first and third quartiles, with whiskers and points distinguished at 1.5 times the interquartile range.
652 Axes are broken to enhance the visibility of data variation.~~The yellow rectangle represents~~



653

Figure 10. ~~s~~Soil moisture and soil temperature ~~plots~~ in each forest type - Ancient River Terrace Forest (AR), White Sand Forest (WS), Upland Forest (Up), and Transects within forest types. Letters indicate statistically significant differences in fluxes between the forest types at $p < 0.05$, N=36 (ANOVA test for normal distribution). Boxes show median and first and third quartiles, with whiskers and points distinguished at 1.5 times the interquartile range. Axes are broken to enhance the visibility of data variation.



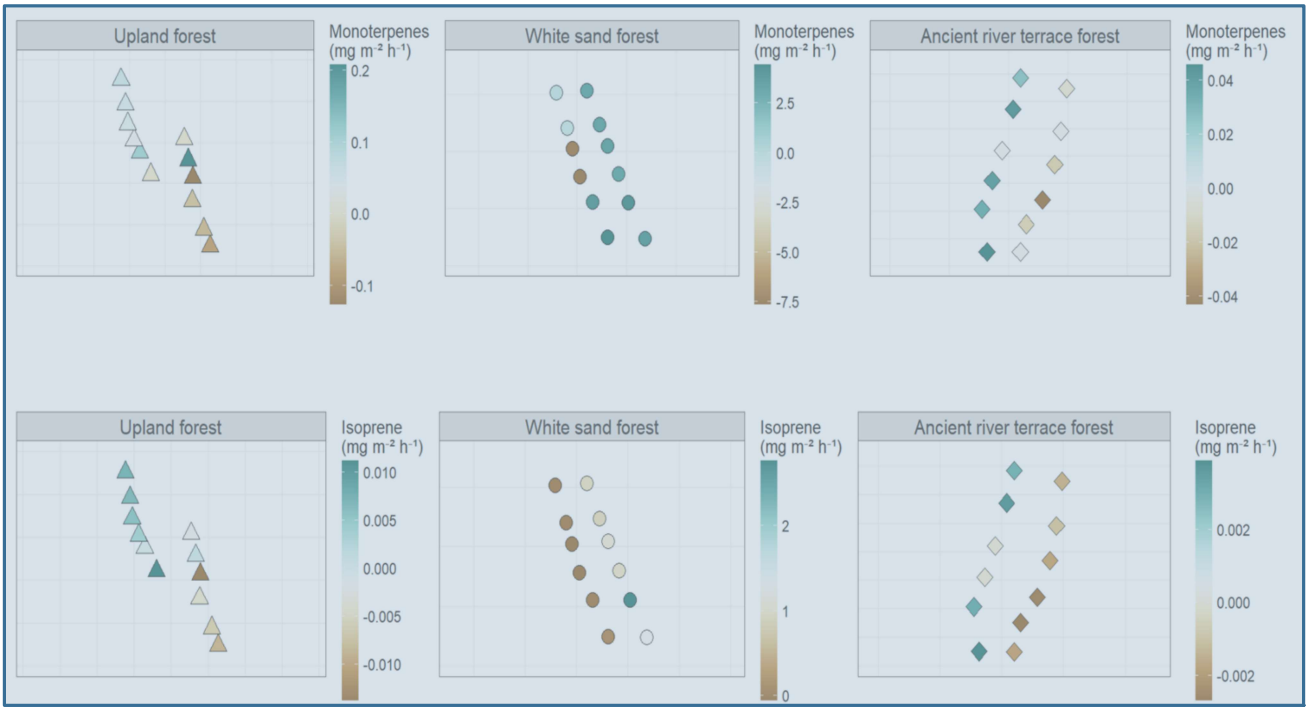


Figure 911. Map of the sampling points visualizing the spatial heterogeneity of BVOC fluxes in each of the three forest types. Each tTransect, sampled on different but subsequent days, contains six sampling points, totaling 12 measurement points per forest type. Left - Transect 1; Right - tTransect 2. Mono = Monoterpenes. The gas flux data are expressed in mg m^{-2} h^{-1}.

4. Discussion

Previous studies investigateding tropical soil BVOC fluxes withusing in-situ measurements and incubation (Bourtsoukidis et al., 2018) and fertilization experiments (Llusià et al., 2022). showed that fluxes were These studies gave insights into how BVOC soil fluxes respond to drought and nutrients, and suggested their magnitudes are much higher than previously anticipated. The present study Although these pioneer studies were very important to understand soil BVOC fluxes from the tropics, our study took one step further by investigating soil-litter BVOC and GHG fluxes across Amazonian Forest types. We found that soil-litter BVOC and GHG fluxes changed across Amazonian forest types and were influenced by differences in nutrient content, soil moisture and temperature, and microbial biomass. The main differences in soil-litter properties, soil-litter gas fluxes, their interaction with soil-litter properties across forest types, and the significance of our findings are discussed in the following sections.

Given the extensive number of measured variables, we chose to focus our discussion on the most relevant and novel findingskey observations related to BVOC and CH_4methane fluxes and their drivers, rather than covering all variables and fluxes. However, since these variables may still be of interest to the reader, detailed analyses are provided in the supplementary material. (Section 2). In the following sections, we first compare soil- –litter properties acrossamong forest types, followed by a comparison of observed BVOC and GHG fluxes both between forest types and with other tropical studies. We then discuss their potential drivers and the broader significance of our findings.

4.1 Differences in soil and litter nutrient contents across forest types

Soil and litter properties showed strong differences between forest types. The ancient river terrace forest stood out for its high litter K and P contents, though the underlying mechanisms –

~~such as nutrient resorption efficiency or soil nutrient availability—remain to be investigated.~~ Variations in soil and litter properties were observed among forest types, particularly concerning their total nutrient contents. These total nutrient pools reflect long-term nutrient availability and reservoirs within each ecosystem, shaped by distinct biogeochemical processes. In the Ancient River Terrace Forest, high concentrations of potassium and phosphorus were found in the litter, suggesting strong nutrient retention and efficient cycling within this forest type. This may result from its history of periodic flooding and the presence of allisols—relatively young, nutrient-rich soils (Andreae et al., 2015).

In the ~~u~~Upland ~~f~~Forest, the dominance of soil iron total content is likely related to the intense leaching common in its ferrasols (oxisols), resulting in iron enrichment due to the removal of other nutrients (Mosquera et al., 2024)~~;~~. ~~in~~In addition, the formation of iron oxides can reduce~~s~~ the mineralization of organic matter, promoting iron accumulation in the leaf litter (Li et al., 2023).

~~Overall, t~~The ~~w~~White ~~s~~Sand ~~f~~Forest ~~exhibited distinct~~showed differences in soil properties when compared to the other ~~studied~~ forest types analyzed. Despite its well-documented low fertility (Mendonça et al., 2015; Demarchi et al., 2022) and arenosol characteristics, this forest type ~~showed~~displayed unexpectedly high soil ~~nutrient~~phosphorus and carbon total concentrations. Phosphorus ~~levels~~total concentrations, for instance, were up to four times higher than in ~~u~~Upland and ~~a~~Ancient ~~r~~River ~~t~~Terrace ~~f~~Forests~~,~~. ~~potentially due to~~This observation may possibly reflect the role of dissolved organic nutrients in mitigating nutrient limitations (Lange et al., 2024)~~.~~, ~~While earlier studies reported higher carbon content in upland forests (Marques et al., 2017), the white sand~~ or the efficient capture and retention of nutrients within the forest's extensive root mats, ~~may~~which can enhance carbon storage~~, as observed~~and nutrient cycling in structurally analogous ecosystems (Draper et al., 2014). ~~Iron~~ Furthermore, iron total concentrations in the soil of ~~white sand~~this forest were lower than expected (Cornu et al., 1997), possibly ~~due~~attributed to spatial variability and seasonal dynamics. During the dry season, the low water~~-~~-retention ~~in~~capacity of sandy soils ~~induces~~ leads to drought stress, ~~while~~whereas in the wet~~-~~ season, leaching redistributes iron, aluminum, and magnesium (García-Villacorta et al., 2016)~~.~~ ~~This~~– a process that can form cemented horizons, impeding drainage and elevating water tables (Franco & Dezzeo, 1994; Demarchi et al., 2022). ~~Additionally, differences in~~Variable iron concentrations, together with wet-season leaching and elemental redistribution, shape the White Sand Forest into a highly

distinct environment. In addition, tree species composition ~~between forest types may~~ could play a role in influence~~e~~ing nutrient ~~levels~~stocks in this forest type (García-Villacorta et al., 2016; Gomes Alves et al., 2022).

4.2 Differences in ~~g~~Gas ~~f~~Fluxes across ~~the different forest types~~Forest Types

Here, by comparing forest type fluxes, it is important to recognize that our chamber measurements represent the combined (net) flux from both soil and litter. Observed differences between sites may therefore reflect variations in the relative contributions of soil and litter, for example, due to different amounts of litter. Because our measurements do not allow us to separate these sources, we cannot determine to what extent the observed differences are attributable to each component. Consequently, we treat soil and litter together as a single compartment in our analysis, and discuss the differences in soil-litter gas fluxes across forest types.

~~Our results revealed that~~ T~~t~~he ~~w~~White ~~s~~Sand ~~f~~Forest ~~showed~~exhibited the highest emissions and consumption of ~~gases~~BVOCs and GHGs, accompanied by the greatest chemical diversity in gas fluxes. ~~This elevated chemical diversity may be attributed to the distinct characteristics of the white sand forest, such as its unique microbiome, seasonality, and species composition (Rinnan et al., 2013; Viros et al., 2021; Vermeuel et al., 2023).~~ Plant ~~S~~species endemic to this ecosystem may influence BVOC emission patterns and their chemical speciation~~.~~: Fine et al. (2004, 2006) showed that tree species adapted to very nutrient-poor sandy soils highly invest in secondary metabolite compounds in defense against herbivory, since leaves are very energetically costly for the plant. This large quantity of secondary compounds can directly influence litter decomposition rate (Chomel et al., 2016) and probably release gases and various compounds into the soil and water (Caetano, 2022).

Isoprenoids were emitted in considerable amounts in the ~~w~~White ~~s~~Sand ~~f~~Forest. As isoprenoids are not expected to be emitted from soil (Bach & Rohmer, 2013; Asensio et al., 2008), the observed high emissions ~~could be attributed to~~might indicate contributions from the activity of microorganisms living in the soil and litter (Carruthers & Lee, 2021; Hernandez-Arranz et al., 2019). In addition, it is important to note that, although emissions in this study are expected to

come from soil and litter, the contribution of root emissions cannot be ruled out, as the main source of isoprenoids is expected to be the plant metabolism (Pulido et al., 2012; Thulasiram et al., 2007).

A previous study on experimental rainforest soils - similar to ~~u~~Upland ~~f~~Forest soils - showed BVOC soil uptake (under wet conditions) primarily for isoprenoids, carbonyls, and alcohols, as well as soil emissions of ~~dimethyl sulfide~~DMS and carbonyl compounds such as acetaldehyde and acetone (Pugliese et al., 2023). Our ~~u~~Upland ~~f~~Forest isoprene fluxes exhibited lower soil uptake (~~-0.1~~0.005 mg m^{-2} h^{-1}) compared to the increased uptake fluxes under drier conditions (~ -2.38 mg m^{-2} h^{-1}) observed by Pugliese et al. (2023). This lower isoprene uptake by the soil observed in the Upland Forest likely reflects the combined effects of the amount of plant-emitted isoprene diffusing into the soil and the subsequent microbial assimilation and soil physical adsorption. These processes are strongly influenced by forest structural attributes and underlying soil properties, which are likely different between this study and Pugliese et al. (2023). Additionally, the higher atmospheric isoprene concentrations reported by Pugliese et al. (2023)~~,~~ compared with those in this study may help explain the greater soil isoprene uptake observed in their work.

~~ ~~In general, our ~~u~~Upland and ~~a~~Ancient ~~r~~River ~~t~~Terrace ~~f~~Forests showed lower average emissions and uptake than those reported by Pugliese et al. (2023). ~~This could also be due to a greater observed abundance of atmospheric isoprene as described in Pugliese et al. (2023), leading to a larger uptake.~~ A study focusing on methanol fluxes in cropland soils observed values ranging from 0.53 to 2.93 mg m^{-2} h^{-1} (Liu et al., 2024), which are higher than those observed in ~~the current~~our study in ~~u~~Upland and ~~a~~Ancient ~~r~~River ~~t~~Terrace ~~f~~Forests but ~~interestingly similar~~comparable to the ~~w~~White ~~s~~Sand ~~f~~Forest fluxes (~~1.5~~0.61 ± 0.81 mg m^{-2} h^{-1}). These higher emissions in crop soils can likely be attributed to factors such as crop species, tillage, fertilization, and irrigation, which can all influence BVOC emission rates; whereas the high methanol emission observed in our study could be related to the root growth of ~~w~~White ~~s~~Sand ~~f~~Forest's extensive root mats~~, (~~although future studies are necessary to confirm this hypothesis~~).~~ ~~Dimethyl sulfide emission fluxes were highest~~

The highest DMS emissions were observed in the ~~w~~White ~~s~~Sand ~~f~~Forest (~ ~~0.92~~1.10 ±1.14 mg m^{-2} h^{-1}), which were higher than the DMS emission of 5.76 µg m^{-2} h^{-1} reported by Jardine et

al. (2015) for Amazon soils~~;~~. ~~h~~However, while an interesting observation, it is important to note that the high magnitude of DMS fluxes presented here might ~~be influenced~~partly be caused by a potential agglomerate of acetaldehyde (mass 45) with water, resulting in the same mass as DMS (63), suggesting that future studies ~~e~~should make use of techniques that differentiate these compounds.

A compound with a mass-to-charge ratio (m/z) of 42 was observed in the ~~w~~White ~~s~~Sand ~~f~~Forest, but its identity could not be confirmed due to technical limitations (Dunne et al., 2012). This m/z 42 is frequently attributed to acetonitrile, a known biomass burning marker primarily associated with anthropogenic sources (Huangfu et al., 2021). However, since it can also be emitted by microorganisms (Raio et al., 2020), it is possible that the microbial communities of the ~~w~~White ~~s~~Sand ~~f~~Forest contributed to potential acetonitrile (m/z 42) ~~-~~emissions.

Methane uptake was observed in the ~~u~~Upland (-0.12 mg m^{-2} h^{-1}) and ~~a~~Ancient ~~r~~River ~~t~~Terrace Forests (-0.10 mg m^{-2} h^{-1}) ~~forests~~, whereas emissions were observed in the ~~w~~White ~~s~~Sand ~~f~~Forest (0.12 mg m^{-2} h^{-1}). ~~These results are probably explained by the shallow water table characteristic of this forest type, which makes the soil saturated and creates an anaerobic environment that favors the growth of methane-producing microorganisms (methanogens), contributing to the observed high emissions.~~ In another central Amazonia site, ~~u~~Upland ~~f~~Forest methane fluxes of similar magnitude were observed (-0.02 to -0.09 mg m^{-2} h^{-1}) (van Asperen et al., 2020). However, ~~-~~the discrepancy in ~~w~~White ~~s~~Sand ~~f~~Forest fluxes, with uptake reported in their study ~~showed uptake instead of emission~~ (-0.38 to -0.25 mg m^{-2} h^{-1}). ~~This difference is probably explained by the natural variations across~~and emissions observed here, can likely be attributed to the high spatial variability characteristic of white sand forest ecosystems~~, especially concerning water table depth (Franco & Dezzeo, 1994; Demarchi et al., 2022).~~.

4.3 ~~General~~ Drivers of Soil and Litter Gas Fluxes

4.3.1 Soil moisture and soil temperature as drivers of soil ~~and~~ litter gas fluxes

~~A principal component analysis (PCA) was performed~~A PCA was initially conducted to identify variables that ~~could collectively~~might differentiate forest types and their gas fluxes. ~~As~~

~~the PCA showed a limited capacity for differentiation~~However, due to the overlapping ellipses~~, a further investigation was carried out using~~and limited discrimination capacity, linear models ~~(LMs).~~were applied to further explore the findings. ~~The LMs showed that~~ These models highlighted soil temperature and ~~soil~~ moisture ~~were important~~as key physical drivers ~~for~~across all three forest types, ~~especially for the white sand forest.~~aligning with observations in other ecosystems (Trowbridge et al., 2020; Pugliese et al., 2023; Liu et al., 2024).

Nevertheless, before evaluating these key drivers, it is important to recognize that external factors inevitably influenced soil moisture and temperature. Although transects were consistently measured at the same time (08:00–10:00 local time), they were conducted on consecutive days under varying weather conditions. In addition, while radiation was not quantified during the campaign, its effects should be considered. Despite the use of opaque chambers, the chamber surrounding environment - and thus the prevailing BVOC flux dynamics - may still be modulated by incoming radiation. ~~Since the white sand forest presents a relatively~~ These factors are particularly important in the White Sand Forest, where the open canopy, ~~with~~ short~~er~~ ~~trees~~stature, and ~~a~~ shallow water table (Adeney et al., 2016; Rossetti et al., 2019)~~, it often experiences extreme conditions and short-term variation, as demonstrated by the highly variable~~promote highly dynamic conditions, reflected in the strong variability of soil temperature and ~~soil moisture values measured over two transects, in two subsequent days.~~moisture between consecutive transects. ~~Here, we discuss the role of soil temperature and moisture, and other potential drivers of gas fluxes.~~While on one hand these factors represent a limitation, it also allowed us to explore the influence of external factors on gas fluxes within the same forest type, such as the rain event which will be discussed hereafter.

~~4.3.1 Soil moisture and soil temperature as drivers of soil and litter gas fluxes~~

In addition to the complicating external factors, we should also note that high soil moisture values were generally accompanied by lower soil temperatures, thereby complicating separating individual drivers. A similar pattern was observed by van Asperen et al., (2024) who showed that the direct effects of temperature and moisture are difficult to differentiate under tropical field conditions, where temperature variation is usually small. Furthermore, it should be noted that this study is additionally limited by a small temporal dataset. Thus, although some BVOC fluxes

showed a positive association with soil moisture and a negative association with soil temperature, distinguishing the primary driver remains difficult. Nevertheless, despite the limitations described above, we discuss the expected effects of soil moisture and temperature on our fluxes below.

We observed a negative relationship between temperature and certain BVOC fluxes, but we interpret this as an indirect effect mediated by the previously described link to soil moisture. In general, elevated temperatures are expected to enhance both BVOC emissions and biological uptake, as described by Baggesen et al. (2022). If the temperature sensitivity of uptake exceeds that of emission, this may result in reduced net emissions or even a net sink for BVOCs (Asensio et al., 2007; Peñuelas et al., 2014; Jiao et al., 2023).

~~Soil temperature and moisture were significant drivers for most gases, especially in the white sand forest, which agrees with what has been observed in other ecosystems (Trowbridge et al., 2020; Pugliese et al., 2023; Liu et al., 2024).~~For soil moisture, we found a clear relation with most of BVOC fluxes, especially for the White Sand Forest. ~~For example,~~The effects of moisture on BVOC fluxes were also described by Pugliese et al. (2023) ~~observed~~who reported that rainforest soils acted as net BVOC sinks under moist conditions and as net BVOC sources under dry conditions. ~~By comparing two transects in~~In the ~~u~~Upland ~~f~~Forest, we observed a similar pattern as Pugliese et al (2023), with the wetter ~~t~~Transect showing BVOC consumption while the drier ~~t~~Transect showed emissions. ~~However, in t~~The ~~w~~White ~~s~~Sand ~~f~~Forest~~,~~ showed even stronger inter-Transect differences, with high BVOC emissions ~~were~~ observed in the wetter ~~t~~Transect, ~~while~~and low emissions and uptake ~~were~~ observed in the drier ~~t~~Transect. Th~~is~~e ~~shows that Amazonian soil emissions may respond differently to soil moisture depending on the soil and forest type.~~pronounced differences between these Transects suggest that the rainfall event preceding Transect 2 was an important driver of the observed variation. ~~Interestingly, soil moisture was shown to be a predictor for methane for all three forest types, suggesting a general mechanism influencing methane fluxes regardless of the forest type, and in agreement with several studies showing the relationship between methane flux and soil moisture (Bridgham et al., 2013; Conrad, 2009; Shah et al., 2024; Van Den Pol-van Dasselaar et al., 1998).~~ A similar hypothesis was posed by Bourtsoukidis et al. (2018), who also observed that sesquiterpene emissions from Upland Forest soils in the dry season (after a rain event) were comparable to those from vegetation. In addition to increasing soil moisture, the physical impact of rainfall may trigger short-term emission bursts

(Miyama et al., 2020). As we observed substantially high isoprene, monoterpenes, and acetaldehyde emissions in tTransect 2 of the wWhite sSand fForest, we argue that these observed BVOC emissions represent a burst induced by the preceding rainfall event,. sSimilar observations have been reported by Greenberg et al.,(2012), who observed increased BVOC emissions during and immediately after rainfall in a Ponderosa pine plantation, and by Jardine et al. (2015), who reported a peak in soil DMS emissions following rainfall.

~~Generally, BVOC fluxes exhibited a positive correlation with soil moisture and an inverse relationship with soil temperature. However, since high soil moisture often coincides with low temperatures, it remains challenging to ascertain whether low temperatures or high moisture levels drive increased fluxes under field conditions. This complexity is particularly relevant given that BVOC uptake and emission are closely tied to biological processes, which typically correlate positively with temperature. High temperatures can enhance BVOC emissions and, at the same time, stimulate biological uptake (Baggesen et al., 2022). Notably, biological uptake may respond more vigorously to elevated temperatures than biological BVOC emission, potentially resulting in lower net emissions or even uptake (Penuelas et al., 2014; Jiao et al., 2023). However, as this study was based on field measurements, wherein soil moisture and temperature are intertwined, it is not possible to disentangle their combined effects.~~

Overall, we hypothesize that the rainfall event induced an emission burst, mostly explaining the elevated BVOC fluxes observed in that transect. Nevertheless, interactions between soil temperature, soil moisture, and BVOC fluxes remain highly complex across heterogeneous forest types, with external drivers contributing to strong spatial and temporal variability and making their combined effects difficult to separate under natural field conditions.

4.3.2 Forest tType-specific Drivers of Soil-litter Gas Fluxes

We observed that drivers of soil and litter gas fluxes varied across forest types, reflecting their unique environmental conditions and nutrient dynamics.

In general, aAncient rRiver tTerrace and uUpland fForests showed many similarities in the predictors of certain gases., In contrast,while other drivers were found infor the wWhite sSand

~~f~~Forest. Here, we ~~discuss the observed key drivers (soil potassium, carbon, phosphorus and~~ focus on the key factors influencing gas fluxes: soil nutrients, microbial biomass~~),~~ ~~for each forest type.~~ and their interactions with environmental conditions.

~~For ancient river terrace and upland forests,~~ ~~s~~Soil potassium was found to be a significant factor influencing ~~soil~~Ancient River Terrace and Upland Forest fluxes, being identified as a predictor of methanol and monoterpenes. In addition, it was also identified as a predictor of m/z 42 fluxes in the ~~u~~Upland ~~f~~Forest. Although we ~~have~~did not f~~ou~~ind studies directly relating BVOCs and GHGs fluxes to soil potassium content, potassium is an essential macronutrient for plant growth and metabolism. Its availability ~~can~~is known to affect plant physiological processes (Wang et al., 2013), and its cycling within the soil environment, often mediated by microbial activity, influences potassium's uptake by plants (Mazahar & Umar, 2022)~~,~~. ~~which~~These plant- and soil-mediated processes can, in turn, ~~can~~indirectly influence the BVOC production and release observed within the soil-litter compartment of our study, by affecting the overall ecosystem health and the quality of organic matter available for decomposition.

In the ~~u~~Upland ~~f~~Forest, our methane consumption fluxes correlated well with soil carbon (in conjunction with soil moisture, as mentioned previously). Soil organic carbon is known to play an important role in supporting methanotrophic bacteria, which are responsible for methane oxidation (Lee et al., 2023); therefore, we suggest that the total soil carbon observed in our study might affect methane uptake through a similar process.

Phosphorus, like carbon, is a key nutrient in the soil and significantly affected BVOC soil-litter fluxes, especially for methanol in the ~~w~~White ~~s~~Sand ~~f~~Forest. The relationship between phosphorus and BVOC emissions is well documented for plants since the availability of phosphorus can influence the production and emission of BVOCs (Ndah et al., 2022). However, some fertilization studies have also shown that increasing soil nutrient status (nitrogen, phosphorus, and potassium) can modify pH levels, affecting microorganisms and their health state (Stotzky et al., 1976), ~~and~~which directly or indirectly promot~~ing~~es or inhibit~~ing~~s soil BVOC fluxes (Liu et al., 2024; Raza et al., 2017). Our findings with bi-directional soil-litter fluxes in the ~~w~~White ~~s~~Sand ~~f~~Forest are consistent with ~~this observation~~these previous studies showing increase or inhibition of soil BVOC fluxes with soil nutrient content.

Interestingly, our results suggested that lower phosphorus levels were associated with higher isoprene emissions. The mechanisms behind this relationship remain unclear. However, studies on soil fertilization in tropical forests by Llusià et al.~~,~~ (2022) found that phosphorus fertilization is less efficient than nitrogen fertilization in increasing monoterpene and sesquiterpene emissions (they did not find isoprene emissions)~~ in a tropical forest~~. They observed that emissions increased when the soil was fertilized only with nitrogen~~—~~ - consistent with a phosphorus-limited system~~—~~ - because excess nitrogen stimulates the enzymes responsible for producing monoterpenes and sesquiterpenes. Conversely, the addition of phosphorus likely redirected this nutrient toward plant growth, resulting in lower emissions of monoterpenes and sesquiterpenes in the phosphorus-fertilized plots compared to those fertilized with nitrogen. As in this study~~,~~ there was no fertilization or a controlled environment, ~~so~~ we can~~-~~not draw similar conclusions. However, our findings provide valuable insights into the possible interactions between phosphorus, nitrogen, and soil-litter BVOC fluxes in tropical ecosystems. These observations align with previous studies on the influence of soil nutrients (Liu et al., 2024; Llusià et al., 2022) and we suggest future soil fertilization studies to explore these relationships across soil and forest types in Amazonia.

For the ~~u~~Upland ~~f~~Forest, it was found that microbial biomass was a significant driver for almost all ~~gas~~soil-litter fluxes, except for isoprene and methane. This aligns with previous studies that have identified microbial biomass as an important driver for soil-litter gas fluxes (Leff & Fierer, 2008; ~~Lamers et al., 2013;~~ Mancuso et al., 2015; ~~Carrion et al., 2017;~~ Tang et al., 2019). For example, research on soil organic matter degradation by Lehnert et al. (202~~3~~4) demonstrated that ~~the degradation of organic matter~~it is an important source of DMS emissions, highlighting the role of microorganisms associated with decomposition. Jardine et al., (2015) point out that DMS emissions in Amazonian soils are related to microbial processes, ~~which was~~a relationship also reported in litter studies by Kesselmeier and Hubert (2002). DMS can be produced in anaerobic environments, such as saturated soils or lakes (~~Carrion et al., 2017;~~ Lehnert et al., 202~~3~~4). This may explain the high emissions observed in transect 2 (wetter and more saturated) of the ~~w~~White ~~s~~Sand ~~f~~Forest, where conditions favorable to anaerobic processes are common and frequently linked to the production of sulfur compounds such as DMS. In contrast, in the drier transect 1 of the upland forest, DMS consumption was observed, suggesting the occurrence of microbial uptake processes. ~~Previous studies, such as the one carried out by Eyice et al.~~In fact, another study has ~~(2015), have~~ shown that bacteria can consume carbon from DMS as an energy source in soil and

lake sediments (Eyice et al., 2015). Therefore, the observed uptake may be the result of microorganisms utilizing the carbon present in DMS as an energy source, leading to uptake rather than production. This dual role of microorganisms - as both producers and consumers of DMS - highlights the complexity of sulfur cycling in terrestrial ecosystems.

~~From the few~~Based on the limited number of studies investigating the relationship between microorganisms and BVOC dynamics, it has been shown that some Proteobacteria, Actinobacteria, and Firmicutes can produce isoprene (Kuzma et al., 1995; McGenity et al., 2018). *Bacillus subtilis* can produce isoprene in response to stress; however, the mechanism is still not clear (McGenity et al., 2018). Some studies have shown that reduced ~~soil~~ microbial diversity, whether in soil (Abis et al., ~~2020; Saunier et al.~~, 2020; Sillo et al., 2024) or associated with plant surfaces (Saunier et al., 2020), can increase BVOC fluxes and alter the chemical composition of emitted compounds~~ (Abis et al., 2020; Saunier et al., 2020; Sillo et al., 2024)~~. Although microbial community data were unavailable in this study, we suggest that potential differences in microbial diversity have influenced emission and consumption patterns. Therefore, we strongly recommend that future studies investigate gas flux measurements with microbial community analyses to better understand these dynamics.

4.4~~. Spatial and temporal variability effects on BVOC fluxes~~

~~While efforts were made in this study to minimize the effects of spatial variability, such as by measuring equidistant points and selecting homogeneous areas, it is important to consider that spatial variability still inevitably influenced our results, as observed in other studies (Durán & Delgado-Baquerizo, 2020). With respect to temporal variability, the transects were measured at the same time (08:00–10:00 am, local time) but on consecutive days, so differences in gas fluxes, soil moisture, and temperature may partly reflect external factors like prior precipitation, cloudiness, and air temperature changes. Just before the measurement of transect 2 at the white sand forest, a heavy rainfall occurred. This coincides with the observation of significantly high BVOC emissions in this transect, while transect 1 showed much lower emissions and more uptake. Bourtsoukidis et al., (2018) also found that sesquiterpenes emissions from upland forest soils in the dry season (after a rain event) were comparable to those from vegetation, suggesting that soil moisture is a crucial factor influencing sesquiterpenes emissions from Amazonian soils. As we~~

~~observed substantially high isoprene, monoterpenes and acetaldehyde emissions in transect 2 of the white sand forest, we argue that these observed BVOC emissions represent a burst induced by the preceding rainfall event, similar to the observed increase in BVOC emissions during and immediately after rainfall in a *Ponderosa pine* plantation (Greenberg et al., 2012). Likewise, Jardine et al., (2016) observed a peak in DMS soil emissions after rainfall. Therefore, higher emissions are expected to result from the interlinked effects of soil temperature and moisture and, as described above, the possible physical effects of rainfall (Miyama et al., 2020).~~

~~4.5~~ The relevance of ~~w~~White ~~s~~Sand ~~f~~Forest ecosystems

This study showed large variability across forest types and unexpectedly high BVOC emissions from the ~~w~~White ~~s~~Sand ~~f~~Forest. In general, ~~R~~relatively few studies have been performed on ~~w~~White ~~s~~Sand ~~f~~Forests, which ~~can~~is partly ~~be~~ explained by the challenging conditions of this forest type, such as flooding and extreme temperatures~~, which require specific infrastructure for data collection~~ (Adeney et al., 2016). In addition, the ~~complex nature of this ecosystem – characterized by~~ scattered patches of differentiated vegetation distributed within extensive ~~u~~Upland ~~f~~Forests (Demarchi et al., 2022) ~~–~~can make access to these sites even more difficult~~.~~ and require specific infrastructure for data collection. While our observations constitute one of the first characterizations of BVOCs in this unique forest type, their capacity to capture the full spectrum of extreme conditions is inevitably limited by the short temporal coverage of the dataset. ~~It is acknowledged that BVOC and GHG studies in white sand forests are limited: so far~~To the best of our knowledge, only one study has provided data on BVOC fluxes with soil incubation lab measurements (Bourtsoukidis et al., 2018), and another measuring GHGs in~~-~~situ (van Asperen et al., 2020) in White Sand Forests. Despite representing only 5% of the Amazon basin area (Adeney et al., 2016) and 8% of the Reserve of this study (Demarchi et al., 2022), ~~w~~White ~~s~~Sand ~~f~~Forests are extremely important environments. Their sandy, nutrient-poor soil type has created a challenging ecosystem for plant growth (Fine & Baraloto, 2016), and this unique condition has selected specialized flora and fauna adapted to thrive in these ecosystems (Adeney et al., 2016; Demarchi et al., 2022). This high level of endemism contributes significantly to the overall biodiversity of the Amazon Basin (García-Villacorta et al. 2016). Moreover, ~~w~~White ~~s~~Sand ~~f~~Forests have been shown to play a crucial role in the chemistry of dissolved organic matter (DOM) in Amazonian blackwater rivers, linking terrestrial ecosystem processes to aquatic

biogeochemistry (Simon et al., 2021). Our results ~~showed that~~suggest a stronger link between ~~w~~White ~~s~~Sand ~~f~~Forest gas fluxes ~~clearly depend on~~ and physical ~~drivers~~factors (more than other forest types), which indicates a possible sensitivity to upcoming climate extremes. Although Costa et al. (2023) did not focus specifically on the ~~w~~White ~~s~~Sand ~~f~~Forest, they showed that regions of the Amazon with shallow water tables~~—~~ - such as the ~~w~~White ~~s~~Sand ~~forest —~~Forests - can act as hydrological refuges during droughts. In these areas, higher productivity under dry conditions may ~~help offset~~maintain relatively stable carbon dynamics, presenting a contrasting response to the substantial carbon losses typically observed in deep water table~~–~~,U~~(u~~pland~~)~~ ~~f~~Forests, during drought. ~~Therefore, it is crucial to recognize that white sand forests have historically been neglected, even with their critical role in regulating the carbon cycle and maintaining Amazonian biodiversity (Rossetti et al., 2019). As for BVOC and GHG measurements, even less information is available for this ecosystem. However, our results suggest that white sand forests may play a significant role in both the emission and uptake of these compounds, reinforcing their importance in regional carbon and trace gas fluxes.~~In addition ~~Notably~~, a recent study reported high atmospheric isoprene concentrations in the northwestern Amazon throughout most of the year (Wells et al., 2022) ~~—~~ - a region characterized by extensive and continuous ~~w~~White ~~s~~Sand ~~f~~Forest cover (Borges et al., 2014). In this context, as White Sand Forests play a critical role in regulating the carbon cycle and maintaining Amazonian biodiversity (Rossetti et al., 2019), our ~~results~~study suggest that ~~w~~White ~~s~~Sand ~~f~~Forests may ~~play a~~represent significant source and sink of BVOCs, ~~T~~together, ~~these findings~~this highlights the need to better integrate ~~w~~White ~~s~~Sand ~~f~~Forests into future BVOC and GHG flux studies and ~~atmospheric~~Earth System model~~s~~ing.

5. Summary and future directions

Multiple interconnected factors influence BVOC and GHG soil-litter fluxes in the central Amazon. This study highlights the significant roles of soil and litter properties, as well as microbial biomass, in driving these fluxes, with distinct patterns observed across forest types. Given the complexity of the mechanisms influencing BVOC and GHG ~~emissions~~fluxes, future studies should prioritize microbial activity and diversity, along with diurnal and seasonal cycles, to better identify the key drivers of emission~~s~~ and consumption in these diverse forest ecosystems.

In addition, itIt is important to note that this research serves as a pilot study aimed at scoping out general trends, and many sampling issues can be addressed in future work. For instance, utilizing a PTR-ToF-MS could alleviate the challenges associated with measuring acetaldehyde, DMS and m/z 42. Longer sampling periods, ideally continuous, would allow for capturing daily variations in emissions.

Surprisingly, despite being the least fertile and diverse forest type, the wWhite sSand fForest exhibited the highest uptake and emission fluxes. This is likely due to intrinsic environmental factors, such as soil temperature and moisture, influencing microbial activity and gas fluxes, as well as -the unique vegetation composition of the white sand forestthis ecosystem. Furthermore, external factors, likesuch as the preceding rainfall event, couldmay have contributed to the observedvery high emissions, potentially reflecting short-term post-rainfall pulses that would have a low or moderated effect when averagingged over longer periods that capture the full range of environmental conditions in these ecosystems. Therefore, future studies extending the measurement duration would provide a clearer understanding of how rainfall events influence average soil BVOC emissions. The exceptionally high emissions observed in the white sand forest may reflect short-term bursts following rainfall, which could be moderated when averaging over longer periods that capture the full range of environmental conditions in these ecosystems. Still, white sand forests may serve as BVOC emission hotspots after rain events, potentially becoming even more significant under climate change. Finally, Ddespite their limited area, they could have substantial ecological and atmospheric impacts.spatial extent in Amazonia, White Sand Forests warrant We encourage further research into this ecosystem to better understand its to elucidate their ecological processes and role intheir influence on atmospheric dynamics,. as forestTheir high BVOC fluxes influencemay substantially affect key physical and chemical processes in the atmosphere, ultimately affectingwith potential implications for the climate system.

Code/Data availability

All data supporting the findings of this study will be made available in a public repository upon publication.

Authors' contributions

Débora Pinheiro Oliveira, Hella van Asperen, and Eliane Gomes Alves contributed to the development and design of the study, as well as the collection, processing, and statistical analysis of the datasets. Murielli Garcia Caetano and Michelle Robin contributed to field data collection and data analysis. Achim Edtbauer helped design the methodology used in the PTR-QMS and contributed to its calibration improvement. Nora Zannoni, Joseph Byron, Jonathan Williams, Sergio Duvoisin-Junior, and Carla Batista contributed to the chemical analysis of BVOC samples with the GC-TOF-MS and GC-MS. Layon Demarchi and Maria T. F. Piedade contributed to the data analysis of the ~~w~~White ~~s~~Sand ~~f~~Forest. Maria T. F. Piedade, Jochen Schöngart, and Florian Wittmann contributed to the dataset for the initial selection of the points in the PELD-MAUA project plots where the soil chambers were installed. Rodrigo Augusto Ferreira de Souza contributed to the development of the study. All authors contributed to the writing of the manuscript.

Competing interests

The authors declare that they have no conflict of interest.

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References

Aaltonen, H., Pumpanen, J., Pihlatie, M., Hakola, H., Hellen, H., Kulmala, L., Vesala, T., and Bäck, J.: Boreal pine forest floor biogenic volatile organic compound emissions peak in early summer and autumn, Agric. For. Meteorol., 151, 682–691, doi:10.1016/j.agrformet.2010.12.010, 2011

Abis, L., Loubet, B., Ciuraru, R., Lafouge, F., Houot, S., Nowak, V., Tripied, J., Dequiedt, S., Maron, P. A., and Sadet-Bourgeteau, S.: Reduced microbial diversity induces larger volatile organic compound emissions from soils. Scientific Reports, 10(1), 1–15. https://doi.org/10.1038/s41598-020-63091-8, 2020

Adeney, J. M., Christensen, N. L., Vicentini, A., and Cohn-Haft, M.: White-sand Ecosystems in Amazonia. Biotropica, 48(1), 7–23. https://doi.org/10.1111/btp.12293, 2016

Alves, E. G., Jardine, K., Tota, J., Jardine, A., Yãnez-Serrano, A. M., Karl, T., Tavares, J., Nelson, B., Gu, D., Stavrakou, T., Martin, S., Artaxo, P., Manzi, A., and Guenther, A.: Seasonality of isoprenoid emissions from a primary rainforest in central Amazonia, Atmos. Chem. Phys., 16, 3903–3925, https://doi.org/10.5194/acp-16-3903-2016, 2016.

Anderson, J.M. and Ingram, J.I.S. Tropical Soil Biology and Fertility: A Handbook of Methods. 2nd Edition, C.A.B. International, Wallingford, UK, 221 pp., DOI: 10.2307/2261129, 1993.

Andreae, M. O., Acevedo, O. C., Araújo, A., Artaxo, P., Barbosa, C. G. G., Barbosa, H. M. J., Brito, J., Carbone, S., Chi, X., Cintra, B. B. L., da Silva, N. F., Dias, N. L., Dias-Júnior, C. Q., Ditas, F., Ditz, R., Godoi, A. F. L., Godoi, R. H. M., Heimann, M., Hoffmann, T., and Yáñez-Serrano, A. M.: The Amazon Tall Tower Observatory (ATTO) in the remote Amazon Basin: overview of first results from ecosystem ecology, meteorology, trace gas, and aerosol measurements. Atmospheric Chemistry and Physics Discussions, 15(8), 11599–11726. https://doi.org/10.5194/acpd-15-11599-2015, 2015

Asensio, D., Owen, S. M., Llusià, J., and Peñuelas, J.: The distribution of volatile isoprenoids in the soil horizons around Pinus halepensis trees. Soil Biology and Biochemistry, 40(12), 2937–2947. https://doi.org/10.1016/j.soilbio.2008.08.008, 2008

~~Aprile, F., and Darwich, A. J.: Nutrients and water-forest interactions in an Amazon floodplain lake: an ecological approach. Acta Limnologica Brasiliensia, 25(2), 169–182. https://doi.org/10.1590/S2179-975X2013000200008, 2013~~

Asensio, D., Peñuelas, J., Llusià, J., Ogaya, R., & Filella, I. Interannual and interseasonal soil CO2 efflux and VOC exchange rates in a Mediterranean holm oak forest in response to experimental drought. Soil Biology and Biochemistry, 39(10), 2471-2484. https://doi.org/10.1016/j.soilbio.2007.04.019, 2007.

Bach, T. J., and Rohmer, M.: Isoprenoid synthesis in plants and microorganisms: new concepts and experimental approaches, Springer, doi:10.1007/978-1-4614-4063-5, 2013.

~~Bachy, A., Aubinet, M., Amelynck, C., Schoon, N., Bodson, B., Moureaux, C., Delaplace, P., De Ligne, A., and Heinesch, B.: Methanol exchange dynamics between a temperate~~

~~cropland soil and the atmosphere. Atmospheric Environment, 176, 229–239. https://doi.org/10.1016/j.atmosenv.2017.12.016, 2018~~

Baggesen, N. S., Davie-Martin, C. L., Seco, R., Holst, T., and Rinnan, R. Bidirectional Exchange of Biogenic Volatile Organic Compounds in Subarctic Heath Mesocosms During Autumn Climate Scenarios. Journal of Geophysical Research: Biogeosciences, 127(6). https://doi.org/10.1029/2021JG006688, 2022.

~~Bao, X., Zhou, W., Xu, L., Zheng, Z., Mu, Z., Llusià, J., Zeng, J., Zhang, Y., Asensio, D., Yang, K., Yi, Z., Wang, X., and Peñuelas, J.: A meta-analysis on plant volatile organic compound emissions of different plant species and responses to environmental stress. Front. Plant Sci., 318, 120886, https://doi.org/10.1016/j.envpol.2022.120886, 2023~~

Beauchamp, J., Herbig, J., Gutmann, R. and Hansel, A. On the use of Tedlar bags for breath-gas sampling and analysis, J. Breath Res., 2, 046001, doi:10.1088/1752-7155/2/4/046001, 2008.

Borges, S. H., Whittaker, A., and de Almeida, R. A. M.: Bird diversity in the Serra do Aracá region, northwestern Brazilian Amazon: Preliminary check-list with considerations on biogeography and conservation. Zoologia, 31, 343–360, https://doi.org/10.1590/S1984-46702014000400006, 2014

Botía, S., Komiya, S., Marshall, J., Koch, T., Gałkowski, M., Lavric, J., Gomes-Alves, E., Walter, D., Fisch, G., Pinho, D. M., Nelson, B. W., Martins, G., Luijkx, I. T., Koren, G., Florentie, L., Carioca de Araújo, A., Sá, M., Andreae, M. O., Heimann, M., and Gerbig, C.: The CO2 record at the Amazon Tall Tower Observatory: A new opportunity to study processes on seasonal and inter-annual scales. Global Change Biology, 28(2), 588–611. https://doi.org/10.1111/gcb.15905, 2022

Bourtsoukidis, E., Behrendt, T., Yañez-Serrano, A. M., Hellén, H., Diamantopoulos, E., Catão, E., Ashworth, K., Pozzer, A., Quesada, C. A., Martins, D. L., Sá, M., Araujo, A., Brito, J., Artaxo, P., Kesselmeier, J., Lelieveld, J., and Williams, J.: Strong sesquiterpene emissions from Amazonian soils. Nature Communications, 9(1), 1–11. https://doi.org/10.1038/s41467-018-04658-y, 2018

~~Bridgham, S. D., Cadillo-Quiroz, H., Keller, J. K., and Zhuang, Q.: Methane emissions from wetlands: Biogeochemical, microbial, and modeling perspectives from local to global scales. Global Change Biology, 19(5), 1325–1346. https://doi.org/10.1111/gcb.12131, 2013~~

~~Brown, P., Watts, P., Märk, T. D., and Mayhew, C. A.: Proton transfer reaction mass spectrometry investigations on the effects of reduced electric field and reagent ion internal energy on product ion branching ratios for a series of saturated alcohols. International Journal of Mass Spectrometry, 294(2–3), 103–111. https://doi.org/10.1016/j.ijms.2010.05.028, 2010~~

Butterbach-Bahl K, Baggs EM, Dannenmann M, Kiese R, Zechmeister-Boltenstern S. Nitrous oxide emissions from soils: how well do we understand the processes and their controls? Philos Trans R Soc Lond B Biol Sci. doi: 10.1098/rstb.2013.0122, 2013.

Caetano Garcia, M.: Biogenic volatile organic compound (BVOC) emissions from decomposing leaf-litter in central Amazonia (Doctoral dissertation, National Institute for Amazonian Research Manaus), 2022

~~Cai, Z. C., Xing, G. X., Shen, G. Y., Xu, H., Yan, X. Y., Tsuruta, H., Yagi, K., and Minami, K.: Measurements of CH4 and N20 emissions from rice paddies in Fengqiu, China. Soil Science and Plant Nutrition, 45(1), 1–13. https://doi.org/10.1080/00380768.1999.10409320, 1999~~

~~Carrión, O., Pratscher, J., Curson, A. R., Williams, B. T., Rostant, W. G., Murrell, J. C., Todd, J. D.,~~ Carruthers, D. N., ~~and~~& Lee, T. S.~~:~~. Diversifying Isoprenoid Platforms via Atypical Carbon Substrates and Non-model Microorganisms. Frontiers in Microbiology, 12, 791089. https://doi.org/10.3389/fmicb.2021.791089, 2021,

~~Chadwick, K. D., and Asner, G. P.: Landscape evolution and nutrient rejuvenation reflected in Amazon forest canopy chemistry. Ecol Lett, 21: 978-988. https://doi.org/10.1111/ele.12963, 2018~~

~~Chen, Y., Ma, S., Jiang, H., Hu, Y., and Lu, X.: Influences of litter diversity and soil moisture on soil microbial communities in decomposing mixed litter of alpine steppe species. Geoderma, 377(March), 114577. https://doi.org/10.1016/j.geoderma.2020.114577, 2020~~

Chomel, M., Guittonny-Larchevêque, M., Fernandez, C., Gallet, C., DesRochers, A., Paré, D., Jackson, B. G., and Baldy, V.: Plant secondary metabolites: A key driver of litter decomposition and soil nutrient cycling. J. Ecol., 104, 1527–1541, https://doi.org/10.1111/1365-2745.12644, 2016.

~~Conrad, R: The global methane cycle: Recent advances in understanding the microbial processes involved. Environmental Microbiology Reports, 1(5), 285–292. https://doi.org/10.1111/j.1758-2229.2009.00038.x, 2009~~

Conrad, R: Methane production in soil environments— anaerobic biogeochemistry and microbial life between flooding and desiccation. Microorganisms, 8(6), 1–12. https://doi.org/10.3390/microorganisms8060881, 2020.

Conrad, R: The global methane cycle: Recent advances in understanding the microbial processes involved. Environmental Microbiology Reports, 1(5), 285–292. https://doi.org/10.1111/j.1758-2229.2009.00038.x, 2009.

Cornu, S., Ambrosi, J. P., Lucas, Y., and Fevrier, D.: A comparative study of the soil solution chemistry of two Amazonian forest soils (Central Amazonia, Brazil). In Hydrology and Earth System Sciences (Vol. 1, Issue 2, pp. 313–324). https://doi.org/10.5194/hess-1-313-1997, 1997

~~Cornwell, W. K., Cornelissen, J. H. C., Amatangelo, K., Dorrepaal, E., Eviner, V. T., Godoy, O., Hobbie, S. E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., Quested, H. M., Santiago, L. S., Wardle, D. A., Wright, I. J., Aerts, R., Allison, S. D., Van Bodegom, P., Brovkin, V., Chatain, A., and Westoby, M.: Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecol. Lett., 11, 1065–1071, https://doi.org/10.1111/j.1461-0248.2008.01219.x, 2008~~

Costa, F. R. C., Schietti, J., Stark, S. C., and Smith, M. N.: The other side of tropical forest drought: do shallow water table regions of Amazonia act as large-scale hydrological refugia from drought? New Phytologist, 237(3), 714–733. https://doi.org/10.1111/nph.17914, 2023

~~de Gouw, J. A., Goldan, P. D., Warneke, C., Kuster, W. C., Roberts, J. M., Marchewka, M., Bertman, S. B., Pszenny, A. A. P., and Keene, W. C.: Validation of proton transfer reaction-~~

mass spectrometry (PTR-MS) measurements of gas-phase organic compounds in the atmosphere during the New England Air Quality Study (NEAQS) in 2002. Journal of Geophysical Research D: Atmospheres, 108(21), 1–18. https://doi.org/10.1029/2003jd003863, 2023

de Mendonça, B. A. F., Filho, E. I. F., Schaefer, C. E. G. R., Simas, F. N. B., and de Paula, M. D.: Os solos das campinaranas na amazônia Brasileira: Ecossistemas arenícolas oligotróficos. Ciencia Florestal, 25(4), 827–839. https://doi.org/10.5902/1980509820581, 2015

de Oliveira Marques, J. D., Luizão, F. J., Teixeira, W. G., Nogueira, E. M., Fearnside, P. M., and Sarrazin, M.: Soil Carbon Stocks under Amazonian Forest: Distribution in the Soil Fractions and Vulnerability to Emission. Open Journal of Forestry, 07(02), 121–142. https://doi.org/10.4236/ojf.2017.72008, 2017

Demarchi, L. O., Klein, V. P., Aguiar, D. P. P., Marinho, L. C., Ferreira, M. J., Lopes, A., da Cruz, J., Quaresma, A. C., Schöngart, J., Wittmann, F., and Piedade, M. T. F.: The specialized white-sand flora of the Uatumã Sustainable Development Reserve, central Amazon, Brazil, Check List, 18, 187–217, https://doi.org/10.15560/18.1.187, 2022

Draper, F. C., Roucoux, K. H., Lawson, I. T., Mitchard, E. T. A., Honorio Coronado, E. N., Lähteenoja, O., Montenegro, L. T., Sandoval, E. V., Zaráte, R., and Baker, T. R.: The distribution and amount of carbon in the largest peatland complex in Amazonia, Environ. Res. Lett., 9, 124017, https://doi.org/10.1088/1748-9326/9/12/124017, 2014https://doi.org/10.1088/1748-9326/9/12/124017, 2014.

Dixon, J. L., Hopkins, F. E., Stephens, J. A., and Schäfer, H.: Seasonal changes in microbial dissolved organic sulfur transformations in coastal waters, Microorganisms, 8, 337, https://doi.org/10.3390/microorganisms8030337, 2020

Drewer, J., Leduning, M. M., Purser, G., Cash, J. M., Sentian, J., and Skiba, U. M.: Monoterpenes from tropical forest and oil palm plantation floor in Malaysian Borneo/Sabah: emission and composition, Environ. Sci. Pollut. Res., 28, 31792–31802, doi: 10.1007/s11356-021-13052-z., 2021.

Dunne, E., Galbally, I. E., Lawson, S., and Patti, A.: Interference in the PTR-MS measurement of acetonitrile at m/z 42 in polluted urban air—a study using switchable reagent ion PTR-MS, Int. J. Mass Spectrom., 319–320, 40–47, https://doi.org/10.1016/j.ijms.2012.05.004, 2012

~~Durán, J., and Delgado-Baquerizo, M.: Vegetation structure determines the spatial variability of soil biodiversity across biomes, Sci. Rep., 10, 1–7, https://doi.org/10.1038/s41598-020-78483-z, 2020~~

Edtbauer, A., Pfannerstill, E. Y., Pires Florentino, A. P., Barbosa, C. G. G., Rodriguez-Caballero, E., Zannoni, N., Alves, R. P., Wolff, S., Tsokankunku, A., Aptroot, A., de Oliveira Sá, M., de Araújo, A. C., Sörgel, M., de Oliveira, S. M., Weber, B., and Williams, J.: Cryptogamic organisms are a substantial source and sink for volatile organic compounds in the Amazon region, Commun. Earth Environ., 2, 1–10, https://doi.org/10.1038/s43247-021-00328-y, 2021

Steeghs, M., Bais, H. P., de Gouw, J., Goldan, P., Kuster, W., Northway, M., Fall, R., and Vivanco, J. M.: Proton-transfer-reaction mass spectrometry as a new tool for real time analysis of root-secreted volatile organic compounds in Arabidopsis, Plant Physiol., 135, 47–58, https://doi.org/10.1104/pp.104.038703, 2004

Emidio, K., Martins, S. V., Antônio, C., and Soares, A.: Structure of 15 hectares permanent plots of terra firme dense forest in central Amazon, 01, 603–615, https://doi.org/10.1590/0100-67622016000400004, 2016.

Empresa Brasileira de Pesquisa Agropecuária. Manual de análise química de solos, plantas e fertilizantes, 2nd Edn., EMBRAPA, Brasília, 1999.

Eyice, Ö., Namura, M., Chen, Y., McGenity, T. J., and Murrell, J. C.: SIP metagenomics identifies uncultivated Methylophilaceae as dimethylsulphide degrading bacteria in soil and lake sediment, ISME J., 9, 2336–2348, https://doi.org/10.1038/ismej.2015.37, 2015

Fan, J., Luo, R., McConkey, B. G., and Ziadi, N.: Effects of nitrogen deposition and litter layer management on soil CO_2, N_2O, and CH_4 emissions in a subtropical pine forestland, Sci. Rep., 10, 1–11, https://doi.org/10.1038/s41598-020-65952-8, 2020

Fan, Y., Zhang, Y., Osborne, B., and Zou, J.: Global patterns of soil greenhouse gas fluxes in response to litter manipulation, Cell Rep. Sustain., 1, 100003, https://doi.org/10.1016/j.crsus.2023.100003, 2024.

~~Franco, W., and Dezzeo, N.: Soils and soil-water regime in the terra-firme-caatinga forest complex near San Carlos de Rio Negro, state of Amazonas, Venezuela, Interciencia, 19, 305–316, 1994.~~

Fine, P. V. A, Mesones, I., & Coley, P. D. Herbivores promote habitat specialization by trees in amazonian forests. Science. https://doi.org/3050663, 2004.

Fine, P. V. A., and Baraloto, C.: Habitat endemism in white-sand forests: insights into the mechanisms of lineage diversification and community assembly of the Neotropical flora, Biotropica, 48, 24–33, https://doi.org/10.1111/btp.12301, 2016.

Fine, P. V. A., Miller, Z. J., Mesones, I., Irazuzta, S., Appel, H. M., Stevens, M. H. H., Sääksjärvi, I., Schultz, J. C., and Coley, P. D.: The growth-defense trade-off and habitat specialization by plants in Amazonian forests, Ecology, 87, 150–162, https://doi.org/10.1126/science.1098982, 2006

Flint, A. L., and Flint, L. E.: Particle density, in: Methods of Soil Analysis, Part 4: Physical Methods, 229–240. https://doi.org/10.2136/sssabookser5.4.c10, ~~2018~~2002.

~~Flores, B. M., and Holmgren, M.: White-sand savannas expand at the core of the Amazon after forest wildfires, Ecosystems, 24, 1624–1637, https://doi.org/10.1007/s10021-021-00607-x, 2021~~

~~Freschet, G. T., Aerts, R., and Cornelissen, J. H. C.: A plant economics spectrum of litter decomposability, Funct. Ecol., 26, 56–65, https://doi.org/10.1111/j.1365-2435.2011.01913.x, 2012~~

Franco, W., and Dezzeo, N.: Soils and soil-water regime in the terra-firme-caatinga forest complex near San Carlos de Rio Negro, state of Amazonas, Venezuela, Interciencia, 19, 305–316, 1994.

García-Villacorta, R., Dexter, K. G., and Pennington, T.: Amazonian white-sand forests show

strong floristic links with surrounding oligotrophic habitats and the Guiana Shield, Biotropica, 48, 47–57, https://doi.org/10.1111/btp.12302, 2016.

Gfeller, A., Laloux, M., Barsics, F., Kati, D. E., Haubruge, E., du Jardin, P., Verheggen, F. J., Lognay, G., Wathelet, J. P., and Fauconnier, M. L.: Characterization of volatile organic compounds emitted by barley (Hordeum vulgare L.) roots and their attractiveness to wireworms, J. Chem. Ecol., 39, 1129–1139,https://doi.org/10.1007/s10886-013-0302-3, 2013

Gomes Alves, E., Taylor, T., Robin, M., Pinheiro Oliveira, D., Schietti, J., Duvoisin Júnior, S., Zannoni, N., Williams, J., Hartmann, C., Gonçalves, J. F. C., Schöngart, J., Wittmann, F., and Piedade, M. T. F.: Seasonal shifts in isoprenoid emission composition from three hyperdominant tree species in central Amazonia, Plant Biol., 24, 721–733, Seasonal shifts in isoprenoid emission composition from three hyperdominant tree species in central Amazonia. Plant Biology, 24(5), 721–733. https://doi.org/10.1111/plb.13419, 2022

Greenberg, J. P., Asensio, D., Turnipseed, A., Guenther, A. B., Karl, T., and Gochis, D.: Contribution of leaf and needle litter to whole ecosystem BVOC fluxes, Atmos. Environ., 59, 302–311, https://doi.org/10.1016/j.atmosenv.2012.04.038, 2012.

Guenther, A. B., Jiang, X., Heald, C. L., Sakulyanontvittaya, T., Duhl, T., Emmons, L. K., and Wang, X.: The model of emissions of gases and aerosols from nature version 2.1 (MEGAN2.1): an extended and updated framework for modeling biogenic emissions, Geosci. Model Dev., 5, 1471–1492, https://doi.org/10.5194/gmd-5-1471-2012~~, 2012~~.

Hair, J. F., Black, W. C., Babin, B. J. and Anderson, R. E. Multivariate data analysis, 7th Edn., Pearson, Upper Saddle River, 2009.

Hebbali, A. (2024). Olsrr: Tools for building OLS regression models.

Hernandez-Arranz, S., Perez-Gil, J., Marshall-Sabey, D., and Rodriguez-Concepcion, M.: Engineering Pseudomonas putida for isoprenoid production by manipulating endogenous and shunt pathways supplying precursors, Microb. Cell Fact., 18, 1–14, https://doi.org/10.1186/s12934-019-1204-z, 2019

Hofmann, K., Pauli, H., Praeg, N., Wagner, A. O., and Illmer, P.: Methane-cycling microorganisms in soils of a high-alpine altitudinal gradient, FEMS Microbiol. Ecol., 92, fiw009, https://doi.org/10.1093/femsec/fiw009, 2016

Huangfu, Y., Yuan, B., Wang, S., Wu, C., He, X., Qi, J., de Gouw, J., Warneke, C., Gilman, J. B., Wisthaler, A., Karl, T., Graus, M., Jobson, B. T., and Shao, M.:Revisiting acetonitrile as tracer of biomass burning in anthropogenic-influenced environments, Geophys. Res. Lett., 48, e2020GL092322, ~~https://doi.org/10.1029/2020GL092322~~https://doi.org/10.1029/2020GL092322, 2021

Jardine, K., Yáñez-Serrano, A. M., Williams, J., Kunert, N., Jardine, A., Taylor, T., Abrell, L., et al.: Dimethyl sulfide in the Amazon rainforest, Glob. Biogeochem. Cycles, 29, 19–32, ~~https://doi.org/10.1002/2014GB004969~~https://doi.org/10.1002/2014GB004969, 2015

Jdanova, M., and Isidorov, V.: Volatile organic compounds from leaves litter, Chemosphere, 48, 2058–2072, doi:10.1016/S0045-6535(02)00365-7, 2002.

Jenkinson, D. S., Brookes, P. C., and Powlson, D. S.: Measuring soil microbial biomass, Soil Biol. Biochem., 36, 5–7, https://doi.org/10.1016/j.soilbio.2003.10.002, 2004

Jiao, Y., Kramshøj, M., Davie-Martin, C. L., Albers, C. N., and Rinnan, R.: Soil uptake of VOCs exceeds production when VOCs are readily available, Soil Biol. Biochem., 185, 109153, https://doi.org/10.1016/j.soilbio.2023.109153, 2023

Kesselmeier, J., & Hubert, A. Exchange of reduced volatile sulfur compounds between leaf litter and the atmosphere. Atmospheric Environment, 36(29), 4679-4686. https://doi.org/10.1016/S1352-2310(02)00413-2, 2002.

Kuzma, J., Nemecek-Marshall, M., Pollock, W. H., and Fall, R.: Bacteria produce the volatile hydrocarbon isoprene, Curr. Microbiol., 30, 97–103, https://doi.org/10.1007/BF00294190, 1995

~~Lamers, L. P., Govers, L. L., Janssen, I. C., Geurts, J. J., Van der Welle, M. E., Van Katwijk, M. M., Smolders, A. J.: Sulfide as a soil phytotoxin—a review, Front. Plant Sci., 4, 268, https://doi.org/10.3389/fpls.2013.00268, 2013~~

Lange, D.F., Schröter, S.A., da Luz, F.M. et al. Cycling of dissolved organic nutrients and indications for nutrient limitations in contrasting Amazon rainforest ecosystems. Biogeochemistry 167, 1567–1588. https://doi.org/10.1007/s10533-024-01187-3, 2024.

Lee, J., Oh, Y., Lee, S. T., Seo, Y. O., Yun, J., Yang, Y., Kim, J., Zhuang, Q., and Kang, H.: Soil organic carbon is a key determinant of CH_4 sink in global forest soils, Nat. Commun., 14, 6–13, https://doi.org/10.1038/s41467-023-38905-8, 2023

Leff, J. W., and Fierer, N.: Volatile organic compound (VOC) emissions from soil and litter samples, Soil Biol. Biochem., 40, 1629–1636,https://doi.org/10.1016/j.soilbio.2008.01.018, 2008

Lehnert, A. S., Cooper, R. E., Ignatz, R., Ruecker, A., Gomes-Alves, E., Küsel, K., Pohnert, G., and Trumbore, S. E.: Dimethyl sulfide emissions from a peatland result more from organic matter degradation than sulfate reduction, J. Geophys. Res. Biogeosci., 129, e2023JG007449, https://doi.org/10.1029/2023JG007449, 2024

Li Q, Hu W, Li L, Li Y. Interactions between organic matter and Fe oxides at soil micro-interfaces: Quantification, associations, and influencing factors. Sci Total Environ. ~~2023 Jan~~ 10;855:158710. doi: 10.1016/j.scitotenv.2022.158710, 2023.

Lin, C., Owen, S. M., and Peñuelas, J.: Volatile organic compounds in the roots and rhizosphere of Pinus spp., Soil Biol. Biochem., 39, 951–960, https://doi.org/10.1016/j.soilbio.2006.11.007, 2007

Lindinger, W., Hansel, A., and Jordan, A.: On-line monitoring of volatile organic compounds at pptv levels by means of proton-transfer-reaction mass spectrometry (PTR-MS) medical applications, food control and environmental research, Int. J. Mass Spectrom. Ion Process., 173, 191–241, ~~https://doi.org/10.1016/s0168-1176(97)00281-4,~~ ~~1998~~https://doi.org/10.1016/s0168-1176(97)00281-4, 1998

Liu, M., and Matsui, H.: Secondary organic aerosol formation regulates cloud condensation nuclei in the global remote troposphere, Geophys. Res. Lett., 49, e2022GL100543,https://doi.org/10.1029/2022GL100543, 2022.

Liu, Y., Ciuraru, R., Abis, L., Amelynck, C., Buysse, P., Guenther, A., Heinesch, B., Lafouge, F., Levavasseur, F., Loubet, B., Voyard, A., and Massad, R.-S.: Emissions of biogenic volatile organic compounds from agricultural lands and the impact of land-use and other management practices: a review, EGUsphere [preprint], 1–35, https://doi.org/10.5194/egusphere-2024-530, 2024

Llusià, J., Asensio, D., Sardans, J., Filella, I., Peguero, G., Grau, O., Ogaya, R., Gargallo-Garriga, A., Verryckt, L. T., Van Langenhove, L., Brechet, L. M., Courtois, E., Stahl, C., Janssens, I. A., and Peñuelas, J.: Contrasting nitrogen and phosphorus fertilization effects on soil terpene exchanges in a tropical forest, Sci. Total Environ., 802, 149769,https://doi.org/10.1016/j.scitotenv.2021.149769, 2022

Luize, B. G., Magalhães, J. L. L., Queiroz, H., Lopes, M. A., Venticinque, E. M., de Moraes Novo, E. M. L., and Silva, T. S. F.: The tree species pool of Amazonian wetland forests: which species can assemble in periodically waterlogged habitats?, PLoS ONE, 13, e0198130, https://doi.org/10.1371/journal.pone.0198130, 2018

~~Venturini, A. M., Gontijo, J. B., Mandro, J. A., Berenguer, E., Peay, K. G., Tsai, S. M., and Bohannan, B. J. M.: Soil microbes under threat in the Amazon rainforest, Trends Ecol. Evol., 38, 693–696, https://doi.org/10.1016/j.tree.2023.04.014, 2023~~

Mäki, M., Heinonsalo, J., Hellén, H., and Bäck, J.: Contribution of understorey vegetation and soil processes to boreal forest isoprenoid exchange, Biogeosciences, 14, 1055–1073, https://doi.org/10.5194/bg-14-1055-2017, 2017

Malavolta, E., Vitti, G.C. and Oliveira, S.A. Avaliação do estadonutricional das plantas: Princípios e aplicações. [Evaluation of the Nutritional Status of Plants: Principles and Applications.] Piracicaba, Potafos, 321 pp., 1989.

Mancuso, S., Taiti, C., Bazihizina, N., Costa, C., Menesatti, P., Giagnoni, L., Arenella, M., Nannipieri, P., and Renella, G.: Soil volatile analysis by proton transfer reaction-time of flight mass spectrometry (PTR-TOF-MS), Appl. Soil Ecol., 86, 182–191, https://doi.org/10.1016/j.apsoil.2014.10.018, 2015

Mazahar, S., and Umar, S.: Soil potassium availability and role of microorganisms in

influencing potassium availability to plants, in: Role of potassium in abiotic stress, 77–87, https://doi.org/10.1007/978-981-16-4461-0_4, 2022

McGenity, T. J., Crombie, A. T., and Murrell, J. C.: Microbial cycling of isoprene, the most abundantly produced biological volatile organic compound on Earth, ISME J., 12, 931–941, https://doi.org/10.1038/s41396-018-0072-6, 2018

Miyama, T., Morishita, T., Kominami, Y., Noguchi, H., Yasuda, Y., Yoshifuji, N., Okano, M., Yamanoi, K., Mizoguchi, Y., Takanashi, S., Kitamura, K., and Matsumoto, K.: Increases in biogenic volatile organic compound concentrations observed after rains at six forest sites in non-summer periods, Atmosphere, 11, 13181, https://doi.org/10.3390/atmos11121381, 2020

Monard, C., Caudal, J. P., Cluzeau, D., Le Garrec, J. L., Hellequin, E., Hoeffner, K., Humbert, G., Jung, V., Le Lann, C., and Nicolai, A.: Short-term temporal dynamics of VOC emissions by soil systems in different biotopes, Front. Environ. Sci., 9, 650701, https://doi.org/10.3389/fenvs.2021.650701, 2021

Mosquera,Q H.; Torres-Torres, J.J.; Pérez-Abadía, D. Influence of Mining on Nutrient Cycling in the Tropical Rain Forests of the Colombian Pacific. Forests 2024, 15, 1222. https://doi.org/10.3390/f15071222

~~Mu, Z., Llusià, J., Zeng, J., Zhang, Y., Asensio, D., Yang, K., Yi, Z., Wang, X., and Peñuelas, J.: An overview of the isoprenoid emissions from tropical plant species, Front. Plant Sci., 13, 833030, https://doi.org/10.3389/fpls.2022.833030, 2022~~

Murphy, J., and Riley, J. P.: A modified single solution method for the determination of phosphate in natural waters, Anal. Chim. Acta, 27, 31–36, https://doi.org/10.1016/S0003-2670(00)88444-5, 1962

Murrell, J. C., McGenity, T. J., and Crombie, A. T.: Microbial metabolism of isoprene: a much-neglected climate-active gas, Microbiology, 166, 600–613, https://doi.org/10.1099/mic.0.000931, 2020

Ndah, F., Valolahti, H., Schollert, M., Michelsen, A., and Kivimäenpää, M.: Influence of

increased nutrient availability on biogenic volatile organic compound (BVOC) emissions and leaf anatomy of subarctic dwarf shrubs under climate warming and increased cloudiness, Ann. Bot., 129, 443–455, doi:10.1093/aob/mcac004, 2022.

Oliveira-Filho, A. T., Dexter, K. G., Pennington, R. T., Simon, M. F., Bueno, M. L., and Neves, D. M.: On the floristic identity of Amazonian vegetation types, Biotropica, 53, 767–777, https://doi.org/10.1093/aob/mcac004, 2021https://doi.org/10.1093/aob/mcac004, 2021

Onwuka, B.: Effects of soil temperature on some soil properties and plant growth, Adv. Plants Agric. Res., 8, 34–37, https://doi.org/10.15406/apar.2018.08.00288, 2018

Olsen, S.R. and Sommers, L.E. Phosphorus. In: Page, A.L., Ed., Methods of Soil Analysis Part 2 Chemical and Microbiological Properties, American Society of Agronomy, Soil Science Society of America, Madison, 403-430, 1982.

Package, T. olsrr: tools for building OLS regression models, R package version 0.5.3, cran.r-project.org, 2024.

Peñuelas, J., and Staudt, M.: BVOCs and global change, Trends Plant Sci., 15, 133–144, https://doi.org/10.1016/j.tplants.2009.12.005, 2010

Peñuelas, J., Asensio, D., Tholl, D., Wenke, K., Rosenkranz, M., Piechulla, B., and Schnitzler, J. P.: Biogenic volatile emissions from the soil, Plant Cell Environ., 37, 1866–1891, https://doi.org/10.1111/pce.12340, 2014.

Pohlman, J. W., Casso, M., Magen, C., and Bergeron, E.: Discrete Sample Introduction Module for Quantitative and Isotopic Analysis of Methane and Other Gases by Cavity Ring-Down Spectroscopy, Environ. Sci. Technol., 55, 12066–12074, https://doi.org/10.1021/acs.est.1c01386 , 2021.

Pugliese, G., Ingrisch, J., Meredith, L. K., Pfannerstill, E. Y., Klüpfel, T., Meeran, K., Byron, J., Purser, G., Gil-Loaiza, J., van Haren, J., Dontsova, K., Kreuzwieser, J., Ladd, S. N., Werner, C., and Williams, J.: Effects of drought and recovery on soil volatile organic compound fluxes in an experimental rainforest, Nat. Commun., 14, 40661, https://doi.org/10.1038/s41467-023-40661-8, 2023

Pulido, P., Perello, C., and Rodriguez-Concepcion, M.: New insights into plant isoprenoid metabolism, Mol. Plant, 5, 964–967, ~~https://doi.org/10.1093/mp/sss088,~~ ~~2012~~https://doi.org/10.1093/mp/sss088, 2012

Quesada, C. A., Lloyd, J., Anderson, L. O., Fyllas, N. M., Schwarz, M., and Czimczik, C. I.: Soils of Amazonia with particular reference to the RAINFOR sites, Biogeosciences, 8, 1415–1440, https://doi.org/10.5194/bg-8-1415-2011, 2011

Quesada, C. A., Lloyd, J., Schwarz, M., Baker, T. R., Phillips, O. L., Patiño, S., Czimczik, C., Hodnett, M. G., Herrera, R., Arneth, A., Lloyd, G., Malhi, Y., Dezzeo, N., Luizão, F. J., Santos, A. J. B., Schmerler, J., Arroyo, L., Silveira, M., Priante Filho, N., and Ramírez, H.: Regional and large-scale patterns in Amazon forest structure and function are mediated by variations in soil physical and chemical properties, Biogeosciences Discuss., 6, 3993–4057, https://doi.org/10.5194/bgd-6-3993-2009, 2009

~~Quesada, C. A., Lloyd, J., Anderson, L. O., Fyllas, N. M., Schwarz, M., and Czimczik, C. I.: Soils of Amazonia with particular reference to the RAINFOR sites, Biogeosciences, 8, 1415–1440, https://doi.org/10.5194/bg-8-1415-2011, 2011~~

Quesada, C. A., Phillips, O. L., Schwarz, M., Czimczik, C. I., Baker, T. R., Patiño, S., Fyllas, N. M., Hodnett, M. G., Herrera, R., Almeida, S., Alvarez Dávila, E., Arneth, A., Arroyo, L., Chao, K. J., Dezzeo, N., Erwin, T., Di Fiore, A., Higuchi, N., Honorio Coronado, E., and Lloyd, J.: Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate, Biogeosciences, 9, 2203–2246, https://doi.org/10.5194/bg-9-2203-2012, ~~2012~~.

Raio, A., Brilli, F., Baraldi, R., Neri, L., & Puopolo, G. Impact of spontaneous mutations on physiological traits and biocontrol activity of Pseudomonas chlororaphis M71. Microbiological Research, 239, 126517. https://doi.org/10.1016/j.micres.2020.126517,2020.

Rasheed, M. U., Kivimäenpää, M., and Kasurinen, A.: Emissions of biogenic volatile organic compounds (BVOCs) from the rhizosphere of Scots pine (Pinus sylvestris) seedlings exposed to warming, moderate N addition and bark herbivory by large pine weevil (Hylobius abietis),

Plant Soil, 463, 379–394, https://doi.org/10.1007/s11104-021-04888-y, 2021

Raza, W., Mei, X., Wei, Z., Ling, N., Yuan, J., Wang, J., Huang, Q., and Shen, Q.: Profiling of soil volatile organic compounds after long-term application of inorganic, organic and organic-inorganic mixed fertilizers and their effect on plant growth, Sci. Total Environ., 607–608, 326–338, https://doi.org/10.1016/j.scitotenv.2017.07.023, 2017

~~Ringsdorf, A., Edtbauer, A., Holanda, B., Poehlker, C., Sá, M. O., Araújo, A., Kesselmeier, J., Lelieveld, J., and Williams, J.: Investigating carbonyl compounds above the Amazon rainforest using PTR-ToF-MS with NO+ chemical ionization, EGUsphere [preprint], https://doi.org/10.5194/egusphere-2024-1210, 2024~~

~~Rinnan, R., Gierth, D., Bilde, M., Rosenørn, T., and Michelsen, A.: Off-season biogenic volatile organic compound emissions from heath mesocosms: responses to vegetation cutting, Front. Microbiol., 4, 224, https://doi.org/10.3389/fmicb.2013.00224, 2013~~

~~Rodrigues, P. M. S., Schaefer, C. E. G. R., De Oliveira Silva, J., Ferreira, W. G., Dos Santos, R. M., and Neri, A. V.: The influence of soil on vegetation structure and plant diversity in different tropical savannic and forest habitats, J. Plant Ecol., 11, 226–236, https://doi.org/10.1093/jpe/rtw135, 2018~~

~~Rosace, M. C., Veronesi, F., Briggs, S., Cardenas, L. M., and Jeffery, S.: Legacy effects override soil properties for CO_2 and N_2O but not CH_4 emissions following digestate application to soil, GCB Bioenergy, 12, 445–457, https://doi.org/10.1111/gcbb.12688, 2020~~

Rossetti, D. F., Moulatlet, G. M., Tuomisto, H., Gribel, R., Toledo, P. M., Valeriano, M. M., Ruokolainen, K., Cohen, M. C. L., Cordeiro, C. L. O., Rennó, C. D., Coelho, L. S., and Ferreira, C. A. C.: White sand vegetation in an Amazonian lowland under the perspective of a young geological history, An. Acad. Bras. Cienc., 91, e20181337, https://doi.org/10.1590/0001-3765201920181337, 2019

~~Sanhueza, E., Holzinger, R., Kleiss, B., Donoso, L., and Crutzen, P. J.: New insights in the global cycle of acetonitrile: release from the ocean and dry deposition in the tropical savanna of Venezuela, Atmos. Chem. Phys., 4, 275–280, https://doi.org/10.5194/acp-4-275-2004, 2004~~

Saggar, S., Jha, N., Deslippe, J., Bolan, N., Luo, J., Giltrap, D., Kim, D., Zaman, M., & Tillman, R. Denitrification and N2O:N2 production in temperate grasslands: Processes, measurements, modelling and mitigating negative impacts. Science of The Total Environment, 465, 173-195. https://doi.org/10.1016/j.scitotenv.2012.11.050, 2013.

Saunier, A., Mpamah, P., Biasi, C., and Blande, J. D.: Microorganisms in the phylloplane modulate the BVOC emissions of Brassica nigra leaves, Plant Signal. Behav., 15, 1728468, https://doi.org/10.1080/15592324.2020.1728468, 2020

~~Schade, G. W., and Goldstein, A. H.: Fluxes of oxygenated volatile organic compounds from a ponderosa pine plantation, J. Geophys. Res. Atmos., 106, 3111–3123, https://doi.org/10.1029/2000JD900592, 2001~~

Schindler, T., Mander, Ü., Machacova, K., Espenberg, M., Krasnov, D., Escuer-Gatius, J., Veber, G., Pärn, J., and Soosaar, K.: Short-term flooding increases CH_4 and N_2O emissions from trees in a riparian forest soil-stem continuum, Sci. Rep., 10, 60058, https://doi.org/10.1038/s41598-020-60058-7, 2020

~~Shah, A., Huang, J., Han, T., Khan, M. N., Tadesse, K. A., Daba, N. A., Khan, S., Ullah, S., Sardar, M. F., Fahad, S., and Zhang, H.: Impact of soil moisture regimes on greenhouse gas emissions, soil microbial biomass, and enzymatic activity in long-term fertilized paddy soil, Environ. Sci. Eur., 36, 943, https://doi.org/10.1186/s12302-024-00943-4, 2024~~

~~Sharkey, T. D., and Monson, R. K.: Isoprene research – 60 years later, the biology is still enigmatic, Plant Cell Environ., 40, 1671–1678, https://doi.org/10.1111/pce.12930, 2017~~

Sillo, F., Neri, L., Calvo, A., Zampieri, E., Petruzzelli, G., Ferraris, I., Delledonne, M., Zaldei, A., Gioli, B., Baraldi, R., and Balestrini, R.: Correlation between microbial communities and volatile organic compounds in an urban soil provides clues on soil quality towards sustainability of city flowerbeds, Heliyon, 10, e23594, https://doi.org/10.1016/j.heliyon.2023.e23594, 2024.

Simon, C., Pimentel, T. P., Monteiro, M. T. F., Candido, L. A., Gastmans, D., Geilmann, H., ... & Gleixner, G.: Molecular links between whitesand ecosystems and blackwater formation in the Rio Negro watershed. Geochimica et Cosmochimica Acta, 311, 274-291.

https://doi.org/10.1016/j.gca.2021.06.036, 2021

~~Steeghs, M., Bais, H. P., de Gouw, J., Goldan, P., Kuster, W., Northway, M., Fall, R., and Vivanco, J. M.: Proton-transfer-reaction mass spectrometry as a new tool for real time analysis of root-secreted volatile organic compounds in Arabidopsis, Plant Physiol., 135, 47–58, https://doi.org/10.1104/pp.104.038703, 2004~~

Sindelarova, K., Granier, C., Bouarar, I., Guenther, A., Tilmes, S., Stavrakou, T., Müller, J.-F., Kuhn, U., Stefani, P., and Knorr, W.: Global data set of biogenic VOC emissions calculated by the MEGAN model over the last 30 years, Atmos. Chem. Phys., 414, ~~275–280~~9317–9341, https://doi.org/10.5194/acp-14-9317-2014, 2014.

Snyder, C. S., Bruulsema, T. W., Jensen, T. L., and Fixen, P. E.: Review of greenhouse gas emissions from crop production systems and fertilizer management effects, Agric. Ecosyst. Environ., 133, 247–266,https://doi.org/10.1016/j.agee.2009.04.021 , 2009.

Stotzky, G., Schenck, S., and Papavizas, G. C.: Volatile organic compounds and microorganisms, Crit. Rev. Microbiol., 4, 333–382, https://doi.org/10.3109/10408417609102303, 1976

~~Stropp, J., Van der Sleen, P., Assunção, P. A., Silva, A. L., and ter Steege, H.: Tree communities of white-sand and terra-firme forests of the upper Rio Negro, Acta Amazon., 41, 521–544, https://doi.org/10.1590/s0044-59672011000400010, 2011~~

~~Svendsen, S. H., Lindwall, F., Michelsen, A., and Rinnan, R.: Biogenic volatile organic compound emissions along a high arctic soil moisture gradient, Sci. Total Environ., 573, 131–138, https://doi.org/10.1016/j.scitotenv.2016.08.100, 2016~~

~~Souza, J. J. L. L., Fontes, M. P. F., Gilkes, R., Costa, L. M., and Oliveira, T. S.: Geochemical signature of Amazon tropical rainforest soils, Rev. Bras. Cienc. Solo, 42, e0170192, https://doi.org/10.1590/18069657rbcs20170192, 2018~~

Tang, J., Schurgers, G., and Rinnan, R.: Process understanding of soil BVOC fluxes in natural ecosystems: a review, Rev. Geophys., 57, 966–986, https://doi.org/10.1029/2018RG000634, 2019

~~Targhetta, N., Kesselmeier, J., and Wittmann, F.: Effects of the hydroedaphic gradient on tree species composition and aboveground wood biomass of oligotrophic forest ecosystems in the central Amazon basin, Folia Geobot., 50, 185–205, https://doi.org/10.1007/s12224-015-9225-9, 2015~~

ter Steege, H., Pitman, N. C. A., Sabatier, D., Baraloto, C., Salomão, R. P., Guevara, J. E., Phillips, O. L., Castilho, C. V., Magnusson, W. E., Molino, J. F., Monteagudo, A., Vargas, P. N., Montero, J. C., Feldpausch, T. R., Coronado, E. N. H., Killeen, T. J., Mostacedo, B., Vasquez, R., Assis, R. L., and Silman, M. R.: Hyperdominance in the Amazonian tree flora, Science, 342, 1243092, https://doi.org/10.1126/science.1243092, 2013

Thulasiram, H. V., Erickson, H. K., and Poulter, C. D.: Chimeras of two isoprenoid synthases catalyze all four coupling reactions in isoprenoid biosynthesis, Science, 316, 73–76, https://doi.org/10.1126/science.1137786, 2007

Tripathi, N., Krumm, B. E., Edtbauer, A., Spracklen, D. V., and Kanzow, T.: Impacts of convection, chemistry, and forest clearing on biogenic volatile organic compounds over the Amazon, Nat. Commun., 16, 4692,https://doi.org/10.1038/s41467-025-59953-2 , 2025.

Trowbridge, A. M., Stoy, P. C., and Phillips, R. P.: Soil biogenic volatile organic compound flux in a mixed hardwood forest: net uptake at warmer temperatures and the importance of mycorrhizal associations, J. Geophys. Res. Biogeosci., 125, e2019JG005479, https://doi.org/10.1029/2019JG005479, 2020

van Asperen, H., Warneke, T., Carioca de Araújo, A., Forsberg, B., José Filgueiras Ferreira, S., Röckmann, T., van der Veen, C., Bulthuis, S., Ramos de Oliveira, L., de Lima Xavier, T., da Mata, J., de Oliveira Sá, M., Ricardo Teixeira, P., Andrews de França e Silva, J., Trumbore, S., and Notholt, J.: The emission of CO from tropical rainforest soils, Biogeosciences, 21, 3183–3199, https://doi.org/10.5194/bg-21-3183-2024, 2024.

van Asperen, H., Warneke, T., Carioca de Araújo, A., Rider Forsberg, B., Ramos de Oliveira, L., de Lima Xavier, T., de Oliveira Sá, M., Ricardo Teixeira, P., Azevedo de Oliveira, R., Sousa de Moura, V., do Socorro Monteiro Leal, L., Botia, S., Lavrič, J., Komiya, S., Frumau, A., Hensen, A., van den Bulk, P., van Dinther, D., and Notholt, J.: Tropical forest CH4: from

flux chambers to micrometeorological tower measurements, EGU General Assembly 2020, Online, 4–8 May 2020, EGU2020-6139, https://doi.org/10.5194/egusphere-egu2020-6139, 2020.

~~Van Den Pol-van Dasselaar, A., Van Beusichem, M. L., and Oenema, O.: Effects of soil moisture content and temperature on methane uptake by grasslands on sandy soils, Plant Soil, 204, 213–222, https://doi.org/10.1023/A:1004371309361, 1998~~

~~Vermeuel, M. P., Novak, G. A., Kilgour, D. B., Claflin, M. S., Lerner, B. M., Trowbridge, A. M., Thom, J., Cleary, P. A., Desai, A. R., and Bertram, T. H.: Observations of biogenic volatile organic compounds over a mixed temperate forest during the summer to autumn transition~~Vella, R., Forrest, M., Pozzer, A., Tsimpidi, A. P., Hickler, T., Lelieveld, J., and Tost, H.: Influence of land cover change on atmospheric organic gases, aerosols, and radiative effects, Atmos. Chem. Phys., ~~23~~25, ~~4123–4148~~243–262, https://doi.org/10.5194/acp-~~23-4123~~25-243-202~~3~~5, 202~~3~~5.

~~Viros, J., Santonja, M., Temime-Roussel, B., Wortham, H., Fernandez, C., and Ormeño, E.: Volatilome of Aleppo pine litter over decomposition process, Ecol. Evol., 11, 6862–6880, https://doi.org/10.1002/ece3.7533, 2021~~

~~Vlasenko, A., MacDonald, A. M., Sjostedt, S. J., and Abbatt, J. P. D.: Formaldehyde measurements by proton transfer reaction–mass spectrometry (PTR-MS): correction for humidity effects, Atmos. Meas. Tech., 3, 1055–1062,https://doi.org/10.5194/amt-3-1055-2010, 2010~~

~~Yáñez-Serrano, A. M., Filella, I., Llusià, J., Gargallo-Garriga, A., Granda, V., Bourtsoukidis, E., Peñuelas, J., et al.: GLOVOCS-master compound assignment guide for proton transfer reaction mass spectrometry users, Atmos. Environ., 244, 117929, https://doi.org/10.1016/j.atmosenv.2020.117929, 2021~~

~~Wachiye, S., Merbold, L., Vesala, T., Rinne, J., Räsänen, M., Leitner, S., and Pellikka, P.: Soil greenhouse gas emissions under different land-use types in savanna ecosystems of Kenya, Biogeosciences, 17, 2149–2167, https://doi.org/10.5194/bg-17-2149-2020, 2020~~

Venturini, A. M., Gontijo, J. B., Mandro, J. A., Berenguer, E., Peay, K. G., Tsai, S. M., and

Bohannan, B. J. M.: Soil microbes under threat in the Amazon rainforest, Trends Ecol. Evol., 38, 693–696, https://doi.org/10.1016/j.tree.2023.04.014, 2023

Wang, H., Liu, X., Wu, C., and Lin, G.: Regional to global distributions, trends, and drivers of biogenic volatile organic compound emission from 2001 to 2020, Atmos. Chem. Phys., 24, 3309–3328, https://doi.org/10.5194/acp-24-3309-2024, 2024.

Wang, M., Zheng, Q., Shen, Q., and Guo, S.: The critical role of potassium in plant stress response, Int. J. Mol. Sci., 14, 7370–7390, https://doi.org/10.3390/ijms14047370, 2013.

~~Warneke, C., Karl, T., Judmaier, H., Hansel, A., Jordan, A., Lindinger, W., and Crutzen, P. J.: Acetone, methanol, and other partially oxidized volatile organic emissions from dead plant matter by abiological processes: significance for atmospheric HO(X) chemistry, Glob. Biogeochem. Cycles, 13, 9–17, https://doi.org/10.1029/98GB02428, 1999~~

Warneke, C., Veres, P., Murphy, S. M., Soltis, J., Field, R. A., Graus, M. G., Koss, A., Li, S. M., Li, R., Yuan, B., Roberts, J. M., and de Gouw, J. A.:

PTR-QMS versus PTR-TOF comparison in a region with oil and natural gas extraction industry in the Uintah Basin in 2013, Atmos. Meas. Tech., 8, 411–420, https://doi.org/10.5194/amt-8-411-~~2015~~2015, 2015.

Wells, K. C., Millet, D. B., Payne, V. H., Vigouroux, C., Aquino, C. A. B., De Mazière, M., de Gouw, J. A., Graus, M., Kurosu, T., Warneke, C., and Wisthaler, A.: Next-generation isoprene measurements from space: detecting daily variability at high resolution, J. Geophys. Res. Atmos., 127, e2021JD036181, https://doi.org/10.1029/2021JD036181, 2022

~~Williams, J., Pöschl, U., Crutzen, P. J., Hansel, A., Holzinger, R., Warneke, C., Lindinger, W., and Lelieveld, J.: An atmospheric chemistry interpretation of mass scans obtained from a proton transfer mass spectrometer flown over the tropical rainforest of Surinam, J. Atmos. Chem., 38, 133–166, https://doi.org/10.1023/A:1006322701523200l, 2001.~~

~~Zanchi, F. B., Waterloo, M. J., Tapia, A. P., Alvarado Barrientos, M. S., Bolson, M. A., Luizão, F. J., Manzi, A. O., and Dolman, A. J.: Igapó (black-water flooded forests) of the Amazon Basin, in: The Amazon: Limnology and landscape ecology of a mighty tropical river~~

~~and its basin, edited by: Sioli, H., Springer, Cham, 59–66, https://doi.org/10.1007/978-3-319-90122-0_7, 2018.~~

Yáñez-Serrano, A. M., Nölscher, A. C., Bourtsoukidis, E., Gomes Alves, E., Ganzeveld, L., Bonn, B., Wolff, S., Sa, M., Yamasoe, M., Williams, J., Andreae, M. O., and Kesselmeier, J.: Monoterpene chemical speciation in a tropical rainforest:variation with season, height, and time of dayat the Amazon Tall Tower Observatory (ATTO), Atmos. Chem. Phys., 18, 3403–3418, https://doi.org/10.5194/acp-18-3403-2018, 2018.

Yáñez-Serrano, A. M., Bourtsoukidis, E., Alves, E. G., Bauwens, M., Stavrakou, T., Llusià, J., Filella, I., Guenther, A., Williams, J., Artaxo, P., Sindelarova, K., Doubalova, J., Kesselmeier, J., & Peñuelas, J. Amazonian biogenic volatile organic compounds under global change. Global Change Biology, 26(9), 4722-4751. https://doi.org/10.1111/gcb.15185, 2020.

Yáñez-Serrano, A. M., Filella, I., Llusià, J., Gargallo-Garriga, A., Granda, V., Bourtsoukidis, E., Peñuelas, J., et al.: GLOVOCS-master compound assignment guide for proton transfer reaction mass spectrometry users, Atmos. Environ., 244, 117929, https://doi.org/10.1016/j.atmosenv.2020.117929, 2021

Zannoni, N., Leppla, D., Lembo Silveira de Assis, P. I., et al.: Surprising chiral composition changes over the Amazon rainforest with height, time and season, Commun. Earth Environ., 1, 4, https://doi.org/10.1038/s43247-020-0007-9, 2020

Zannoni, N., Wikelski, M., Gagliardo, A., et al.: Identifying volatile organic compounds used for olfactory navigation by homing pigeons, Sci. Rep., 10, 15879, https://doi.org/10.1038/s41598-020-72525-2, 2020.

~~Zhang, B., Jia, Y., Bai, G., Han, H., Yang, W., Xie, W., and Li, L.: Characterizing BVOC emissions of common plant species in northern China using real world measurements: towards strategic species selection to minimize ozone forming potential of urban greening, Urban For. Urban Green., 96, 128341, https://doi.org/10.1016/j.ufug.2024.128341, 2024~~