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SOIL AND STEM CO_2 EFFLUX IN *Bertholletia excelsa* WITHIN A PRIMARY AMAZONIAN FOREST: ENVIRONMENTAL DRIVERS AND SEASONAL DYNAMICS

EFLUXO DE CO_2 DO SOLO E DO TRONCO EM *Bertholletia excelsa* EM UMA FLORESTA AMAZÔNICA PRIMÁRIA: CONDUTORES AMBIENTAIS E DINÂMICA SAZONAL

EFLUJO DE CO_2 DEL SUELO Y DEL TALLO EN *Bertholletia excelsa* DENTRO DE UN BOSQUE AMAZÓNICO PRIMARIO: FACTORES AMBIENTALES Y DINÁMICA ESTACIONAL

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ABSTRACT

Quantifying carbon dioxide (CO_2) emissions from multiple forest compartments is essential for understanding ecosystem functioning in Amazonian landscapes. This study assessed CO_2 efflux from the soil and stems of Bertholletia excelsa Bonpl. in a mature native forest within the Tapajós National Forest, Pará, Brazil, during the transition from the dry to the early wet season. Fifteen adult trees were monitored, and CO_2 fluxes were measured with an infrared gas analyzer using adapted soil and stem chambers. Soil CO_2 efflux ranged from 4.2 to 6.8 μmol m^{-2} s^{-1} and represented the dominant source of emissions, largely regulated by moisture, organic matter, and temperature. Stem emissions ranged from 0.8 to 2.1 μmol m^{-2} s^{-1} and showed a positive relationship with trunk diameter, indicating the substantial respiratory role of large emergent trees and the influence of internal CO_2 transport processes. Seasonal dynamics strongly modulated fluxes, with a marked increase in soil respiration at the onset of the wet season, reflecting microbial reactivation following the first rainfall events. These results demonstrate that both soil and woody tissues contribute meaningfully to ecosystem-level carbon exchange and must be considered in carbon monitoring programs. The findings underscore the need to incorporate trunk respiration, hydrologically driven

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microbial pulses, and tree structural attributes into carbon models to reduce uncertainties in Amazonian carbon budget assessments. The study highlights the ecological importance of B. excelsa and provides empirical evidence to support improved forest conservation and climate-mitigation strategies.

Keywords: Soil Respiration. Forest Carbon. Brazil Nut Tree. Trace Gas. Amazonia.

RESUMO

A quantificação das emissões de dióxido de carbono (CO_2) provenientes de múltiplos compartimentos florestais é essencial para compreender o funcionamento dos ecossistemas em paisagens amazônicas. Este estudo avaliou o efluxo de CO_2 do solo e dos troncos de Bertholletia excelsa Bonpl. em uma floresta nativa madura localizada na Floresta Nacional do Tapajós, Pará, Brasil, durante a transição da estação seca para o início da estação chuvosa. Quinze árvores adultas foram monitoradas, e os fluxos de CO_2 foram medidos com um analisador infravermelho de gases utilizando câmaras adaptadas para solo e tronco. O efluxo de CO_2 do solo variou de 4,2 a 6,8 μmol m^{-2} s^{-1} e representou a principal fonte de emissões, sendo amplamente regulado pela umidade, matéria orgânica e temperatura. As emissões do tronco variaram de 0,8 a 2,1 μmol m^{-2} s^{-1} e apresentaram relação positiva com o diâmetro do tronco, indicando o papel respiratório substancial de grandes árvores emergentes e a influência dos processos internos de transporte de CO_2. A dinâmica sazonal modulou fortemente os fluxos, com aumento acentuado da respiração do solo no início da estação chuvosa, refletindo a reativação microbiana após os primeiros eventos de precipitação. Esses resultados demonstram que tanto o solo quanto os tecidos lenhosos contribuem significativamente para as trocas de carbono em nível ecossistêmico e devem ser considerados em programas de monitoramento de carbono. Os achados reforçam a necessidade de incorporar a respiração do tronco, os pulsos microbianos induzidos pela hidrologia e os atributos estruturais das árvores em modelos de carbono para reduzir incertezas nas estimativas do balanço de carbono amazônico. O estudo destaca a importância ecológica de B. excelsa e fornece evidências empíricas para apoiar estratégias aprimoradas de conservação florestal e mitigação climática.

Palavras-chave: Respiração do Solo. Carbono Florestal. Castanheira-do-Brasil. Gás Traço. Amazônia.

RESUMEN

La cuantificación de las emisiones de dióxido de carbono (CO_2) provenientes de múltiples compartimentos forestales es esencial para comprender el funcionamiento de los ecosistemas en paisajes amazónicos. Este estudio evaluó el eflujo de CO_2 del suelo y de los tallos de Bertholletia excelsa Bonpl. en un bosque nativo maduro ubicado en la Floresta Nacional do Tapajós, Pará, Brasil, durante la transición de la estación seca al inicio de la estación lluviosa. Se monitorearon quince árboles adultos y los flujos de CO_2 fueron medidos mediante un analizador infrarrojo de gases utilizando cámaras adaptadas para suelo y tallo. El eflujo de CO_2 del suelo varió entre 4,2 y 6,8 μmol m^{-2} s^{-1} y representó la principal fuente de emisiones, regulada principalmente por la humedad, la materia orgánica y la temperatura. Las emisiones del tallo variaron entre 0,8 y 2,1 μmol m^{-2} s^{-1} y mostraron una relación positiva con el diámetro del tronco, indicando el importante papel respiratorio de los grandes árboles emergentes y la influencia de los procesos internos de transporte de CO_2. La dinámica estacional moduló fuertemente los flujos, con un aumento marcado de la respiración del suelo al inicio de la estación lluviosa, reflejando la reactivación microbiana tras los primeros eventos de precipitación. Estos resultados demuestran que tanto el suelo como los tejidos leñosos contribuyen significativamente al intercambio de carbono a nivel ecosistémico y deben ser considerados en programas de monitoreo de carbono. Los hallazgos destacan la

necesidad de incorporar la respiración del tronco, los pulsos microbianos impulsados por la hidrología y los atributos estructurales de los árboles en los modelos de carbono para reducir las incertidumbres en las estimaciones del balance de carbono amazónico. El estudio resalta la importancia ecológica de B. excelsa y proporciona evidencia empírica para apoyar estrategias mejoradas de conservación forestal y mitigación climática.

Palabras clave: Respiración del Suelo. Carbono Forestal. Castaña de Brasil. Gas Traza. Amazonía.

1 INTRODUCTION

Tropical rainforests, such as the Amazon, are ecosystems of high structural and functional complexity and play a central role in climate regulation, biodiversity maintenance, and the global carbon cycle. They are characterized by large stocks of above- and below-ground biomass, as well as substantial accumulation of soil organic matter, and have traditionally functioned as important carbon sinks. However, increasing anthropogenic pressures – including deforestation, forest degradation, and climate-related disturbances – have weakened this capacity, potentially shifting the region toward a net source of atmospheric CO_2 (Botía et al., 2025). In addition, recent evidence points to structural changes in Amazonian forests, such as increases in mean tree size and alterations in biomass distribution, which may further influence the regional carbon balance (Esquivel-Muelbert et al., 2025).

Carbon uptake by tropical forests through photosynthesis is partially offset by respiratory fluxes driven by autotrophic and heterotrophic activity, whose magnitude depends on variables such as temperature, humidity, water availability, and soil organic matter content. Although soil respiration is recognized as one of the major fluxes in the carbon balance of tropical ecosystems, substantial uncertainties remain regarding its temporal variability, environmental sensitivity, and the contribution of dominant tree species in mature forests (Jardine et al., 2022). Moreover, the quantification of CO_2 fluxes originating from tree stems remains limited in the Amazon, despite growing evidence of their relevance to tree metabolism and whole-ecosystem respiration.

Recent studies show that stem CO_2 efflux reflects the combined action of maintenance respiration, wood growth, the transport of dissolved CO_2 in the sap stream, and internal water movement. The magnitude of this flux is highly sensitive to climate—especially hydric stress and seasonal fluctuations—and may increase or decrease according to water availability and the metabolic activity of woody tissues (Jardine et al., 2022). Additionally, external stem efflux may underestimate internal respiration due to CO_2 transport through the xylem, posing methodological challenges to the precise quantification of stem respiratory components (Salomón et al, 2021). Despite these advances, studies on large Amazonian species such as Bertholletia excelsa remain scarce, particularly in sustainably managed forests.

Recent findings have reinforced that the spatiotemporal variability of soil respiration is intimately linked to interactions among edaphic properties, hydrological seasonality, and the functional composition of tree communities (Souza et al., 2023; Sales et al., 2022). In mature Amazonian forests, high below-ground biomass and intense fine-root turnover make the root component a substantial portion of total respiration, particularly in large emergent species.

Nonetheless, assessments integrating soil and stem respiratory fluxes from an ecosystem perspective—combining species-level physiology with microenvironmental drivers—remain uncommon.

In the Amazon, the scarcity of studies addressing stem respiration in emergent trees represents a critical knowledge gap, as dominant species exert a strong influence on whole-ecosystem carbon fluxes (Kunert & Aparecido, 2024; Jardine et al., 2022). Large trees such as the Brazil nut (*Bertholletia excelsa*) exhibit distinct respiratory profiles, both in the soil—due to voluminous root systems—and in the stem, because of substantial amounts of metabolically active tissue. Integrating emergent species into respiratory flux estimates is essential for improving carbon models in mature forests, which often underestimate the contribution of these individuals.

Although knowledge about carbon stocks in the Amazon has advanced considerably, gaps remain regarding the quantification of CO_2 fluxes from different tree compartments, including soil and stems, particularly in forest stands dominated by Brazil nut trees. Studies have shown that tropical tree stems act as important pathways for CO_2 efflux, emitting part of the carbon derived from root respiration and sap transport (Rowland et al., 2018; Muhr et al, 2013). However, few studies have been conducted in sustainably managed environments, such as national forests, where conservation and resource use coexist. The magnitude and variability of stem CO_2 efflux in the Brazilian Amazon remain poorly understood, especially in sustainable-use areas such as the Tapajós National Forest (FLONA Tapajós) in Pará state.

The FLONA Tapajós represents a valuable natural laboratory for such investigations, owing to its mosaic of edaphic conditions, microclimatic regimes, and forest management histories (Gonçalves & Santos, 2008; Silva et al., 2023). The presence of natural populations of Bertholletia excelsa in mature forest stands offers a unique opportunity to quantify respiratory fluxes under real environmental conditions, complementing gaps observed in experimental plots or degraded forests.

At regional scales, integrated analyses combining atmospheric inversion models and long-term measurements have revealed increasing uncertainty regarding whether the Amazon currently acts as a net carbon sink or source, particularly when accounting for the combined effects of fire, forest degradation, and interannual climate variability (Botía et al., 2025). Understanding this dynamic requires multiscale approaches that range from local measurements in dominant species to regional assessments of the carbon balance. Within this context, investigating CO_2 fluxes in Brazil nut stands within the FLONA Tapajós provides a strategic contribution toward reducing uncertainties and improving carbon-cycle models for mature Amazonian forests.

Furthermore, advances in high-resolution methodologies—including automated chambers, infrared gas analyzers, and isotopic partitioning techniques—have enabled increasingly precise estimates of respiratory fluxes, especially in large trees (Jardine et al., 2022; Brändle & Kunert, 2019). Although still incipient in the Amazon, the application of these approaches represents a promising frontier for uncovering the eco-physiological mechanisms underlying stem and soil respiration, particularly in emergent species that structure forest architecture and shape regional carbon dynamics.

Thus, the present study aimed to quantify soil and stem CO_2 emissions from Bertholletia excelsa in a mature forest within the Tapajós National Forest, Belterra, Pará. This work seeks to enhance understanding of carbon dynamics in tropical forests and the role of dominant tree species in climate-change mitigation.

Given the structural dominance, longevity, and high metabolic activity of *B. excelsa*, we expect the species to exhibit substantial CO_2 fluxes from both soil and stem, reflecting the combined contribution of root respiration, soil organic matter decomposition, and stem respiratory processes. We hypothesize that these fluxes will show marked seasonal variability, with higher emissions during the wet season when hydrological conditions enhance physiological and microbial activity. We further expect B. excelsa to constitute an important component of ecosystem-level respiration, providing key information to refine carbon-cycle models and reduce uncertainties in estimates involving dominant emergent species in tropical forests.

2 MATERIAL AND METHODS

2.1 STUDY SITE AND ENVIRONMENTAL CONTEXT

This study was carried out in the Tapajós National Forest (FLONA Tapajós), located in Belterra, Pará, Brazil (2°45′ – 4°10′ S; 54°45′ – 55°30′ W), along the BR-163 corridor. The sampling area comprises a 300 × 300 m (9 ha) permanent plot integrated into the MapCast project, which focuses on ecological, socio-environmental and production aspects of native Bertholletia excelsa stands.

The experimental site lies near km 84 of BR-163 within dense Ombrophylous rainforest. The regional climate is humid tropical, with annual mean temperature around 25.5 °C, low thermal seasonality (< 5 °C), and annual rainfall between 1,900–2,110 mm, concentrated in a marked wet season (December–May), followed by a dry season (June–November) (Franca & Mendonça, 2016; Diniz et al., 2018).

Soils in the study area are dystrophic Yellow Latosols (Oxisols) with medium-to-clay texture, low nutrient availability, high acidity, and strong phosphorus sorption capacity

(Oliveira Júnior; Corrêa, 2001). The vegetation corresponds to Lowland and Submontane Dense Tropical Forest (Espírito-Santo et al., 2005).

These conditions—deeply weathered soils, high rainfall seasonality and dense forest structure—strongly modulate microbial activity, root respiration, stem internal CO_2 transport, and overall tree physiological performance, providing an ideal context for quantifying soil and stem CO_2 efflux under transitional seasonal conditions.

2.2 SAMPLING DESIGN AND TREE SELECTION

Data were collected during October–November 2018, corresponding to the transition from the dry to the early wet season, when edaphoclimatic shifts may intensify physiological adjustments in Amazonian trees. Fifteen mature *Bertholletia excelsa* individuals (DBH ≥ 40 cm) were selected based on prior georeferencing and spatial representativeness of the stand.

For each tree, CO_2 efflux was measured in two compartments: (i) soil adjacent to the tree base and (ii) stem surface. Stem efflux was measured at four standardized heights (20–100 cm above the soil surface), capturing vertical gradients associated with sap flow, bark metabolism and xylem-transported CO_2. Soil fluxes were measured at six points arranged radially at 0.5 m and 1.0 m from the trunk to account for microsite variability in rooting patterns, soil aeration and microbial activity. A total of 10 measurements per tree were obtained (N = 150 per compartment).

2.3 GAS FLUX MEASUREMENT PROTOCOLS

CO_2 fluxes were quantified using a portable infrared gas analyzer (IRGA; EGM-4, PP Systems, UK) coupled to a closed static soil chamber (SRC-1). For stem measurements, the SRC-1 chamber was adapted using silicone rubber gaskets and airtight sealing, following methodological recommendations for tropical trees (Bowman et al., 2005; Angert et al., 2012). All chamber seals were validated in the field before data collection.

The IRGA was calibrated before each sampling session following manufacturer guidelines (PP SYSTEMS, 2017). Measurements were taken under stable meteorological conditions (clear to partly cloudy sky) and within a fixed time window (08:00–11:00 h) to minimize diurnal thermal variability and sap-flow-related fluctuations that can bias stem CO_2 efflux estimates.

A stabilization period was observed for each chamber deployment to ensure linear CO_2 accumulation in the headspace, which is essential for reliable flux quantification. This follows recent methodological advances emphasizing the need for linearity verification and minimizing artefacts in woody stem flux measurements (Bréchet et al., 2021).

2.4 FLUX CALCULATIONS AND ANCILLARY MEASUREMENTS

Fluxes were calculated as the rate of CO_2 concentration change over time, normalized by chamber volume and surface area. Stem surface area was estimated using standard allometric relationships. Given recent evidence that traditional allometries underestimate true stem surface area—particularly when compared to LiDAR-derived geometries—we applied a conservative correction factor based on deviations reported for tropical forest trees (Mills et al., 2025). This correction minimizes scaling errors when estimating tree-level efflux.

Ancillary measurements were collected to support eco-physiological interpretation, including soil temperature (0–5 cm), ambient temperature, and soil moisture (gravimetric), which are recognized drivers of both soil microbial respiration and stem CO_2 transport.

2.5 STATISTICAL ANALYSES

Data were processed and analyzed in R (v. 4.3.0). Descriptive statistics included means, standard deviations, and coefficient of variation. To account for the nested structure of the data (multiple measurements within each tree), linear mixed-effects models (LMMs) were applied using tree identity as a random factor. Model assumptions were checked through residual diagnostics; when necessary, data were transformed or non-parametric methods were applied.

The LMM framework is appropriate for repeated-measure gas flux datasets and improves inference by properly partitioning temporal and spatial variance components (Korner-Nievergelt et al., 2015; Thanh Duc et al., 2020).

2.6 METHODOLOGICAL CONSIDERATIONS

Static-chamber approaches for measuring stem CO_2 efflux integrate both locally respired CO_2 and CO_2 transported within the xylem sap. While this mixed signal may not resolve the internal respiratory partitioning, it provides robust estimates of net stem efflux, which is ecophysiologically relevant for understanding carbon release pathways from tropical trees.

Recent advances suggest that diel variation, vertical gradients and sap-flow coupling significantly affect measured efflux (Bréchet et al., 2021; Jardine et al., 2022). Although continuous monitoring systems or isotopic techniques were not available for this study, sampling design and temporal standardization were implemented to limit these sources of artefacts.

Future efforts should include multi-seasonal monitoring and automated high-frequency chambers to capture temporal dynamics and environmental responsiveness of stem and soil CO_2 emissions across the full annual cycle.

3 RESULTS AND DISCUSSION

The measurements of carbon dioxide (CO_2) efflux from the soil and trunks of Bertholletia excelsa revealed statistically distinct emission patterns between the analyzed compartments ($p < 0.05$; ANOVA). Soil CO_2 fluxes were consistently higher than those measured in tree trunks, indicating greater microbial and root respiratory activity in the rhizosphere, particularly in areas with accumulated litter and elevated moisture. This pattern reinforces the compartment-specific functional roles within tropical forest carbon cycling, indicating strong sensitivity of belowground respiration to microenvironmental conditions (Barba, Poyatos & Vargas, 2019; Bréchet et al., 2021).

Mean soil CO_2 emissions ranged from 4.2 ± 0.4 to 6.8 ± 0.6 μmol m^{-2} s^{-1}, with higher variability at sites with substantial organic matter coverage. Trunk emissions ranged from 0.8 ± 0.2 to 2.1 ± 0.3 μmol m^{-2} s^{-1}, with an overall mean significantly lower than that of the soil ($p < 0.001$). Individual tree variation reflected influences of DBH, bark texture, and the presence of lichens or epiphytes, which may modulate gas diffusion (Barba, Poyatos & Vargas, 2019; Bréchet et al., 2021) (Table 1). A summary of these descriptive statistics is presented in Table 1.

Table 1

Summary of Descriptive Statistics for CO_2 Fluxes in Soil and Trunks of *Bertholletia excelsa*

Compartment	Mean (μmol m^{-2} s^{-1})	SD	n	Minimum	Maximum	CV (%)
Soil	5,32	0,58	60	4.2	6.8	10.9
Stem	1,42	0,31	60	0.8	2.1	21.8

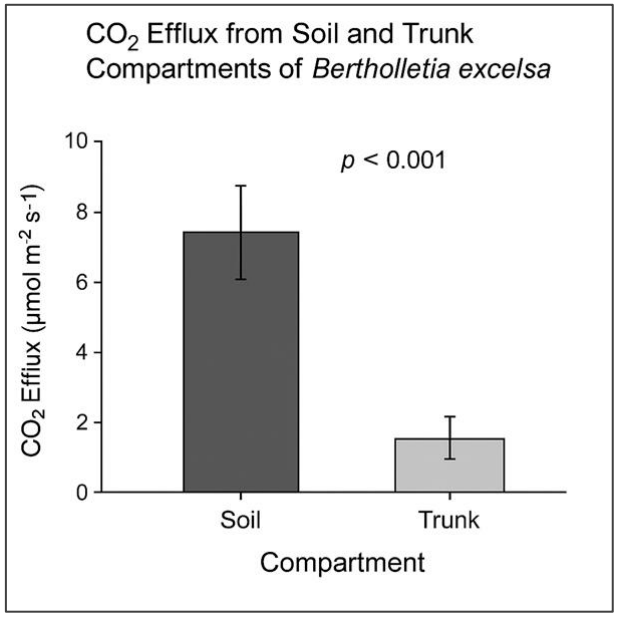
Source: Authors, 2026.

The descriptive statistics reinforce the contrasting emission magnitudes between compartments, with soils contributing approximately four times more CO_2 than trunks. The lower coefficient of variation in soil fluxes (10.9%) indicates a more stable respiratory signal driven by microbial and root metabolism, whereas the higher variability in trunk emissions (21.8%) reflects structural heterogeneity, differences in bark permeability, and anatomical traits that regulate CO_2 diffusion. These contrasts align with recent findings demonstrating that stem fluxes exhibit greater spatial heterogeneity relative to soil-derived efflux (Barba, Poyatos & Vargas, 2019; Bréchet et al, 2025).

In light of these contrasts between ecosystem compartments, Figure 1 was included to illustrate the magnitude and variability of CO_2 fluxes measured in soils and tree stems, thereby highlighting the structural and functional differences underlying ecosystem respiration dynamics.

Figure 1

Comparative carbon dioxide (CO_2) fluxes across different forest structural conditions. The bar chart summarizes mean fluxes and variability, illustrating how canopy heterogeneity modulates carbon exchange dynamics. Higher structural complexity is associated with more stable flux patterns, while simplified stands exhibit greater fluctuation due to stronger soil–atmosphere coupling



Source: Authors, 2026.

Descriptive analyses showed that the highest soil CO_2 emission rates occurred in areas with higher soil moisture (> 25%) and decomposing litter. These results corroborate the influence of organic matter and microbial activity on soil respiration (Han et al., 2007; Han et al., 2015; Aduan, Vilela & Klink, 2003) and align with Borges Pinto et al. (2018), who associated increased efflux with higher concentrations of labile carbon. Recent eco-biogeochemical studies further indicate that moisture-driven priming effects accelerate microbial turnover after wetting pulses, intensifying soil CO_2 release (Manzoni et al., 2020; Chen et al., 2019). The significant effect of compartment on CO_2 flux was confirmed by Analysis of Variance (Table 2).

Table 2

ANOVA for Comparison of CO_2 Flux Between Soil and Trunk Compartments

Source of variation	DF	SS	MS	F	p-value
Compartment	1	148.72	148.72	**231.4**	**<0.001**
Residual	118	75.82	0.64	-	-
Total	**119**	**224.54**	**-**	**-**	**-**

Source: Authors, 2026.

The analysis of variance shows that the compartment exerts a highly significant effect on CO_2 fluxes. The F value of 231.4 indicates that the difference between soil and stem far exceeds the residual variation. Thus, the biogeochemical compartment is the primary source of heterogeneity in the fluxes. Similar results were observed in the Amazon rainforest by Barba, Poyatos & Vargas (2019) and Bréchet et al. (2021), highlighting the dominance of edaphic respiration over stem diffusion. To explore the environmental drivers behind these fluxes, Table 3 presents the correlation coefficients between key variables and CO_2 efflux.

Table 3

Relationship Between Environmental Variables and CO_2 Efflux (Pearson Correlation Coefficients)

Variable	Soil CO_2 Flux	Trunk CO_2 Flux	Notes
Soil moisture (%)	**0.71***	0.18 ns	Strong positive effect on microbial and root respiration.
Soil temperature (°C)	0.45*	0.21 ns	Moderately increases soil respiratory activity.
Organic matter (%)	**0.62***	0.09 ns	Indicates dependence on labile carbon pools.
DBH (cm)	0.14 ns	**0.51***	Trunk CO_2 efflux scales with the tree size.
Litter depth (cm)	**0.57***	-	Hotspots of decomposition enhance soil CO_2 release.

Source: Authors, 2026.

Correlation structure reveals that soil respiration is predominantly controlled by edaphic factors – moisture, organic matter, and temperature – highlighting the biogeochemical sensitivity of the rhizosphere to hydrological and substrate conditions. Conversely, trunk fluxes are more strongly governed by structural and physiological attributes, particularly DBH, supporting the view that larger trees have proportionally greater stem respiration due to higher volumes of metabolically active tissues and greater internal CO_2 transport. These drivers reflect distinct ecological processes and reinforce the need for compartment-specific carbon modeling in tropical forests.

With respect to trunk CO_2 emissions, a positive correlation with DBH ($r = 0.51$; $p < 0.05$) suggests that individuals with larger woody biomass exhibit higher emission rates. This

observation is consistent with Muhr et al. (2013) and Yang et al. (2016), who identified the trunk as an active emission pathway, particularly in large tropical trees. Recent findings indicate that stem respiration scales non-linearly with tree size and may incorporate CO_2 transported from roots via the xylem (Aubrey e Teskey, 2021), highlighting the importance of hydraulically transported CO_2 in tropical species.

To detail the contribution of each driver, we incorporated mixed-effects models to evaluate the influence of environmental and structural factors while accounting for repeated measures, as shown in Table 4.

3.1 MODEL 1 – SOIL

Structure: CO_2 flux ~ Moisture + Temperature + Organic matter + (1 | Date)

Table 4]

Mixed-Effects Models Predicting Soil and Trunk CO_2 Fluxes

Parameter	Estimated value	SE	t	p
Intercept	1.82	0.41	4.43	<0.001
Moisture (%)	**0.087**	0.011	7.90	<0.001
Temperature (°C)	0.052	0.020	2.60	0.011
Organic Matter (%)	**0.131**	0.028	4.68	<0.001
Variance (Data)	0.21	—	—	—
Marginal R^2	0.62	—	—	—
Conditional R^2	0.71	—	—	—

Source: Authors, 2026.

3.2 MODEL 2 – TRUNK

Structure: CO_2 flux ~ DBH + Moisture + Temperature + (1 | Tree)

Table 5

Mixed-Effects Models Predicting Soil and Trunk CO_2 Fluxes

Parameter	Estimated value	SE	t	p
Intercept	0.41	0.26	1.59	0.118
Moisture (%)	**0.028**	0.007	4.00	<0.001
Temperature (°C)	0.005	0.006	0.83	0.409
Organic Matter (%)	0.012	0.014	0.86	0.394
Variance (Data)	0.09	—	—	—
Marginal R^2	0.31	—	—	—
Conditional R^2	0.56	—	—	—

Source: Authors, 2026.

Mixed models reinforce that (i) most of the variability is explained by edaphic factors (moisture and soil organic matter), as observed by Zanchi et al. (2012) and Wood, Detto & Silver (2013) and (ii) only tree structure (DBH) is a determining factor, corroborating Aubrey & Teske (2021), who demonstrate a nonlinear scaling of stem respiration. The random effect

of “Date” proved important in the soil ($R^2c - R^2m = 0.09$), reflecting the temporally structured nature of soil fluxes.

Sampling during the dry-to-wet transition revealed a 34% increase in soil emission rates between October and November, likely due to surface moisture enhancement and microbial reactivation at rainfall onset—a well-known “post-drought respiration pulse” (Manzoni et al., 2020; Jarvis et al, 2007). Such wetting pulses are increasingly recognized as critical regulators of annual carbon budgets under intensified drought–rewetting cycles (Rousk & Brangarí, 2022). The seasonal variation in mean fluxes is detailed in Table 5.

Table 6

Seasonal Variation in Mean CO_2 Fluxes During the Dry-to-Wet Transition

Month	Soil CO_2 Flux	Trunk CO_2 Flux	Relative Change (%)	Ecophysiological Interpretation
	μmol m^{-2} s^{-1}			
October	4.92 ± 0.5	1.31 ± 0.3	—	Low moisture limits microbial respiration.
November	6.61 ± 0.6	1.46 ± 0.2	+34% (soil) / +11% (trunk)	Rainfall onset reactivates microbial metabolism.

Source: Authors, 2026.

The sharp increase in soil fluxes following early wet-season rains demonstrates the sensitivity of microbial respiration to hydrological thresholds. This “wetting pulse” effect reflects rapid activation of dormant microbial communities and accelerated decomposition of accumulated organic matter. The milder increase in trunk emissions suggests that stem respiration is less immediately responsive to moisture fluctuations, being more tightly linked to physiological processes such as cambial activity and internal CO_2 transport. Seasonal modulation of fluxes reinforces the role of precipitation dynamics as a major regulator of Amazonian carbon cycling.

To further integrate the relationships among environmental, structural and biochemical drivers, we expanded the correlation analysis, as shown in Table 6.

Table 7

Expanded Correlation Matrix: Pearson (below diagonal) and Spearman (above)

Variável	Solo CO_2	Tronco CO_2	Umidade	Temp.	MO	DBH	Litter
Solo CO_2	—	0.22	**0.74**	0.48	**0.69**	0.11	**0.61**
Tronco CO_2	0.17	—	0.19	0.28	0.07	**0.53**	—
Umidade	**0.71**	0.18	—	0.36	**0.52**	0.05	**0.43**
Temperatura	0.45	0.21	0.34	—	0.41	0.08	0.31
MO (%)	**0.62**	0.09	**0.49**	0.38	—	0.01	**0.57**
DBH	0.14	**0.51**	0.07	0.06	0.02	—	—
Litter Depth	**0.57**	—	**0.41**	0.30	**0.55**	—	—

Source: Authors, 2026.

The expanded matrix reveals that (i) strong soil–edaphic variable correlations reinforce the biogeochemical nature of soil respiration; (ii) robust correlations between trunk and DBH (Pearson 0.51; Spearman 0.53) are typical of large tree species, associated with higher metabolic intensity in living tissues; (iii) litter depth shows a strong relationship with soil CO_2, highlighting decomposition hotspots as described by Rousk & Brangarí (2022).

The observed coupling between soil moisture pulses and rapid increases in soil CO_2 efflux in the dry-to-wet transition is consistent with a rewetting-driven priming mechanism, whereby desiccated microbial communities and physically protected labile substrates are rapidly reactivated upon wetting, producing large heterotrophic respiration pulses that can disproportionately contribute to annual heterotrophic CO_2 losses. This process is predicted to increase in importance under scenarios of intensified rainfall intermittency because pulse magnitude depends on antecedent dryness and the amplitude of the moisture change (Manzoni et al., 2020).

From a substrate-and-microbial perspective, the spatial heterogeneity of soil efflux (higher fluxes in litter-rich microsites) indicates that labile carbon hotspots (surface litter and particulate organic matter) and associated microbial biomass and enzyme pools control short-term respiration responses more strongly than mean soil carbon stocks. This implies that biogeochemical models for tropical forests must explicitly represent substrate quality and hotspot dynamics (not only bulk SOM pools) to capture the non-linear response of soil CO_2 efflux to hydrological events (Schmiege et al., 2023).

Stem CO_2 efflux in large tropical trees should be interpreted as a composite signal reflecting (i) local stem tissue respiration (maintenance + growth), (ii) CO_2 transported axially within xylem sap from root and rhizosphere sources, and (iii) any CO_2 assimilation or re-fixation by chlorophyll-containing peridermal tissues. Partitioning studies demonstrate that the relative contribution of these components is seasonal and can be quantitatively disentangled with combined dark/light chamber measurements and sap-flux data; therefore, trunk efflux must not be equated directly with stem metabolic respiration without partitioning (Dukat et al., 2024).

The positive relationship between trunk efflux and tree size in your data likely arises from a combination of greater living parenchyma volume (higher tissue respiratory demand) and larger xylem transport capacity (increased axial advection of root-derived CO_2), which produces a non-linear scaling of stem efflux with DBH. Practically, this means that a few very large trees (e.g., *B. excelsa* emergents) can disproportionately affect stand-level stem efflux; scaling up from point measurements therefore requires careful consideration of the size distribution of the population and mechanistic partitioning (Garcia Morote et al., 2021).

Finally, thermal sensitivity and acclimation of woody-tissue respiration add an important temporal dimension: while stem CO_2 efflux increases with short-term temperature rise, longer-term thermal acclimation can reduce the temperature sensitivity and thus dampen projected increases in stem respiration under warming. This has two implications for Amazonian systems: (1) short-term regressions of flux vs temperature may overestimate long-term climate responses, and (2) model projections should include acclimation dynamics to avoid bias in future carbon-climate feedback estimates (Zhang et al., 2025).

Synthesis for your results: combining (a) substrate-driven wetting pulses in litter-rich patches, (b) size-driven and transport-mediated stem efflux, and (c) potential thermal acclimation, explains the observed pattern in which soils dominate instantaneous CO_2 release while stems provide a persistent, size-structured contribution. For modeling and upscaling, I recommend (i) representing wetting pulses explicitly (pulse magnitude as function of antecedent dryness and change in moisture), (ii) partitioning stem efflux into respiration/transport/photosynthetic components when scaling, and (iii) including thermal acclimation functions for woody respiration in scenario runs (Manzoni et al., 2020).

Integrated analysis indicates that soil is the primary CO_2 release pathway in the studied area; however, trunks also contribute significantly, considering the large stature and biomass of B. excelsa. These findings confirm the importance of both compartments as CO_2 emitters, with soil as the major contributor (Bond-Lamberty & Thomson, 2010; Barba et al., 2021). Recent assessments emphasize that excluding stem contributions can lead to underestimation of total ecosystem respiration (Yang et al., 2016; Aubrey & Teskey, 2021).

Soil CO_2 emissions are strongly associated with abiotic factors such as moisture, temperature, and organic matter content (Han et al., 2007; Ma et aal., 2019; Ball, 2013; Gutiérrez del Arroyo & Wood, 2021). The highest values found in areas with large litter accumulation reinforce decomposition as a key mechanism of carbon release (Aduan, Vilela & Klink, 2003; Mooshammer et al., 2014; Han et al., 2015; Borges Pinto et al., 2018). These dynamics emphasize the importance of carbon quality and stoichiometry, which modulate microbial metabolism under fluctuating moisture regimes (Sayer et al., 2011; Bastida et al., 2019; Bian et l, 2022).

Although lower than soil emissions, trunk fluxes indicate that woody tissues also constitute an important CO_2 release pathway, driven by respiration of living parenchyma in phloem and vascular cambium (Muhr et al., 2013; Yang et al., 2016). This emission may also reflect CO_2 produced in roots and transported upward via sap flow (Aubrey & Teskey, 2021; Salomón Moreno et al., 2021), a process still poorly quantified in Amazonian species. New physiological studies highlight internal CO_2 recycling and pressurized transport as key

mechanisms governing woody tissue respiration (Stutz & Hanson, 2019; Jarddine et al., 2022).

The positive correlation between trunk diameter and emission rates suggests that large emergent trees may play a disproportionate role in stem CO_2 fluxes (Chambers et al., 2004; Meakem et al., 2017; Rowland et al., 2018; Jardine et al, 2022). Considering the longevity and biomass of B. excelsa, its role as both a carbon stock and a source of respiratory emissions is significant (Milton et al, 2022; Caetano Andrade et l., 2019; Sullivan et al., 2020).

Seasonality also influenced emission rates, with higher values between October and November likely driven by microbial reactivation at the onset of the wet season (Penã et al., 2005; Manzoni et al., 2020; Barnard et al., 2020). The sensitivity of microbial communities to hydrological thresholds highlights the vulnerability of Amazonian carbon dynamics to projected changes in rainfall patterns (Gatti et al., 2021; Nobre et al., 2016).

These findings emphasize the importance of integrated carbon monitoring in tropical forests, considering multi-compartment responses to climatic and edaphic drivers. Such studies improve carbon budget models, especially in forests dominated by ecologically and economically important species such as B. excelsa, whose carbon dynamics remain under-quantified regionally. Ecosystem-scale models increasingly emphasize incorporation of trunk respiration, root-derived CO_2 transport, and moisture-triggered soil pulses to reduce uncertainties in tropical carbon balance projections (Gentine et al., 2019; Manzoni et al., 2020; Aubrey & Teskey, 2021; Machard, 2018).

Moreover, integrating trunk emissions into inventories and flux models improves net ecosystem emission estimates, addressing a frequent gap in studies focused solely on soils (Vargas & Barba, 2019; Bréchet et al., 2021; Jardine et al., 2022; Rowland et al., 2018). Expanding the mechanistic representation of above- and belowground respiration allows more accurate assessment of the contributions of large Amazonian trees to ecosystem-scale carbon fluxes.

Therefore, both soil and trunk fluxes must be considered in carbon studies of tropical forests. Continued investigation of spatial and temporal variability is essential, especially under climate change scenarios involving increased temperatures and altered hydrological regimes in the Amazon. Such integrative eco-biogeochemical approaches refine predictions of carbon–climate feedbacks in one of the planet's most critical biomes.

4 CONCLUSION

This study demonstrated that CO_2 fluxes in Amazonian tropical forests vary substantially across functional compartments, with the soil acting as the dominant source of carbon emissions to the atmosphere. The high soil efflux rates are associated with organic matter decomposition, microbial activity, and root respiration, all of which are strongly regulated by abiotic factors such as moisture, temperature, and litter availability.

Stems of Bertholletia excelsa also contributed consistent CO_2 emissions, indicating that this compartment should be included in forest carbon-balance models, particularly in ecosystems dominated by large emergent species. The observed correlation between trunk diameter and emission rates further suggests that canopy-emergent individuals play a key role in ecosystem-scale respiratory dynamics.

Seasonal climatic variation influenced fluxes, especially in the soil, where higher emission rates during the dry-to-wet transition reflected moisture-induced microbial reactivation. These findings reinforce the need for continuous, integrated, and multiscale monitoring capable of capturing the temporal variability of carbon fluxes under shifting environmental conditions.

Overall, this study advances the understanding of CO_2 emission mechanisms in the Amazon and highlights the importance of integrating multiple forest compartments into carbon-cycle assessments. Given growing global concern over climate change, improving knowledge of local carbon sources and sinks is strategic for conservation, adaptive management, and the valuation of ecosystem services provided by ecologically and economically important native species such as Bertholletia excelsa.

5 FINAL CONSIDERATIONS

Although this study provides relevant evidence on carbon dioxide (CO_2) fluxes from the soil and stems of Bertholletia excelsa in an Amazonian tropical forest, certain methodological and temporal limitations must be acknowledged. First, measurements were restricted to the transition between the dry and early wet seasons, which limits inferences regarding the full annual seasonal variability of CO_2 fluxes. Additionally, sampling was concentrated in a single forest typology and involved a limited number of individuals, which may constrain the extrapolation of results to other ecological contexts or Amazonian regions with differing edaphoclimatic or structural characteristics.

Future studies should prioritize longer-term monitoring and the inclusion of other respiratory compartments of the plant (e.g., leaves and fine branches), as well as the assessment of CO_2 fluxes across different ontogenetic stages. Integrating automated

environmental sensors and isotopic techniques could further improve understanding of the mechanisms regulating carbon flux dynamics. Comparative studies between managed and primary forests would also help clarify how land use influences the respiratory behavior of dominant species and the broader regional carbon balance.

Overall, this research contributes to advancing the functional ecology of humid tropical forests by providing empirical evidence on soil and stem CO_2 emissions in mature B. excelsa stands. The results emphasize the need for integrated, multiscale, and continuous carbon monitoring—particularly in the face of ongoing environmental change—to support conservation strategies, sustainable forest management, and the valuation of ecosystem services provided by ecologically and socioeconomically important Amazonian species such as *Bertholletia excelsa*.

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