



Quantifying canopy CO₂ storage to improve long-term estimates of net ecosystem carbon exchange in the southern Amazon forest

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Abstract.

The Amazon rainforest plays a critical role in the global carbon cycle, yet large uncertainties remain regarding its net carbon balance. Accurate estimates of net ecosystem exchange (NEE) require accounting for the CO₂ storage term, which is commonly derived from vertical CO₂ profile measurements that are scarcely available at long-term flux tower sites. Here, we evaluated three approaches for estimating canopy CO₂ storage at the Rebio Jaru forest site in Rondônia, Brazil: (1) a multi-point CO₂ profile (MPP), (2) a single-point profile (SPP) based on a closed-path gas analyzer, and (3) a single-point eddy covariance approach (SPE) using CO₂ measurements from an open-path gas analyzer. Although the methods operated simultaneously for less than two years, both simplified approaches showed strong agreement with the reference MPP method, with coefficients of determination of $R^2 = 0.87$ for SPP and $R^2 = 0.79$ for SPE, whereas neglecting the storage term resulted in poor agreement ($R^2 = 0.24$). Using the SPE approach, we reconstructed a 13-year NEE time series that revealed pronounced interannual variability, with the forest generally acting as a carbon sink during La Niña conditions and shifting toward a carbon source during El Niño events and during consecutive years due to drought legacy effects. The seasonal cycle exhibited a marked carbon source peak during the transition from the dry to the wet season, likely associated with enhanced litter decomposition and increased soil respiration following the first rainfall events after prolonged dry periods. These results demonstrate that simplified single-point approaches can reliably reconstruct long-term NEE dynamics and substantially improve estimates of Amazonian carbon balance at sites where complete CO₂ profile measurements are unavailable.

Keywords. Amazon rainforest, net ecosystem exchange, CO₂ storage flux, eddy covariance, ENSO



1 Introduction

The Amazon rainforest plays a crucial role in the global carbon cycle and is widely recognized as a key component in regulating Earth's climate. However, the combined effects of deforestation, recurrent droughts (Doughty et al., 2015; Marengo et al., 2024), and rising temperatures provide increasing evidence of a transition from a carbon sink to a carbon source (Davidson et al., 2012; Tavares et al., 2023; Flores et al., 2024; Botía et al., 2026). This transition appears particularly pronounced in southeastern Amazonia, where a net CO₂ source has already been observed (Gatti et al., 2021). In this context, Gatti et al. (2021) showed that the Amazon has become a net carbon source of 0.29 PgC yr⁻¹, driven by historical degradation in the southeastern portion of the region. Nevertheless, Botía et al. (2025) revised these estimates by applying humidity corrections to atmospheric measurements, identifying a near-neutral balance (−0.04 PgC yr⁻¹), although the regional balance remains affected by emissions from the adjacent Cerrado and Caatinga biomes. More recently, Botía et al. (2026) demonstrated that this neutrality is highly sensitive to climatic anomalies; during the 2023 El Niño event, the basin rapidly shifted to a temporary carbon source, with emissions ranging between 0.15 and 0.20 PgC, affecting even preserved areas.

A representative example of this environmental shift is the Jaru Biological Reserve (Rebio Jaru), located within the “Arc of Deforestation” (Csillik et al., 2024). This region contains large areas of fragmented and degraded forests, characterized by increasing edge effects and the progressive loss of original forest structure (Feitosa et al., 2023; Trejo et al., 2025). Subjected to intense anthropogenic pressure and highly vulnerable to drought, Rebio Jaru reflects broader processes occurring across the southern Amazon and is therefore an important site for understanding regional forest carbon balance dynamics (Chen et al., 2024).

Proper monitoring of CO₂ fluxes between the biosphere and the atmosphere is essential for determining whether a region acts as a carbon source or sink. Robust quantification of net ecosystem exchange (NEE) is one of the most effective direct approaches for assessing ecosystem carbon balance over time (Baldocchi et al., 2024). However, accurate NEE estimation requires accounting for the storage term (F_s), which represents the CO₂ accumulated in the air column beneath the flux-measurement sensors (Aubinet et al., 2012). This component becomes particularly important during periods of low atmospheric turbulence (Acevedo et al., 2009; Peltola et al., 2021). Ideally, F_s should be calculated using detailed vertical CO₂ concentration profiles measured at multiple heights, typically at least six levels, to capture the complex stratification within the canopy air space (Aubinet et al., 2012). Such multi-level instrumentation is essential for robust NEE estimates in dense vegetation, including tropical and temperate forests (Buchmann et al., 1997; Hutrya et al., 2008; Araújo et al., 2010; Paul-Limoges et al., 2017; Rodrigues et al., 2024).

Despite its importance, maintaining complete vertical CO₂ concentration profiles over long periods is often difficult at remote Amazonian sites because of major logistical constraints. These include complex maintenance requirements, frequent power supply interruptions, and rapid degradation of sensors and cables caused by high humidity and biological activity. Consequently, there is a clear need to evaluate simpler yet reliable methods for estimating the storage term that can be applied to long-term flux datasets.



Several approaches have been proposed to estimate F_s when measurements at multiple heights are unavailable. One widely used method, introduced by Hollinger et al. (1994), assumes that temporal variations in CO₂ concentration measured at a single reference height (typically from the eddy covariance gas analyzer) represent the entire air column below the sensor. Early evaluations of this approach reported relatively small errors in daily carbon balance estimates. For example, Greco and Baldocchi (1996) found that the residual error associated with this approximation averaged approximately -0.20 ± 2.32 gC m⁻² day⁻¹ over 24-hour periods, suggesting that uncertainties introduced by omitting the full vertical profile are relatively small compared with those associated with gradient systems.

Another approach involves reconstructing the vertical distribution of CO₂ by assuming a theoretical profile, such as a logarithmic function of the form $C(z) = a + b \ln(z)$, consistent with canopy micrometeorological theory (Finnigan, 2004; Aubinet et al., 2012). This allows estimation of F_s even with measurements at a limited number of heights. More recently, data-driven approaches have also been proposed to reconstruct storage fluxes when observational data are incomplete. Machine learning techniques can be used to predict F_s based on meteorological and eddy covariance variables, including CO₂ concentration measured by the eddy covariance system, air temperature, vapor pressure deficit (VPD), friction velocity (u^*), wind speed, and incoming radiation. In this approach, F_s values calculated from periods with available profile measurements are used to train regression models, which are then applied to reconstruct the storage flux during periods without vertical profile observations (Pastorello et al., 2020).

Previous studies in the Amazon have addressed the lack of multi-level CO₂ profiles by simplifying the storage term to single-point measurements or by restricting analyses to periods of strong atmospheric turbulence (von Randow et al., 2004; Cirino et al., 2014). Other studies incorporated advection components to better represent complex flow dynamics, as performed at the Cuieiras Reserve (Araújo et al., 2002) and the Tapajós National Forest (Tóta et al., 2008).

In this study, we evaluate the single-point storage estimation approach proposed by Hollinger et al. (1994), which uses CO₂ concentration measurements from a single height to estimate F_s . Previous studies comparing single-point and multi-point approaches indicate that the performance of this method depends strongly on atmospheric turbulence conditions. For example, Saito et al. (2005) reported that the single-point approach underestimated the storage term by approximately 22% under low-turbulence conditions, whereas Moureaux et al. (2008) found only a 6% overestimation under well-mixed conditions. Together, these studies suggest that simplified storage estimates can provide reliable results when atmospheric mixing is sufficiently strong.

Here, we present the first long-term (13-year) evaluation of single-point CO₂ storage estimation at an Amazon forest site and investigate its implications for NEE variability under different climatic conditions. Using long-term flux measurements collected at Rebio Jaru, we assess the performance of this approach and reconstruct the NEE time series for one of the oldest flux tower sites in Amazonia, where complete vertical CO₂ profile measurements were available only for a limited period. This reconstruction allows us to evaluate whether this portion of the southern Amazon currently behaves as a net carbon sink or source. In addition, the approach tested here can be extended to other Amazonian sites, providing a practical framework for investigating regional carbon dynamics using long-term flux observations.



Table 1. Overview of measured variables, micrometeorological sensors, gas instrumentation, and measurement heights at the tower.

Variable	Description	Instrument	Sampling rate (Hz)	Heights (m)
u, v, w, T_s	Turbulent 3D wind speed and sonic temperature	Sonic anemometer	10	63.4
c, q	CO ₂ and H ₂ O concentration	Infrared gas analyzer	10	63.4
c	CO ₂ concentration	Closed-path infrared gas analyzer	0.0167	2, 12, 22, 34, 50, 62
T_{air}	Air temperature	Thermohygrometer	0.00056	62
S_{in}	Shortwave solar radiation	Pyranometer	0.00056	52
P	Precipitation	Rain gauge	0.00056	62

85 2 Material and Methods

2.1 Site Description and Measurements

The Rebio Jaru is a fully protected conservation unit covering approximately 350,000 hectares in the state of Rondônia, Brazil. The vegetation is predominantly classified as Open Ombrophilous Forest (Culf et al., 1997) and is also characterized as semideciduous or seasonally dry forest (Costa et al., 2010). The leaf area index (LAI) exhibits a marked seasonal cycle, varying from 90 5.56 [5.44–5.69] m² m⁻² in July to 6.53 [6.26–6.74] m² m⁻² in January (Barbino et al., 2023). A 62 m tall micrometeorological tower (10.19° S, 61.87° W), part of the Large-Scale Biosphere–Atmosphere Program (LBA), has been operational at the site since 1999 (Fig. 1). The regional climate is characterized by a mean annual precipitation of approximately 2200 mm (Gomes et al., 2015; Antonucci et al., 2025). The site elevation is approximately 220 m above sea level, and the vegetation has an average canopy height of 33 m, with emergent trees reaching nearly 45 m (Rummel et al., 2002).

95 Measurements at the site have been conducted continuously since early 1999, making this one of the longest-running micrometeorological monitoring towers currently operating in the Amazon. In 2003, a temporary interruption occurred due to the relocation of the tower; however, the continuity of the CO₂ measurement series was maintained, as reported by Aguiar et al. (2012). Measurements resumed in 2004 at the current tower location. Additional data gaps occurred during subsequent periods, primarily associated with limitations in financial support and logistical constraints.

100 Fig. 2 presents the temporal evolution of the instrumentation deployed at the site between 1999 and 2020, including eddy covariance systems, CO₂ profile measurements, and supporting meteorological observations. The long-term observational program involved successive replacements of sonic anemometers and infrared gas analyzers while preserving the continuity and consistency of the atmospheric monitoring record. Eddy covariance flux measurements and CO₂ profile observations were simultaneously available only during a restricted period, from March 2008 to September 2009. Additional information 105 regarding the measured variables, sensor models, sampling rate and measurement heights is provided in Table 1 and Fig. 2.

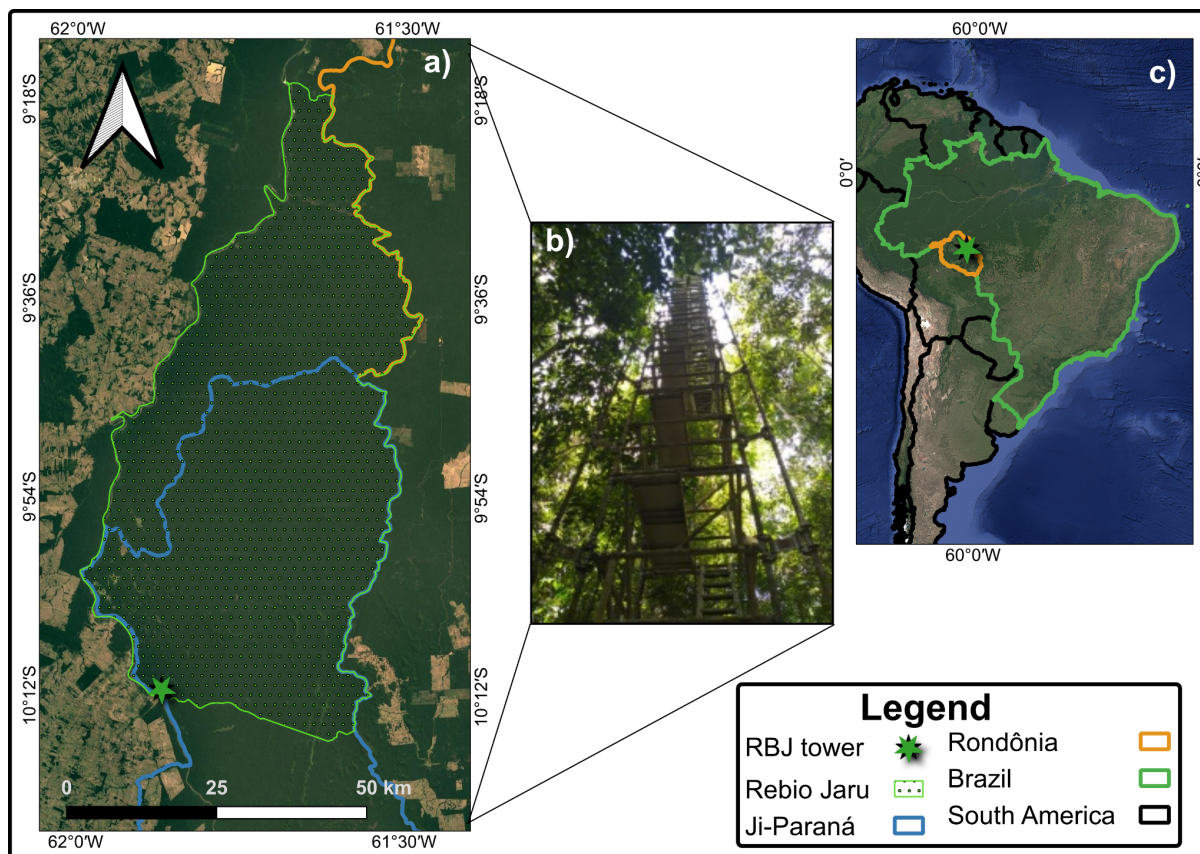


Figure 1. Location and infrastructure of the study site. (a) Spatial delimitation of the Jaru Biological Reserve (Rebio Jaru), Rondônia, Brazil; (b) view of the micrometeorological tower (LBA site); (c) geographic position of the study area in South America. The map was generated using satellite imagery from Google Earth (Google, 2026) and cartographic data from the Brazilian Institute of Geography and Statistics (IBGE, 2022).

2.2 Determination of the Net Ecosystem CO₂ Exchange

Assuming steady-state turbulent flow and horizontal surface homogeneity, net ecosystem exchange (NEE) was calculated as the sum of the turbulent CO₂ flux (F_c) and the storage flux (F_s) (Aubinet et al., 2012):

$$NEE = F_c + F_s \tag{1}$$

110 The turbulent flux was obtained from high-frequency eddy covariance measurements as:

$$F_c = \overline{w'c'} \tag{2}$$

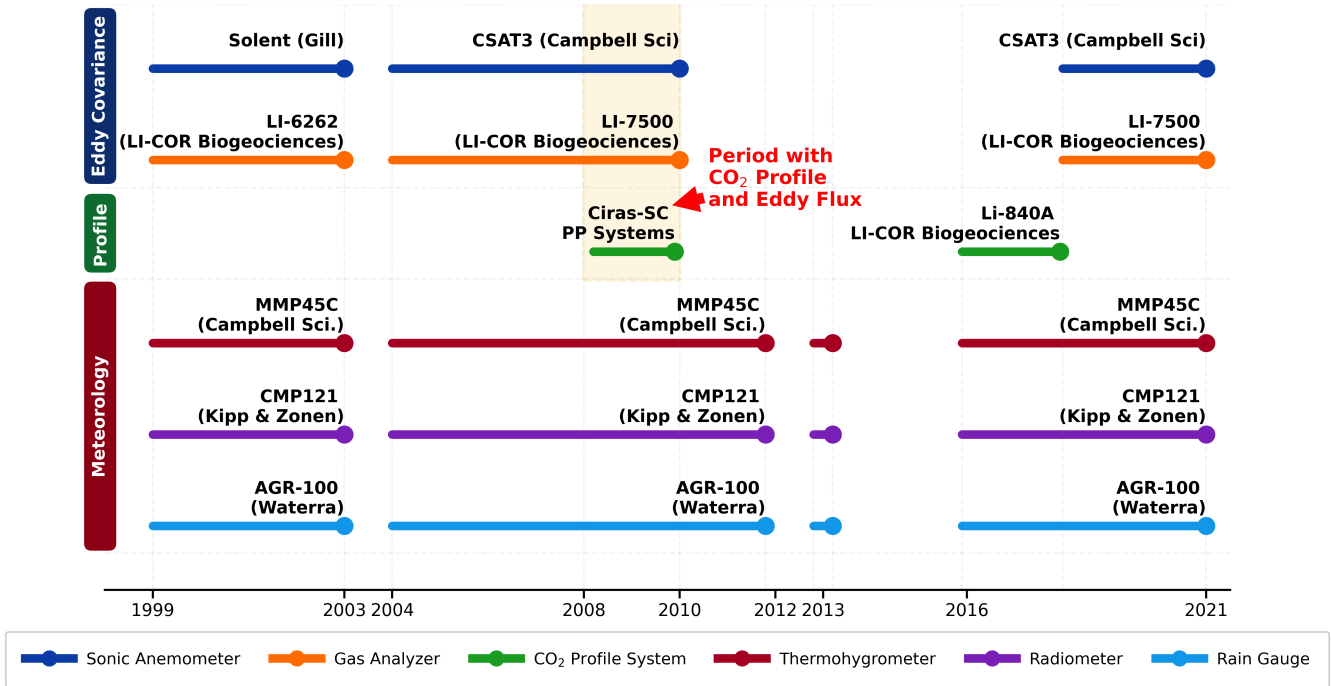


Figure 2. Models of instruments and their operational periods at the Rebio Jaru site from 1999 to 2021. The largest data gaps occurred in 2003 and between 2011 and 2015.

where w' is the fluctuation of the vertical wind velocity and c' is the fluctuation of the CO_2 concentration.

The storage flux represents the temporal change in CO_2 content within the air column between the surface and the integration height (z). Assuming constant dry air density (ρ), it can be expressed as (Baldocchi and Meyers, 1988; Aubinet et al., 2012):

$$115 \quad F_s(t) = \rho \int_0^z \frac{\partial c(z,t)}{\partial t} dz \quad (3)$$

In this study, F_s was calculated using three approaches: (i) multi-point profile (MPP), (ii) single-point profile (SPP), and (iii) single-point eddy (SPE). These approaches were derived from Eq. (3).

The MPP method uses CO_2 concentrations measured at discrete heights and can only be calculated when the complete CO_2 profile is available (z_1, z_2, \dots, z_n), requiring a numerical approximation of the vertical integral:

$$120 \quad F_s(t_i) = \rho \sum_{i=1}^n \left(\frac{c_i(t + \Delta t) - c_i(t)}{\Delta t} \right) \Delta z_i \quad (4)$$

where c_i is the CO_2 concentration at height z_i , Δt is the time interval between measurements, and Δz_i is the vertical layer thickness associated with each level.



For the SPP and SPE approaches, the CO₂ concentration was assumed to be vertically uniform between the surface and the measurement height. Applying a finite-difference approximation to Eq. (3) yields:

$$125 \quad F_s(t) \approx \rho z \frac{\partial c(t)}{\partial t} \approx \rho z \frac{c(t + \Delta t) - c(t)}{\Delta t} \quad (5)$$

Equation (5) was applied using the CO₂ concentration measured at 62 m for the SPP approach, whereas for the SPE approach the CO₂ concentration was obtained from the open-path infrared gas analyzer installed at 63.4 m.

Atmospheric turbulence intensity was characterized by the friction velocity (u^*):

$$u^* = \left[(\overline{u'w'})^2 + (\overline{v'w'})^2 \right]^{1/4} \quad (6)$$

130 where u' and v' are the fluctuations in the longitudinal and lateral wind components, respectively.

Atmospheric stability was evaluated using the dimensionless stability parameter z/L , defined according to Monin–Obukhov similarity theory as:

$$\frac{z}{L} = - \frac{\kappa g z \overline{w'\theta'_v}}{\overline{\theta_v} u^{*3}} \quad (7)$$

135 where κ is the von Kármán constant (0.4), g is the gravitational acceleration, $\overline{w'\theta'_v}$ is the kinematic virtual potential temperature flux, $\overline{\theta_v}$ is the mean virtual potential temperature, and u^* is the friction velocity. Atmospheric stability conditions were classified according to the value of z/L as: very unstable ($z/L < -3$), unstable ($-3 \leq z/L < -0.1$), neutral ($-0.1 \leq z/L \leq 0.1$), stable ($0.1 < z/L < 2$), and very stable ($z/L \geq 2$).

2.3 Processing and quality control

Eddy covariance fluxes averaged over 30-minute intervals, including CO₂ exchange, were computed using the Alteddy software 140 for the 1999–2010 period. For subsequent years, fluxes were processed using EddyPro (LI-COR, Lincoln, NE, USA). Both software packages were configured using standardized processing routines to ensure consistency and comparability throughout the long-term dataset.

The processing chain included double-axis coordinate rotation to align the coordinate system with the mean wind direction, forcing the mean vertical wind velocity component (w) to zero. Additional procedures included time-lag compensation, 145 frequency response corrections, and corrections for cross-wind effects, humidity, and sonic temperature. The Webb–Pearman–Leuning (WPL) correction was applied to account for air-density fluctuations (Aubinet et al., 2012).

F_s and NEE were calculated separately using the outputs generated by Alteddy and EddyPro. An additional quality-control routine was implemented to remove physically inconsistent values and periods affected by instrumental malfunction, including NEE spikes exceeding $\pm 50 \text{ mol m}^{-2} \text{ s}^{-1}$. Data collected during rainfall events, when water droplets obstructed the sonic 150 anemometer measurement path, were also excluded from the analysis.



To minimize the underestimation of nighttime respiration under stable atmospheric conditions, a u^* threshold was applied to filter periods with insufficient turbulence. The definition of an appropriate u^* threshold is widely recognized as one of the main sources of uncertainty in NEE estimates (Aubinet et al., 2012), particularly in Amazon forests, where strong decoupling often occurs between the air below and above the canopy (Santana et al., 2018). Miller et al. (2004) evaluated different u^* thresholds by comparing NEE derived from eddy covariance measurements with independent inventory-based estimates for a forest near Santarém, Pará, Brazil, and reported an optimal threshold of 0.2 m s^{-1} , which excluded approximately 60% of the nocturnal data.

However, applying a threshold of 0.2 m s^{-1} to the Rebio Jaru site would remove more than 90% of the nighttime observations. Therefore, a site-specific threshold corresponding to the exclusion of 60% of the nocturnal data was adopted for Rebio Jaru, resulting in a u^* threshold of 0.12 m s^{-1} . The same threshold was applied throughout the entire dataset, since the seasonal variability of u^* was relatively small, as shown in Fig. 3.

Finally, remaining gaps in the dataset were filled using a modified Marginal Distribution Sampling (MDS) approach based on temporal similarity (Reichstein et al., 2005). The algorithm reconstructed missing values using averages from observations acquired at the same half-hourly time step within moving temporal windows of ± 7 , ± 14 , and ± 30 days, requiring a minimum number of valid samples for gap filling. Long gaps exceeding 90 days were not reconstructed.

3 Results and Discussion

3.1 Characterizing meteorology

The observational record from the Rebio Jaru tower is not sufficiently long to establish a local climatological normal, which conventionally requires at least 30 years of continuous measurements. Therefore, long-term precipitation data from the municipality of Porto Velho, Rondônia, Brazil, the nearest location with an extended meteorological record, were used as a regional climatological reference. Both precipitation time series are presented in Fig. 3.

Precipitation distribution is characterized by marked seasonality, with the wet season presenting average monthly totals above 250 mm at Rebio Jaru and the dry season showing precipitation below 100 mm between May and September. The Porto Velho climatology presents slightly higher precipitation values in some months, such as January, likely associated with geographical and land-cover differences between the two regions. Nevertheless, the seasonal pattern remains consistent, reinforcing the robustness and representativeness of the rainfall regime observed at Rebio Jaru (Antonucci et al., 2025).

Shortwave radiation exhibits its lowest values during the peak the rainy season, from December to March, when persistent cloud cover limits incoming solar radiation. As rainfall decreases and cloudiness is reduced, radiation progressively increases from April onward, reaching maximum values during the dry season, particularly in July and August (approximately 225 W m^{-2}). During this period, clearer skies allow greater solar input to reach the surface, enhancing surface heating and atmospheric instability (Aguiar et al., 2012). From September onward, shortwave radiation gradually declines with the onset of the wet season and the associated increase in cloud formation and precipitation.

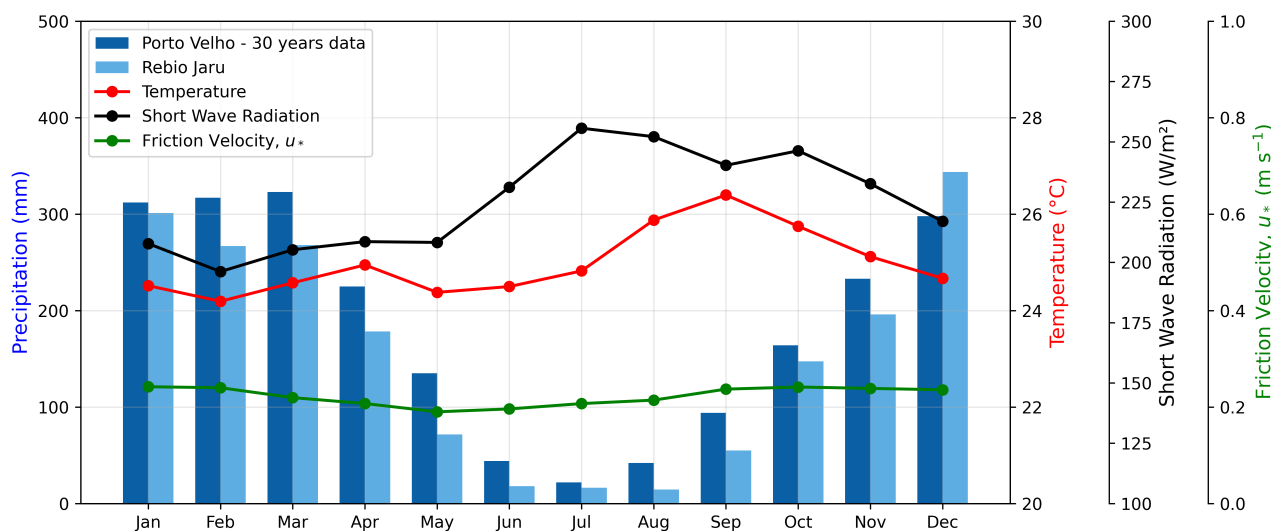


Figure 3. Monthly seasonal cycle of precipitation, air temperature, incoming shortwave radiation, and friction velocity (u_*). Light blue bars represent the monthly accumulated precipitation at Rebio Jaru (13 years of data), while dark blue bars represent the 30-year mean monthly precipitation from Porto Velho, Rondônia.

Between May and September, the region is frequently influenced by incursions of polar air masses (Garreaud, 1999; Fisch et al., 2004). These events, locally known as *friagens*, strongly affect Rebio Jaru and contribute to reductions in average air temperature to approximately 25 °C during the May–July period (Fig. 3). Such episodes typically last from two to four days and can produce sharp decreases in minimum temperature, reaching extremes of 13 °C in 2001 (de Oliveira et al., 2004) and 11 °C in 2017 (Antonucci et al., 2023).

3.2 Evaluation of the single-point CO₂ storage flux

The diurnal cycle of the F_s is strongly controlled by atmospheric stability regimes. During nighttime, ecosystem respiration combined with weak turbulence promotes CO₂ accumulation within and above the canopy, leading to progressively larger positive F_s values throughout the night, as shown in Fig. 4. Similar behavior was reported for the Tapajós National Forest in Pará, Brazil, by Hutyrá et al. (2008).

After sunrise, increasing solar radiation enhances turbulent mixing and promotes flushing events that transport CO₂-rich air from the sub-canopy to the tower top, mainly during very calm nights. As a consequence, F_s increases rapidly, frequently exceeding 30 $\mu\text{mol m}^{-2} \text{s}^{-1}$, a pattern commonly observed in forest ecosystems (Araújo et al., 2002).

Following the morning transition, photosynthetic activity intensifies and the forest begins to act as a carbon sink. Consequently, F_s becomes negative, indicating net CO₂ uptake by the ecosystem. During this period, storage fluxes can reach magnitudes close to 40 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 4).

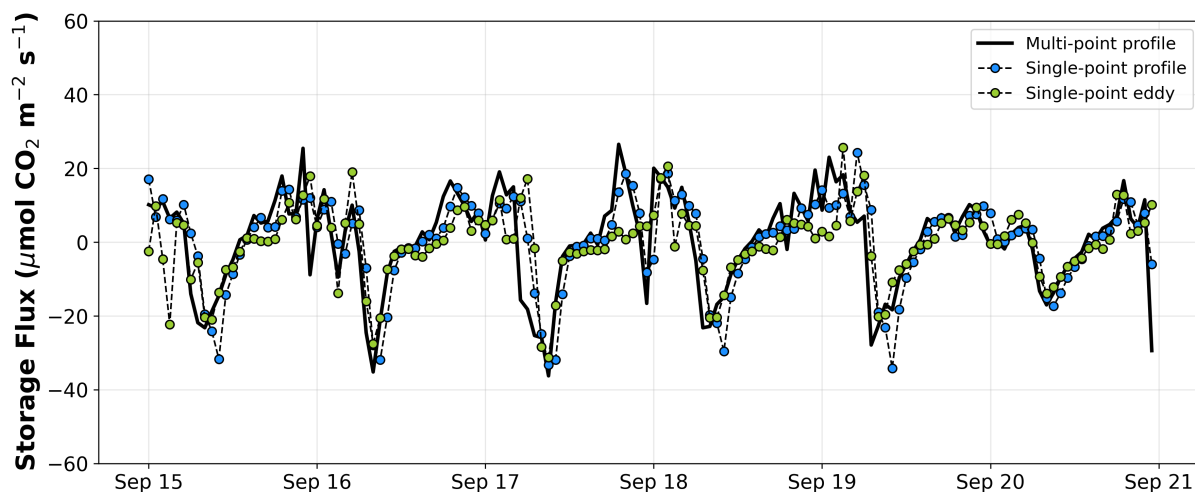


Figure 4. Example of the diurnal evolution of CO₂ storage flux (F_s) during 15–21 September 2008 at the Rebio Jaru site. Storage was calculated using the multi-point profile (MPP), single-point profile (SPP), and single-point eddy (SPE) methods.

The overall behavior shown in Fig. 4 is remarkably consistent among the three methods studied here, with all approaches capturing the same diurnal patterns, including the pronounced nocturnal accumulation and daytime depletion of CO₂. In other words, both single-point methods capture the main characteristics of the behavior exhibited by the multi-point profile (MPP) method, even though small differences occur in the instantaneous measurements between the methods.

The comparison between storage estimates using single-point profile (SPP) and single-point eddy (SPE) against MPP across stability regimes reveals a clear dependence on atmospheric stability, with generally stronger agreement under more turbulent conditions and a progressive decline in skill as stratification increases (Table 2). Both SPP and SPE show improved and more coherent relationships with MPP, particularly under very unstable, unstable, and neutral conditions, where enhanced turbulent mixing promotes stronger vertical coupling.

As atmospheric stability increases further, both methods show a clear degradation in performance, although the decline is more pronounced for SPE. In stable conditions, SPP remains relatively robust ($R^2 = 0.81$), outperforming SPE ($R^2 = 0.62$), with both methods showing comparable RMSE values and moderate biases. Under very stable conditions, performance deteriorates substantially, especially for SPE, which exhibits very low agreement with MPP ($R^2 = 0.09$) and a large bias (3.51), indicating a breakdown in its ability to capture storage variability. SPP also weakens ($R^2 = 0.37$) but retains some predictive skill and more stable error characteristics. Overall, SPP consistently shows lower RMSE and more stable behavior across regimes, while SPE is more sensitive to stability, particularly under strongly stratified conditions. These results confirm that storage estimates are most reliable under turbulent conditions and progressively deteriorate with increasing atmospheric stability.

In the very unstable regime, SPP achieves strong agreement with MPP ($R^2 = 0.85$), while SPE shows slightly lower skill ($R^2 = 0.71$) with larger RMSE values. Similarly, in unstable conditions, SPP remains robust ($R^2 = 0.83$) and exhibits the



Table 2. Statistical comparison between the multi-point profile storage method (MPP) and the two single-point approaches across atmospheric stability classes. The coefficient of determination (R^2), root mean square error (RMSE), and mean bias are shown for each comparison.

Stability class	Comparison	R^2	RMSE ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Bias ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
Very Unstable	SPP vs. MPP	0.85	5.37	2.43
Very Unstable	SPE vs. MPP	0.71	7.63	1.59
Unstable	SPP vs. MPP	0.83	4.83	4.42
Unstable	SPE vs. MPP	0.68	6.30	-0.19
Neutral	SPP vs. MPP	0.74	5.57	1.95
Neutral	SPE vs. MPP	0.65	6.04	0.74
Stable	SPP vs. MPP	0.81	5.03	2.74
Stable	SPE vs. MPP	0.62	6.92	0.07
Very Stable	SPP vs. MPP	0.37	5.49	-0.33
Very Stable	SPE vs. MPP	0.09	6.71	3.51

SPP: single-point profile method; SPE: single-point eddy covariance method; MPP: multi-point profile method.

lowest RMSE (4.83), whereas SPE shows lower explanatory power ($R^2 = 0.68$) and higher RMSE (6.30), despite a relatively small bias (-0.19). In the neutral regime, performance decreases slightly for both methods, although SPP retains stronger skill ($R^2 = 0.74$) than SPE ($R^2 = 0.65$) and maintains lower RMSE values.

Fig. 5 shows the relationship between the NEE calculated using F_s from the MPP (NEE_{MPP}) and the NEE calculated using alternative approaches for estimating F_s : (a) SPP (NEE_{SPP}); (b) SPE (NEE_{SPE}); and (c) $F_s = 0$ (i.e., $NEE = F_c$). The results reveal that the highest coefficient of determination ($R^2 = 0.87$) was observed between NEE_{MPP} and NEE_{SPP} (Fig. 5a).

Likewise, the comparison between NEE_{MPP} and NEE_{SPE} (Fig. 5b) also showed a strong correlation ($R^2 = 0.79$). These similarities indicate that the temporal variability of CO_2 storage in Rebio Jaru is largely controlled by concentration changes near the upper canopy, where measurements are available from both the profile and eddy covariance systems. This suggests that, despite vertical stratification under stable atmospheric conditions, the dominant storage signal can be captured at a representative height, allowing the single-point approach to reliably reproduce long-term carbon exchange dynamics.

This result is particularly relevant because the time series of eddy covariance in Rebio Jaru is substantially longer than the period during which CO_2 profile measurements were available (See Fig. 2). Furthermore, NEE_{SPP} is considered more reliable than NEE_{SPE} , because the latter was derived from measurements obtained with an open-path gas analyzer, which is generally more susceptible to environmental interferences such as rain, wind, and signal contamination than a closed-path system.

Conversely, the simplified approach of assuming $NEE = F_c$ yielded a substantially lower regression coefficient ($R^2 = 0.24$). This result demonstrates that neglecting the storage flux (F_s) is an inadequate approximation for dense forest sites, in

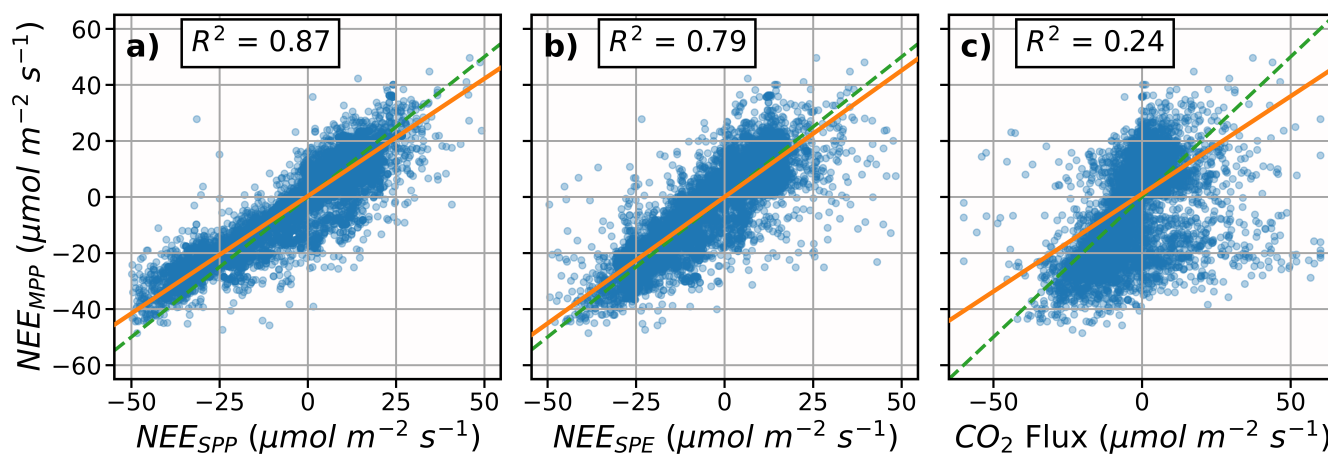


Figure 5. Relationship between the net ecosystem exchange (NEE) calculated using the storage flux (F_s) of the multi-point profile (NEE_{MPP}) and the NEE calculated using the following approaches for F_s : (a) single-point profile (NEE_{SPP}); (b) single-point eddy (NEE_{SPE}); and (c) $F_s = 0$, resulting in $NEE = F_c$. The analysis was performed using data from 2008 to 2009, when both the CO₂ profile and CO₂ flux measurements were available simultaneously. The solid line represents the linear regression fit, while the dashed line indicates the 1:1 relationship.

contrast to approaches adopted for savanna ecosystems in the Orinoco River region of the Colombian Amazon by Morales-Rincon et al. (2021). For Rebio Jaru, von Randow et al. (2004) and Cirino et al. (2014) occasionally relied on CO₂ flux measurements as a proxy for NEE when CO₂ profile observations were unavailable. Our results emphasize the critical importance of the storage estimates proposed here to minimize the underestimation of NEE in tall forests. Even when simplified proxies are applied, including a storage term provides a substantially more realistic representation of CO₂ dynamics than neglecting it entirely, while the MPP remains the most robust approach for representing ecosystem carbon exchange dynamics.

3.3 Interannual and Seasonal Variability of NEE

Since the SPE approach provided a reliable estimate of the storage term for the Rebio Jaru forest, we reconstructed the NEE time series for the entire period in which eddy covariance measurements were available. From this point onward, we assume $NEE = NEE_{SPE}$. Figure 6 presents the reconstructed time series from 1999 to 2020 as monthly accumulated values (Fig. 6b) and annual accumulated values (Fig. 6c), together with the Oceanic Niño Index (ONI; Fig. 6a).

The 1999–2000, 2000–2001, and 2007–2008 La Niña events coincided with periods during which Rebio Jaru generally acted as a carbon sink, as indicated by negative cumulative NEE values (Fig. 6b and Fig. 6c). However, despite the influence of the 2007–2008 La Niña event, the year 2008 exhibited a net carbon source behavior due to a pronounced emission peak during the late dry season, when La Niña conditions had already dissipated.

In contrast, following the 2002–2003 El Niño event, the forest frequently behaved as a carbon source and maintained this behavior during subsequent years, suggesting a possible drought legacy effect (Kannenberg et al., 2020; Wigneron et al., 2020;

Gonçalves et al., 2020). Previous studies have shown that severe droughts associated with El Niño events can produce persistent impacts on tropical forests, including enhanced tree mortality, delayed aboveground carbon recovery, and long-lasting alterations in leaf phenology and photosynthetic capacity. For example, Wigner et al. (2020) demonstrated that tropical humid forests in the Americas did not fully recover their aboveground carbon stocks after the 2015–2016 El Niño drought, indicating prolonged ecosystem responses. Similarly, Gonçalves et al. (2020) reported persistent post-drought anomalies in canopy phenology and leaf demography in Amazon forests, suggesting that drought effects on ecosystem functioning may extend for more than one year after the climatic event.

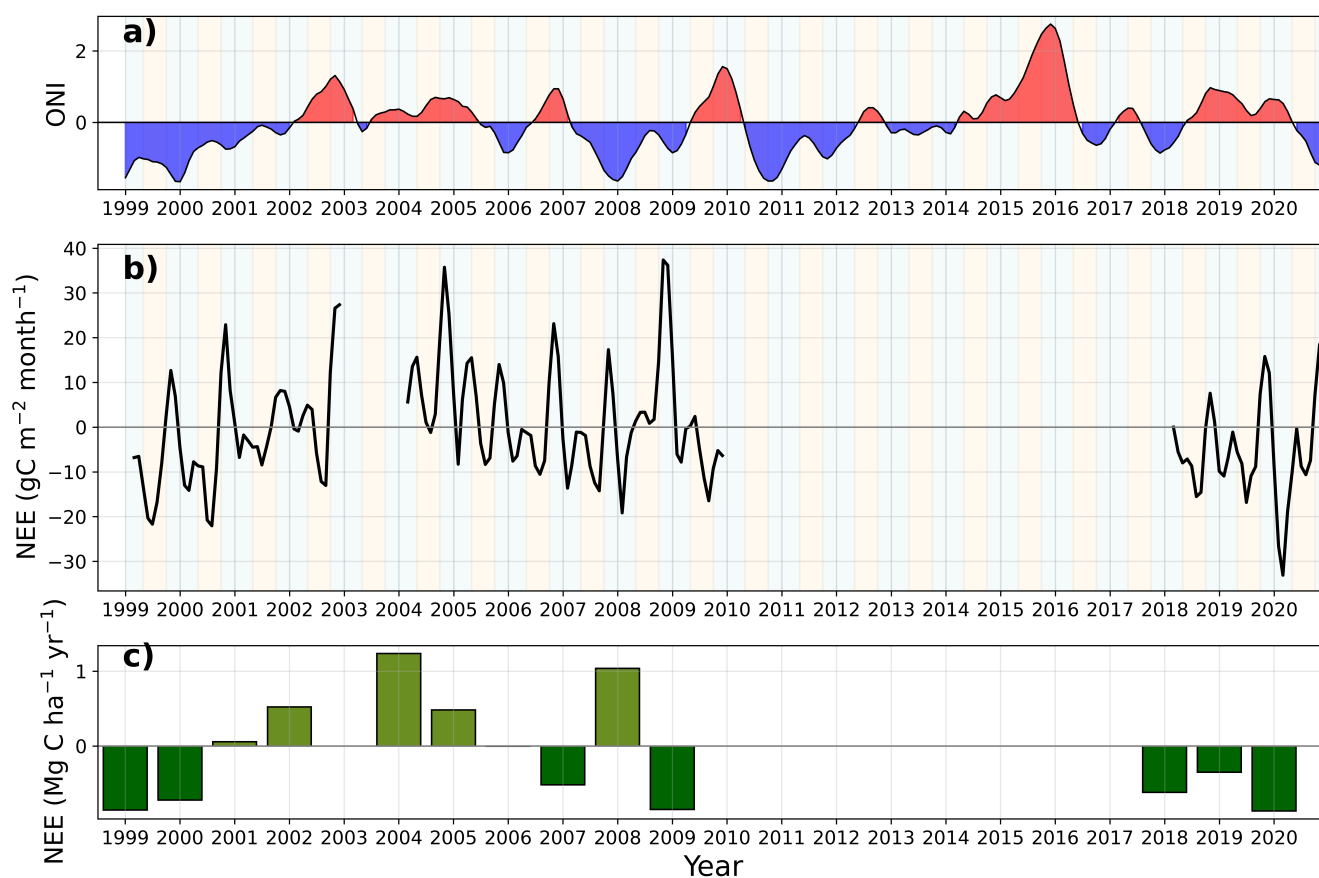


Figure 6. Time series of net ecosystem exchange (NEE) and the Oceanic Niño Index (ONI) at the Rebio Jaru site from 1999 to 2020. (a) Monthly ONI values, where positive anomalies (red) indicate El Niño conditions and negative anomalies (blue) indicate La Niña conditions. (b) Three-month running mean of monthly accumulated NEE expressed in $\text{g C m}^{-2} \text{ month}^{-1}$. (c) Annual accumulated NEE expressed in $\text{Mg C ha}^{-1} \text{ yr}^{-1}$. Negative NEE values indicate periods when the ecosystem acted as a carbon sink, while positive values indicate a carbon source. Years with insufficient or missing data (2003 and 2010–2017) were excluded from the analysis and represented as gaps in the time series.



260 Taken together, the results shown in Fig. 6 suggest that El Niño events weaken the ecosystem carbon sink, whereas La Niña events tend to enhance it. This pattern contrasts with the findings of Restrepo-Coupe et al. (2023) for central Amazonia, where enhanced carbon assimilation was observed during the 2015–2016 El Niño event, although the authors also reported evidence of drought legacy effects persisting after the event.

The seasonal cycle of NEE at Rebio Jaru (Fig. 7) exhibits a pronounced carbon source peak in October, coinciding with the transition between the late dry season and the onset of the wet season. This pattern differs from those reported by Hayek et al. (2018) and Restrepo-Coupe et al. (2023) for a tropical forest near Santarém, Pará, Brazil, as well as by Botía et al. (2022) at the Amazon Tall Tower Observatory (ATTO), near Manaus, Amazonas, Brazil.

A possible explanation for this peak is the semi-deciduous character of the Rebio Jaru forest, which likely experiences enhanced leaf senescence and litterfall during the dry season. The accumulated litter may then undergo rapid decomposition with the arrival of the first rains at the beginning of the wet season, increasing heterotrophic respiration and consequently enhancing CO₂ emissions from the soil to the atmosphere. This mechanism may contribute to the observed increase in ecosystem carbon release during this transition period.

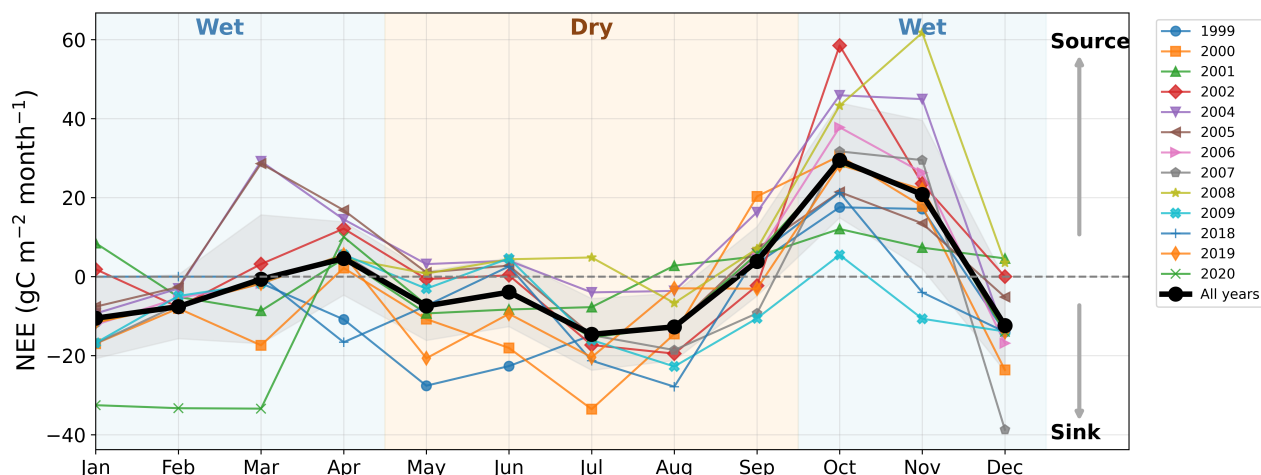


Figure 7. Seasonal cycle of monthly net ecosystem exchange (NEE) at Rebio Jaru for all available years. Colored lines represent individual years, while the thick black line indicates the climatological mean and the shaded gray region denotes ± 1 standard deviation. Negative NEE values indicate net carbon uptake (sink), whereas positive values indicate net carbon release (source). Shaded background regions represent the wet season (October–April; blue) and dry season (May–September; orange).

For the same reason, a peak in CO₂ assimilation is observed in July, likely because ecosystem respiration is relatively low during this period while sufficient leaf area is still maintained to sustain high photosynthetic activity. During most of the remaining months, NEE remains close to carbon neutrality, except for pronounced source peaks observed in March 2004 and 2005, which may be associated with drought legacy effects following the 2002–2003 El Niño event. However, the mechanisms underlying these anomalies require further investigation and are beyond the scope of the present study. In contrast, the year



2020 exhibited a particularly strong carbon sink behavior, which also deserves a more detailed investigation to better understand the processes controlling this anomalous response.

280 4 Conclusions

This study demonstrates that reliable estimates of canopy CO₂ storage and net ecosystem exchange (NEE) can be obtained at Rebio Jaru using simplified single-height approaches when complete vertical CO₂ profile measurements are unavailable. The strong agreement between NEE derived from the traditional multi-point profile and the single-point profile approach ($R^2 = 0.87$), together with the good performance of the single-point eddy method ($R^2 = 0.79$), indicates that simplified storage
285 estimates are capable of reproducing the dominant temporal variability of ecosystem carbon exchange in this tall Amazonian forest. In contrast, neglecting the storage term and assuming $NEE = F_c$ resulted in much poorer agreement ($R^2 = 0.24$), demonstrating that canopy CO₂ storage is an essential component of NEE at Rebio Jaru.

The comparison among atmospheric stability regimes showed that the performance of the simplified methods strongly depends on turbulence conditions. Both single-point approaches reproduced the multi-point profile more accurately under
290 stable and neutral conditions, whereas performance deteriorated under very stable nighttime conditions, especially for the single-point eddy method. Even so, the overall agreement between simplified and profile-based estimates supports the use of the single-point eddy approach to reconstruct long-term NEE variability at this site, particularly because the eddy covariance record is substantially longer than the available CO₂ profile measurements.

The reconstructed NEE time series revealed a strong influence of ENSO variability on the carbon balance of the Rebio Jaru
295 forest. La Niña periods generally coincided with enhanced carbon uptake, whereas El Niño events were associated with weaker carbon sinks or even net carbon release. In particular, following the 2002–2003 El Niño event, the forest frequently behaved as a carbon source during subsequent years, suggesting the occurrence of drought legacy effects. These results indicate that interannual hydroclimatic variability exerts a stronger control on ecosystem carbon exchange than the regular seasonal cycle.

The seasonal cycle of NEE exhibited a pronounced carbon source peak during the transition from the dry to the wet season,
300 particularly in October. This behavior differs from patterns reported for central and eastern Amazonian forests and may be associated with the semi-deciduous character of the Rebio Jaru forest. Enhanced litterfall during the dry season followed by rapid decomposition after the first rainfall events likely increases soil respiration and contributes to elevated CO₂ emissions during this transition period. Conversely, a peak in carbon uptake was observed during July, when ecosystem respiration is likely reduced while sufficient leaf area is maintained to sustain photosynthesis.

305 Overall, this study provides a practical framework for reconstructing long-term NEE at Amazonian flux towers where complete CO₂ profile measurements are intermittent or unavailable. These findings improve our understanding of carbon exchange dynamics in seasonally dry Amazon forests and highlight the importance of accurately representing canopy storage fluxes in studies of ecosystem carbon balance, atmospheric inversion modeling, and regional carbon budget assessments.



310 *Code availability.* The software code used in this study is publicly available in the Zenodo repository at [10.5281/zenodo.20534199](https://zenodo.org/record/20534199) (Santana et al., 2026)

Data availability. The research data supporting this study are available through the Large-Scale Biosphere–Atmosphere Experiment in Amazonia (LBA) data request system at <https://programa-lba.atlassian.net/servicedesk/customer/portal/1>. Due to the consortium’s data policy, access requires user registration and a formal data request through the platform.

315 *Author contributions.* B.A. conceived the study, processed the data, performed the analyses, and wrote the manuscript. R.A.S. contributed to data analysis, interpretation of the results, and manuscript revision. N.L.R.A., E.G.A., S.B., C.M.A.S., and S.K. contributed to field measurements, data processing, and scientific discussion. D.H.H., N.R.C., G.B.C., and C.Q.D.-J. contributed to the interpretation of the results and manuscript revision. C.Q.D.-J. supervised the study. All authors reviewed and approved the final manuscript.

Competing interests. The authors declare that they have no conflict of interest.

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