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Estimating Carbon Dynamics in an Intact Lowland Mixed Dipterocarp Forest Using a Forest Carbon Model

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Abstract: Intact dipterocarp forests in Asia act as crucial carbon (C) reservoirs, and it is therefore important to investigate the C dynamics in these forests. We estimated C dynamics, together with net ecosystem production (NEP), in an intact tropical dipterocarp forest of Brunei Darussalam. Fifty-four simulation units (plots; 20 m × 20 m) were established and initial C stocks were determined via direct field measurement. The C dynamics were annually simulated with a regression model and the Forest Biomass and Dead organic matter Carbon (FBDC) model. The initial C stock (Mg C·ha⁻¹) of biomass, litter, dead wood and mineral soil were 213.1 ± 104.8, 2.0 ± 0.8, 31.3 ± 38.8, and 80.7 ± 15.5, respectively. Their annual changes (Mg C·ha⁻¹·year⁻¹) were 3.2 ± 1.1, 0.2 ± 0.2, −3.7 ± 6.1, and −0.3 ± 1.1, respectively. NEP was −0.6 ± 6.1 Mg C·ha⁻¹·year⁻¹, showing large heterogeneity among the plots. The initial C stocks of biomass and dead wood, biomass turnover rates and dead wood decay rates were elucidated as dominant factors determining NEP in a sensitivity analysis. Accordingly, investigation on those input data can constrain an uncertainty in determining NEP in the intact tropical forests.

Keywords: carbon dynamics; net ecosystem production; forest carbon model; intact dipterocarp forest

1. Introduction

Intact tropical forests, not disturbed by anthropogenic activity and natural disasters, are repositories of biodiversity and carbon (C). In particular, these forests contain abundant C and contribute to global C sinks [1,2]. Therefore, they have been the focus of international protection efforts [3]. Mixed dipterocarp forests are among the most important types of forest in Southeast Asia, as they contain substantial amounts of biomass C, especially in intact forests [4]. Understanding the C dynamics in these forests is crucial because they can also indicate the C status of preserved tropical forests in the future. However, the C dynamics in such forests are poorly understood owing to a paucity of empirical data.

The C dynamics have been investigated in detail using various methodologies in tropical forests. Most studies have focused on estimating tree-biomass C stocks in tropical forests [5–9]. These studies involved destructive tree sampling in order to develop allometric functions, which are useful tools for

estimating biomass using simple field measurements. Recently, eddy covariance technologies have been widely used to measure overall C dynamics in Neotropical and Paleotropical tropical forests [10–12]. This advanced technique can be used to calculate the exchange rate of atmospheric C by comparing vertical air fluxes and concentrations of atmospheric C [13]. The accumulation of empirical data can contribute to enhancing the understanding of C dynamics in the tropical forests. Unfortunately, however, most of these earlier studies were conducted in the Amazonian forests and data that can be used to integrate C dynamics in other tropical forests are still lacking [11].

Ecosystem models have been utilized to supplement the paucity of empirical data. These models facilitate the quantification of forest C dynamics without requiring direct measurement of all C fluxes [14]. Several previous studies have simulated C dynamics in tropical forests using ecosystem models [15–18]. These studies mainly estimated annual forest C dynamics using various factors (e.g., disturbance, climate change, and CO₂ concentration) in Amazonian forests owing to the higher availability of empirical data. Availability of model input data is, however, a limiting factor in the utilization of ecosystem models in other tropical forests.

In this context, another simple ecosystem model that can be utilized with less empirical data is required to estimate the C dynamics of intact mixed dipterocarp forests in Southeast Asia, owing to the limited availability of research data. The Forest Biomass and Dead organic matter Carbon (FBDC) model might be appropriate because of the low data requirements and flexibility in the model structure [19,20]. Thus, we aimed to estimate annual C dynamics in an intact dipterocarp forest of Brunei Darussalam using the FBDC model. A minimum level of field measurement was conducted to initialize C stocks and to prepare parameters for the FBDC model. In addition, the most dominant factors on C dynamics in the forest were also explored.

2. Materials and Methods

2.1. Study Site

The study was carried out in an undisturbed lowland mixed dipterocarp forest in Kuala Belalong, Brunei Darussalam (4°63'50.3" N, 115°22'79.1" E; Table 1). Mean annual air temperature ranged between 24.0 and 24.9 °C (unpublished data) and mean annual precipitation was 4582 mm [4]. Dipterocarpaceae is the dominant tree family and 1064 trees (diameter at breast height (DBH) ≥ 5 cm) were found in a 1-ha plot [21]. Inceptisols and Ultisols consist of major soil order [22]. Experimental plots (simulation units) were established by laying out 54 plots (20 m × 20 m), included in six large quadrats (60 m × 60 m), within a 25-ha permanent plot of the Center for Tropical Forest Science.

Table 1. Stand condition of the study site.

	Mean Annual Temperature (°C) ^a	Annual Precipitation (mm) ^b	Number of Stems (N·ha ⁻¹)		
			DBH < 20 cm	20 cm ≤ DBH < 50 cm	50 cm ≤ DBH
Maximum	24.9	5677.4	7606	236	58
Average	24.6	4582.0	6504	204	42
Minimum	24.0	3236.9	5467	167	28

^a Observation data from the automatic weather system at the experimental plot; ^b Observation data from Semabat Agricultural Station [4]; DBH, diameter at breast height.

2.2. Estimation of Biomass C Stock and Growth Rate

C stocks in biomass and other pools were estimated using both field measurements and previously published equations. DBH was measured for all trees in all 54 plots in 2011 to estimate biomass C stocks. The aboveground biomass (AGB) was estimated by using a function derived from a study in the lowland dipterocarp forests of Borneo ([6]; $n = 122$, Adjusted $r^2 = 0.963$):

$$\text{AGB (kg)} = \exp(-1.201 + 2.196 \times \ln(\text{DBH (cm)})) \quad (1)$$

This reference was used because of the proximity of the study sites, the similarities of species (dipterocarp forest) and the range of DBH (< 150 cm) compared to other studies [7,23,24]. The proportions of stem, branch, and foliage in AGB were determined based on the ratios of the mean tree biomass (10 cm ≤ DBH) of these compartments (stem:branch:foliage = 83.4:15.2:1.4) in a virgin tropical dipterocarp forest in Borneo (5; DBH < 140 cm), rather than these ratios in disturbed dipterocarp forests in Borneo (25; DBH < 100 cm). Belowground biomass (BGB) was estimated using the root:shoot ratio (18:100) derived from the ratio of mean BGB to mean AGB in a primary lowland dipterocarp forest in Peninsular Malaysia (26; DBH < 116 cm). The reference was particularly selected among previous studies [7,23,25,26] by consideration of the proximity of the study sites and the similarities of species (dipterocarp forest) and the DBH range. Total biomass C stock was calculated by multiplying the total biomass by 0.5 [27]. The biomass C stock within each plot (Mg C·ha⁻¹) was calculated by summing the individual tree C stocks followed by unit conversion to 1 ha. To estimate annual biomass C stocks, DBHs were re-measured at three large quadrats (27 plots), which were randomly selected from six large quadrats in 2014. The annual biomass growth rate (Mg·ha⁻¹·year⁻¹) at each plot was estimated by a difference between the biomass C stock in 2014 and that in 2011 at these 27 plots. Annual biomass growth was estimated using Equation (2) (SAS 9.4 (SAS Institute, Cary, NC, USA) PROC NLIN; $r^2 = 0.43$, [28]):

$$\text{Annual biomass growth (Mg C}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}) = 2.34 \times \ln(\text{AGB (Mg C}\cdot\text{ha}^{-1})) - 9.15 \quad (2)$$

This regression model was applied to estimate annual growth rate and biomass at all plots from 2011. The annual growth of biomass at each plot was successively estimated by summing annual growth and biomass stock in the previous year at the plot scale.

2.3. Simulation of Forest C Dynamics with the FBDC Model

The FBDC model can simulate C dynamics at diverse spatial and temporal scales [19,20]. This generic model includes C dynamics in biomass and dead organic matter compartments. C dynamics, such as growth of biomass, turnover (litterfall and mortality) of biomass, and fluxes of organic matter (mineral soil, dead wood and litter) can be quantified using this model [19]. In the FBDC model, C stocks of five biomass pools (stems, branches, foliage, coarse roots, and fine roots) are estimated separately using empirical growth models [19,20]. Changes in the C stocks of litter and dead wood pools are determined based on a balance between organic matter input (litterfall and mortality from biomass pools) and output (decomposition of litter and dead wood) [19]. Litterfall and mortality are estimated using biomass C stock and the turnover rate of each tree compartment [19]. Decomposition of dead organic matter is estimated using the C stocks of dead organic matter and decay rate, which is a function of mean air temperature and the decay constant at standard temperature [19]. Finally, some portion of the output from litter and dead wood pools becomes organic matter input to the mineral soil C pool and it determines changes in the C stock of mineral soil with decomposition in the mineral soil pool [19].

The FBDC model was selected to simulate C dynamics in this intact tropical forest because the model requires a small amount of input data and has a relatively flexible model structure [19,20]. Mean annual temperature, stand age, and site productivity are the major input data required for this model, but the latter two data were not required due to the growth function developed for this study (Equation (2)). In addition, this model consists of relatively fewer parameters than other models. Thus, parameterization of the FBDC model to other environments is relatively easy. The FBDC model has already been applied to forest ecosystems in some countries using a new parameterization process with limited empirical data [19,20].

Initialization of the C pools was based on the field measurements. The calculated biomass C stock of each component was directly used as initial biomass C stock. For initialization of the dead organic matter C pools in the FBDC model, the C stocks in litter (fallen twigs and foliage), coarse woody

debris (CWD), and mineral soil (1 m in depth) were directly measured in 2014. These pools were investigated by direct sampling with random collection (litter), auger (soil), and line intersect (dead wood) method. The C concentration of each pool was measured using an elemental analyzer, vario MACRO (Elementar, Langensfeld, Germany). The detailed methodologies used for measurements of C stocks have been described by [4]. The measured C stocks of the CWD were used as the initial aboveground dead wood C stocks of the FBDC model. The measured C stocks of fallen branches and foliage were used as the initial litter C stocks, and the measured C stocks of mineral soil were directly used for the FBDC model. The initial C stocks of dead fine roots were estimated using the mass ratio of dead fine roots to coarse roots in tropical lowland natural forests in Indonesia (0.064; [29]). As no empirical data are available on C stock of dead coarse roots, the initial C stocks of dead coarse roots were estimated using the following relationship; branch:coarse root = dead branch:dead coarse root. Two assumptions underlie this relationship: (1) dead coarse roots and dead fine root are simultaneously generated with coarse woody debris and litterfall, respectively; and (2) their decomposition rates are similar. Meanwhile, the parameters of the FBDC model were prepared to simulate dead organic matter C dynamics (Table 2). The original parameters were substituted with other parameters representing the environmental conditions of the study site. The turnover (litterfall) rates of branch and foliage, along with the decay constant of CWD, were substituted with field data acquired directly from the study site (unpublished data).

Table 2. Model parameters.

Category	Pools	Value	Reference
Turnover rate (year ⁻¹)	Stem	0.0075	[30]
	Branches	0.04	Lee et al. (unpublished data)
	Foliage	1.458	Lee et al. (unpublished data)
	Coarse roots	0.04	Assumption: equal to the Branch
	Fine roots	0.6635	[31]
	AWDS	0.209	Lee et al. (unpublished data)
	AWDB	1.07	[32]
Decay constant (k; year ⁻¹)	ALT	2.27	[32]
	BWD	1.07	Assumption: equal to the AWDB
	BLT	0.96	[33]
	AHUM and BHUM	0.02	[34,35]
	SOC	0.0017	[34,35]

Abbreviations: aboveground woody debris from stem (AWDS); aboveground woody debris from branch (AWDB); aboveground litter (ALT); belowground wood debris (BWD); belowground litter (BLT); aboveground humus (AHUM); belowground humus (BHUM); soil organic carbon (SOC) [19].

The C dynamics in the 54 plots were simulated monthly, and the annual changes in C stocks were calculated by difference between the C stocks in 2015 and those in the following year. Those changes were separately provided by C pools (biomass, litter, dead wood, and mineral soil). Net ecosystem production (NEP), which is defined as net C accumulation by ecosystems (gross primary production–ecosystem respiration), was calculated by summing the changes in the forest C stocks within each plot. Correlation analysis on the initial C stocks and simulated changes in C stocks was also conducted with SAS 9.4 software [28].

A sensitivity analysis on NEP was conducted to determine the order of importance of input data for estimating accurate NEP. The analysis can quantify the response of the model output to uncertainties in input data and parameters. The initial C stocks in four pools (biomass, dead wood, mineral soil and litter), the turnover rates of the biomass and decay rates of the other three C pools (Table 2) were evaluated. The average of NEP was used as a reference level for the sensitivity analysis. Each run of the sensitivity analysis was carried out by changing an input data ranging from 60% to –60% in a 20% scale.

3. Results

3.1. Initial C Stocks

The total C stock (average \pm standard deviation; $\text{Mg C}\cdot\text{ha}^{-1}$) was estimated to be 327.0 ± 102.2 (Table 3). The biomass pools accounted for most of the total C stocks, whereas large variations were observed in the dead wood and biomass. The C stock of biomass was $213.1 \pm 104.8 \text{ Mg C}\cdot\text{ha}^{-1}$, accounting for 65.2% of total C stock on average. The relative contribution of biomass particularly increased with increasing total forest C stock ($r = 0.54$). Meanwhile, the C stocks of litter and mineral soil were 2.0 ± 0.8 and 80.7 ± 15.5 , respectively, exhibiting relatively small variation. Litter C stock decreased with increasing total forest C stocks ($r = -0.53$). In particular, mineral soil C stock showed a small variation, although this C pool accounted for 24.7% of the total C stock on average. The relative contribution of the mineral soil pool decreased with increasing total forest C stock ($r = -0.73$), in contrast to the trend observed for the biomass pool. The dead wood C stock was $31.3 \pm 38.8 \text{ Mg C}\cdot\text{ha}^{-1}$, with a coefficient of variation of 124%. This pool explained 9.6% of total C stocks, and the proportion did not show a significant correlation with total forest C stock ($p > 0.05$).

Table 3. Initial carbon (C) stocks and their relative contribution to the total forest C stock.

Variables	Biomass	Litter	Dead Wood	Mineral Soil	Total
C stock ($\text{Mg C}\cdot\text{ha}^{-1}$)	213.1 ± 104.8	2.0 ± 0.8	31.3 ± 38.8	80.7 ± 15.5	327.0 ± 102.2
Relative contribution (%)	65.2	0.5	9.6	24.7	100

3.2. Changes in C Stocks and NEP

Estimated changes in annual C stocks varied greatly among the C pools of the study site, particularly displaying large variations in the dead wood and biomass pools (Figure 1). The C stocks ($\text{Mg C}\cdot\text{ha}^{-1}$) of biomass, litter, dead wood, and mineral soil were annually changed by 3.2 ± 1.1 , 0.2 ± 0.2 , -4.6 ± 7.3 , and -0.3 ± 1.2 , approximately equivalent to 38.6%, 2.2%, 55.6%, and 3.6% of NEP, respectively. The biomass pool positively contributed to the C sequestration. The litter and mineral soil pools exhibited almost C neutral status, showing small variations. In contrast, dead wood pool was obviously C source in spite of large variation in C balance. Consequently, NEP averaged $-0.6 \pm 6.1 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$, exhibiting a large degree of spatial heterogeneity; NEP of the study site showed both positive and negative C sinks.

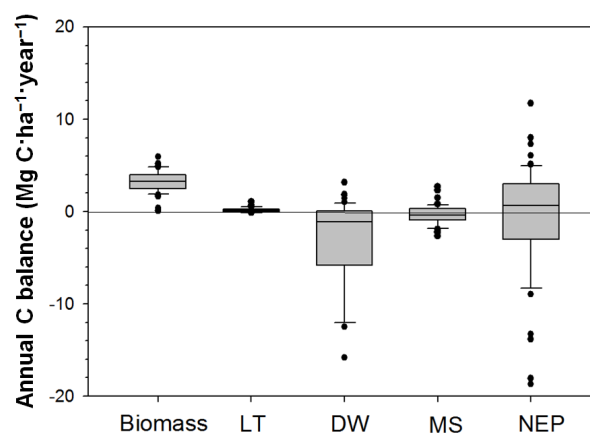


Figure 1. Annual carbon (C) stock changes in biomass, litter (LT), dead wood (DW), and mineral soil (MS), and net ecosystem production (NEP).

The annual changes in C stocks were correlated with the initial C stocks (Table 4). The annual changes in the C stocks of dead organic matter pools decreased with increasing initial C stocks because C emissions from these pools increase with increasing initial C stocks ($r \leq -0.41$; $p < 0.05$). The biomass C stock was positively correlated with the annual changes in C stocks and NEP. It might be attributed to the fact that the growth and dead organic matter input from biomass increased with increasing biomass C stock in this study. Dead wood C stock negatively correlated with NEP ($r = -0.94$) while the C stock positively correlated with the increase in mineral soil C stock ($r = 0.79$). It implied the change in C allocation from dead wood to mineral soil during the decomposition process.

Table 4. Correlation coefficients between forest carbon (C) stocks and their changes (Δ).

	NEP	Biomass C	LT C	DW C	MS C
Δ Bio	0.57 *	0.94 *	0.05	-0.20	-0.13
Δ LT	0.55 *	0.90 *	-0.41 *	-0.23	0.08
Δ DW	0.95 *	0.32 *	-0.11	-1.00 *	0.05
Δ MS	-0.42 *	0.37 *	0.19	0.73 *	-0.50 *
NEP	-	0.59 *	-0.09	-0.92 *	-0.06

Abbreviations: NEP, net ecosystem production; LT, litter; DW, dead wood; MS, mineral soil. *: $p < 0.05$.

3.3. Sensitivity Analysis

The sensitivity analysis assessed the influence of input data (initial C stocks) and parameters on the NEP (Figure 2). The changes in NEP ($\text{Mg C}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$) started from $-3.8, 0.2, 2.5$ and 1.5 (-60% of the initial C stocks) to $2.7, -0.23, -2.5$ and -1.5 (60% of the initial C stocks) for biomass, litter, dead wood and mineral soil pools, respectively. Meanwhile, the changes in NEP ($\text{Mg C}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$) started from $-1.9, 0.9, 2.5$, and 1.8 (-60% of the parameters) to $1.9, -0.1, -1.5$ and -1.3 (60% of the parameters) for biomass turnover rate, litter decay rate, dead wood decay rate and mineral soil decay rate, respectively. Those results implied that the initial C stocks of biomass and dead wood, turnover rate of biomass and decay rate of dead wood are dominant factors on determination of NEP in the forests. The influence of variation in mineral soil C stock on the NEP would be constrained due to the small variation (%) in the initial C stock of mineral soil. The other input data in terms of litter seemed to affect the NEP while its role might be smaller than the other pools. Accordingly, the NEP was especially sensitive to the components in the following order: biomass > dead wood > mineral soil > litter.

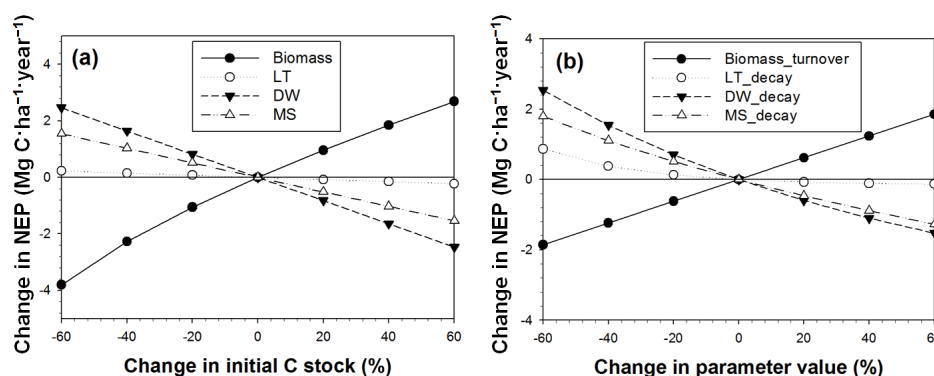


Figure 2. The sensitivity of NEP to changes in the (a) initial C stocks and (b) parameter values. Abbreviations: NEP, net ecosystem production; LT, litter; DW, dead wood; MS, mineral soil.

4. Discussion

4.1. C Dynamics in the Intact Tropical Forests

In this study, C balance in an intact tropical dipterocarp forest in Southeast Asia was found to be weakly negative, with substantial variation ($-0.6 \pm 6.1 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$; Figure 1). This estimate corresponded to those of previous studies on dipterocarp forests [10,12]. The large variation in NEP observed in the present study was most likely due to the spatial heterogeneity of changes in C stocks among the C pools. Biomass was particularly correlated with NEP (Table 4, Figure 2). The biomass pool is well known to be a major C sink in tropical forest ecosystems. The positive correlation between biomass and its growth, which was estimated using Equation (2), appropriately reflected the fact that the growth of trees in tropical forests is positively correlated with light availability and tree size [36,37]. The canopy layer can develop with the presence of large-DBH trees (tall and emergent), which corresponds to the increase in biomass in intact mixed dipterocarp forests [38]. Furthermore, biomass is a source of annual dead organic matter input. Accordingly, the assessment of biomass C stock and turnover rates is highly recommended for the reliable estimation of NEP in forests.

The most important contribution of the present study to the field is the exploration of an underestimation of the role of dead wood in C balance in intact tropical forests. Dead wood C dynamics was a key component of NEP and contributed to the spatial heterogeneity of NEP (Figures 1 and 2). The substantial amount of C loss from dead wood was attributed to a substantial amount of CWD C stock in the study site, which occurred owing to the mortality of emergent individual trees, which accounted for most of the biomass C stocks [4]. The CWD C stocks in some study plots ($> 100 \text{ Mg C}\cdot\text{ha}^{-1}$) were more than those in other tropical forests, and a substantial amount of C can be emitted from CWD [4,11,39,40]. Previous studies have primarily focused on biomass C dynamics, and information regarding the effects of CWD is lacking. Thus, the inclusion of dead wood, especially CWD, will help us gain an enhanced understanding of C dynamics in intact tropical forests.

Contributions of litter and mineral soil to NEP were negligible in the model (Figure 1). The rapid decay rates of litter in tropical climatic zones can constrain the annual increase in litter C stocks [32,40]. Meanwhile, only small annual changes were estimated in the mineral soil C stocks despite abundant C stocks. The mineral soil is actually the least sensitive C pool to decomposition in forests [19,34].

4.2. Implications

Using forest C models to quantify the C dynamics of this dipterocarp forest has several advantages. First, modeling can provide estimates of C dynamics when data are inadequate; the FBDC model used in this study is particularly effective when only small amounts of input data are available. The ability to estimate the annual change in the C stock of each pool is another advantage of the approach adopted in this study. The classification of C pools that we used followed the international guidance: biomass, litter, dead wood, and soil [27]. Thus, this approach provides a reliable way of estimating the forest C inventories of intact tropical forests when available data are insufficient.

The sensitivity analysis revealed an order of priority for reducing uncertainty in estimations of C balance in intact tropical forests (Figure 2). The C stocks in biomass, dead wood, and mineral soil and their parameters (turnover and decay rates) substantially affected C balance and could even change the sign of NEP as a result of 20% uncertainty in the study site. In particular, the assumption regarding initial C stocks (branch:coarse root = dead branch:dead coarse root) and parameters (Table 2), which are included in the categories of these dominant factors (biomass turnover and initial dead wood C stock), might be a source of uncertainty. Accordingly, appropriate investigation and preparation of C stocks and parameters, especially considering the order of their effects on NEP (biomass > dead wood > mineral soil > litter), in ecosystem models are highly recommended to reduce uncertainty in estimating NEP in tropical intact forests.

5. Conclusions

We estimated the annual changes in C stocks and NEP in an intact lowland dipterocarp forest in Asia. Both the changes in C stocks and the NEP exhibited large variation among the C pools and the plots due to the large spatial heterogeneities in the C stocks. Intact tropical forest ecosystems can be either C sinks or C sources, and C balance is largely determined by initial C stocks and related parameters of the biomass and dead wood pools. Investigation on those C stocks and parameters should be firstly conducted to reduce uncertainty in estimating C dynamics in the forests. Most notably, the role of CWD on C balance in intact tropical forests must be further explored in the future. We also found that forest C modeling can contribute to a better understanding of forest C dynamics in intact tropical forests when available data are limited.

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