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TROLL 4.0: representing water and carbon fluxes, leaf phenology, and intraspecific trait variation in a mixed-species individual-based forest dynamics model – Part 2: Model evaluation for two Amazonian sites

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1 **TROLL 4.0: representing water and carbon fluxes, leaf phenology,**
2 **and intraspecific trait variation in a mixed-species individual-based**
3 **forest dynamics model – Part 2: Model evaluation for two Amazonian**
4 **sites**

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26 **Summary.** We evaluate the capability of TROLL 4.0, a simulator of forest dynamics, to represent tropical forest structure,
27 diversity and functioning in two Amazonian forests. Evaluation data include forest inventories, carbon and water fluxes
28 between the forest and the atmosphere, and leaf area and canopy height from remote-sensing products. The model realistically
29 predicts the structure and composition, and the seasonality of carbon and water fluxes at both sites.

30

31

32

33 **Abstract.** TROLL 4.0 is an individual-based forest dynamics model that jointly simulates the structure, diversity and
34 functioning of tropical forests, including their water balance, carbon fluxes and leaf phenology, while accounting for
35 intraspecific trait variation for a large number of species. In a companion paper, we describe how the model represents the
36 physiological and demographic processes that control the tree life cycle in a one-metre-resolution spatially-explicit scene and
37 uses plant functional traits measurable in the field to parameterize such processes across species and individuals (Maréchaux
38 et al., [submitted companion paper](#)). Here we evaluate the performance of TROLL 4.0 for two Amazonian sites with contrasting
39 soil and climate properties. We assessed the model's ability to represent forest structure and composition using lidar-derived
40 canopy height distributions and forest inventories combined with information on plant functional traits. We also evaluated the
41 model's ability to represent carbon and water fluxes, as well as leaf area variation, at daily and fortnightly resolution over a
42 decade, using detailed information from on-site eddy covariance towers, satellite data and ground-based or air-borne lidar data.
43 We finally compared the responses of carbon and water fluxes to environmental drivers between simulated and observed data.
44 Overall, TROLL 4.0 provided a realistic representation of forests at both sites. The simulated canopy height distribution
45 showed a high correlation coefficient (CC) with observed aerial and satellite data (CC>0.92), while the species and functional
46 composition were well represented (CC>0.75). TROLL 4.0 also realistically simulated the seasonal variability of carbon and
47 water fluxes (CC>0.46) and their responses to environmental drivers, while capturing temporal variations in leaf area
48 (CC>0.76) and its partitioning in leaf age cohorts. However, TROLL 4.0 overestimated annual gross primary productivity at
49 both sites (mean RMSEP=0.94 kgC m⁻² yr⁻¹) and evapotranspiration at one site (mean RMSEP=0.75 mm day⁻¹), likely due to
50 an underestimation of the soil water depletion and stomatal control during the dry season. This evaluation highlights the
51 potential of TROLL 4.0 to represent ecosystem fluxes and the structure and diversity of plant communities at a fine resolution,
52 paving the way for model predictions of the effects of climate change, fragmentation and forest management on forest structure
53 and dynamics.



54 1 Introduction

55 Tropical forests cover just 7% of the Earth's land surface, yet they play a disproportionately large role in the biosphere, store
56 around 25% of terrestrial carbon and contribute to more than a third of global terrestrial productivity (Bonan 2008). Regionally,
57 tropical forests recycle around a third of precipitation through evapotranspiration, contributing to the generation and
58 maintenance of a humid climate (Harper et al., 2013), effects that extend well beyond the tropics (Lawrence & Vandecar 2015).
59 However, tropical forests remain a major source of uncertainty in simulations of global biogeochemical cycles (Fisher et al.,
60 2014; Koch et al., 2020).

61
62 As an illustration, for light-limited tropical forests, dynamic global vegetation models (DGVMs, Prentice et al., 2007) typically
63 simulate a decrease in productivity with a seasonal decline in precipitation (Restrepo-Coupe et al., 2017, Chen et al., 2020),
64 while observations from eddy covariance data point to an increase in gross primary productivity during the dry season (Guan
65 et al., 2015; Aguilos et al., 2018). Similarly, simulated forest responses to experimental and natural droughts have highlighted
66 large model-data discrepancies and variation across models (Powell et al., 2013; Joetzjer et al., 2014; Yao et al., 2023; Paschalis
67 et al., 2022). Improving the representation of tropical forest functioning in models is needed to enhance our understanding and
68 ability to predict biogeochemical cycles.

69
70 One challenge is to better integrate the structure, diversity and functioning of forests into vegetation models (Purves and Pacala,
71 2008; McMahon et al., 2011; Evans, 2012; Mokany et al., 2016). In spite of progress (Fisher et al., 2018), most models still
72 adopt a coarse grained representation of vegetation, which makes it difficult to use field data to parameterize and evaluate the
73 models. Also, several processes driving the variation of tropical forest productivity and water fluxes remain incompletely
74 represented in vegetation models. These include water uptake by the root system and seasonal variation of leaf quantity and
75 quality at the ecosystem-level, which are driven by leaf phenology and allocation processes at the individual-level (Chen et
76 al., 2020; Wu et al., 2021; Restrepo-Coupe et al., 2017, Cusak et al., 2024).

77
78 In a companion paper, we described the individual-based forest dynamics model TROLL 4.0 (Maréchaux et al., submitted
79 companion paper). This model jointly simulates tropical forest structure, diversity and functioning, including forest water
80 balance, carbon fluxes and leaf phenology, and accounts for intraspecific trait variation for a large number of species. TROLL
81 4.0 represents the processes underlying ecosystem fluxes, such as leaf gas exchanges and their responses to environmental
82 variation, and is thus similar to DGVMs in that respect, with its outputs comparable with data from eddy covariance towers.
83 However, unlike DGVMs that are designed for global applications and typically represent plant diversity with a few functional
84 types, TROLL 4.0 represents diversity at the species level (e.g., 10s to 100s of tropical tree species). TROLL 4.0 is spatially-
85 explicit and represents plant community structure and diversity at a spatial resolution of one metre, which is consistent with
86 that used by field ecologists. Physiological and demographic processes are integrated using a parameterisation based on plant
87 traits measurable in the field, relying on recent knowledge in plant physiology and functional ecology. The individual-based,



88 species-specific and spatially explicit representation of forest structure and composition enables TROLL 4.0 outputs to be
89 directly compared with spatially explicit forest inventories, trait distributions or fine-scale remote sensing products.

90

91 In this paper, we evaluate TROLL 4.0 for two Amazonian sites with contrasting soil and climate properties. We parameterized
92 the model using functional trait and soil data at both sites. We first calibrated three major forest structure parameters using
93 inventory data, and then the three parameters of the phenological module that control leaf shedding as a function of soil water
94 availability using litterfall data. We then ran simulations and evaluated the model's representation of forest structure and
95 composition against independent data, including lidar-derived canopy height distribution, understory inventories and
96 functional trait distribution. We also assessed the model ability to represent carbon and water fluxes at daily resolution, as well
97 as leaf area variation at fortnightly resolution, against eddy covariance, satellite and terrestrial or drone lidar data. We finally
98 compared the response of simulated and observed fluxes to incoming radiation, vapour pressure deficit, temperature, and wind
99 speed. Finally, we discuss the potential model-data discrepancies and identify priorities for future developments.

100 **2 Methods**

101 TROLL represents individual trees explicitly in an aboveground voxelized space (1 m^3), in which light diffusion is modelled,
102 and in a belowground space, which consists of several layers with user-defined thickness and horizontal resolution (here 25
103 m^2). Belowground water flow is simulated using a bucket model. Each tree belongs to a species, and we provide as input
104 species-specific mean plant trait values and intraspecific trait variances and covariances. At recruitment, individual trait values
105 are randomly drawn from the intraspecific trait distribution. These traits parameterize the physiological and demographic
106 processes that govern the life cycle of trees, from recruitment to growth, seed dispersal, and finally death. Carbon assimilation
107 by trees is computed using the photosynthesis model of Farquhar, von Caemmerer and Berry (1980), coupled to the stomatal
108 conductance model of Medlyn et al. (2011), as a function of leaf micro-environmental conditions, tree access to water, and
109 leaf photosynthetic capacity and leaf respiration rate. Sugars produced during photosynthesis are used for tree respiration and
110 allocation to plant tissues, including foliar production, carbon storage and woody growth.

111

112 We conducted model calibration and evaluation at two lowland Amazon forest sites: the Paracou research station in French
113 Guiana ($5^{\circ}28'N$, $52^{\circ}92'W$), hereafter Paracou (Gourlet-Fleury et al., 2004; Bonal et al., 2008), and the Tapajos National Forest
114 in Brazil in the K67 site also named BR-Sa1 ($2^{\circ}86'S$, $54^{\circ}96'W$), hereafter Tapajos (Silver et al., 2000; Saleska et al., 2003).
115 Both sites are covered by a high biomass and species rich lowland moist tropical forest, and they present contrasting soil
116 characteristics and climate (Table 1). The two sites have been intensively monitored for several decades, mainly through
117 repeated forest inventories and eddy flux tower measurements.

118

119 At each site, we calibrated six global parameters, three parameters related to forest structure, to which TROLL is known to be
120 sensitive: the reference background mortality rate m , and the intercept a_{CR} and slope b_{CR} of the crown radius scaling relationship



121 (Table A1; Maréchaux and Chave, 2017; Fischer et al., 2019), and three parameters pertaining to the phenological module,
 122 new to TROLL 4.0 ($a_{T,o}$, $b_{T,o}$ and δ_o ; Table A1). In TROLL 4.0, the shedding of old leaves is accelerated as soil water
 123 availability decreases (Maréchaux et al., [submitted companion paper](#)). When the leaf predawn water potential (ψ_{pd} , MPa) falls
 124 below a threshold $\psi_{T,o}$ (MPa), the residence time of old leaves is decreased using a multiplicative factor $f_0 < 1$. The parameter
 125 $\psi_{T,o}$ varies with the tree leaf drought tolerance and its size as follows:

$$126 \quad \psi_{T,o} = \min(a_{T,o} \times \pi_{tlp}, -0.01 \times h - b_{T,o})$$

127 where π_{tlp} is the leaf water potential at turgor loss point in MPa and h is the tree height in m. f_0 is decremented (resp.
 128 incremented) by δ_o when $\psi_{pd} < \psi_{T,o}$ (resp. $\psi_{pd} > \psi_{T,o}$). The parameters $a_{T,o}$, $b_{T,o}$ and δ_o control the intensity and the
 129 timing of the peak of litterfall under drying soil conditions. This scheme is consistent with field observations (Maréchaux et
 130 al. [submitted companion paper](#)), uncertainties remain on the values of $a_{T,o}$, $b_{T,o}$ and δ_o however, and they need to be calibrated.
 131 After calibration, we compared model outputs with site-specific data for evaluation at each site.

132
 133 **Table 1: Site overview with climate, vegetation and soil properties.**

Variables	Units	Paracou	Tapajos	References
Climate				
Annual rainfall	mm	3,041	2,075	P: Aguilos et al., 2018; T: Silver et al., 2000
Average air temperature	°C	25.7	26.1	
Vegetation				
Aboveground biomass ($DBH \geq 10$)	Mg ha ⁻¹	419	287	P: Rutishauser et al., 2010; T: Rice et al., 2004
Abundance ($DBH \geq 10$)	ha ⁻¹	612	470	P: Derroire et al., 2023; T: Rice et al., 2004
Basal area ($DBH \geq 10$)	m ² ha ⁻¹	31	24	P: Derroire et al., 2023; T: Goncalves et al., 2018
Soil				
Type	-	Sandy clay loam	Clay	-
Depth	m	2.50	16.10	P: Hiltner et al., 2021; T: Nepstad et al.,



2002

Layer thickness (top to bottom)	m	0.10 / 0.23 / 0.40 / 0.80 / 0.97	0.10 / 0.40 / 1.00 / 2.50 / 12.10	-
Sand	%	65.25	37.27	P: Van Langenhove et al., 2021; T: Silver et al., 2000
Clay	%	21.50	60.09	
Silt	%	13.25	2.64	
Soil Organic Content	%	2.37	2.54	P: Van Langenhove et al., 2021; T: Quesada et al., 2010
Dry Bulk Density	g cm ⁻³	1.040	1.125	P: Van Langenhove et al., 2021; T: Silver et al., 2000
Cation Exchange Capacity	mEq 100g ⁻¹	2.98	2.97	P: Sabatier et al., 1997; T: Quesada et al., 2010
pH		4.34	3.84	P: Sabatier et al., 1997; T: Quesada et al., 2010

134 2.1 Simulation inputs and climatic drivers

135 TROLL 4.0 uses 35 global parameters defined by the user and provided as inputs. These parameters relate to atmospheric
 136 constants, light transmission, leaf carbon acquisition, leaf shedding, tree carbon allocation, tree shape, reproduction, and death,
 137 and intraspecific trait variability (Table A1). Except for the three parameters of forest structure mentioned above and the three
 138 parameters of the leaf shedding module that have been calibrated at each site, all values are assumed site independent.

139
 140 TROLL 4.0 requires trait parameters for each species: values need to be provided as input for six functional traits and three
 141 scaling parameters. The scaling parameters are species maximum diameter at breast height (dbh_{max} , cm), and parameters
 142 defining the relationship between height and diameter at breast height (dbh), which are the asymptotic height (h_{lim} , m) and the
 143 parameter a_h (see Maréchaux et al. [submitted companion paper](#), Eqs (16) and (62)). We used forest inventories from Paracou
 144 (Derroire et al., 2023) and Tapajos (Goncalves et al., 2018) to create a species list for each site, and computed dbh_{max} as the
 145 95th quantile of species diameter at breast height for species including more than 10 individuals. We used the TALLO global
 146 database of height and diameter measurements (Jucker et al., 2022) to infer species-specific values of h_{lim} and a_h for the 496
 147 species of the database that are present in Amazonia (latitude between 10°N and 18°S and longitude between 39°W and 78°W;



148 n = 24,609 trees with a mean of 49.62 ± 730 trees per species). Parameters a_h and h_{lim} were inferred using Bayesian inference
149 as follows:

$$150 \log(h) \sim N\left[\log\left(h_{lim} \times \frac{dbh}{a_h + dbh}\right), \sigma^2\right] \mid h_{lim} \sim N(h_{lim,0}, \sigma^2_h), a_h \sim N(a_{h,0}, \sigma^2_a)$$

151 with the logarithm of height (h , in m) following a normal distribution centred on the log of a Michaelis-Menten model with
152 asymptotic height h_{lim} , height-dbh scaling parameter a_h , and variance σ^2 . The two species-specific parameters h_{lim} and a_h
153 are random parameters following a normal distribution centred respectively on $h_{lim,0}$ and $a_{h,0}$ with variances σ^2_h and σ^2_a .

154

155 The functional traits used in the parameterization include leaf area (LA, in cm^2), leaf mass per area (LMA, g m^{-2}), leaf nitrogen
156 content per dry mass (N, mg g^{-1}), leaf phosphorus content per dry mass (P, mg g^{-1}), leaf water potential at turgor loss point
157 (π_{tlp} , MPa), and wood specific gravity (wsg, g cm^{-3}). We used several datasets to retrieve species-specific mean values for
158 these traits (Vleminckx et al. 2021, Boisseaux et al., submitted; Kattge, Bönisch, and al., 2020; Maréchaux et al., 2015;
159 Maréchaux et al., 2019; Nemetschek et al., 2024; Ziegler et al., 2019). Finally, we used predictive mean matching (Van Buuren
160 and Groothuis-Oudshoorn, 2011) to impute missing trait values for a_h , h_{lim} , dbh_{max} , and π_{tlp} only. Overall, this procedure
161 leads to a parameterization of 114 species for Paracou and 113 species for Tapajos. These species pools are representative of
162 the functional trait spaces of the two sites (Fig. A1).

163

164 TROLL 4.0 requests nine soil parameters to describe the texture, depth and chemistry. These were gathered from the literature,
165 assuming a single soil type and depth per site for simplicity and setting the number of soil layers to five (Table 1). Testing the
166 influence of horizontal and vertical soil heterogeneity on model outputs is left for future work.

167

168 TROLL 4.0 simulations are forced with six climatic drivers. Two of them are daily: cumulative rainfall (mm), and average
169 nighttime temperature ($^{\circ}\text{C}$). The remaining four drivers are provided every half hour during the daytime (defined below):
170 incoming shortwave radiation (SW, W m^{-2}), temperature (T, $^{\circ}\text{C}$), vapour pressure deficit (VPD, kPa), and wind speed (WS, m
171 s^{-1}). Historical time series for these climatic variables have been retrieved from the FLUXNET 2015 dataset (Pastorello et al.,
172 2020), which provides standardised data from eddy flux towers located at each site (2004-2014 for Paracou, and 2002-2011
173 for Tapajos). However, at Tapajos, rainfall data from FLUXNET 2015 is not reliable due to issues with rain gauges (Restrepo-
174 Coupe et al., 2017). Instead, we used rainfall data from the ERA5-Land reanalysis dataset (Muñoz-Sabater et al., 2021)
175 available at hourly resolution between 2002 and 2011. For other climatic variables, data from ERA5-Land showed high
176 correlation with FLUXNET 2015 data. A more in-depth evaluation of ERA5-Land precipitation data is left for future. We used
177 spline interpolation to derive half-hourly time series from the hourly FLUXNET 2015 data in Tapajos. The half-hourly net
178 radiation time series was used to define daytime hours (i.e. with $S_{net} > 0$) which were set from 6 a.m. to 6 p.m. in Paracou, and
179 from 7 a.m. to 7 p.m. in Tapajos. The dry season was defined as a period with fortnightly rainfall below 50 mm on average
180 across years, consistent with the 100 mm per month used by Bonal et al. (2008). This leads to a 4-month dry season in Paracou
181 (August 1st to December 1st), and a 4.5-month dry season in Tapajos (June 15 to November 1st). Dry seasons were defined



182 for illustration purposes only and have no effect on the model behaviour, which is driven by the meteorological inputs described
183 above.

184 2.2 Calibration and simulation set-up

185 We calibrated the three forest structure parameters (m , a_{CR} and b_{CR}) for each site. a_{CR} and b_{CR} are not independent, and we used
186 the TALLO global database of crown radius (CR) and diameter (dbh) measurements (Jucker et al., 2022) to infer their
187 relationship. To do so, we restricted the TALLO database to observations located within 10 km around sites from which we
188 generated a thousand pairs of (a_{CR}, b_{CR}) values. Each pair of values was determined by randomly drawing 10 individuals per 10-
189 cm diameter class to generate a size-balanced dataset to which the following model was fitted: $\log(CR) \sim N[a_{CR} +$
190 $b_{CR} \times \log(dbh), \sigma^2]$. This resulted in the following linear relationship between the two parameters: $b_{CR} = -0.39 +$
191 $0.59 \times a_{CR} + \epsilon_{b_{CR}}$, with $\epsilon_{b_{CR}}$ the error around the relation. This relationship constrained the exploration of the three-
192 dimensional parameter space, so we only had to calibrate a_{CR} , $\epsilon_{b_{CR}}$, and m . Based on preliminary exploratory analyses with
193 the previous version of TROLL, we defined the range of calibration for each parameter and site as follows: a_{CR} varied from
194 1.60 to 2.00 in Paracou and from 2.3 to 2.7 in Tapajos with a step of 0.05, $\epsilon_{b_{CR}}$ from -0.30 to 0.10 in both sites with a step of
195 0.05, and m from 0.030 to 0.050 in both sites with a step of 0.0025. This resulted in $9 a_{CR} \times 5 \epsilon_{b_{CR}} \times 9 m \times 2 site = 810$
196 triplets of parameter values.

197
198 For each set of three parameter values, we performed a 600-year simulation from bare ground over a 4-ha area. Simulations
199 were run with an external seed rain uniformly distributed across species, so that the simulated community structure is an
200 emergent property resulting from the community assembly mechanisms embedded in the model. As succession unfolds and
201 the number of mature trees increases in the simulation, internal seed production increases according to the assumed
202 relationships between individual size and fecundity. An alternative to uniform seed rain across species would be to prescribe
203 non-uniform seed rain based on species' regional abundances. This approach would tend to make the simulated species
204 abundances more closely resemble the observed regional abundances. In contrast, uniform seed rain as simulated here, biases
205 the simulated abundances towards evenness across species, and differences in simulated abundances reflect differences in
206 demographic performance controlled by the model trait-based parameterization rather than prescribed differences in the seed
207 rain. Each simulation was forced each year by randomly drawing a year among the ten years of climatic data. In doing so, we
208 avoided applying a periodic climatic forcing or any potential trend linked to global warming.

209
210 To evaluate the forest structure simulated with each triplet of parameter values, we compared simulated to observed total
211 aboveground biomass (AGB^{tot} , $Mg\ ha^{-1}$), total tree abundance (N^{tot} , ha^{-1}), and tree abundances per 5-cm diameter class (N^i , ha^{-1}
212 1 for dbh class i) at the end of the 600-year regeneration. The Paracou reference dataset was a 2015 inventory of trees with dbh
213 >10 cm in six 6-ha plots (Derroire et al., 2023). The Tapajos reference dataset was a 1999 inventory of trees with $dbh > 10$ cm



214 in 19.75 ha along four 1-km transects (Rice et al., 2004). At both sites, we calculated the relative root mean squared error
215 defined as:

$$216 \quad RRMSEP = \frac{AGB_o^{tot} - AGB_s^{tot}}{AGB_o^{tot}} + \frac{N_o^{tot} - N_s^{tot}}{N_o^{tot}} + \frac{\sqrt{\frac{1}{n} \times \sum_{i=1}^n (N_o^i - N_s^i)^2}}{|N_o^i|}$$

217
218 where AGB_o^{tot} , N_o^{tot} and N_o^i are observed values, and AGB_s^{tot} , N_s^{tot} and N_s^i are the simulated values. n is the number of dbh
219 classes and $|N_o^i|$ is the mean tree abundances among dbh classes. We extracted the simulation with the lowest $RRMSEP$ at each
220 site and used the corresponding values for m , a_{CR} and b_{CR} in all subsequent simulations.

221
222 After 600 simulated years of forest dynamics the system reached a mature forest stage with stable forest structure, composition,
223 and functioning at both sites. This is referred to as the ‘spin-up phase’. We then used this mature forest stage to calibrate the
224 three parameters of the phenological module. We performed an exhaustive search in the parameter space for combinations of
225 $a_{T,o}$ in [0.01, 0.025, 0.05, 0.075, 0.1, 0.2, 0.3, 0.4, 0.5], $b_{T,o}$ in [0.01, 0.015, 0.02, 0.05, 0.04, 0.06, 0.08, 0.10], and δ_o in [0.1,
226 0.2, 0.3, 0.4, 0.5] resulting in $9 a_{T,o} \times 8 b_{T,o} \times 5 \delta_o \times 2 sites = 720$ simulations. For each triplet, we ran a 20-year
227 simulation with historical weather repeating the 10 years of data twice with the mature forest as an initial condition. Only the
228 last 10 years were used for the calibration to allow the leaf dynamics to adjust to new parameter values.

229
230 To evaluate each simulation, we used leaf litter data from litter traps at both sites (unpublished data at Paracou, Rice et al.,
231 2008 at Tapajos). Litter traps were typically collected fortnightly (although time intervals between consecutive litter trap
232 collections were sometimes higher and up to 80 days in Paracou) between 2004 and 2023 in Paracou, and between 2000 and
233 2005 in Tapajos. The litter collected from the traps was oven-dried until the mass stabilised, partitioned between leaves, fruits
234 and woody debris, and then the fraction were weighed. We computed observed leaf litterfall flux in $Mg ha^{-1} year^{-1}$ as the mean
235 across traps converted from trap surface to hectare and time interval in days to year. We also recorded the time interval between
236 consecutive trap collections to account for the smoothing effect of the longer time intervals in simulated data. Simulated leaf
237 litterfall fluxes over the last 10 years of simulation for each triplet of parameter values were compared to the observed fluxes
238 using the same observation dates and corresponding time intervals.

239
240 To compare simulations against observations, we defined two yearly indices that quantify the timing and intensity of the
241 litterfall peak. The two indices are (i) the day of the litterfall peak as the Julian day of the maximum annual litterfall flux value
242 (*day*), and (ii) the ratio between the maximum value (computed as the average of litterfall flux over the two consecutive time
243 intervals before and after the peak day) divided by the basal flux (computed as the yearly average between January and April)
244 (*ratio*). Both indices are key features of litterfall patterns in tropical rainforests (Chave et al., 2010; Yang et al., 2021). For
245 each simulation we calculated the root mean squared error defined as:



246

$$RMSEP = \sqrt{\frac{\sum_{y=y_0}^{y=y_{max}} (ratio_{y,o} - ratio_{y,s})^2}{N_{year}} + \frac{\sum_{y=y_0}^{y=y_{max}} (day_{y,o} - day_{y,s})^2}{N_{year}}}$$

247

248

249

250

251

252

253

where $day_{y,o}$ and $ratio_{y,o}$ are observed z-scores (i.e., standard deviations from the mean) for year y , and $day_{y,s}$ and $ratio_{y,s}$ are simulated z-scores for year y . Thus a unit $RMSEP$ corresponds to a ratio error of one standard deviation, i.e. 7.6 folds, or to a day error of one standard deviation, i.e. 45.5 days. The best-fit parameters were those corresponding to the lowest $RMSEP$ at each site.

Finally, to quantify the envelopes of stochastic simulation outputs, we ran ten replicates of 600-year simulations starting from bare ground with the six calibrated parameter values.

254 2.3 Evaluation of forest structure and composition

255 To assess the model's ability to simulate forest structure, species and functional composition, we used airborne lidar scanning
 256 (ALS) and satellite data, as well as forest inventories combined with functional traits. Independently from the calibration, we
 257 evaluated the diameter distribution of the forest understory at Paracou using an independent 9-ha inventory of trees with dbh
 258 between 1 and 10 cm from 2020-2023 (unpublished data). We evaluated the structure of the simulated forest at the end of the
 259 600-year replicates against observed basal area (BA, $m^2 ha^{-1}$) and logarithm of tree abundance (ha^{-1}) per 1-cm diameter class
 260 below 10 cm. We evaluated tree height distributions using ALS data from 2015 at Paracou (unpublished data) and from 2012
 261 at Tapajos (dos-Santos et al., 2019), which were processed into canopy height models with a standardised pipeline (Fischer et
 262 al., 2024). From both simulated and ALS-derived canopy height models, we derived the distribution of canopy height,
 263 expressed in proportion of 1- m^2 pixels per 1-m height class. We evaluated the species composition after the 600-year replicates
 264 against the observed rank-abundance curve of the 114 most abundant species at both sites, and the functional composition
 265 against the observed density distribution of each trait for each site and each plot. Due to a lower taxonomic resolution of
 266 botanical identification at the Tapajos site, we used genus level functional trait data at Tapajos and species level functional
 267 trait data at Paracou.

268 2.4 Evaluation of total leaf area dynamics

269 We assessed the model's ability to represent the dynamics of total leaf area and its partitioning into three leaf age cohorts
 270 (Maréchaux et al., submitted companion paper). For evaluation, we gathered leaf area index (LAI) datasets as follows: LAI
 271 from MODIS satellites at both sites, LAI from terrestrial lidar at Tapajos (Smith et al., 2019), and LAI from UAV-borne lidar
 272 at Paracou (unpublished data; Vincent et al., 2017). The MODIS LAI product was at 8 day and 500 m resolution, and pre-
 273 processed in PLUMBER2 (Ukkoloo et al., 2020). At Tapajos, plant area index (PAI) was derived from terrestrial lidar scanning
 274 (TLS) performed every 1-2 months in 2010, 2012, 2015 and 2017 along four 1-km long transects representing 0.4 ha with a
 275 spatial resolution of about 3 m to characterise canopy porosity (Smith et al., 2019). PAI was derived from lidar hits following
 276 Stark et al. (2012) and based on the MacArthur–Horn transformation (MacArthur & Horn, 1969). This PAI was then converted



277 to LAI using an annual mean LAI of 5.7 (Stark et al., 2012). In Paracou, the PAI was derived from repeated UAV-borne lidar
278 surveys, resulting in PAI mapping at 21 day and 1 m resolution between 2020 and 2022 over a 2.5 ha forest area. This PAI
279 derived from UAV lidar was obtained by vertical integration of Plant Area Density (PAD) profiles previously recalibrated to
280 match a TLS-derived PAD profile of a common 1-ha plot scanned in October 2019. This was required because the limited
281 penetration of the UAV lidar yielded overestimation of raw PAD values (Vincent et al., 2023). This PAI was converted to LAI
282 variation with a factor of 0.68, where the conversion factor is derived from other products.

283
284 Simulated LAI variation per leaf age cohort (Eqs 56-57, Maréchaux et al. [submitted companion paper](#)) were compared
285 qualitatively against the one derived from phenological cameras by Wu et al., (2016) at Tapajos and from the reanalysis of
286 Yang et al. (2023) at both sites. Wu et al. (2016) analysed 478 images collected over 24 months from 65 tree crowns and fitted
287 the transition from young to mature and from mature to old leaf pools, assumed to occur at 1 and 3 months, respectively. Yang
288 et al. (2023) used global satellite observations of the TROPOMI satellite Solar Induced Fluorescence (SIF) sensor as an
289 indicator of leaf photosynthesis variation, validated by *in situ* measurements, and set the transition from young to mature and
290 from mature to old leaf pools, occurring at 1.71 and 5.14 months, respectively. By comparison, simulated leaf age per cohort
291 depends on the individual leaf lifespan in TROLL 4.0 (see Maréchaux et al. [submitted companion paper](#)).

292 **2.5 Evaluation of carbon and water fluxes**

293 To assess the model's ability to simulate carbon and water fluxes, we evaluated gross primary productivity (GPP, kgC m⁻²
294 year⁻¹) and evapotranspiration (ET, mm day⁻¹). We extracted GPP and latent heat flux (LE, W m⁻² half-hour⁻¹) from the
295 FLUXNET 2015 dataset (Pastorello et al., 2020). ET was derived from LE and temperature (T, in °C) using $ET =$
296 $\frac{LE \times 60 \times 30 \times 10^{-6}}{\lambda(T)}$ with $\lambda(T) = 2.501 - (2.361 \times 10^{-3}) \times T$ (Allen et al., 1998). GPP was obtained from net ecosystem
297 exchange with the nighttime partitioning method (Reichstein et al., 2005). We summarised half-hourly GPP and ET into daily
298 values by calculating the daily mean and sum. TROLL 4.0 carbon fluxes were also compared with a remotely sensed product
299 of GPP derived from TROPOMI SIF using the formula $GPP = 15.343 \times SIF$ (Chen et al. 2022). We compared how the
300 fluxes depended on environmental drivers in both simulated and observed data. Using the FLUXNET 2015 dataset (Pastorello
301 et al., 2020), daily values of cumulative photosynthetically active radiation (PAR, mol m⁻²), maximum vapour pressure deficit
302 (VPD, kPa), mean temperature (T, °C), and mean wind speed (WS, m s⁻¹) were calculated, and simulated and observed
303 responses of GPP and ET to PAR, VPD, T and WS were compared. TROLL 4.0 water fluxes were assessed using the relative
304 variation of soil water content (RSWC, %) of the top horizon from the Paracou eddy flux tower (Bonal et al., 2008) and the
305 relative variation of soil water content of the top horizon reanalysed against the climatic water deficit at Tapajos (Restrepo-
306 Coupe et al., 2024). RSWC is defined as the daily mean of soil water content (m³ m⁻³) divided by the annual 95th quantile of
307 the daily mean.

308



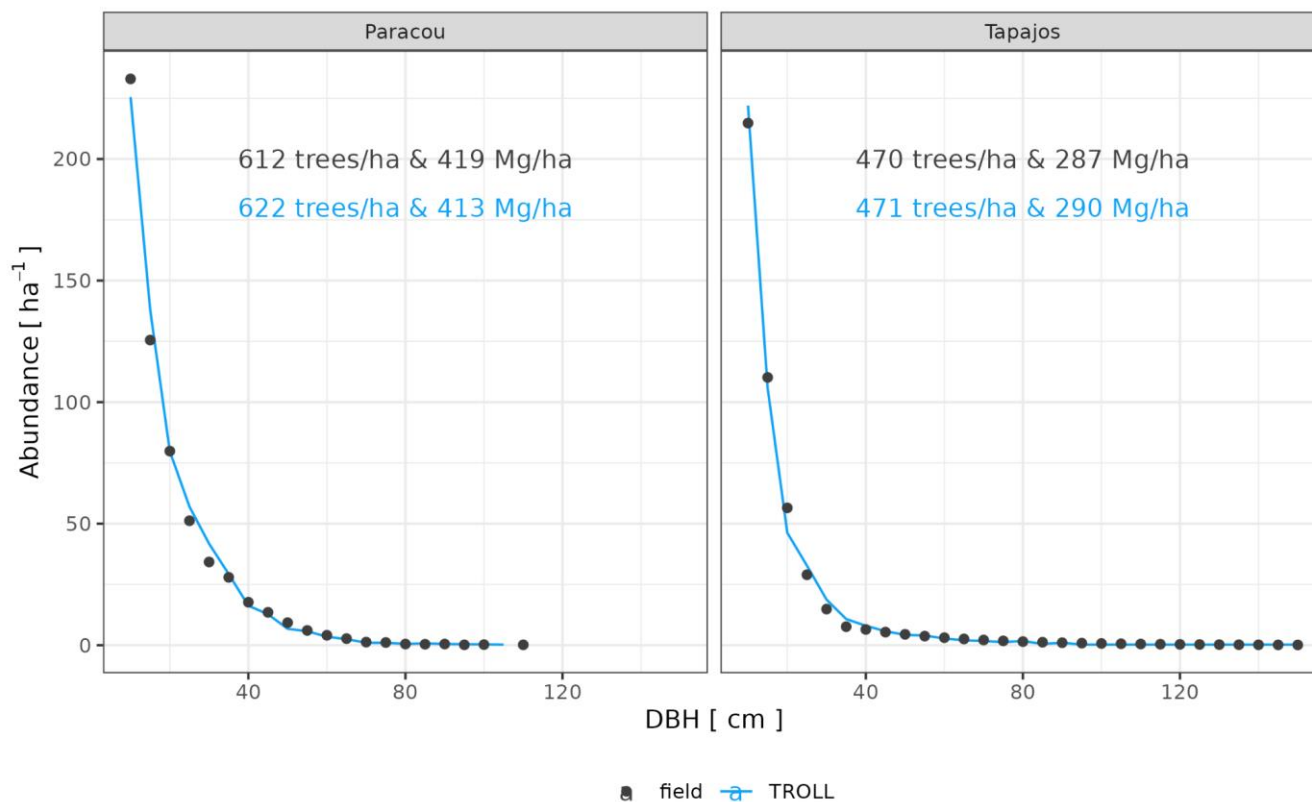
309 All simulations were run using TROLL 4.0 (Maréchaux et al., [submitted companion paper](#)) wrapped in the R package *rcontrol*
310 (Schmitt et al., 2023) and encapsulated in a Singularity image (Kurtzer et al., 2017) leveraging a Python Snakemake workflow
311 (Köster et al., 2012) on a high performance computing platform using 100 cores.

312 3 Results

313 3.1 Forest structure and composition

314 We calibrated background mortality rate (m) and crown radius scaling parameters (a_{CR} and b_{CR}) at Paracou and Tapajos against
315 observed aboveground biomass, total abundance and abundance per 5-cm dbh classes, and found $m=0.035$, $a_{CR}=1.80$ and
316 $b_{CR}=0.3860$ at Paracou, and $m=0.040$, $a_{CR}=2.45$ and $b_{CR}=0.7565$ at Tapajos. The modelled aboveground biomass, total
317 abundance and abundance per 5-cm dbh classes were in good agreement with observations (correlation coefficient, $CC>0.99$
318 at both sites, Fig. 1). The three parameter values were very similar across the five best simulations, i.e. the ones minimising
319 RRMSEP ($m\pm 0.0025$, $a_{CR}\pm 0.1$ and $b_{CR}\pm 0.057$ at Paracou and $m\pm 0.01$, $a_{CR}\pm 0.1$ and $b_{CR}\pm 0.0285$ at Tapajos), and we used the
320 values of the best simulation in all subsequent simulations.

321



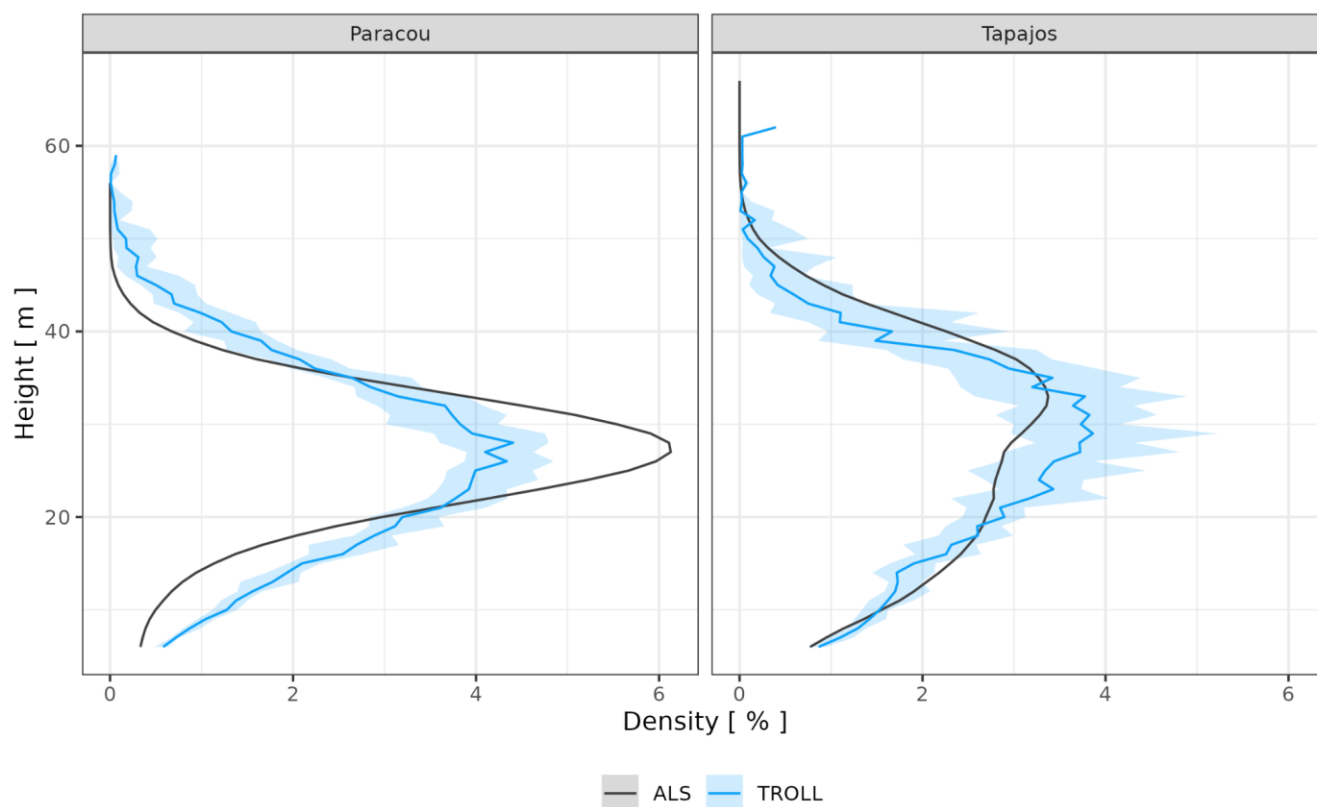
322



323 **Figure 1: Tree size structure at Paracou and Tapajos, expressed in terms of tree abundances per 5 cm-dbh classes. Comparison**
 324 **between distributions simulated by TROLL 4.0 after calibration of m , a_{CR} and b_{CR} in blue and the ones derived from field inventories**
 325 **of trees with dbh >10 cm in black, at Paracou (left) and Tapajos (right). Observed (black) and simulated (blue) densities of trees**
 326 **with dbh > 10 cm, and aboveground biomass are also provided. All simulated values correspond to the end-state of a 600-year**
 327 **regeneration from bare ground with calibrated values for m , a_{CR} and b_{CR} at each site.**

328 After calibration, the canopy height distribution simulated by TROLL 4.0 matched that measured by lidar aerial scanning
 329 (ALS), with a root mean square error of prediction (RMSEP) of the proportion of 1-m² pixels per 1-m height class below 0.8%
 330 and a correlation coefficient (CC) above 0.91, despite a slight overestimation of low canopy areas in Paracou, at heights below
 331 20 m, and a slight underestimation of high canopy areas, above 40 m in Tapajos (Fig. 2). For example, in Paracou, 4% of the
 332 1-m² pixels scanned by ALS had a canopy height around 25m. An RMSEP of 0.8% means that TROLL simulations could lead
 333 to 3.2 or 4.8% of pixels with a canopy height of 25m. TROLL 4.0 simulations also reproduced the forest understory structure
 334 characterised by basal area (BA) and tree abundance distribution per 1-cm diameter classes for trees < 10 cm dbh at Paracou
 335 (Fig. 3). However, TROLL 4.0 underestimated the number of small trees (2,139 vs. 3,787 trees ha⁻¹), resulting in an
 336 underestimation of basal area (BA = 2.9 vs. 3.7 m² ha⁻¹).

337



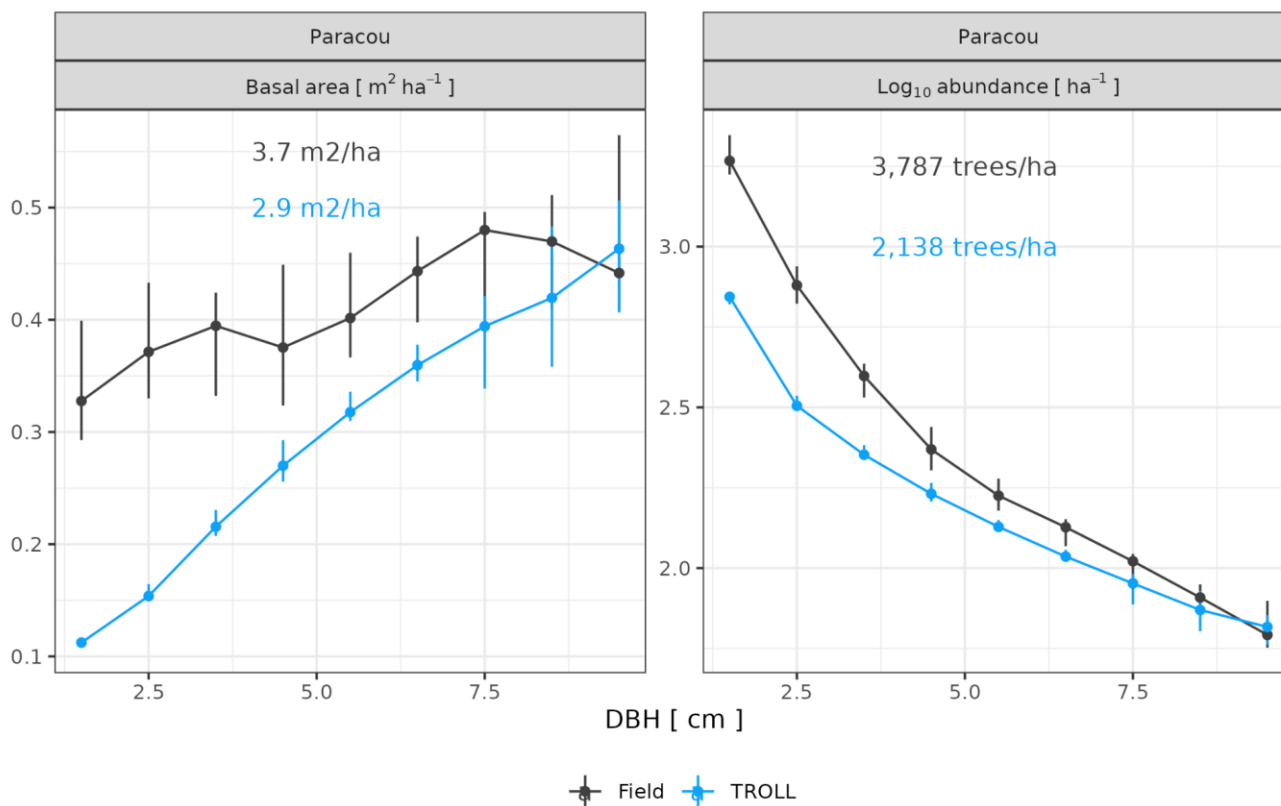
338

339 **Figure 2: Canopy height distribution at Paracou and Tapajos, expressed in proportion of 1-m² pixels (%) per 1-m height classes.**
 340 **Comparison between distributions derived from a canopy height model simulated by TROLL 4.0 (blue lines), the ones derived from**



341
342

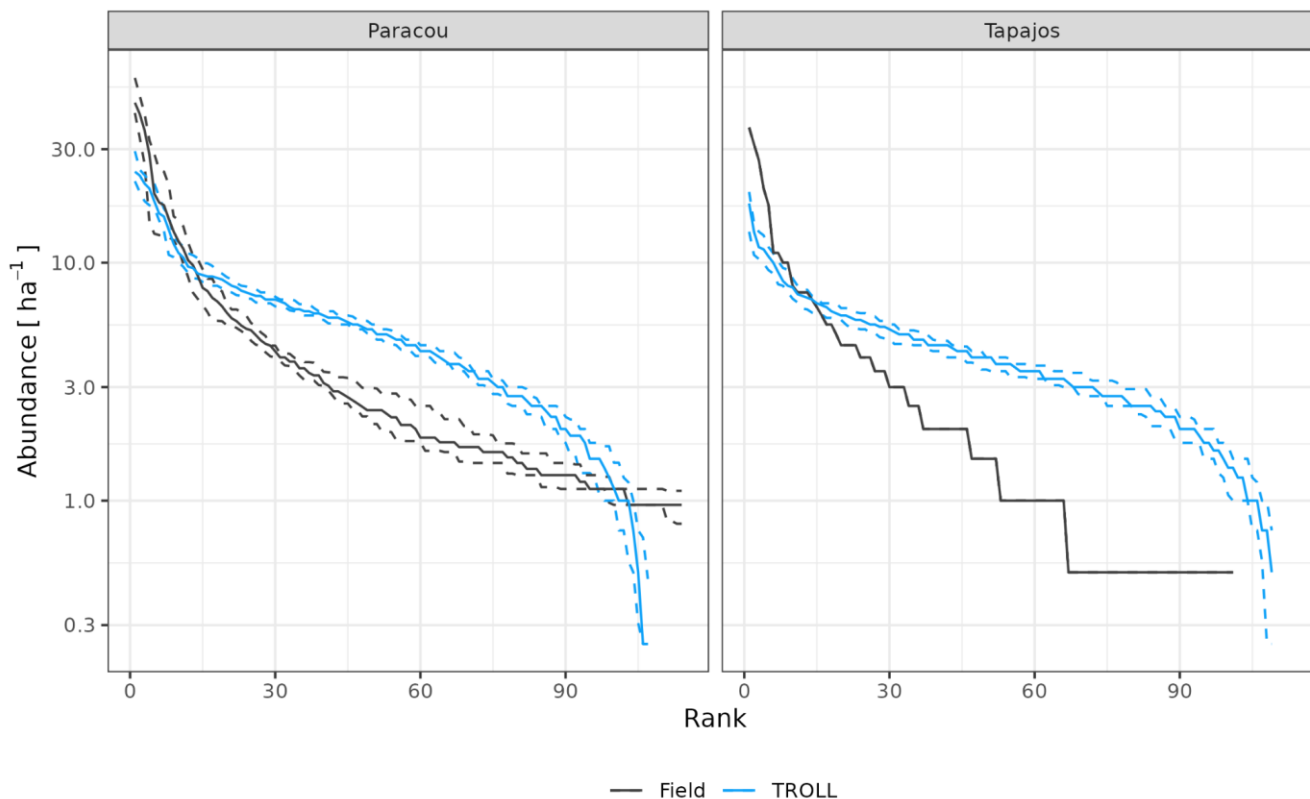
a canopy height model from airborne laser scanning (black lines). Simulated values and their confidence intervals correspond to the end-state of simulations of ten 4-ha 600-year regeneration from bare ground for each site.



343

344 **Figure 3: Understory tree size structure at Paracou, expressed in terms of basal area distributions (left) and tree abundance (right)**
 345 **per 1 cm-dbh classes. The figures compare distributions simulated by TROLL 4.0 in blue and field inventory observations in black.**
 346 **Simulated values and their confidence intervals correspond to the end-state of simulations of ten 4-ha 600-year regeneration from**
 347 **bare ground. Confidence intervals at 95 % are shown with error bars and are based on variations among plots (9 plots of 1 ha) for**
 348 **the observations. Simulated (blue) and observed (black) total basal area (left) and densities (right) for trees with dbh >1 cm and <**
 349 **10 cm are also provided. To the best of our knowledge, similar data was not available in Tapajos.**

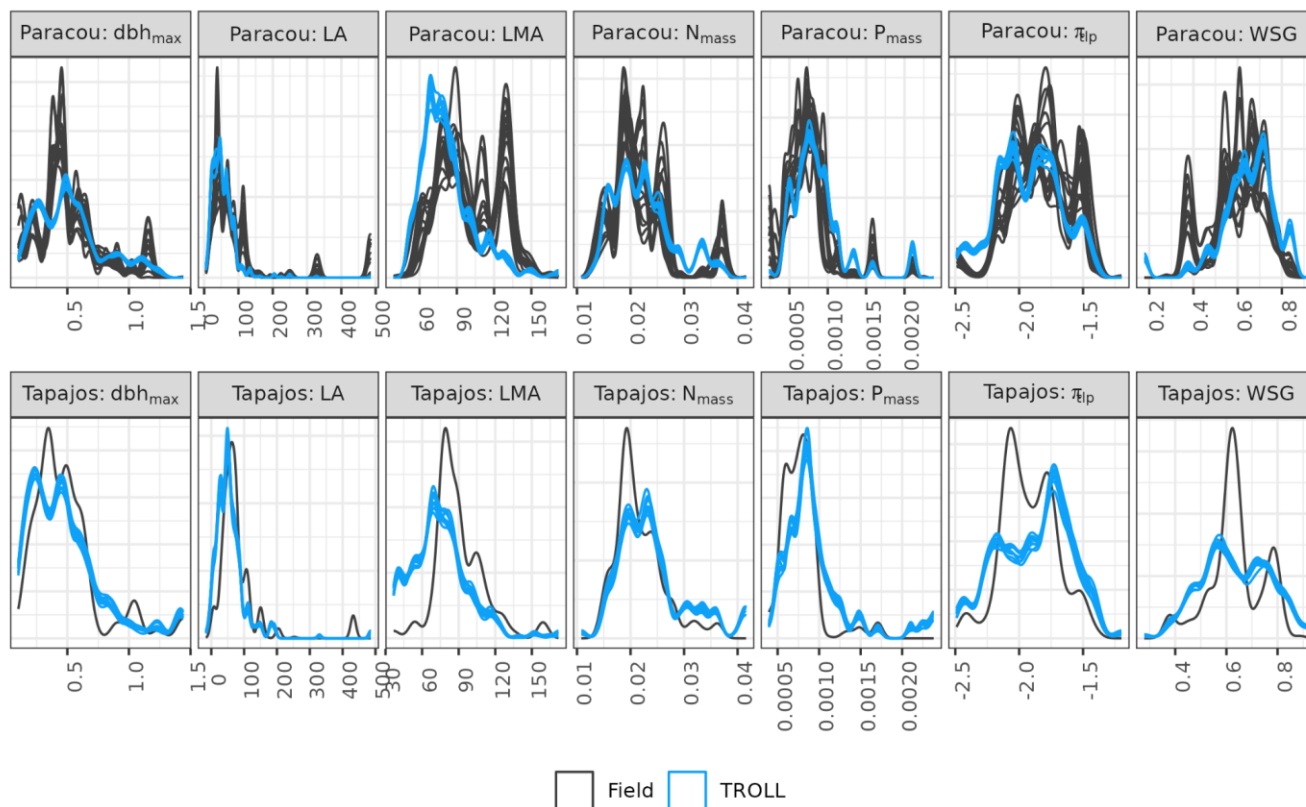
350 At Paracou, the simulated and observed species rank-abundance curves were similar (Fig. 4), with a RMSEP of 3.67 trees ha⁻¹
 351 and a CC of 0.93, but with an underestimation in the abundance of dominant species and an overestimation in the
 352 abundance of rare species resulting in a higher evenness overall. At Tapajos, the simulated and observed rank-abundance
 353 curves displayed similar patterns as at Paracou (RMSEP=3.62 trees ha⁻¹ and CC=0.94) but amplified, with a strong
 354 underestimation of the abundance of dominant species and an overestimation of the abundance of rare species.



355

356 **Figure 4: Species-rank abundance curves at Paracou and Tapajos. Comparisons between curves simulated by TROLL 4.0 (blue)**
357 **and derived from field inventories at both sites. Simulations included 114 and 113 species at Paracou and Tapajos respectively.**
358 **Curves derived from inventories were cut at the 114th species. Simulated values and their confidence intervals correspond to the**
359 **end-state of ten 4-ha 600-year regeneration from bare ground. Confidence intervals at 95 % are shown with error bars and are**
360 **based on variations among plots for observations.**

361 Functional trait distributions simulated by TROLL 4.0 were consistent with empirical ones at Paracou and Tapajos (Fig. 5),
362 with a CC from 0.91 to 1.00 for all traits at both sites, except for leaf area at Paracou (CC=0.74) and Tapajos (CC=0.87).
363 However, abundances of low wood density trees, high LA trees, and high LMA trees were underestimated in simulations
364 when compared to observations at Paracou.



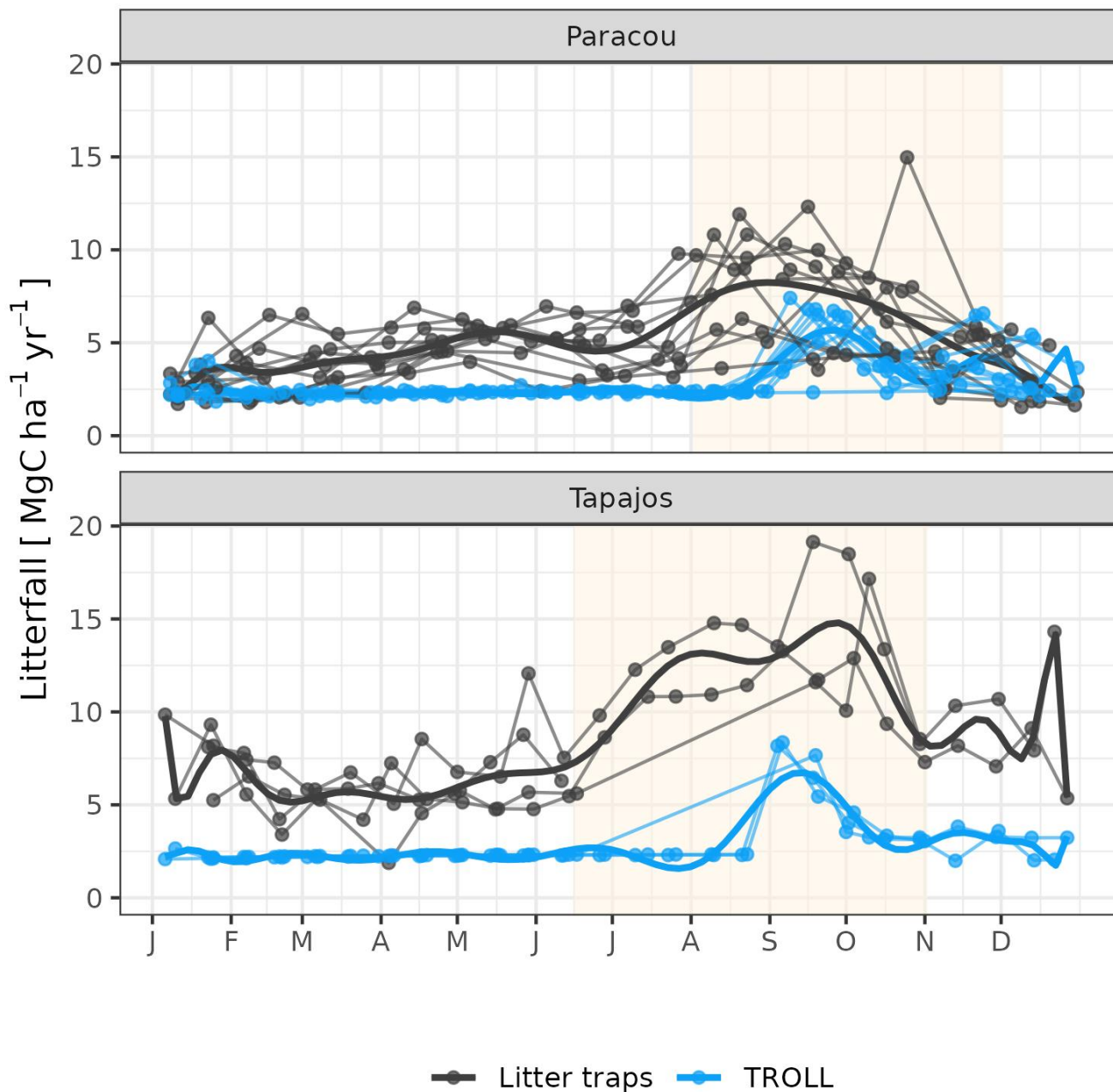
365

366 **Figure 5: Functional trait distributions at Paracou and Tapajos. Distributions derived from field inventories (black) were based on**
 367 **botanical identification at the species level in Paracou and the genus level in Tapajos. Simulated distributions (blue) were based on**
 368 **the final stage of ten 4-ha 600-year regeneration from bare ground. Confidence intervals are shown with repeated lines and are**
 369 **based on variations among plots for observations and among repetitions for simulations. dbh_{max} : maximum diameter in m, LA: leaf**
 370 **area in cm^2 , LMA: leaf mass per area in $g\ cm^{-3}$, N_{mass} : leaf nitrogen content per dry mass in $mg\ g^{-1}$, P_{mass} : leaf phosphorus content**
 371 **per dry mass in $mg\ g^{-1}$, π_{tlp} : leaf water potential at turgor loss point in MPa, WSG: wood specific gravity in $g\ cm^{-3}$.**

372 3.2 Leaf phenology

373 The calibration of the three parameters of the leaf shedding module against observed litterfall illustrated how each parameter
 374 affects the simulated timing and intensity of the litterfall peak during the dry season, with no or little effect on the background
 375 litterfall rate (Fig. A2). Calibration resulted in a best-fit $a_{T,o}$ value of 0.2, and a $b_{T,o}$ value of 0.015 at both sites. The
 376 calibrated δ_o differed across sites ($\delta_o=0.1$ at Paracou and $\delta_o=0.2$ at Tapajos). The simulated seasonal variation of litterfall
 377 at Paracou and Tapajos shows qualitative agreement with the observed data (Fig. 6). Both empirical and simulated data showed
 378 a marked peak in litterfall during the dry season, despite a clear under-estimation of simulated litterfall flux during both wet
 379 and dry seasons, particularly at Tapajos, and a delayed peak during the dry season, particularly at Paracou, in comparison to
 380 observations.

381



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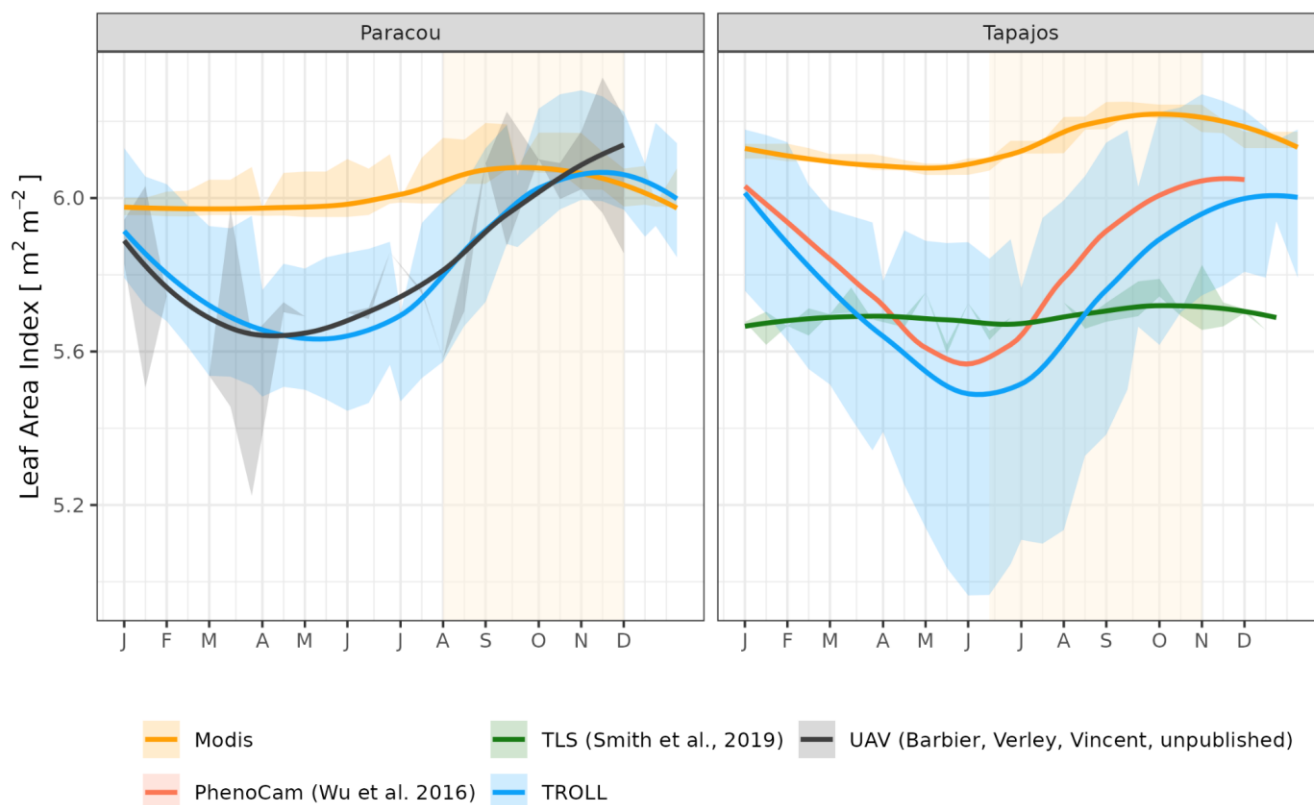
383 **Figure 6: Litterfall annual cycle from fortnightly litterfall fluxes at Paracou and Tapajos. Each thin line represents one year with**
384 **points showing values at sampling dates, the thick lines represent polynomial smoothing among years, and the vertical yellow bands**
385 **in the background correspond to the site's climatological dry season. Simulated values correspond to the last 10 years of 20-year**
386 **simulations starting from the end-state of 600-year regeneration from bare ground with calibrated parameters at each site.**

387 The empirical LAI datasets displayed strikingly different results, illustrating the challenge of estimating LAI with confidence
388 in dense tropical forests (Fig. 7, Tab. A2). MODIS-derived LAI displayed almost no seasonality with mean LAI values



389 around $6.0 \text{ m}^2 \text{ m}^{-2}$ at both sites. At Paracou, LAI derived from UAV-borne lidar showed a clear seasonality, with lowest
 390 values around $5.5 \text{ m}^2 \text{ m}^{-2}$ from April to June and highest values of almost $6.0 \text{ m}^2 \text{ m}^{-2}$ in December, at the end of the dry
 391 season. At Tapajos, LAI derived from terrestrial lidar showed no seasonality, around $5.8 \text{ m}^2 \text{ m}^{-2}$ throughout the year, but LAI
 392 derived from phenological cameras (PhenoCams) did display some seasonality, with lowest values at $5.5 \text{ m}^2 \text{ m}^{-2}$ in June and
 393 highest values above $6.0 \text{ m}^2 \text{ m}^{-2}$ in December, at the end of the dry season. These observations were compared with
 394 simulations. At Paracou, simulated LAI matched the one derived from UAV-borne lidar, both showing an increase during
 395 the dry season ($\text{CC}=0.84$, $\text{RMSEP}=0.11 \text{ m}^2 \text{ m}^{-2}$). At Tapajos, simulated LAI matched the empirical LAI derived from
 396 PhenoCams ($\text{CC}=0.91$, $\text{RMSEP}=0.15 \text{ m}^2 \text{ m}^{-2}$; Table A2).

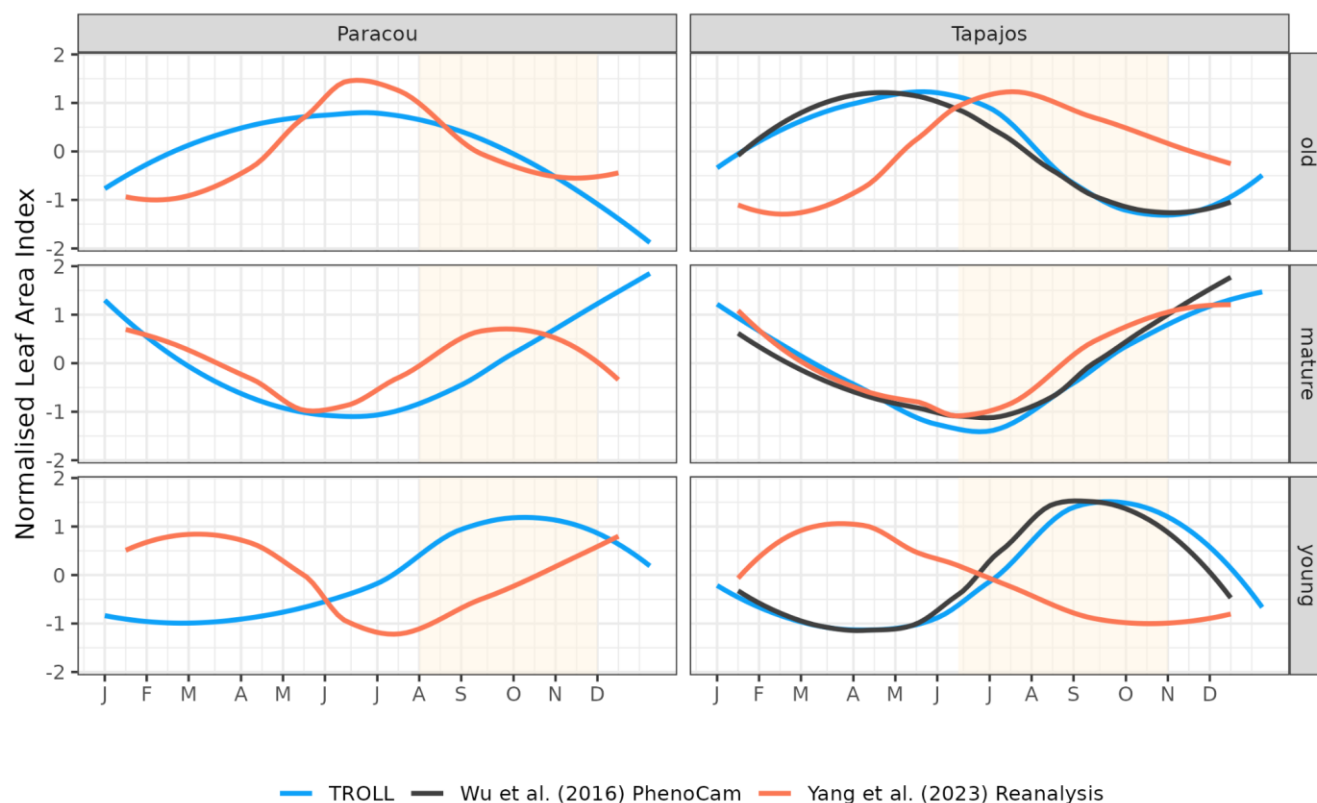
397
 398 The different datasets gathered to estimate LAI dynamics per cohorts also showed contrasted patterns (Fig. 8 and Fig. A3).
 399 At Tapajos, PhenoCams indicate a maximum young leaf LAI reached during the dry season and a minimum during the wet
 400 season, with inverse patterns for old leaf LAI. TROLL 4.0 simulations yielded patterns consistent with these observations
 401 (Fig. 8). However, Yang et al.'s (2023) reanalysis predicts the exact opposite trends for young and old leaves, with a
 402 maximum young leaf LAI during the wet season and a minimum during the dry season. At Paracou, we could only compare
 403 simulated trends against Yang et al. (2023)'s reanalysis and the match was relatively poor (Fig 8).



404



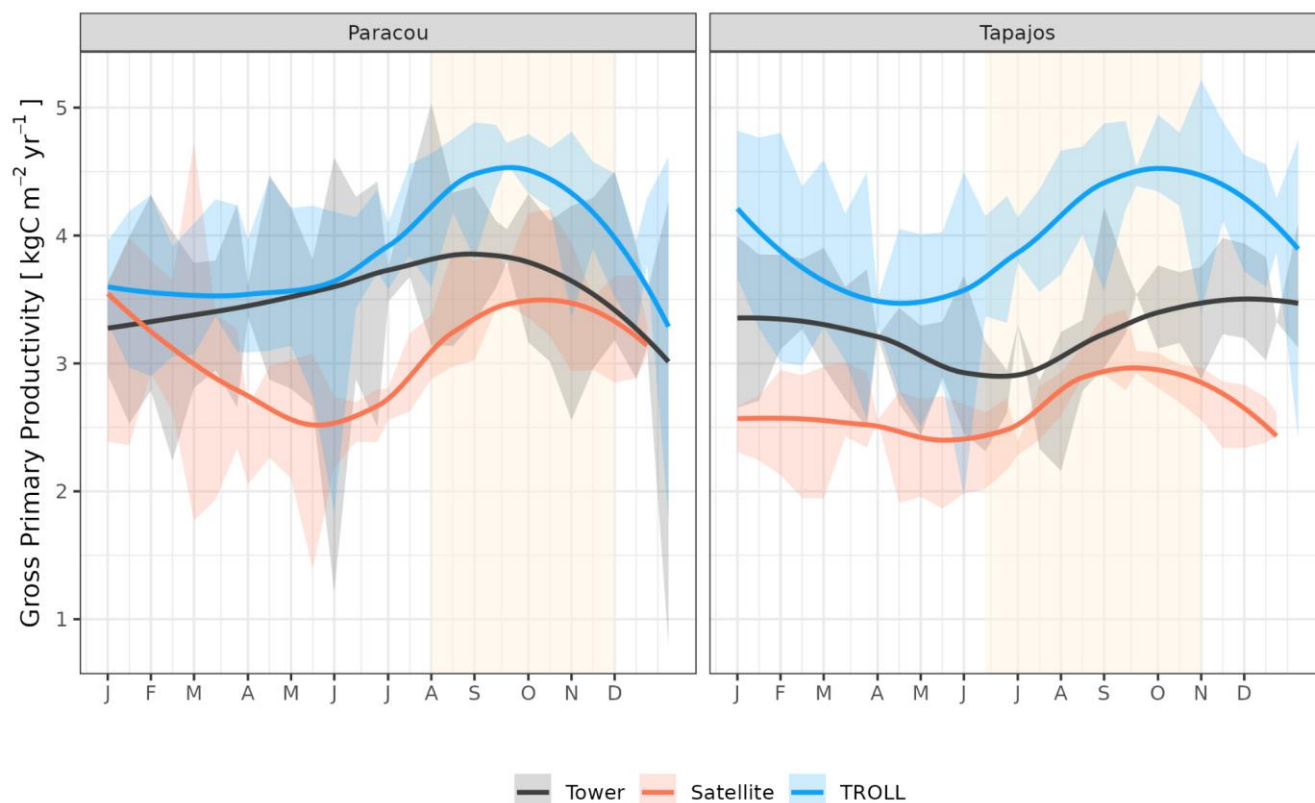
405 **Figure 7: Mean annual cycle of leaf area index (LAI) at Paracou and Tapajos, derived from fortnightly means, from different sources**
 406 **(see methods). Bands are the intervals of means across years, and the vertical yellow bands in the background correspond to the**
 407 **site's climatological dry season. Simulated values correspond to 10 years of simulations starting from the end-state of 600-year**
 408 **regeneration from bare ground with calibrated parameters at each site.**



409 **Figure 8: Mean annual cycle of normalised leaf area index per leaf age cohorts, derived from fortnightly means, at Paracou and**
 410 **Tapajos. Note that the three leaf age cohorts (young, mature and old leaves) are not defined the same way in the three sources. Leaf**
 411 **age per cohort depends on the individual leaf lifespan in TROLL 4.0 (see Maréchaux et al., submitted companion paper), while the**
 412 **transition from young to mature and mature to old are respectively fixed to 1.71 and 5.14 months in Yang et al. (2023) and fitted to**
 413 **1 and 3 months in Wu et al. (2016). The vertical yellow bands in the background correspond to the site's climatological dry season.**
 414 **See figure A3 for absolute variation per cohort, site and dataset. Simulated values correspond to 10 years of simulations starting**
 415 **from the end-state of 600-year regeneration from bare ground with calibrated parameters at each site.**
 416

417 3.3 Water and carbon fluxes

418 TROLL 4.0 captured the seasonality of gross primary productivity (GPP) observed at the two sites, with an increase before the
 419 onset of the dry season, reaching its maximum during the dry season, and a decrease starting before or at the onset of the wet
 420 season (Fig. 9 and see Fig. A4 for interannual variations, Tab. A2). Comparison with eddy flux estimates with simulations
 421 were high both at Paracou (CC=0.60) and Tapajos (CC=0.46). TROLL 4.0 overestimated GPP at both sites, particularly during
 422 the dry season, with a RMSEP of 0.75 and 1.12 kgC m⁻² year⁻¹ when compared with both eddy flux and TROPOMI SIF
 423 estimates at Paracou and Tapajos, respectively.

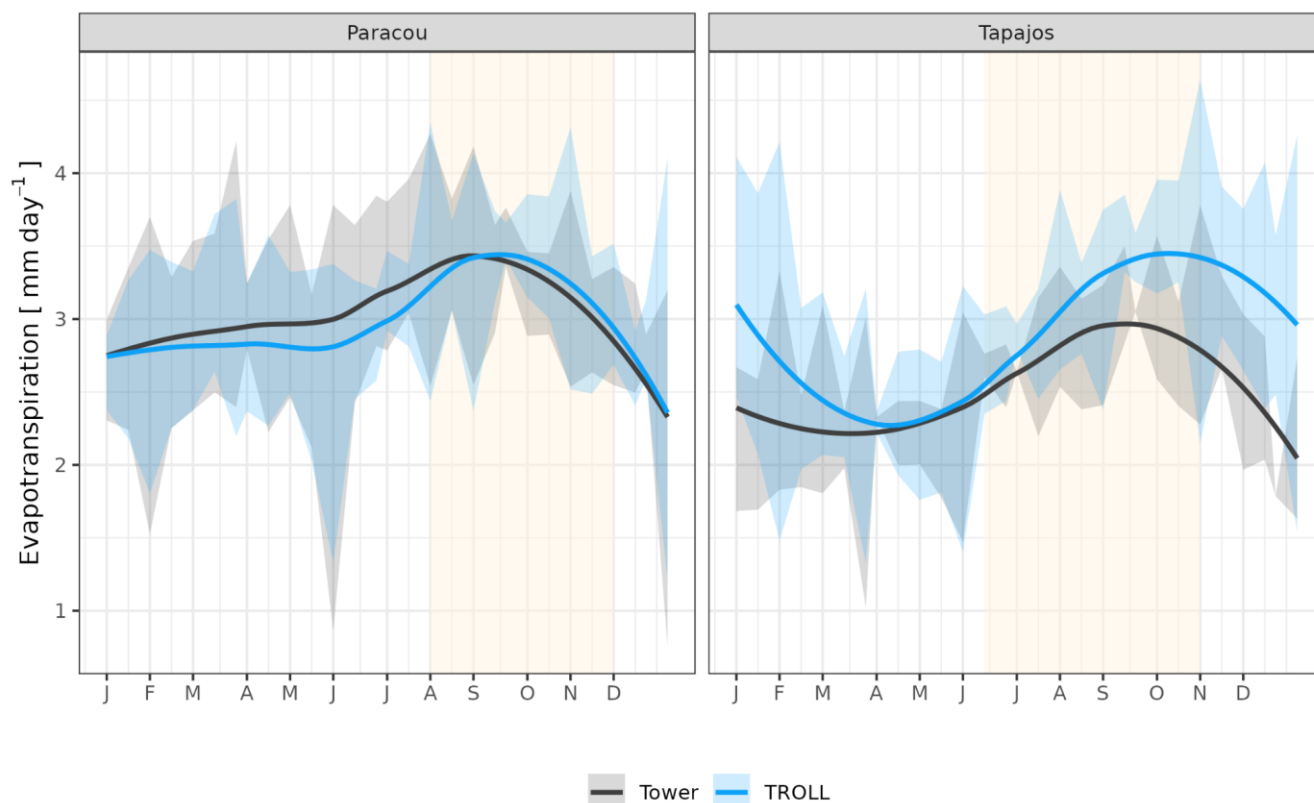


424

425 **Figure 9: Mean annual cycle of gross primary productivity for Paracou and Tapajos, derived from fortnightly means. The red lines**
 426 **represent the gross primary productivity estimated from TROPOMI SIF while the black lines represent the one derived from eddy**
 427 **flux measurements, and the blue lines the simulated gross primary productivity with TROLL 4.0. Bands are the intervals of means**
 428 **across ten years, and the vertical yellow bands in the background correspond to the site's climatological dry season. Simulated values**
 429 **correspond to 10 years of simulations starting from the end-state of 600-year regeneration from bare ground with calibrated**
 430 **parameters at each site. Inter-annual variations are shown in Figure A4.**

431 The seasonality of water flux was captured by TROLL 4.0 (Fig. 10 and see Fig. A5 for interannual variations, Tab. A2), with
 432 a pronounced increase in evapotranspiration (ET) during the dry season at both sites, and leading to CC of 0.66 and 0.70 when
 433 compared with eddy flux estimates at Tapajos and Paracou respectively. Although intra-annual variations of simulated and
 434 observed values overlapped, TROLL 4.0 tended to overestimate ET in Tapajos during the dry season, leading to RMSEP
 435 values of 0.60 and 0.75 mm day⁻¹ when compared with eddy flux estimates at Paracou and Tapajos respectively. TROLL 4.0
 436 also captured the seasonality in RSWC of the top soil layer at Paracou and Tapajos (Fig. A6, Table A2, see Fig. A7 for absolute
 437 variation with varying depth), with a high RSWC in the wet season close to 100% and a sharp decrease in RSWC in the dry
 438 season, although overall smoother in simulations than field estimates.

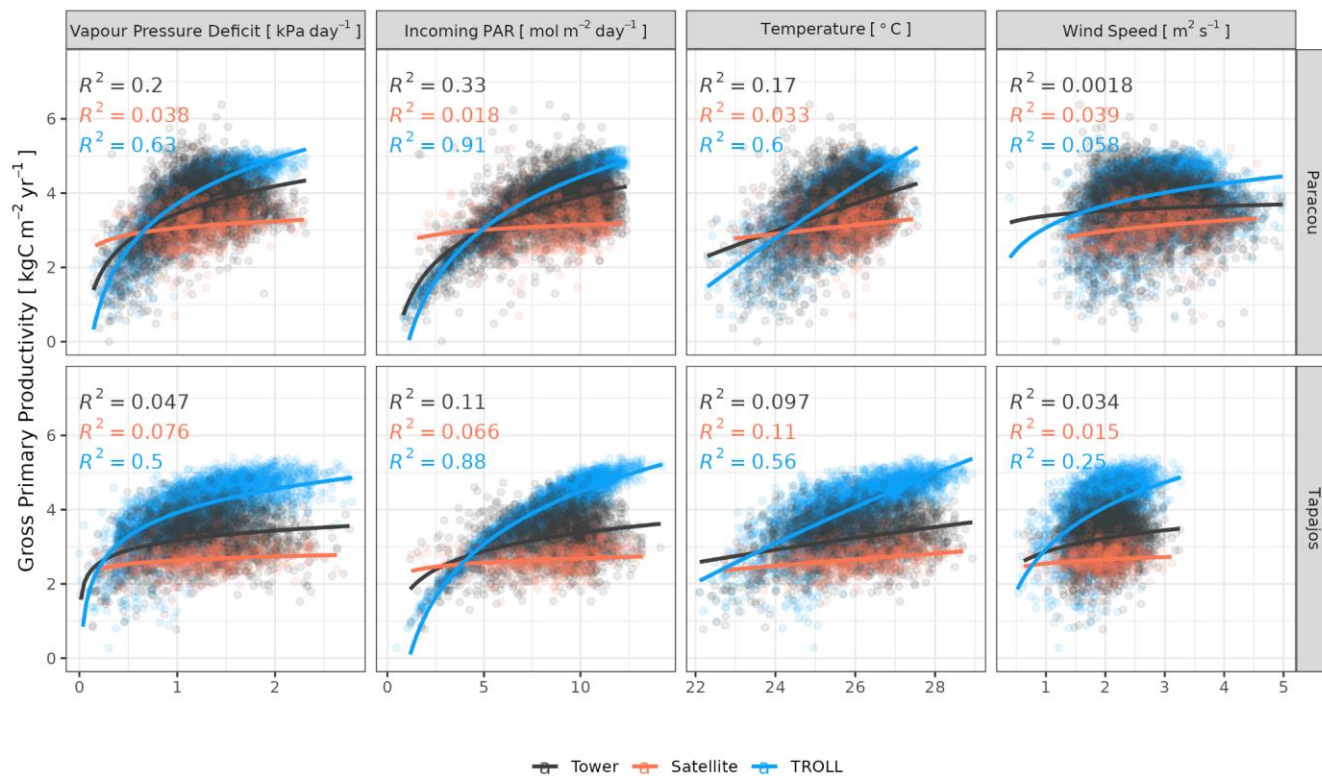
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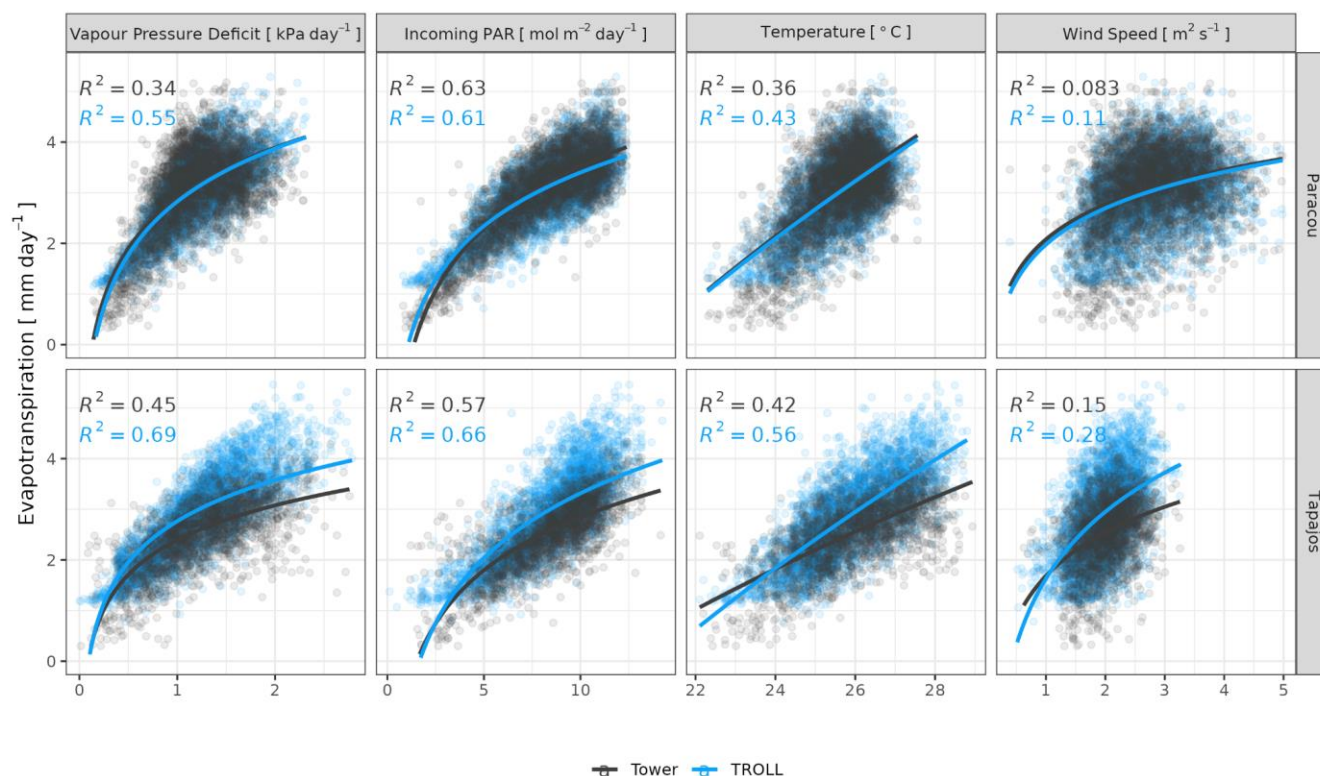
441 **Figure 10: Mean annual cycle of evapotranspiration for Paracou and Tapajos, derived from fortnightly means. The black lines**
 442 **represent the evapotranspiration derived from eddy flux measurements and the blue lines the evapotranspiration simulated with**
 443 **TROLL 4.0. Bands are the intervals of means across years, and the yellow vertical bands in the background correspond to the site's**
 444 **climatological dry season. Simulated values correspond to 10 years of simulations starting from the end-state of 600-year**
 445 **regeneration from bare ground with calibrated parameters at each site. Inter-annual variations are shown in Figure A5.**

446 Both eddy flux-derived and simulated GPP showed a positive logarithmic relationship with cumulative incoming PAR and
 447 maximum VPD, and a positive linear relationship with mean temperature at daily scale (Fig. 11). TROLL 4.0 predicted a
 448 higher PAR conversion to carbon under high irradiance, high VPD and high temperature conditions when compared to eddy
 449 flux estimates, consistent with the higher dry-season GPP in simulations (Fig. 9). Responses of SIF-derived GPP to climatic
 450 variables were weak in comparison to simulated and eddy flux derived GPP. Simulated ET was positively correlated with
 451 maximum VPD, cumulative PAR and mean temperature, similarly to eddy flux derived ET (Fig. 12). At Paracou, the
 452 relationships between environmental drivers and simulated ET, closely aligned with the ones obtained from eddy flux
 453 estimates. However, at Tapajos, simulated ET was overestimated under high irradiance, VPD, temperature and windy
 454 conditions in comparison to eddy flux estimates. Simulated GPP and ET at both sites were more strongly controlled by
 455 environmental variables (higher R^2 in Figs. 11-12) than eddy flux derived GPP and ET.



456

457 **Figure 11: Daily averages of gross primary productivity as a function of daily maximum vapour pressure deficit, total incoming**
 458 **photosynthetically active radiation, average temperature, and average wind speed for model-, satellite- and eddy flux-based**
 459 **estimates at Paracou (top) and Tapajos (bottom). Lines illustrate the linear regression of form $y \sim \log(x)$, and text the squared**
 460 **Pearson's R correlation coefficient.**



461

462 **Figure 12: Daily total evapotranspiration as a function of daily maximum vapour pressure deficit, total incoming photosynthetically**
463 **active radiation, average temperature, and average wind speed for model- and eddy flux estimates at Paracou and Tapajos. Lines**
464 **illustrate the linear regression of form $y \sim \log(x)$, and text the squared Pearson's R correlation coefficient.**

465 **4 Discussion**

466 Here we tested the performance of TROLL 4.0 in reproducing observed forest structure and diversity, but also water and
467 carbon fluxes, and leaf dynamics. We conducted a detailed model evaluation for two Amazonian rainforest sites, Paracou and
468 Tapajos, presenting contrasting climate and soil properties. Both sites have been intensively monitored over the past decades,
469 and we compared the model outputs with available data. We now discuss the consistencies and discrepancies between
470 simulated and observed patterns, potential uncertainties in our results, and the advantages and possible improvements of
471 TROLL 4.0.

472 **4.1 Forest structure and composition**

473 TROLL 4.0 was found to jointly simulate realistic forest structure and species composition (Maréchaux et Chave, 2017). The
474 calibration of three global parameters led to simulated tree abundances across size classes and basal area or aboveground
475 biomass in good agreement with observations from forest inventories. Also, aerial lidar data allowed forest structure to be
476 assessed independently of calibration data. This revealed a good ability of TROLL 4.0 to simulate the horizontal and vertical



477 structure of both forests, which is promising for various applications, including biomass estimation (Knapp et al., 2018).
478 Understory inventories at Paracou also allowed us to independently evaluate TROLL 4.0's ability to simulate tree community
479 structure in the 1 to 10-cm tree diameter range. TROLL 4.0 simulated the distribution of smaller trees reasonably well, although
480 it underestimated individuals from the smallest cohorts. This underestimation of the density of small trees may be partly
481 explained by the fact that the one-metre resolution of the voxel grid used in TROLL 4.0 only allows for one tree per square
482 metre of ground, whereas smaller trees may be squeezed into certain areas of the understory. However the number of
483 simulated small stems remains lower than the maximal potential number in simulations. Another explanation could be the lack
484 of light heterogeneity in the understory in simulations in comparison to observations (Montgomery and Chazdon, 2001), thus
485 limiting the opportunities for recruitment of small stems. Explorations of simulated micro-environmental variations within the
486 canopy (de Frenne et al., 2019) and inclusion of trait ontogenetic shifts (Fortunel et al., 2019) could further help understand
487 and improve TROLL's ability to simulate forest structure in the understory.

488
489 TROLL 4.0 attributes individual trees to botanical species and it permits tree functional traits to vary within species. It thus
490 provides a finer-grained description of biodiversity compared to models based on plant functional types (e.g. Longo et al.,
491 2018), and uses a description matching the one of ecologists, in contrast with taxonomy-free continuous trait spectrum
492 approaches (e.g. Sakschewski et al., 2015). The simulated species composition presented classically observed L-shaped profile
493 of species rank abundance distribution in the two sites, but with an over-estimated species evenness resulting in under-abundant
494 dominant species and over-abundant rare species, as already observed in previous versions of the model (Maréchaux and
495 Chave, 2017). Several simulation factors could have resulted in the overestimation of species evenness. The species trait values
496 were extracted from global databases and partially imputed and may therefore not represent the true trait values for the region
497 concerned, which could affect the behaviour of individual species in the model. However, as this noise is random, it seems
498 unlikely that the global values and imputation have led to the skewed species abundance. More likely, the simulations used an
499 external seed rain representing immigration from a continuous forest matrix. We here implemented a homogeneous seed rain,
500 in which all species are equally-abundant, as a conservative test of the model's ability to represent community assembly. Here,
501 the simulated composition after regeneration from bare ground is determined by species traits and their simulated effect on
502 demographic processes and species fitness, rather than prescribed differences in seed rain. However, this homogeneous, and
503 therefore unrealistic, seed rain maintains diversity in the simulated forest with a rescue effect, and can dampen species
504 dominance by promoting less dominant species through a high immigration. The effects of the representation of seed
505 production, dispersal and recruitment on simulated communities should be further explored in the future, especially for
506 projections under disturbance scenarios where forest regeneration is key (Diaz-Yanez et al., 2024, Hanbury-Brown et al.,
507 2022).

508
509 TROLL 4.0 also explicitly simulates forest functional diversity in the community. Simulated functional trait distributions
510 matched well the observed distributions at both sites, as already observed in previous versions of the model (Maréchaux and
511 Chave, 2017). In Paracou, the main discrepancies were the lack of individuals with high LMA (between 120 and 150 g m⁻²),



512 low wood specific gravity (below 0.4 g cm^{-3}) and/or high leaf area (above 100 cm^2). In contrast, in Tapajos, the model tended
513 to simulate lower LMA and less negative turgor loss points on average. Since trait combinations are structured at the species
514 level, and trait integration is high dimensional in tropical forests, with decoupled leaf and wood economic spectra (Baraloto et
515 al., 2010) and weak associations between leaf turgor loss point and other leaf traits (Maréchaux et al., 2019), these
516 discrepancies can be more easily interpreted at Paracou where the trait distributions are built on species-level (and not genus-
517 level) information. Regarding the lack of high LMA individuals, TROLL 4.0 underestimated the abundance of common species
518 such as *Lecythis persistens* or *Licania alba*, which present high LMA. These species come from genera that are hyperdominant
519 across the Amazon basin (ter Steege et al., 2013) but may be underrepresented in the simulations due to the overestimation of
520 species evenness in TROLL 4.0 as discussed above. The lack of light wood and high leaf area individuals can be related to the
521 underestimated abundances of light demanding and pioneer species with fast growth (Chave et al., 2009), such as the ones of
522 the genus *Cecropia*. These species are known to quickly colonise forest gaps under high light conditions, thanks to fast carbon
523 assimilation and growth, and the dispersal of a high number of small, potentially dormant, seeds, leading to an omnipresence
524 of these species in the forest seed bank (Holthuijzen and Boerboom, 1982; Alvarez-Buylla and Martínez-Ramos, 1990). In
525 TROLL 4.0, the seed-size mediated tolerance-fecundity trade-off (Muller-Landau et al., 2010) is assumed to be perfectly
526 equalising, and all species present in the local seed bank and able to strive under the local light availability have the same
527 probability of being recruited per seed. However, this assumption likely disadvantages gap-affiliated species with a
528 colonisation strategy, and could easily be revisited in future model developments.

529 4.2 Leaf phenology

530 We calibrated and evaluated the new phenology module of TROLL 4.0. The calibration of the three module parameters ($a_{T,o}$,
531 $b_{T,o}$ and δ_o), which together control the variation of old leaf fall under drying conditions, was conducted using litterfall trap
532 data. This resulted in a realistic litterfall seasonality with a peak during the dry season as already documented (Manoli et al.,
533 2018, Chave et al., 2010, van Langenhove et al., 2020). Interestingly, the calibration resulted in the same values for two
534 parameters at the two sites ($a_{T,o}$, $b_{T,o}$) and close values for the third one (δ_o) to which the simulated litterfall pattern is less
535 sensitive (Fig. A2). At both sites, simulations with the mean value of the third parameter resulted in similar evaluations (not
536 shown). This suggests a good transferability of the phenology module across sites without the need for site-specific calibration,
537 although this remains to be further tested at additional sites and in contrasted conditions (e.g. Restrepo-Coupe et al., 2017). A
538 faster shedding of old leaves was assumed to depend on soil water potential in the root zone, rather than soil water content, on
539 individual leaf water potential at turgor loss point, and on tree size. These are biologically reasonable hypotheses and this
540 supports a good generality of the module. However, the current implementation of leaf dynamics in TROLL 4.0 leads to an
541 underestimation of the flux of litterfall in wet and dry seasons and, as a result, of total annual litterfall at both sites. In TROLL
542 4.0, leaf lifespan was parameterized based on an empirical relationship with leaf structure (leaf mass per area; Maréchaux et
543 al., companion paper). Previous relationships provided in the literature (Reich et al., 1991; Reich et al., 1997; Wright et al.,
544 2004) provided contrasting leaf lifespan estimates, with the one implemented in TROLL 4.0 providing among the highest
545 values, calling for a more in-depth exploration of the reliability and transferability of these empirical relationship. Alternative



546 representations, such as the ones based on optimality principles (Kikuzawa 1991, Franklin et al., 2020, Manzoni et al., 2015),
547 and their combination with the environmentally-driven old leaf shedding acceleration implemented in the new module could
548 be explored in the future.

549
550 The evaluation of leaf area index (LAI) and its dynamics was difficult due to the number of products that yield inconsistent
551 time series. Remotely sensed MODIS LAI showed a very small seasonal variation with a slight increase of LAI starting at the
552 beginning of the dry season at both sites. However, MODIS LAI data products are known to be susceptible to the uncertainty
553 affecting the bidirectional reflectance, and to saturate at high LAI values (Petri and Galvão, 2019). Local measurements of
554 LAI through UAV-borne lidar in Paracou showed a stronger increase of total LAI of $0.5 \text{ m}^2 \text{ m}^{-2}$ starting at the beginning of
555 the dry season, and leading to a maximum in the dry season. This pattern of variation was in strong agreement with that
556 simulated for LAI by TROLL 4.0. Similarly, local measurements of top canopy LAI derived from phenological cameras in
557 Tapajos (Wu et al., 2016) also showed a high increase of total LAI in the dry season, above $0.5 \text{ m}^2 \text{ m}^{-2}$, also in good agreement
558 with the seasonal LAI variation simulated by TROLL 4.0 at that site. By contrast, the LAI derived from terrestrial vertical
559 lidar in Tapajos showed almost no variations (Smith et al., 2019), and such differences with both the patterns derived from
560 phenological cameras and simulations need to be further scrutinised. Among potential explanations, LAI from TLS in Tapajos
561 was adjusted to the annual mean of 5.7 (Stark et al., 2012), leading to lower absolute variations than what was obtained
562 elsewhere, and used coarse spatial and temporal resolutions over small spatial and temporal extents (see material and methods).
563 The discrepancy with simulated patterns could also be linked to uncertainties in LAI variations in the understory in our
564 simulations. Recent studies have suggested opposite variations in LAI between the canopy and the understorey (Nunes et al.,
565 2022), which should be further explored with TROLL 4.0. Overall, while obtaining a robust estimate of LAI temporal variation
566 in tropical forests remains a challenge (Vincent et al., 2023; Bai et al., 2023), the relative variation of LAI simulated by TROLL
567 4.0 matched the most reliable products at each site, providing an encouraging assessment of this model's ability. Importantly,
568 while total LAI variation remains limited on average within a year in tropical rainforests, this hides important turnover across
569 leaf ages and species, and to ensure robust predictions models should endeavour to represent such turnover and its underlying
570 processes (Wu et al., 2017).

571
572 The dry-season increase in total LAI simulated in TROLL 4.0 corresponds to a rejuvenation of the canopy leaf cover associated
573 with a decrease in the LAI of old leaves at the beginning of the dry season, directly followed by an increase in the LAI of
574 young leaves during the dry season. This turnover is in very good agreement with the one captured by phenological cameras
575 at Tapajos (Wu et al., 2016) and documented in other studies (Yang et al., 2021; Doughty and Goulden, 2008), while the SIF-
576 derived young LAI pattern (Yang et al., 2023) showed an opposite pattern at this site. The main difference in simulated cohorts
577 between the two sites is the continuous dominance of old LAI in Tapajos while mature leaves dominated at the end of the dry
578 season in Paracou. This dominance of older (and less efficient) leaves in Tapajos simulations may be linked to the
579 underestimated litterfall flux and soil water depletion during the dry season at this site. However, the relative proportion of
580 leaf area across the different leaf age pools within and across datasets strongly depends on the definition of the leaf age pools



581 themselves. These pools depend on the individual leaf lifespan in TROLL 4.0 (see section 2.6.2 in Maréchaux et al., [submitted](#)
582 [companion paper](#)), while the transition from young to mature and mature to old are respectively fixed to 1.71 and 5.14 months
583 in Yang et al. (2023) and fitted to 1 and 3 months in Wu et al. (2016). These contrasting approaches may explain the higher
584 relative importance of old leaves in Wu et al. (2016) compared to Yang et al. (2023) and the intermediate values of TROLL
585 4.0 (Fig. 6). The seasonal dynamics of leaf cohorts remains poorly known in tropical forests and additional high-resolution
586 optical imagery, *e.g.* by drones or phenological cameras, would be extremely useful to better document these patterns.

587 **4.3 Water and carbon fluxes**

588 At Tapajos, DGVMs simulated opposite seasonal trends in carbon and water fluxes compared to the observed ones (*e.g.* Fig.
589 1 in Chen et al., 2020; Fig. 5 in Longo et al., 2019b; Fig. 3 in Restrepo-Coupe et al., 2017). In contrast, TROLL 4.0 showed a
590 good ability to represent the dynamics of both carbon and water fluxes estimated with eddy covariance data. In particular,
591 TROLL 4.0 captures the dry season increase in gross primary productivity (GPP) and evapotranspiration (ET) documented for
592 light-limited forests (Guan et al. 2017, Wagner et al. 2016, Aguilos et al. 2018). Simulated GPP and ET also presented realistic
593 daily responses to environmental drivers, namely vapour pressure deficit (VPD), temperature, incident radiation and wind
594 speed, both in direction and relative magnitude.

595
596 However, at Tapajos, we found that TROLL 4.0 overestimated ET during the dry season in comparison to eddy flux-derived
597 ET values, under high irradiance, high VPD and high temperature. Simulated ET consists in tree transpiration summed over
598 simulated individuals, water evaporation from the topsoil layer, and the direct evaporation of the rainfall intercepted by the
599 canopy (Kunert et al., 2017). TROLL 4.0 may underestimate the stomatal control of transpiration during the dry season at
600 Tapajos. Accordingly, the control of ET by atmospheric conditions in Tapajos was overestimated in simulated data in
601 comparison to observations, suggesting a stronger coupling of vegetation and atmosphere at that site than simulated (de Kauwe
602 et al., 2017). Underestimation of stomatal control can result from the representation of stomatal conductance and its responses
603 to soil water availability. These are active areas of research and alternative representations could be considered in the future
604 (Wolf et al. 2016; Anderegg et al. 2018; Sabot et al., 2022, Lamour et al., 2022; see sections 2.5.2 and 2.5.3 and Appendix B
605 in Maréchaux et al. [submitted companion paper](#)). Alternatively, during the dry season, a lack of stomatal control can be due to
606 an overestimation of soil water availability in the model. Soil water content dynamics depend on both the soil depth (Fig. A7)
607 and on the soil hydraulic properties. The two sites are known to present heterogeneity in soil properties but we here performed
608 simulations with homogenous soil properties, both horizontally and vertically. For instance in Paracou, the topsoil layer is
609 sandier than the 15-30 cm layer (Van Langenhove et al., 2021). Although TROLL 4.0 quantitatively captures the soil water
610 depletion observed during the dry season, it appears to underestimate this depletion compared to empirical estimates at both
611 sites (Fig. A6). This underestimation occurs in spite of the agreement between simulated and eddy covariance-derived ET
612 during the dry season in Paracou, and of the higher simulated than eddy-covariance-derived ET during the dry season at
613 Tapajos. Testing the model's sensitivity to soil layer thickness and properties will be important to perform prior to forest
614 projections under drier future conditions and model spatial up-scaling (Meunier et al., 2022). For example, simulations with



615 the ED2 model suggested that forest responses to drier conditions at Tapajos strongly depended on soil texture (Longo et al.,
616 2018). Finally, the greater disagreement between simulated and eddy-covariance-derived ET at Tapajos than Paracou also calls
617 for an in-depth evaluation of the global reanalysis precipitation data at this site. More generally, climate of the Amazon is
618 notoriously challenging for models and it is important to further explore climate forcings in vegetation models.

619
620 TROLL 4.0 tended to overestimate empirical GPP estimates, particularly during the dry season, in comparison to both eddy
621 covariance- and SIF-derived GPP. GPP is driven by the photosynthetic activity of the canopy, which depends on multiple
622 processes (Diao et al., 2023; Slot et al., 2024) and further work would be needed to precisely discriminate among them, while
623 accounting for eddy covariance uncertainties (Cui and Chui, 2019). Among others, simulated GPP is sensitive to the parameters
624 that control light transmission and absorbance (light extinction coefficient, apparent quantum yield; Maréchaux & Chave,
625 2017). Both are assumed fixed and constant in simulations, but are known to vary with leaf angle distribution and leaf optical
626 properties, depending on micro-environmental conditions and species (Long et al., 1993; Poorter et al., 1995; Meir et al., 2000;
627 Kitajima et al., 2005). Also, the response of leaf-level gas exchanges to soil water availability shows no clear consensus across
628 models (Powell et al., 2013; Trugman et al., 2018), and could be underestimated during the dry season in TROLL 4.0
629 simulations. Simulated GPP was higher than inferred from eddy covariance data, which was itself higher than GPP inferred
630 from SIF satellite data (Chen et al., 2022). The eddy covariance-derived GPP were obtained from the net ecosystem exchanges
631 using the nighttime partitioning method (Reichstein et al., 2005). This method was developed for temperate forests with greater
632 temperature variations than tropical forests, which could therefore bias the empirical estimates. In addition, the eddy flux
633 method has long been reported to underestimate CO₂ fluxes (Baldocchi, 2003; Gao et al., 2019). Similarly, even though solar
634 induced fluorescence offers a great potential for the evaluation or the calibration of seasonal carbon fluxes in vegetation
635 models, especially as the tropics are underrepresented by eddy flux tower networks (Villarreal et Vargas, 2021), current SIF
636 products should be used with care (Marrs et al., 2020).

637 **5 Conclusions**

638 Here we evaluated the TROLL 4.0 individual-based forest dynamics model, which is capable of jointly simulating forest
639 structure, diversity and functioning. To this end, we assembled data from forest inventories, eddy flux towers, litterfall traps,
640 UAV-borne and terrestrial lidar, phenological cameras, and satellite products at two Amazonian forest sites and found that
641 TROLL 4.0 was able to realistically simulate the forest structure and composition, water and carbon fluxes, and leaf area
642 dynamics. In using data of different nature and under the control of different processes, we limited the emergence of equi-
643 finality issues (Medlyn et al., 2005), suggesting a good transferability and robustness of TROLL 4.0.

644
645 Comparison with field inventories, aerial and satellite data confirm TROLL 4.0's ability to realistically simulate the structure
646 and composition of tropical forests, without imposing constraints beyond the species pool and calibrating more than three
647 parameters. Discrepancies between observed and simulated tree abundances in small size classes and abundance of trait values



648 specific to colonising species suggest further developments of regeneration processes are needed, a worthy endeavour in the
649 context of increased disturbance regimes. TROLL 4.0 was further able to simultaneously simulate the seasonality of
650 productivity, evapotranspiration and leaf area in these two light-limited forests, as opposed to many current DGVMs (Chen et
651 al., 2020; Restrepo-Coupe et al., 2017; Longo et al., 2019). The model's ability to simulate ecosystem fluxes is further shown
652 by the responses of carbon and water fluxes to environmental drivers, whose direction and relative importance were well
653 aligned with observations at both sites despite contrasting climate and soil properties. Additionally, the dynamics of total leaf
654 area appeared realistically partitioned into different leaf pools, as shown by the leaf rejuvenation during the dry season in these
655 systems (Wu et al., 2016; Yang et al., 2021). However, further inspection of the leaf area dynamics across the canopy vertical
656 profile would be useful. Also, the model overestimation of productivity and evapotranspiration during the dry season calls for
657 a more in-depth exploration of the model representation of respiration, plant hydraulics (e.g., stomatal control), and soil
658 hydrology.

659

660 Overall, our analyses establish the suitability of TROLL 4.0 for simulating forest structure, diversity and ecosystem functioning
661 in short- and long-term studies of tropical forest dynamics, paving the way for multiple applications (Maréchaux et al., 2021).
662 TROLL 4.0 could thus be used for projections of the effects of climate change on tropical forests, and exploration of the effect
663 of biodiversity on forest resilience to these changes (Sakschewski et al., 2016). Similarly, as TROLL 4.0 retains the species-
664 level taxonomic description, it can also help explore the effects of management practices such as timber production, for which
665 half of tropical forests are designated (Blaser et al., 2011). While the development of TROLL 4.0 will continue, in light of
666 knowledge improvement, novel data collection and identification of uncertainties and discrepancies, we believe it represents
667 a valuable tool for addressing the major challenges tropical forests are currently facing.

668 **Code and data availability**

669 The TROLL version 4.0 and further developments are publicly available on GitHub as a C++ standalone at
670 <https://github.com/TROLL-code/TROLL> or wrapped into an R package at <https://github.com/sylvainschmitt/rcontrol/>. All the
671 code associated with the analyses described in this paper are available at https://github.com/sylvainschmitt/troll_eval and
672 permanently stored at [add a zenodo doi after acceptance](#) with corresponding analyses notebook at
673 https://sylvainschmitt.github.io/troll_eval/. Inventories data for Paracou trees over 10 cm are available through request on the
674 CIRAD dataverse: <https://dataverse.cirad.fr/dataverse/paracou>. Paracou trees understory trees are available through request,
675 PI: GS, GD, JC. Aerial Lidar Scanning from Paracou are available through request (PI: GV) and from dos-Santos et al. (2019)
676 for Tapajos. Species data are available from Jucker et al., (2022), Maréchaux et al., (2015), Guillemot et al., (2022), Vleminckx
677 et al., (2021), Maréchaux et al., (2019), Nemetschek et al., (2024), Schmitt and Boisseaux (2023), Boisseaux et al., (submitted),
678 Ziegler et al., (2019), Baraloto et al., (2010), and from TRY (Kattge, Bönišch, et al., 2020). Soil data have been collected from
679 Van Langenhove et al., (2021), Silver et al., (2000), Quesada et al., (2010), Sabatier et al., (1997), and Nepstad et al., (2002).
680 Eddy covariance data from Paracou and Tapajos sites are available on FLUXNET at <https://fluxnet.fluxdata.org> (last access:



681 6 September 2023). ERA5-Land data are available on the Climate Data Store:
682 <https://cds.climate.copernicus.eu/cdsapp#!/dataset/reanalysis-era5-land?tab=overview>. TROPOMI SIF satellite data are
683 available in Chen et al., (2022). Litterfall data at Tapajos are available online through the Oak Ridge National Laboratory
684 (ORNL) Distributed Active Archive Center (DAAC): https://daac.ornl.gov/LBA/guides/CD10_Litter_Tapajos.html and upon-
685 request at Paracou, PI: DB. MODIS LAI data are available online and were extracted from PLUMBER2 on Research Data
686 Australia: <https://researchdata.edu.au/plumber2-forcing-evaluation-surface-models/1656048>. Terrestrial LAD data from
687 Tapajos are available in Smith et al., (2019). Lidar PAD data from Paracou are available upon-request, PIs: NB and GV. LAI
688 variations among young, mature and leaf cohorts are available from the reanalysis of Yang et al. (2023) at:
689 [https://figshare.com/articles/dataset/Leaf_age-dependent_LAI_seasonality_product_Lad-](https://figshare.com/articles/dataset/Leaf_age-dependent_LAI_seasonality_product_Lad-LAI_over_tropical_and_subtropical_evergreen_broadleaved_forests/21700955/4)
690 [LAI_over_tropical_and_subtropical_evergreen_broadleaved_forests/21700955/4](https://figshare.com/articles/dataset/Leaf_age-dependent_LAI_seasonality_product_Lad-LAI_over_tropical_and_subtropical_evergreen_broadleaved_forests/21700955/4) and from the phenological camera of Wu et
691 al., (2016) at: <https://datadryad.org/stash/dataset/doi:10.5061/dryad.8fb47>. Tapajos soil moisture data from Restrepo-Coupe et
692 al. (2024) are available at: <https://datadryad.org/stash/dataset/doi:10.5061/dryad.d51c5b08g>.

693 **Author contributions**

694 SS and IM designed the model assessment and carried out the TROLL 4.0 simulations. SS, FJF, JC and IM developed TROLL
695 4.0. SS, FJF, NB, MB, DB, BB, XC, GD, JL, DM, NRC, ScS, GS, PV, GV, CZ, JC, IM contributed to the data collection and
696 compilation. SS and IM wrote the paper.

697 **Competing interests**

698 The authors declare that they have no conflict of interest.

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1153 **Appendix**

1154 **Table A1: TROLL 4.0 global parameters.**

Abbreviation	Definition	Units	Value	Nature*	Reference
c_a	Carbon free air concentration	$\mu\text{mol mol}^{-1}$	375	Constant	
P_{ress}	Atmospheric pressure	kPa	101	Constant	
k_{geom}	Light extinction coefficient, reflecting leaf geometric arrangement	unitless	0.5	Constant	Ross 1981
$\text{absorptance}_{\text{leaves}}$	leaves absorptance	unitless	0.83	Literature	Long et al., 1993; Poorter et al., 1995
θ	Curvature factor (Farquhar model parameter)	unitless	0.7	Literature	Farquhar et al., 1980
g_0	leaf minimum conductance for water vapor	$\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$	5	Literature	Duursma et al., 2019
$a_{T,o}$	Phenological parameter that modulates old leaf drought tolerance	unitless		Calibrated	
$b_{T,o}$	Phenological parameter that modulates the height dependence of leaf susceptibility to drought	MPa		Calibrated	
δ_o	Phenological parameter that controls the pace of old leaf shedding acceleration	unitless		Calibrated	
f_{wood}	Fraction of carbon allocated to wood	unitless	0.35	Literature	Aragão et al., 2019; Malhi et al., 2011
f_{canopy}	Fraction of carbon allocated to canopy		0.25	Literature	Aragão et al., 2019; Malhi et al., 2011
f_{gap}	Fraction of gaps in the tree crown		0.15	Literature	Fischer et al., 2019



a_{CR}	Crown radius intercept	unitless		Calibrated	
b_{CR}	Crown radius slope	unitless		Calibrated	
a_{CD}	Crown depth intercept	m	0	Literature	Chave et al., 2005
b_{CD}	Crown depth slope	unitless	0.2	Literature	Chave et al., 2005
$shape_{crown}$	Crown shape parameter		0.72	Calibrated	
N_{tot}	Intensity of the external seed rain	seeds ha ⁻¹	50,000	Assumed	
n_s	Number of reproduction opportunities per mature tree	seeds tree ⁻¹	10	Assumed	
m	Reference background mortality	death year ⁻¹		Calibrated	
v_T	Variance of the flexion moment for treefall		0.021	Calibrated	
σ_h	Intraspecific variation in height (log scale)	m	0.19	Inferred	Baraloto et al., 2010
σ_{cr}	Intraspecific variation in crown radius (log scale)	m	0.29	Calibrated	Fischer et al., 2019
σ_{cd}	Intraspecific variation in crown depth (log scale)	m	0		
σ_{dbhmax}	Intraspecific variation in maximum diameters (log scale)	m	0.05	Inferred	Baraloto et al., 2010
$corr_{cr-h}$	Intraspecific correlation between crown radius and height		0		
σ_P	Intraspecific variation in phosphorus (log scale)	mg g ⁻¹	0.24	Inferred	Baraloto et al., 2010
σ_N	Intraspecific variation in nitrogen (log scale)	mg g ⁻¹	0.12	Inferred	Baraloto et al., 2010
σ_{LMA}	Intraspecific variation in leaf mass per area (log scale)	g m ⁻²	0.24	Inferred	Baraloto et al., 2010



σ_{wsg}	Intraspecific variation in wood specific gravity	g cm^{-3}	0.06	Inferred	Baraloto et al., 2010
σ_{LA}	Intraspecific variation in leaf area (log scale)	cm^2	0.48	Inferred	Schmitt and Boisseaux 2023
σ_{tlp}	Intraspecific variation in turgor loss point (log scale)	MPa	0.10	Inferred	Schmitt and Boisseaux 2023
$corr_{N-P}$	Intraspecific correlation between nitrogen and phosphorous		0.65	Inferred	Baraloto et al., 2010
$corr_{N-LMA}$	Intraspecific correlation between nitrogen and leaf mass per area		-0.43	Inferred	Baraloto et al., 2010
$corr_{P-LMA}$	Intraspecific correlation between phosphorus and leaf mass per area		-0.39	Inferred	Baraloto et al., 2010

1155 *Assumed is a value that is supposed; Calibrated is a value that was previously calibrated; Constant is a fundamental physic constant;
 1156 Literature is a value prescribed from the literature.

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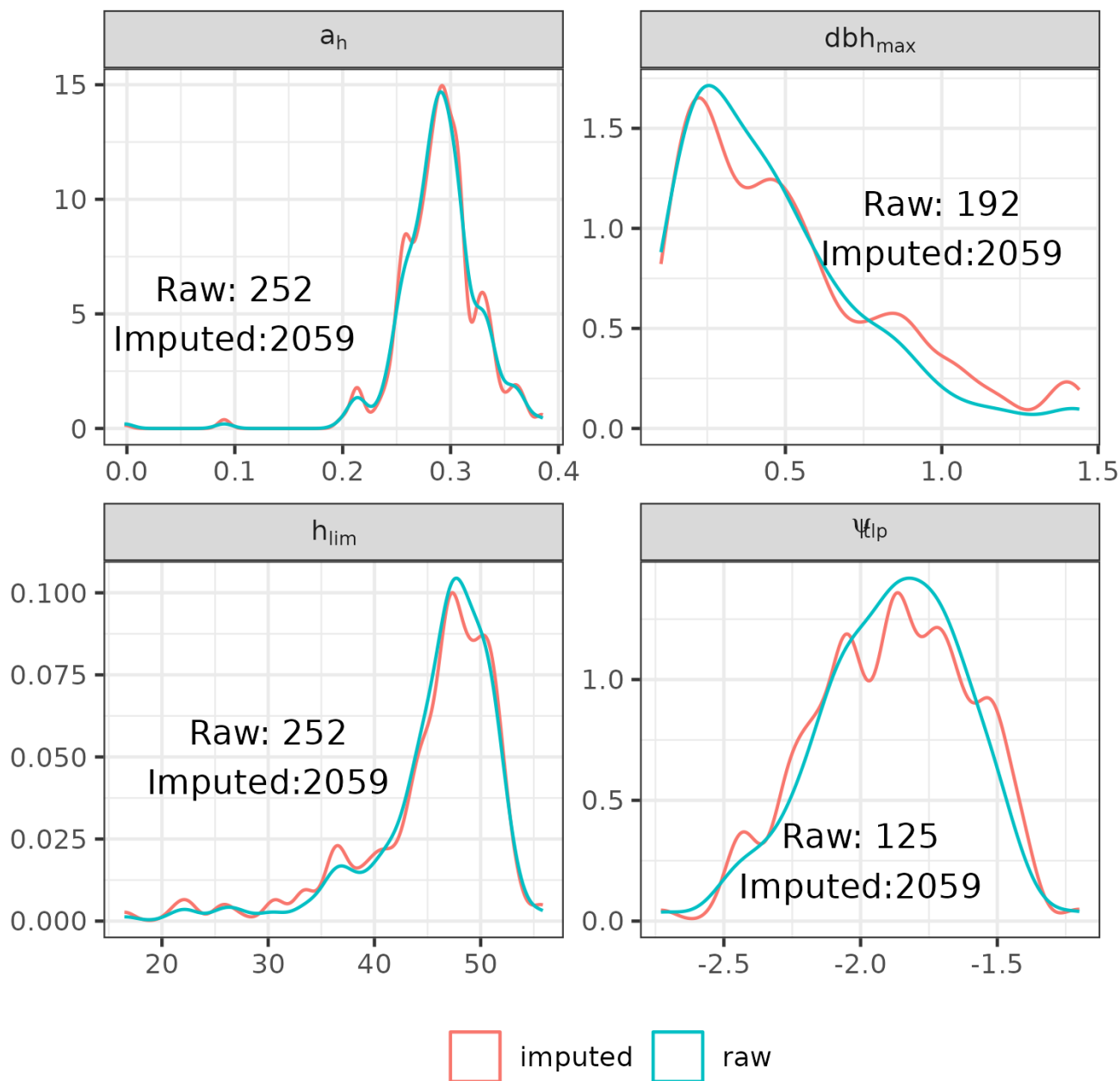


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Table A2: Evaluation of forest structure, composition and fluxes explored at Paracou and Tapajos. Evaluations include the goodness-of-fit R^2 from the linear regression with a null intercept, the Pearson's r correlation coefficient CC , the root mean square error of prediction $RMSEP$, the standard deviation of the error of prediction SD .

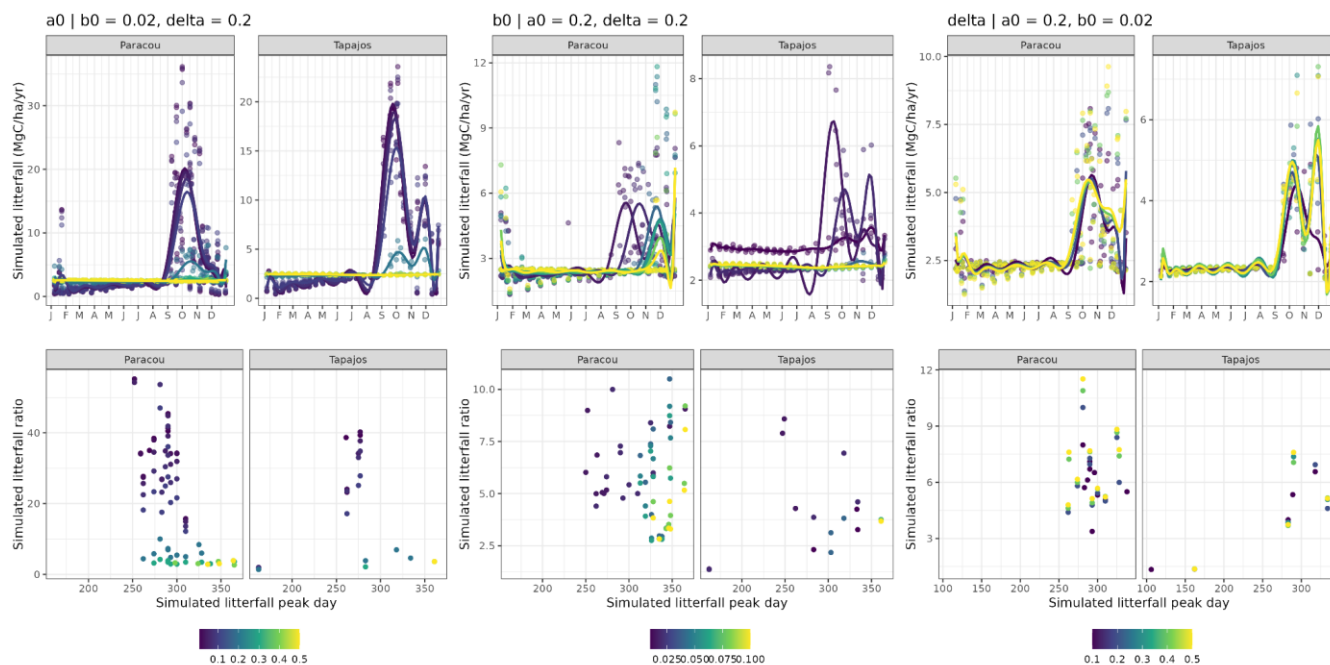
Site	Variable	Unit	Observations	Temporal resolution	R^2	CC	$RMSEP$	SD
Paracou	height	%	Plane	single	0.93	0.95	0.76	0.76
Tapajos	height	%	Plane	single	0.94	0.94	0.56	0.55
Paracou	height	%	Satellite	single	0.95	0.96	0.55	0.55
Tapajos	height	%	Satellite	single	0.92	0.91	0.69	0.62
Paracou	BA understory	$m^2 ha^{-1}$	Inventory	single	0.94	0.90	0.12	0.08
Paracou	Abundance understory	ha^{-1}	Inventory	single	0.99	1.00	342.15	309.81
Paracou	Rank-abundance	ha^{-1}	Inventory	single	0.85	0.93	3.67	3.58
Tapajos	Rank-abundance	ha^{-1}	Inventory	single	0.74	0.94	3.63	3.48
Paracou	GPP	$kgC m^{-2} year^{-1}$	eddy flux	day	0.97	0.60	0.75	0.67
Tapajos	GPP	$kgC m^{-2} year^{-1}$	eddy flux	day	0.97	0.45	1.12	0.67
Paracou	GPP	$kgC m^{-2} year^{-1}$	Satellite	day	0.95	0.45	1.18	0.80
Tapajos	GPP	$kgC m^{-2} year^{-1}$	Satellite	day	0.96	0.22	1.54	0.28
Paracou	LAI	$m^2 m^{-2}$	Satellite	15 days	1.00	0.69	0.29	0.13
Tapajos	LAI	$m^2 m^{-2}$	Satellite	15 days	1.00	0.55	0.26	0.17
Paracou	LAI	$m^2 m^{-2}$	Drone	15 days	1.00	0.84	0.11	0.11
Tapajos	LAI	$m^2 m^{-2}$	Terrestrial	15 days	1.00	0.25	0.32	0.20
Tapajos	LAI	$m^2 m^{-2}$	Phenocam	15 days	1.00	0.91	0.11	0.08
Paracou	ET	$mm day^{-1}$	eddy flux	day	0.96	0.69	0.60	0.60
Tapajos	ET	$mm day^{-1}$	eddy flux	day	0.96	0.75	0.75	0.63
Paracou	RSWC	%	eddy flux	day	0.97	0.77	0.24	0.13
Tapajos	RSWC	%	eddy flux	day	0.99	0.39	0.20	0.11

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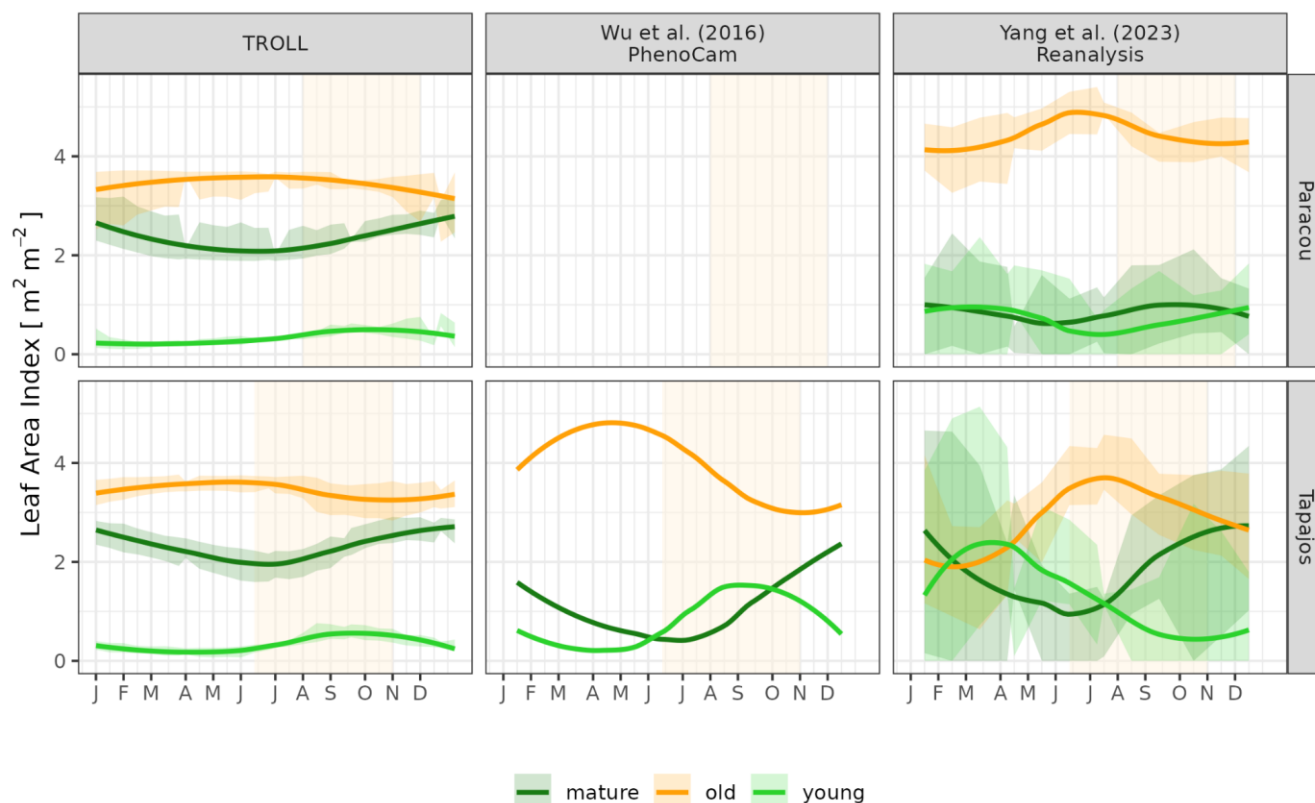
1163 **Figure A1: Representativity of imputed functional traits values (red) against raw functional trait values (blue) from various datasets**
1164 **(see methods). Traits were imputed using predictive means matching for dbh_{max} , h_{lim} , and π_{tlp} only. The number in each subplots**
1165 **represents the number of species with a trait value in the raw data and after imputation composing respectively the blue and red**
1166 **curves.**



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1168 **Figure A2.** Effect of each parameter of the new leaf shedding module on the simulated timing and intensity of the litterfall peak
 1169 during the dry season. Top panels illustrate simulated variations of litterfall at both sites for varying $a_{T,0}$, $b_{T,0}$, and δ_0 with the other
 1170 parameters fixed to a calibrated value. Bottom panels illustrate the corresponding timing and intensity of the dry season litterfall
 1171 peak: (i) the day of the litterfall peak as the julian day of the maximum annual value (day), and (ii) the ratio between the peak value
 1172 (computed as the average of litterfall flux over the two consecutive time intervals before and after the peak day) divided by the basal
 1173 flux (computed as the average between January and April) (ratio). $a_{T,0}$ mainly limited the intensity of the peak with a peak up to 60
 1174 times the wet season base litter flux with small parameter values close to 0.01 and no peak with values greater than 0.3, when
 1175 $b_{T,0}=0.02$ and $\delta_0=0.2$. Values of $a_{T,0}$ greater than 0.1 also resulted in a later peak during the dry season. $b_{T,0}$ mainly influenced the
 1176 date of the simulated peak during the dry season, as well as the intensity of the simulated peak for values greater than 0.1. Indeed,
 1177 low values of $b_{T,0}$, close to 0.01, resulted in a peak starting in September, while high values showed a peak starting in December,
 1178 when $a_{T,0}=0.2$ and $\delta_0=0.2$. Finally, δ_0 appeared to have a smaller influence on the intensity and timing of the simulated litter peaks.
 1179 Higher values of δ_0 increased the duration of the simulated peaks or the litter flux between two peaks during the same dry season.

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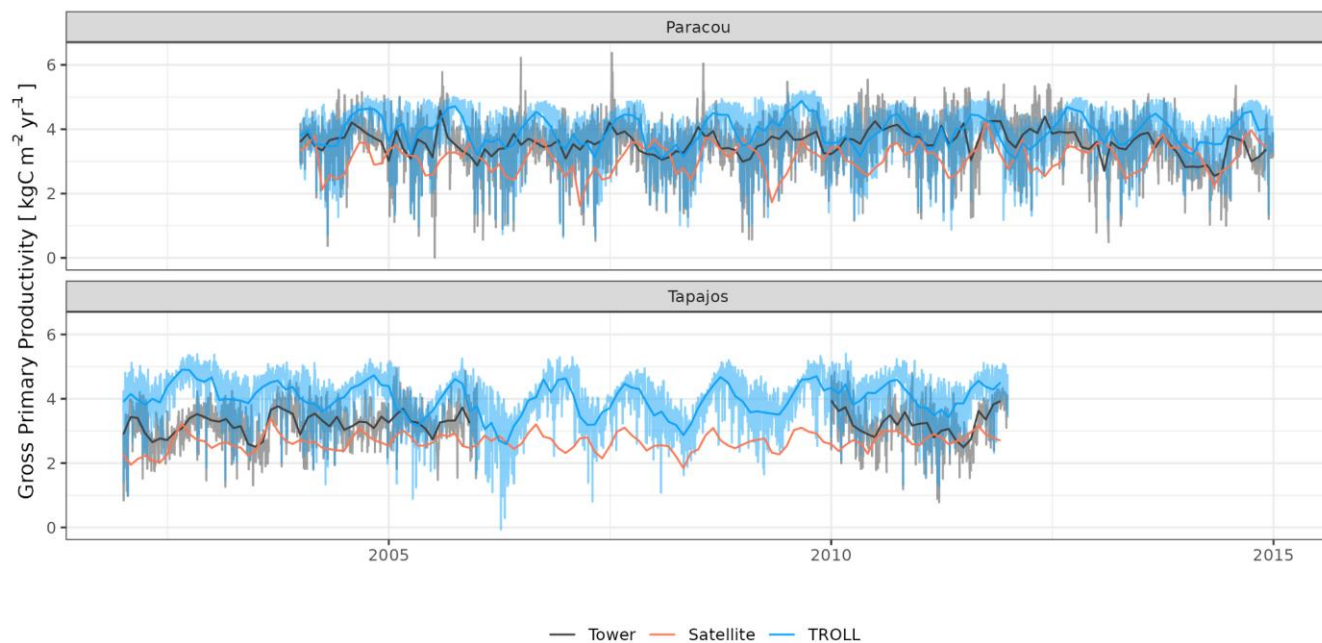
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Figure A3: Mean annual cycle of leaf area index per leaf age cohorts, derived from fortnightly means, at Paracou and Tapajos. Note that the three leaf age cohorts (young, mature and old leaves) are not defined the same way in the three sources. Leaf age per cohort depends on the individual leaf lifespan in TROLL 4.0 (see Maréchaux et al., [submitted companion paper](#)), while the transition from young to mature and mature to old are respectively fixed to 1.71 and 5.14 months in Yang et al. (2023) and fitted to 1 and 3 months in Wu et al. (2016). Bands are the intervals of means across years, and the vertical yellow bands in the background correspond to the site's climatological dry season.



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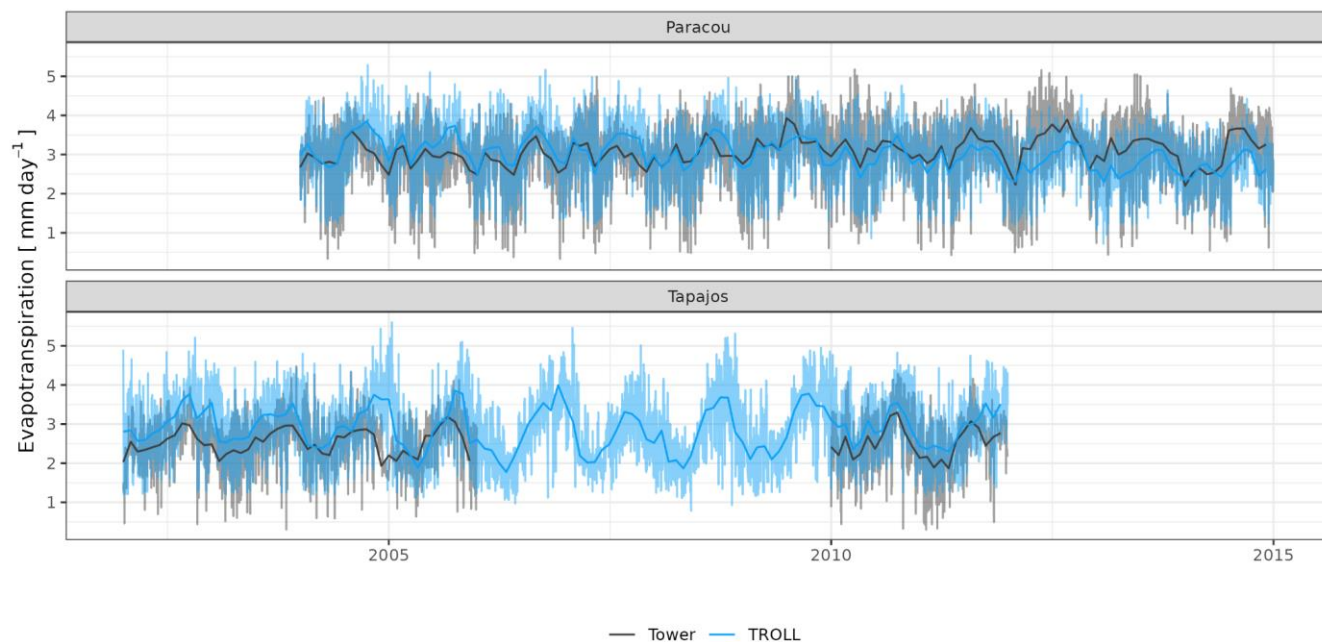


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1191 **Figure A4: Daily and monthly means of gross primary productivity for Paracou and Tapajos. Dark lines are the monthly means,**
1192 **semi-transparent lines are the daily means variations with the exception of satellite data for which data are available only every 8**
1193 **days.**



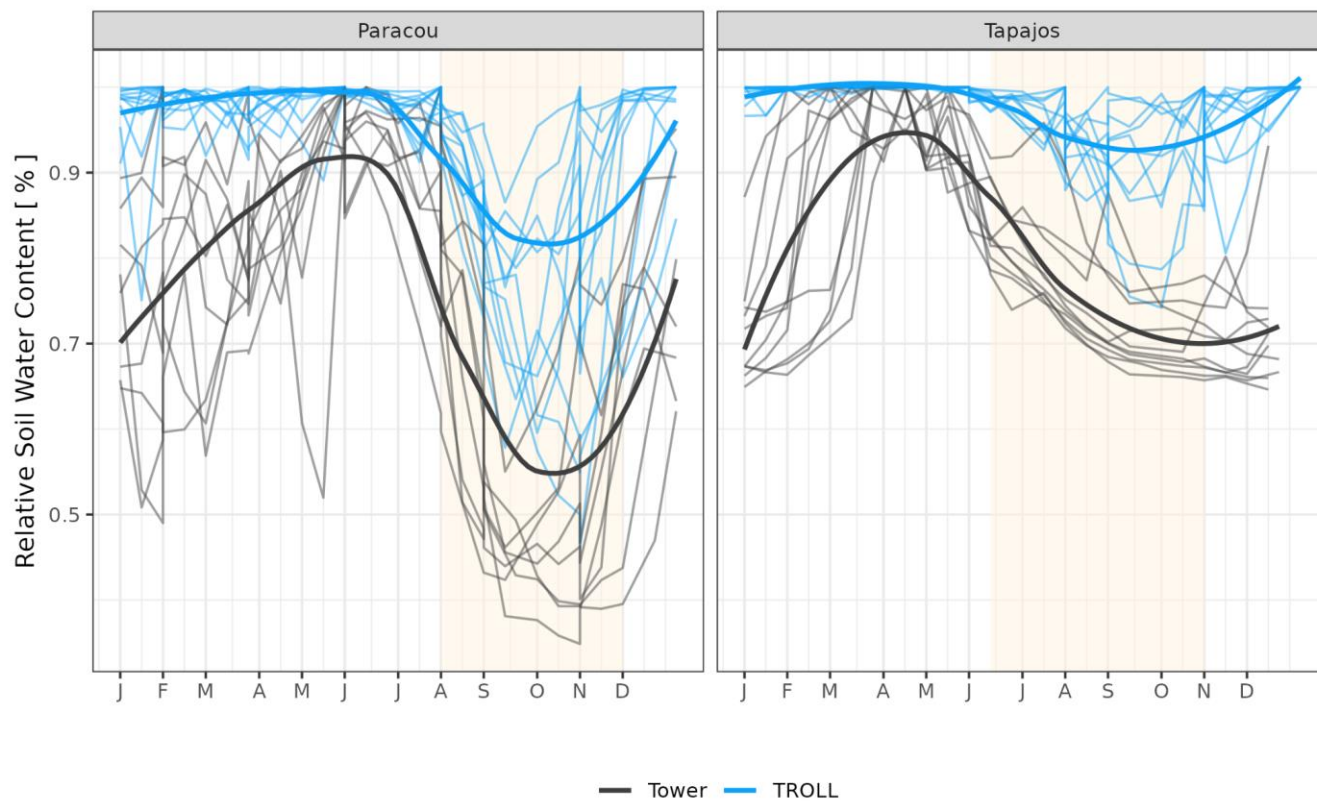
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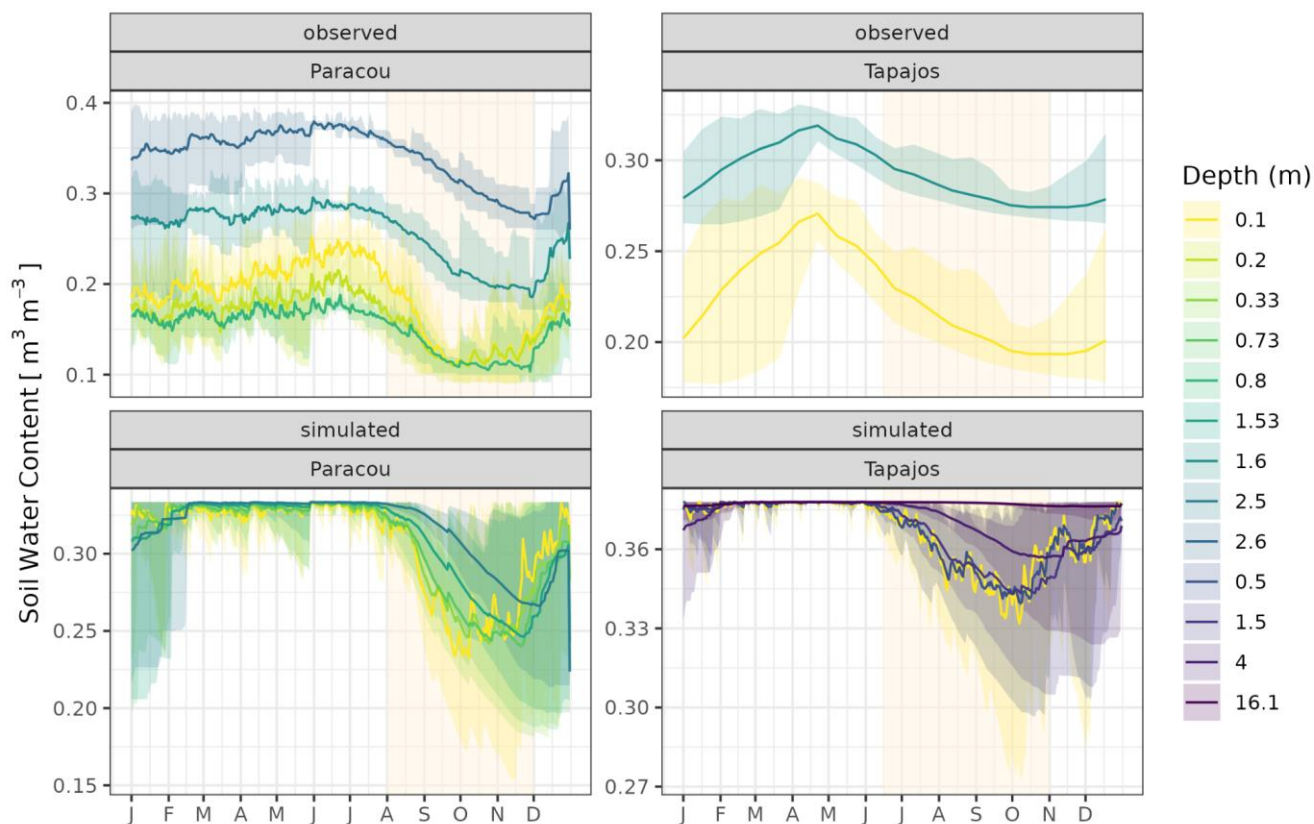
1196 **Figure A5: Daily and monthly total of evapotranspiration for Paracou and Tapajos. Dark lines are the monthly means, semi-**
1197 **transparent lines are the daily means variations.**

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Figure A6: Mean annual cycle from daily means of relative soil water content for Paracou and Tapajos for the topsoil layer up to 10 cm. Dark lines are the daily mean across years, semi-transparent lines are the daily means per year. The vertical yellow bands in the background correspond to the site's climatological dry season.



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Figure A7: Mean annual cycle from daily means of soil water content for Paracou and Tapajos at different depths. The depth value indicates the maximum depth of the layer. Dark lines are the daily means across years, and bands are the intervals of means across ten years. The vertical yellow bands in the background correspond to the site's climatological dry season.