Impacts of Degradation on Water, Energy, and Carbon Cycling of the Amazon Tropical Forests

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Abstract

Selective logging, fragmentation, and understory fires directly degrade forest structure and composition. However, studies addressing the effects of forest degradation on carbon, water, and energy cycles are scarce. Here, we integrate field observations and high-resolution remote sensing from airborne lidar to provide realistic initial conditions to the Ecosystem Demography Model (ED–2.2) and investigate how disturbances from forest degradation affect gross primary production (GPP), evapotranspiration (ET), and sensible heat flux (H). We used forest demography information retrieved from airborne lidar samples (13,500 ha) and calibrated with 817 inventory plots (0.25 ha) across precipitation and degradation gradients in the Eastern Amazon as initial conditions to ED-2.2 model. Our results show that the magnitude and seasonality of fluxes were modulated by changes in forest structure caused by degradation. During the dry season and under typical conditions, severely degraded forests (biomass loss [?] 66%) experienced water-stress with declines in ET (up to 34%) and GPP (up to 35%), and increases of H (up to 43%) and daily mean ground temperatures (up to 6.5°C) relative to intact forests. In contrast, the relative impact of forest degradation on energy, water, and carbon cycles markedly diminishes under extreme, multi-year droughts, as a consequence of severe stress experienced by intact forests. Our results highlight that the water and energy cycles in the Amazon are not only driven by climate and deforestation, but also the past disturbance and changes of forest structure from degradation, suggesting a much broader influence of human land use activities on the tropical ecosystems.

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Key Points:

- Airborne lidar can be used to inform degradation-driven changes in structure to vegetation models

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- Forest degradation typically depletes evapotranspiration and productivity and increases flammability
- Extreme droughts reduce functional differences between degraded and intact tropical forests

Abstract

Selective logging, fragmentation, and understory fires directly degrade forest structure and composition. However, studies addressing the effects of forest degradation on carbon, water, and energy cycles are scarce. Here, we integrate field observations and high-resolution remote sensing from airborne lidar to provide realistic initial conditions to the Ecosystem Demography Model (ED–2.2) and investigate how disturbances from forest degradation affect gross primary production (GPP), evapotranspiration (ET), and sensible heat flux (H). We used forest demography information retrieved from airborne lidar samples (13,500 ha) and calibrated with 817 inventory plots (0.25 ha) across precipitation and degradation gradients in the Eastern Amazon as initial conditions to ED-2.2 model. Our results show that the magnitude and seasonality of fluxes were modulated by changes in forest structure caused by degradation. During the dry season and under typical conditions, severely degraded forests (biomass loss $\geq$ 66%) experienced water-stress with declines in ET (up to 34%) and GPP (up to 35%), and increases of H (up to 43%) and daily mean ground temperatures (up to 6.5°C) relative to intact forests. In contrast, the relative impact of forest degradation on energy, water, and carbon cycles markedly diminishes under extreme, multi-year droughts, as a consequence of severe stress experienced by intact forests. Our results highlight that the water and energy cycles in the Amazon are not only driven by climate and deforestation, but also the past disturbance and changes of forest structure from degradation, suggesting a much broader influence of human land use activities on the tropical ecosystems.

Plain Language Summary

In the Amazon, timber extraction and forest fires that are ignited by people are the chief causes of damages that we call forest degradation. Degradation is as widespread as deforestation, and change the way forests behave. Degraded forests may pump less water to the atmosphere and absorb less carbon dioxide from the atmosphere. To understand the differences in behavior between degraded and intact forests, we used high-resolution scanning laser data collected from aircraft flights over regions in the Amazon where we knew if and when the forest was degraded. Then, we provided these data to a computer program that calculates the exchange of water and carbon between the forest and the atmosphere. We found that, during the dry season, degraded forests are 6.5°C warmer, pump 1/3 less water, absorb 1/3 less carbon, and show higher fire risk than in-

tact forests. To our surprise, when the Amazon is hit by severe droughts, intact forests start to behave like degraded forests, because all forests run out of water and become hot. Our results are important because they show that forest degradation caused by people can have large impacts on dry-season climate and favor more fire, especially during typical, non-drought years.

1 Introduction

Tropical forests account for 25–40% of total carbon stocks in terrestrial ecosystems (Sabine et al., 2004; Meister et al., 2012), but their maintenance and functioning have been weakened by climate and land-use change. As a result, tropical forests may shift to net sources of carbon to the atmosphere, with residence time of carbon in forests declining by 50% (Davidson et al., 2012; Grace et al., 2014; Lewis et al., 2015; Erb et al., 2016). Land use and land cover changes contribute to nearly 15% of total annual carbon emissions (Harris et al., 2012; Friedlingstein et al., 2019). However, most studies assessing the effects of land use change on tropical forest stocks and fluxes have focused on the effects of deforestation (e.g., Harris et al., 2012; Achard et al., 2014). The effects of logging, understory fires and forest fragmentation — collectively known as *forest degradation* (Hosonuma et al., 2012) — could play a comparable role in the forest's energy, water, and carbon cycle, but they remain poorly quantified.

Significant fractions of the remaining tropical forests are located within 1 km to the forest's edge (Haddad et al., 2015; Lewis et al., 2015) and thus are probably degraded (Asner et al., 2006; Morton et al., 2013; Pütz et al., 2014; Tyukavina et al., 2016; Potapov et al., 2017). The area impacted by forest degradation in the Amazon each year is highly uncertain, but likely comparable to deforestation (Asner et al., 2006; Morton et al., 2013; Tyukavina et al., 2017). Total carbon losses attributable to degradation may be similar or exceed deforestation-related losses in tropical forests (Berenguer et al., 2014; Pearson et al., 2017; Baccini et al., 2017; Aragão et al., 2018; Erb et al., 2018), and degradation may even dominate the carbon losses in indigenous lands and protected areas (Walker et al., 2020). At the local scale, carbon stocks in degraded forests are extremely variable. Lightly disturbed forests (e.g., reduced-impact logging) store as much carbon as intact forests, while forests impacted by severe or multiple disturbances may lose 65–95% of their original carbon stocks (Berenguer et al., 2014; Alamgir et al., 2016; Longo et al., 2016; Rappaport et al., 2018; Ferraz et al., 2018). Unquestionably, estimates of fluxes

from forest degradation and regeneration are more uncertain than emissions from deforestation (Aragão et al., 2014; Morton, 2016; Bustamante et al., 2016), because their impacts on forests are more subtle than deforestation and thus more difficult to detect and quantify with traditional remote sensing techniques.

Selective logging and fires also modify the forest structure, composition and functioning. For example, selective logging in the tropics generally targets large trees (diameter at breast height, DBH $\geq$ 40–60 cm) from a few marketable species (e.g., Feldpausch et al., 2005; Blanc et al., 2009; Pinagé et al., 2019), but the other logging structures such as skid trails and log decks kill or damage mostly small trees (DBH $<$ 20 cm) (Feldpausch et al., 2005). Likewise, fire mortality decreases with tree size and the bark thickness (e.g., Brando et al., 2012; Pellegrini et al., 2016), although areas disturbed by recurrent fires also show significant losses of large trees (Martins et al., 2012). Consequently, degradation creates more open canopies and thinner understory (e.g., d'Oliveira et al., 2012; Pinagé et al., 2019; Silvério et al., 2019) and increased abundance of fast-growing, low wood-density species (Barlow et al., 2016; Both et al., 2019; Brando, Silvério, et al., 2019).

Previous studies indicate an increase in dry-season length in parts of the Amazon where both deforestation and forest degradation are pervasive (e.g., Fu et al., 2013; Sena et al., 2018), and that the onset of the wet season is modulated by forest transpiration (J. S. Wright et al., 2017). Temperature and vapor pressure deficit (VPD), important drivers of evapotranspiration (ET), were found by Kapos (1989) to be significantly higher near forest edges. Likewise, Jucker et al. (2018) installed a network of micrometeorological measurements across a study area in Sabah, Malaysia, that included intact forests, a broad range of degraded forests and oil-palm plantations, and found that forest structure, along with topographic features, explained most of the variance in understory temperature. Yet, only a few studies on experimental sites quantified the magnitude, seasonality, and interannual variability of water, and energy cycles in degraded forests. For example, S. D. Miller et al. (2011) analyzed the impact of reduced-impact, low-intensity selective logging in the Amazon using eddy covariance towers and found only minor impacts of logging on sensible and latent heat fluxes. Recently, Brando, Silvério, et al. (2019) compared eddy covariance data from two towers at an experimental fire site in the Amazon forest, and found declining differences in gross primary productivity and small differences in evapotranspiration between the control and burned area between 4 and 8 years after the last burn.

Field inventory plots are fundamental to sample the structure and species composition of tropical forests, but they also have important limitations to characterize the heterogeneity of degraded landscapes. First, the number of plots required to characterize stands increase with heterogeneity, often reaching impractical numbers (Marvin et al., 2014). In addition, most tropical forest degradation occurs in private landholdings and privately managed logging concessions, where limited access by researchers may create sampling bias towards well-managed areas, which generally experience less intensive degradation. However, airborne laser scanning (airborne lidar) can circumvent these limitations over large areas with sub-meter resolution. Airborne lidar data have been used successfully to quantify structural characteristics of the canopy such as height and leaf area distribution (Hunter et al., 2013; Shao et al., 2019). Moreover, these data have also been used to quantify changes in canopy structure and carbon stocks at local to regional scale that experienced multiple levels of degradation (e.g., Asner et al., 2010; Longo et al., 2016; Ferraz et al., 2018; Meyer et al., 2019).

Numerical models can be used to understand the links between changes in forest structure, light and water availability for different local plant communities, and the overall impact on energy, water, and carbon fluxes between forests and the atmosphere. In the past, *big-leaf* models have been modified to account for the long-term impacts of selectively logged tropical forests on the carbon cycle of tropical forests (e.g., Huang et al., 2008; Huang & Asner, 2010). However, big-leaf models cannot represent the mechanisms that control access and availability of light and water in complex and heterogeneous forest structures (Purves & Pacala, 2008; Fisher et al., 2018). Individual-based models can represent the changes in the population structure and micro-environments due to degradation (R. Fischer et al., 2016; Maréchaux & Chave, 2017), but the complexity and computational burden of these simulations often limit their application to single sites. Cohort-based models, such as the Ecosystem Demography (ED-2.2) model (Medvigy et al., 2009; Longo, Knox, Medvigy, et al., 2019), strike a balance between these end-members because they can efficiently represent the horizontal and vertical heterogeneity of forests, provided that they are informed with initial conditions and accurate parameterizations that can capture the landscape variability.

In this study, we use airborne lidar data to quantify forest structure variability across the Amazon in order to provide critical initial conditions for ecosystem demography models. We also investigate the role of forest degradation on the Amazon forest productiv-

ity, flammability, as well as the degradation impacts on the water and energy cycles. Specifically, we seek to answer the following questions:

1. What are the relationships between degradation metrics (e.g. biomass loss) and changes in carbon, water, and energy fluxes, and how does it vary across seasons and regions with different rainfall regimes?
2. How do droughts affect the relationships between degradation and ecosystem functioning?
3. Does forest degradation make Amazon forests more susceptible to fires? If so, which parts of the Amazon experience the largest flammability response to degradation?

To this end, we integrate field inventory plots with high-resolution airborne lidar data over five study regions in the Eastern Amazon along a precipitation gradient and with a broad range of anthropogenic disturbance histories, to provide initial conditions to ED-2.2 that realistically represent the structural diversity of degraded forests. While limited to specific regions in the Amazon where detailed degradation information exists, our goal is to provide a framework that can be extended to larger scales, including biome- and pantropical scales.

2 Materials and Methods

2.1 Study regions

We selected five study regions across a gradient of disturbance and climate conditions where ground and airborne lidar are available to study the forest function (Figure 1; Table 1). Three of these sites include eddy covariance tower measurement of energy, water, and carbon dioxide fluxes for comparison with the model simulations, and have been the focus of several ecological studies in the past.

1. *Paracou, French Guiana (GYF)* is a field station where a logging experiment was conducted between 1987 and 1988 that includes intact forest controls and three selective logging treatments: timber extraction using conventional logging techniques, timber extraction and canopy thinning, and timber and fuelwood extraction followed by canopy thinning (Gourlet-Fleury et al., 2004). The eddy covariance tower at the site is located in the undisturbed forest and has been operational since 2004 (Guyaflux; Bonal et al., 2008).

Table 1. Overview of the study regions, including mean annual precipitation (MAP) and dry-season length (DSL).

Region (Code)	Coordinates	MAP[a] [mm]	DSL[b] [mo]	Lidar [ha]	Inventory [ha]	Disturbances[c]
Paracou (GYF)	5.28°N; 52.91°W	3040	2(0)	963	79.8	INT, CL1, LTH
Belterra (BTE)	3.09°S; 54.95°W	1890	5(1)	4057	16.7	INT, RIL, BN1, BN2, BN3
Paragominas (PRG)	3.15°S; 47.61°W	1850	6(2)	3217	35.6	INT, RIL, CL1, BN1, LB1, BN2, BN3
Feliz Natal (FZN)	12.14°S; 54.68°W	1940	5(4)	4210	14.0	INT, CL1, CL2, BN1, LB1, BN2, BN3
Tanguro (TAN)	13.08°S; 52.41°W	1800	5(4)	1006	22.9	INT, BN1, BN3, BN6

[a] Source for mean annual precipitation (MAP) data: GYF – Gourlet-Fleury et al. (2004); other regions – nearest site available at INMET (2019).
[b] Dry-season length (DSL): number of months with precipitation below 100 mm; numbers in parentheses indicate number of severely dry months (precipitation below 30 mm).
[c] Disturbance history classes: INT – intact; RIL – reduced-impact logging; CLx – conventional logging (x times); LTH – conventional logging and thinning; LB1 – conventional logging and burned (once); BNx – burned x times.

2. *Belterra, Brazil (BTE).* Over the past 100 years, this region experienced cycles of economic growth and recession that created a complex landscapes dominated by deforestation, degradation and second-growth (VanWey et al., 2007), with intact areas in the Tapajós National Forest. An eddy covariance tower known as Km 67 overlaps with one of the surveyed sites and has data for 2001–2005, and 2008–2011 (Hayek et al., 2018).
3. The *Paragominas, Brazil (PRG)* region used to be within the largest timber production area in Brazil and has undergone selective logging since the 1970s (Veríssimo et al., 1992). Since the 1990s, the economy has shifted towards agriculture, introducing large-scale deforestation such that nearly half of the original forest cover has been lost, and most of the remaining areas have been logged (Pinto et al., 2009).
4. *Feliz Natal, Brazil (FZN)* is located at the southern fringe of the Amazon in a mosaic landscape of soybean fields, grazing lands, and logged forests. This region regularly experiences severe dry seasons and frequent understory fires (Morton et al., 2013; Rappaport et al., 2018).
5. *Tanguro, Brazil (TAN)* is located in an experimental fire study area within a larger landscape covered by intact forests and forests that were disturbed with low-intensity understory fires (one, three, and six times) between 2004 and 2010 (Brando et al., 2014). The surveyed region also includes two eddy covariance towers that have been operating since 2014 both at the intact and burned forests (Brando, Silvério, et al., 2019).

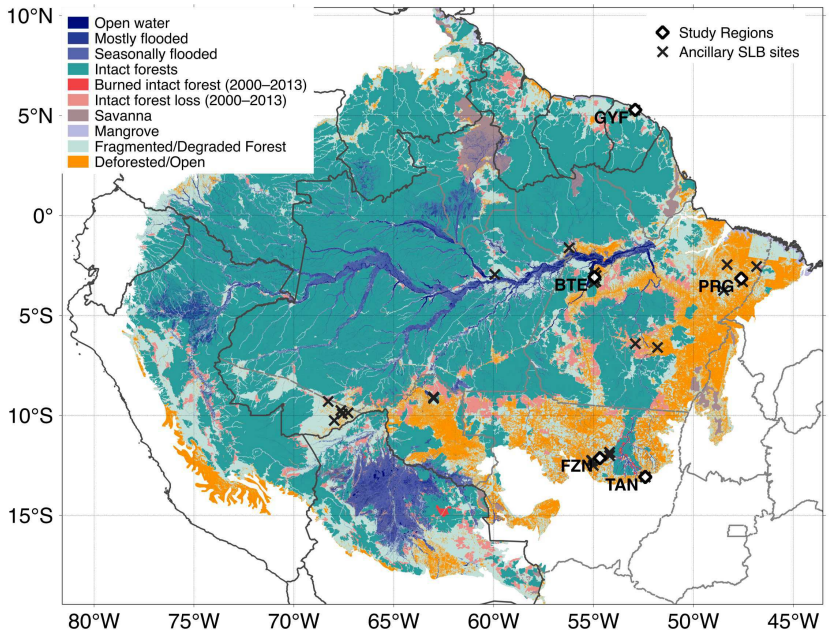

Figure 1. Location of the five study regions within the Amazon biome region, along with land classification as of 2013. Intact forest and intact forest loss were obtained from Potapov et al. (2017); open and deforested areas were obtained from PRODES-INPE (2018) (Brazil) and areas with tree cover below 20% according to Hansen et al. (2013) (other countries); wetlands and water bodies in the Amazon River Basin were from Hess et al. (2015) and savannas and mangroves were obtained from Olson et al. (2001).

These five study regions were sampled at multiple sites by small-footprint, multiple-return airborne lidar. The lidar data provided both the terrain elevation at high spatial resolution (1-m) and detailed information about the vertical structure of forests from a uniform point cloud density to meet a minimum return density of 4 returns per m^2 over 99.5% of the area (Leitold et al., 2015). Living trees of diameter at breast height DBH $\geq$ 10 cm were either botanically identified (experimental plots in GYF) or identified from field characteristics by local parataxonomists. To characterize the disturbance history, we used either published information from the experimental regions GYF (Gourlet-Fleury et al., 2004; Bonal et al., 2008; Wagner et al., 2013) and TAN (Brando et al., 2012, 2014), or the disturbance history analysis from (Longo et al., 2016), which was based on a visual interpretation of the Normalized Burn Ratio (NBR) of cloud-free Landsat images since 1984, and complemented with information from logging companies for the reduced-impact logging sites (e.g., Pinagé et al., 2019). Details on site-specific data used in this

study are available in Text 1 and previous work (Longo et al., 2016; Vincent et al., 2017; Brando, Silvério, et al., 2019), and were obtained through the Paracou Experimental Station and the Sustainable Landscapes Brazil data servers (Paracou Portal, 2016; Sustainable Landscapes Brazil, 2019; dos-Santos et al., 2019).

2.2 Overview of the modeling framework

In this study, we used the Ecosystem Demography model, version 2.2 (ED-2.2) (Moorcroft et al., 2001; Medvigy et al., 2009; Longo, Knox, Medvigy, et al., 2019) to simulate the impacts of forest structure on energy, water, and carbon cycles. For any point of interest, the ED-2.2 model simulates the forest structure and functional diversity across a landscape, and simulates the energy, water, and carbon budgets for multiple canopy environments, which represent the forest heterogeneity (Longo, Knox, Medvigy, et al., 2019). ED-2.2 has been successfully evaluated and used in both short-term and long-term studies in the Amazon forest (Powell et al., 2013; Zhang et al., 2015; Levine et al., 2016; Longo, Knox, Levine, et al., 2019). In ED-2.2, the horizontal and vertical heterogeneities of forests are represented through a hierarchical structure. Each area with the same climate (e.g., footprint of an eddy covariance tower or a grid cell in a gridded meteorological driver) is called a *polygon*. Each polygon is subdivided into *patches*, which represent collections of forest gaps within a polygon that share a similar age since last disturbance and same disturbance type (although not necessarily contiguous in space). Patches are further subdivided into *cohorts*, which are collections of individual plants that have similar size and similar functional group. Importantly, because ED-2.2 incorporates the horizontal heterogeneity of the plant community structure and composition, the model can efficiently incorporate and simulate the dynamics of degraded forests.

Most of the ED-2.2 modules used in this study have been previously described in Longo, Knox, Medvigy, et al. (2019). The main changes used in this study include (1) a modified height-diameter allometry based on the Jucker et al. (2017) approach and locally collected field data that can be used consistently by the initialization and model; (2) an improved allocation to living and structural tissues, which is now based on more recent allometric equations (Chave et al., 2014; Falster et al., 2016) and datasets (Falster et al., 2015); (3) a revised photosynthesis solver, which now accounts for the maximum electron transport ratio and the maximum triose-phosphate utilization (von Caemmerer, 2000; Oleson et al., 2013; Lombardozzi et al., 2018); (4) updated values of traits and trade-

offs, using multiple studies and trait databases, including GLOPNET, TRY, and NGEE-Tropics (I. J. Wright et al., 2004; Santiago & Wright, 2007; Chave et al., 2009; Kattge et al., 2009, 2011, 2020; Baraloto et al., 2010; Powers & Tiffin, 2010; Gu et al., 2016; Bahar et al., 2017; Norby et al., 2017). These changes are described in Text 2. Moreover, we used an approach developed by X. Xu (unpublished) and based on Lloyd et al. (2010) to account for light-dependent plasticity of three leaf traits (specific leaf area, leaf turnover rate, and carboxylation capacity), and calibrated using existing data (Lloyd et al., 2010; Russo & Kitajima, 2016; Keenan & Niinemets, 2016).

To obtain initial conditions for ED-2.2 from airborne lidar, we devised a multi-step approach that links airborne lidar data with ecosystem properties (Figure 2). Here we provide a summary of the initialization procedure; the technical details of this approach are described in Text 3. For step 1, we split all collected point cloud data into 50×50 m columns, simulated waveforms from the discrete returns (Blair & Hofton, 1999; Popescu et al., 2011; Hancock et al., 2019) to obtain unscaled leaf area density profiles based on the vertical distribution of returns (e.g., MacArthur & Horn, 1969; Ni-Meister et al., 2001; Stark et al., 2012; Antonarakis et al., 2014; Tang & Dubayah, 2017), and assigned the relative proportion of each plant functional type provided by one of the 769 training plots that had the most similar vertical structure; the similarity was based on the profile comparison that yielded the smallest Kolmogorov-Smirnov statistic. The vertical profile was split into cohort layers centered around local maxima or saddle points, using a modified procedure based on function `peaks` (package `RSEIS`, Lees, 2017) of the `R` statistical software (R Core Team, 2019). For step 2, we used a collection of 817 forest inventory plots (0.16–0.26 ha) that were also surveyed by airborne lidar, which included plots from all study regions as well additional sites available from Sustainable Landscapes Brazil (SLB) and used in a previous study (ancillary SLB sites, Figure 1; Longo et al., 2016); we developed statistical models based on subset selection of regression (A. J. Miller, 1984) and heteroskedastic distribution of residuals (Mascaro et al., 2011) to estimate plot-level properties (aboveground biomass, basal area, stem number density, leaf area index) from point cloud metrics and field estimates, following the approach by Longo et al. (2016). For step 3, we sought to obtain a plot-specific scaling factor to the leaf area density profile that produced the best agreement between the four estimated plot-level properties from step 1 and the plot-level properties obtained by integrating the vertical distribution from step 2, by minimizing the sum of relative square differences of the four properties. For step

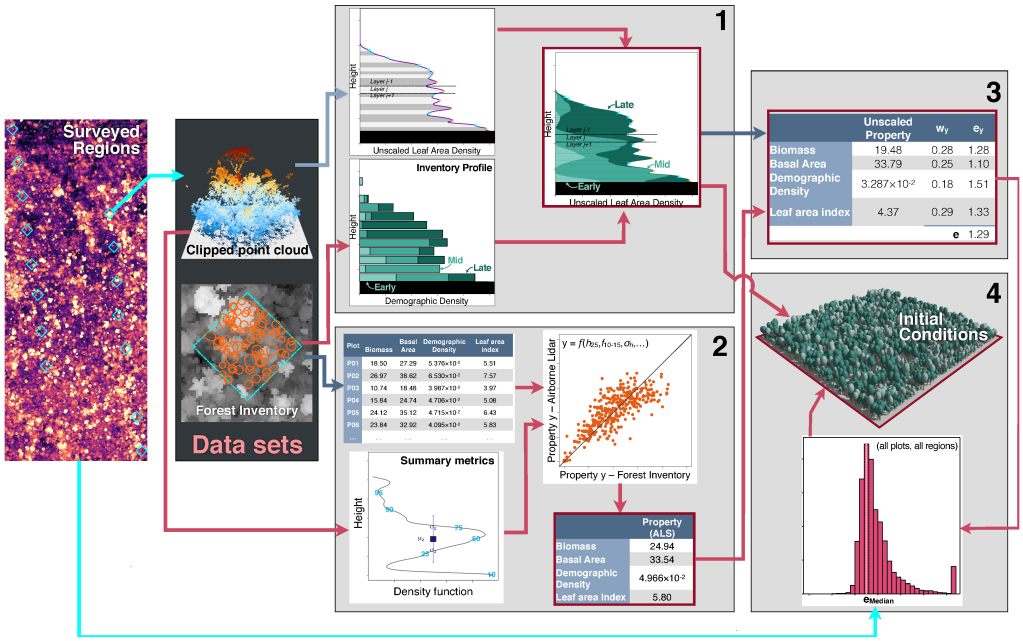

Figure 2. Schematic representation of the method to obtain initial conditions for ED-2 from airborne lidar. Each light box represents one step in the procedure. The results of each step are highlighted with a red border. Dark blue arrows are stages that require individual-based allometric equations, and light blue arrows are stages that require a light extinction model.

4, we analyze the scaling factor distribution for all plots for which we could test the approach, and define a unique and global scaling factor, based on the median scaling factor, that is used to correct all predicted profiles.

Once we obtained the initial conditions for each 50×50 m column, we grouped individual columns based the disturbance history (degradation level) and the study region (Table 1). We used the following broad categories for disturbance history: intact (INT), reduced-impact logging (RIL), conventional logging (CLx, where x is the number of logging disturbances), conventional logging and thinning (LTH), logged and burned once (LB1) and burned (BNx, where x is the number of burns). Importantly, we did not perform any averaging or sampling of the individual columns before providing them to ED-2.2; instead, we provided all columns to the model, so the initial conditions characterize the observed distribution of forest structures that exist within each group.

2.3 Assessment of the modeling framework

We evaluated three characteristics to assess the ability of model framework to represent the forest structure heterogeneity caused by degradation, and to represent components of the energy, water, and carbon cycle. First, we quantified the ability of the airborne lidar initialization to capture the differences in forest structure caused by degradation. Second, we assessed whether the model can realistically represent fluxes and storage of water, energy and carbon across different regions. Third, we compared the model sensitivity to degradation-driven effects on fluxes and storage with independent observations.

To evaluate the airborne lidar initialization, we used a cross-validation approach in which we replicated the procedure described above (Section 2.2) 2000 times, using a hierarchical bootstrap approach. We first sampled regions (with replacement), to ensure that some regions would be entirely excluded from the replicate, then we sampled plots (also with replacement), to ensure that the replicate had the same number of plots as the original training data set. We then predicted the structure of all plots in the excluded regions, using iterations that did not have any plot in the training data set; to make this number consistent across regions, we used the smallest number of iterations that met this criterion across all regions (n = 612). Finally, for each region, we compared the average forest structure from all cross-validation replicates that excluded the region from the training stage. Because estimates of forest properties have larger uncertainties in smaller plots (Chave et al., 2004; Meyer et al., 2013; Mauya et al., 2015), we only evaluated the method when a disturbance class within a region had at least 20 plots.

To verify the model's ability to realistically represent the regional variability of fluxes and storage, we carried out ED-2.2 simulations initialized with airborne lidar for the intact forests regions where eddy covariance tower and forest inventory plots co-located with airborne lidar were available (GYF and BTE). Region TAN had two eddy-covariance towers, one within the footprint of the burned forests and a second in intact forest (Brando, Silvério, et al., 2019), which allowed us to contrast the model's predicted impacts of degradation on fluxes and biophysical properties with the pair of tower measurements.

2.4 Model configuration and analyses

Our main focus is to understand the role of degradation-driven changes in forest structure in altering both the state and the fluxes of energy, water, and carbon, both under typical and extreme climate. To account for regional differences in climate and to sample a broad range of interannual variability, we used time series of meteorological drivers pooled from gridded reanalyses (one set of time series per region). For most meteorological variables required by ED-2.2 (pressure, temperature, humidity, incoming shortwave and longwave radiation, and winds), we used $0.625° \times 0.5°$, hourly averages (1980–2016) from the version 2 of the Modern-Era Retrospective Analysis for Research and Applications (MERRA-2, Gelaro et al., 2017). MERRA-2 precipitation is known to have significant negative biases in the tropics (Beck et al., 2019); therefore we used the $0.1° \times 0.1°$, 3-hourly precipitation rates from the version 2 of the Multi-Source Weighted Ensemble Precipitation product (MSWEP-2, Beck et al., 2019). To ensure that the only difference between simulations in the same study region was the distribution of forest structures, we imposed the same edaphic conditions: free-drainage soils with 8 m deep, and nearly equal fractions of sand (32%), silt (34%), and clay (34%). To avoid confounding effects from post-disturbance mortality and recovery, all simulations were carried out without enabling dynamic vegetation, such that the differences in forest structure would remain the same for the entire time series, and all differences between simulations in the same region could be attributable to well-characterized differences in forest structure.

To investigate the role of degradation on fire risk, we built on the original fire model from ED-1 (Moorcroft et al., 2001) to determine when fire-prone conditions would occur in each patch. The flammable area α_F ($\%\,\mathrm{yr}^{-1}$) is calculated from the fire disturbance rate λ_F (yr^{-1}):

$$\alpha_F = 100\,\left[1 - \exp\left(-\lambda_F\,\Delta t\right)\right], \tag{1}$$

$$\lambda_F = \begin{cases} I\,C_{\mathrm{Fuel}} & \text{, if } \left[\dfrac{1}{|z_F|}\displaystyle\int_{z_F}^{0} \vartheta\left(z\right)\mathrm{d}z\right] < \left(1-f\right)\,\vartheta_{\mathrm{Wp}} + f\,\vartheta_{\mathrm{Fc}} \\ 0 & \text{, otherwise} \end{cases}. \tag{2}$$

where $\Delta t = 1\,\mathrm{yr}$; $I = 0.5\,\mathrm{m}^2\,\mathrm{kgC\,yr}^{-1}$ is a fire intensity parameter; $z_F = 30\,\mathrm{cm}$ is the depth of the soil layer used to estimate dryness; ϑ ($\mathrm{m}^3\,\mathrm{m}^{-3}$) is the soil moisture; ϑ_{Wp} is the permanent wilting point and ϑ_{Fc} is the field capacity, both defined as in Longo, Knox, Medvigy, et al. (2019); and $f = 0.02$ is a phenomenological parameter that defines dry conditions. Because understory fires are the dominant type of fire in the Ama-

zon (A. Alencar et al., 2006; Morton et al., 2013), we considered fuels to be comprised by above-ground litter, above-ground coarse woody debris, and above-ground biomass from grasses and seedlings (trees with height $< 2\,\mathrm{m}$); canopy trees were not considered to be fuels. The fire parameterization, although simple, has been previously demonstrated to capture the general features of fire regime across tropical South America (Longo, Knox, Levine, et al., 2019).

3 Results

3.1 Evaluation of the model initialization and simulated dynamics

The ED-2.2 model initialization approach from airborne lidar (Figure 3) captured the main differences in forest structure and composition, both across study regions and along degradation gradients. To illustrate the initialization, we focus on the basal area distribution obtained from cross-validation at disturbance histories within study regions that had at least 20 plots (Figure 3). At sites GYF, PRG, and TAN, the airborne lidar initialization predicted the total basal area with absolute biases ranging from 3% (GYF) to 13% (TAN), and root mean square error of the order of 18–27% (Figures 3c, 3f and 3i). The largest absolute discrepancies occurred for intermediate-sized trees ($20 \leq$ DBH $< 40\,\mathrm{cm}$) at GYF and PRG, where the airborne lidar initialization underestimated basal area by 2.9 and $4.3\,\mathrm{cm^2\,m^{-2}}$, respectively (Figures 3c and 2f). The largest overestimation of airborne lidar was observed among larger trees ($60 \leq$ DBH $< 100\,\mathrm{cm}$) in intact forests at GYF ($2.4\,\mathrm{cm^2\,m^{-2}}$; Figure 3c). The size distribution of most degraded forests were well characterized (Figures 3a-b, 3d-e and 3g); the largest deviations from inventory were observed in logged and burned forests in PRG, where airborne lidar underestimated total basal area by $3.0\,\mathrm{cm^2\,m^{-2}}$ (Figure 3d). Likewise, the initialization algorithm represented the higher relative abundance of early successional plants in the most degraded sites, and the dominance of mid- and late-successional plants at intact forests at GYF and PRG (Figure S1), and realistically represented the leaf area distribution across regions and degradation levels (Figure S2).

ED-2.2 simulations using forest inventory and airborne lidar as initial conditions were compared with eddy covariance tower estimates of all sites (Figures 4 and S4-S9, and Table S1). Gross primary productivity (GPP) generally showed small biases relative to tower estimates (-0.046 to $+0.394\,\mathrm{kgC\,m^{-2}\,yr^{-1}}$), and relatively small errors (less

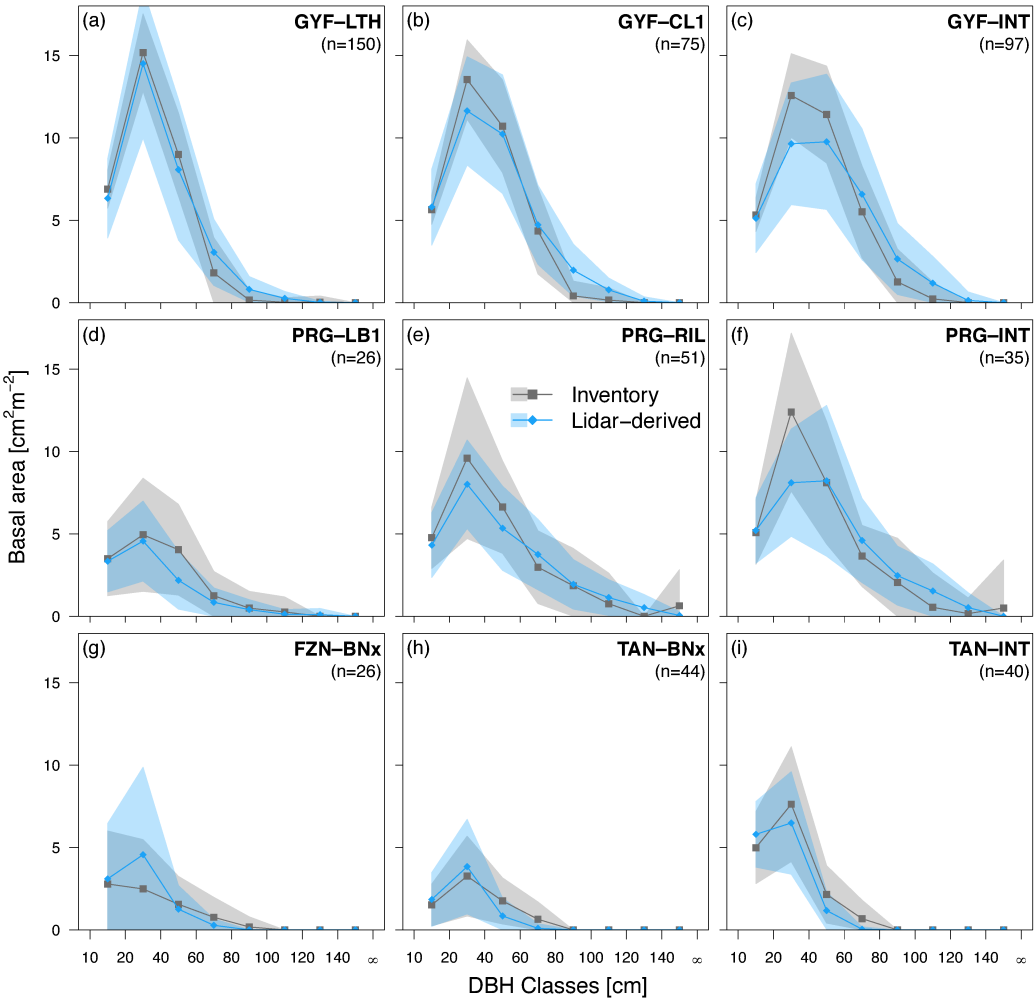

Figure 3. Assessment of basal area distribution as a function of diameter at breast height (DBH) for different study regions and degradation levels. Grey points are obtained from forest inventory plots, and blue points are obtained from the airborne lidar initialization (Figure 2) using a 612-fold regional cross-validation (i.e. excluding all plots from region in the calibration stage). Bands around points correspond to the standard deviation either across all plots in the same category (inventory) or across all plots and replicates (lidar). Sites: GYF – Paracou, PRG – Paragominas, FZN – Feliz Natal, TAN – Tanguro. Disturbance classes: BNx – Burned twice or more, CL1 – conventional logging (once), LB1 – logged and burned once, LTH – logged and thinned, RIL – reduced-impact logging, INT – intact. Additional comparisons are shown in the Supporting Information: basal area as functions of plant functional type (Figure S1); leaf area index profiles as functions of height (Figure S2); comparisons for Belterra (BTE-RIL) (Figure S3).

than observed variability) at all sites, regardless of the initial conditions (Figure 4; Table S1). While the GPP seasonality was correctly represented at GYF, the model did not capture the late wet-season decrease and early dry-season increase of GPP at BTE, and it showed a delayed dry-season decline GPP at TAN compared to tower estimates (Figure S4). Net ecosystem productivity (NEP), on the other hand, showed significant biases, large errors, and relatively small correlation with tower estimates (Figure 4; Table S1), which were driven by excessive seasonality of heterotrophic respiration (Figure S5). Because the initial carbon stocks in necromass pools are uncertain, and the results on magnitude and seasonality of ecosystem respiration (and consequently NEP) are inconsistent with tower estimates, we will not discuss the simulation results in terms of respiration and NEP.

Water fluxes also showed small biases relative to the observed variability at GYF, TNF and TAN (Burned), regardless of the initialization (-0.01 to $+0.54\,\mathrm{mm\,day^{-1}}$; Figures 4a and 4c; Table S1); biases at TAN (Intact) were larger ($0.69-0.82\,\mathrm{mm\,day^{-1}}$). With the exception of TAN (Burned), the correlation between ED-2.2 and tower was high at daily averages (Figures 4b and 4d; Table S1). At TAN (Burned), the poorer agreement with tower estimates was caused by the model predicting a similar seasonality of water flux at both control and burned forests, whereas towers suggest an increase in water flux during the earlier part of the dry season (Figure S6). ED-2.2 predictions of sensible heat flux had high correlation with observations at all sites (Figures 4b and 4d; Table S1), although sensible heat flux shows significant biases at BTE, and dampened seasonality at GYF and TAN (Burned) (Figures 4a and 4c; Table S1; Figure S6). Outgoing shortwave radiation correctly captured the seasonality at the wettest sites, but it did not capture the sharp dry-season increase at TAN (Figure S8), which may be associated with dry-season leaf senescence and shedding that was likely underestimated by ED-2.2. In addition, ED-2.2 simulations overestimated outgoing longwave radiation at all sites except at TAN (Burned) using inventory initialization (Figure S9). Nonetheless, the seasonality and the intra-seasonal variation of outgoing longwave radiation were correctly captured by ED-2.2, resulting in generally high correlation and small standard deviation of residuals at most sites (Figure 4; Table S1).

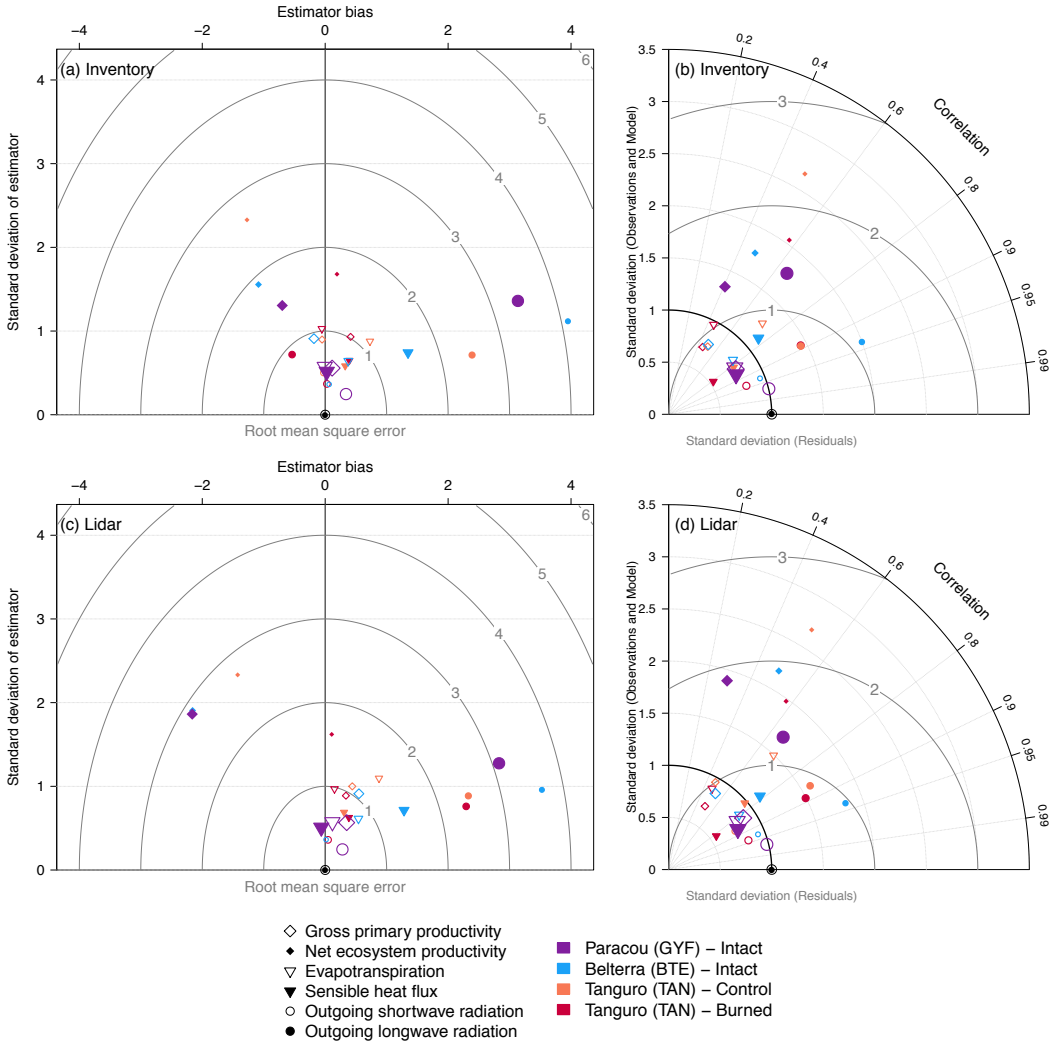

Figure 4. Summary of ED-2.2 model assessment using eddy covariance towers as benchmarks, using simulations initialized with forest inventory and airborne lidar. (a,c) Bias-variance diagram and (b,d) Taylor diagram of multiple daily-averaged fluxes of carbon, energy, and water for Paracou (GYF), Belterra (BTE) and Tanguro (TAN, control and burned), for simulations initialized with (a,b) forest inventory plots and (c,d) airborne lidar. In the bias-variance diagram, bias (x axis), standard deviation of residuals (y axis) and root mean square error (concentric arcs) are normalized by the standard deviation of observations, as is the standard deviation of models in the Taylor diagram. In both diagrams, $\odot$ corresponds to the perfect model prediction. In all plots, we only compare daily averages of days with no measurement gaps. Comparisons of the seasonal cycle for all variables included in the diagrams are available at Figures S4-S9.

3.2 Degradation effects on seasonality of fluxes

From ED-2.2, we found that forest degradation can have substantial impacts on the ecosystem function such as evapotranspiration (ET) or ground temperature in severely or recently degraded forests, and in parts of the Amazon with a longer dry season. At GYF, the airborne lidar survey sampled only intact forests and areas that were logged 25 years prior to the data acquisition: consequently, the average water vapor flux and ground temperature were nearly indistinguishable across degraded and intact forests (Figures 5a,S10a). At the equatorial sites, degradation effects were small during the wet season but showed marked reduction in ET (2.1–6.7% in BTE and 4.3–31.8% in PRG) and increase in daytime temperature (0.4–0.9°C in BTE and 1.0–6.0°C in PRG) during the dry season, with the largest changes relative to intact forests found at burned areas (Figures 5b, 5c, S10b,c). At the southern (driest) sites, the seasonal changes were even more pronounced: at both FZN and TAN, ET decreased by 21–25% early in the dry season (Jun) at the most severely burned forests, whereas ET in intact forests peaked in the middle of the dry season (Jul–Aug; Figures 5d and 5e). Similarly, burned forests were warmer year-round than intact forests at the southern sites (FZN and TAN), with minimum warming during the wet season (Dec–Mar; 0.5–0.8°C), and maximum warming occurring at the peak of the dry season (Jul–Aug; 1.0–6.5°C; Figures S10d and S10e).

Importantly, the ED-2.2 results in Figures 5 and S10 emerge from the different distribution of forest structures associated with degradation histories. ED-2.2 accounts for the diversity of forest structures within each disturbance history by means of patches; each patch represents a different forest structure found within any disturbance regime, and patch area is proportional to the probability of finding such forest structure (Longo, Knox, Medvigy, et al., 2019). For example, the ground temperature is consistently warmer at the low biomass patches, but the differences between the lowest and highest patch temperatures are as low as 1°C at GYF (Figure 6a) and less than 4°C during the wet season even at the southern regions (Figures 6d and 6e). In contrast, differences along biomass gradients exceed 9°C during the dry season at all regions except GYF (Figure 6).

Likewise, when all simulated patches are considered, we observe strong coherence between biomass and gross primary productivity (GPP) across all regions and throughout the year (Figures 7 and S11). However, the effect of local communities on GPP is seasonal: differences in typical GPP between low-biomass and high-biomass patches do

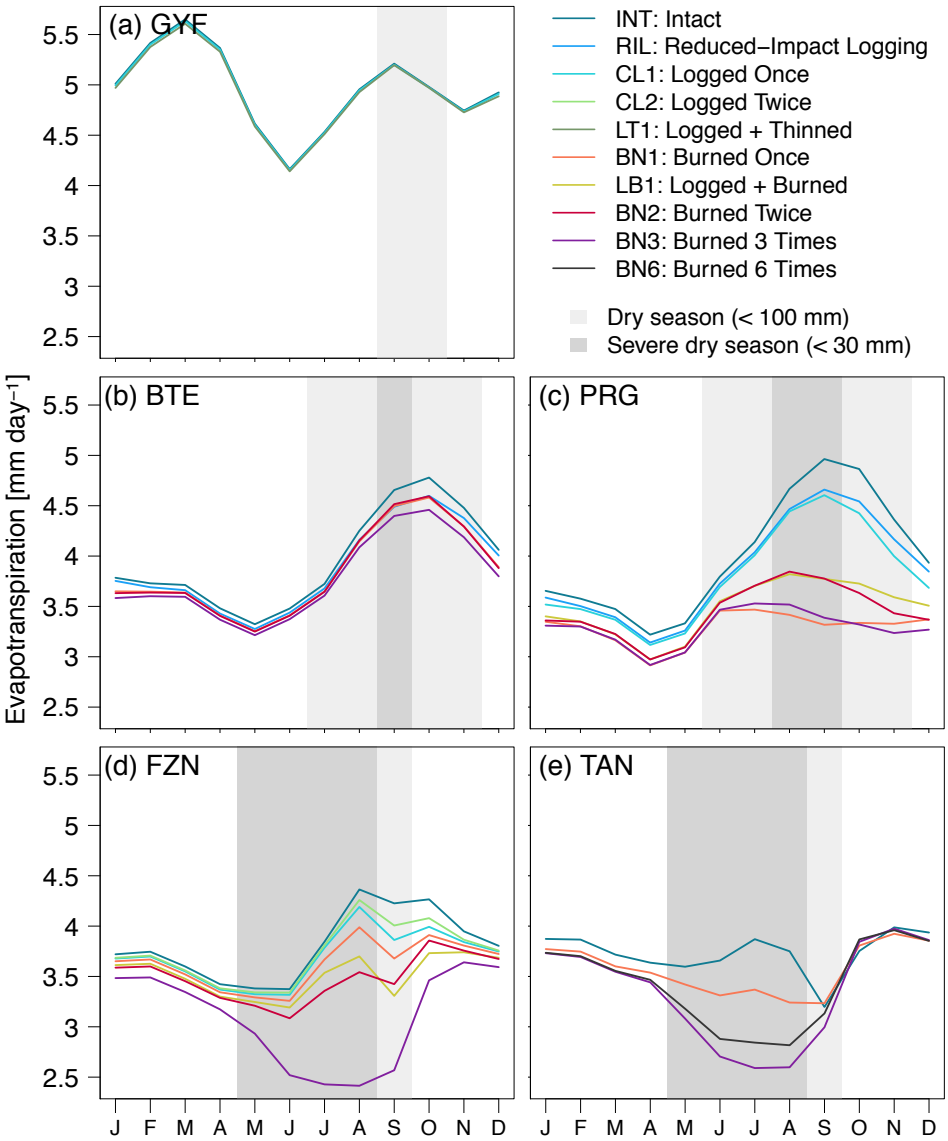

Figure 5. Monthly mean evapotranspiration (ET) as a function of region and degradation. Monthly averages correspond to the 1980–2016 period, simulated by ED-2.2 for (a) Paracou (GYF), (b) Belterra (BTE), (c) Paragominas (PRG), (d) Feliz Natal (FZN), and (e) Tanguro (TAN), aggregated by degradation history within each region (lines). Grey rectangles in the background correspond to the average dry season.

not exceed 1.1 $\mathrm{kgC\,m^{-2}\,yr^{-1}}$ during the wettest months (Figures 7a–7c), whereas the range of GPP reaches 0.7 $\mathrm{kgC\,m^{-2}\,yr^{-1}}$ at the short dry-season at GYF and exceeds 2.0 $\mathrm{kgC\,m^{-2}\,yr^{-1}}$ during the dry season at the most degraded and driest sites (Figures 7e and 7f). Sim-

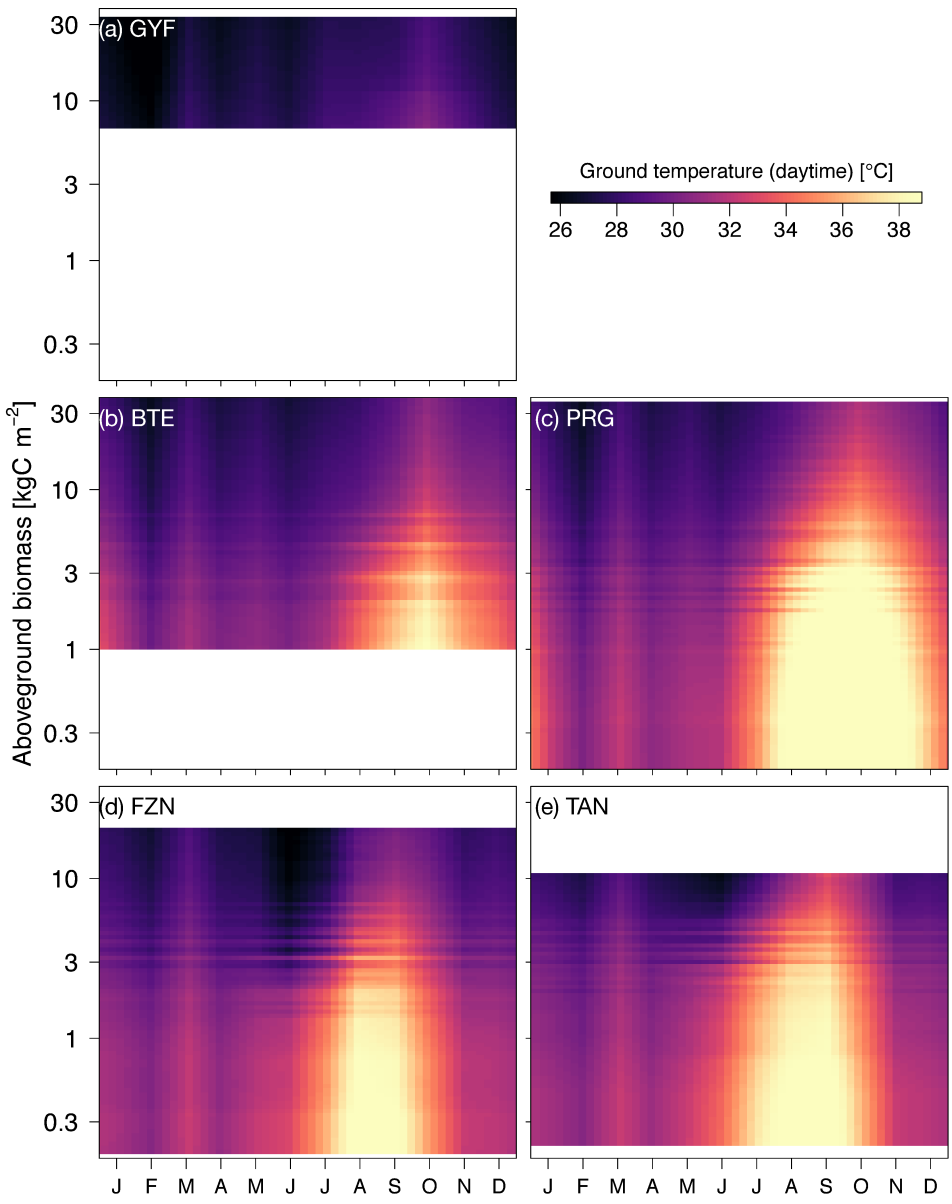

Figure 6. Monthly mean daytime ground temperature as a function of region and local (patch) aboveground biomass. Monthly averages correspond to the 1980–2016 period, simulated by ED-2.2 for (a) Paracou (GYF), (b) Belterra (BTE), (c) Paragominas (PRG), (d) Feliz Natal (FZN), and (e) Tanguro (TAN), and the y axis corresponds to the aboveground biomass for each patch, linearly interpolated for visualization. White areas are outside the range of biomass of each region and thus excluded.

ilar effects were observed in evapotranspiration, where differences along biomass are the strongest during the dry season (Figure S12).

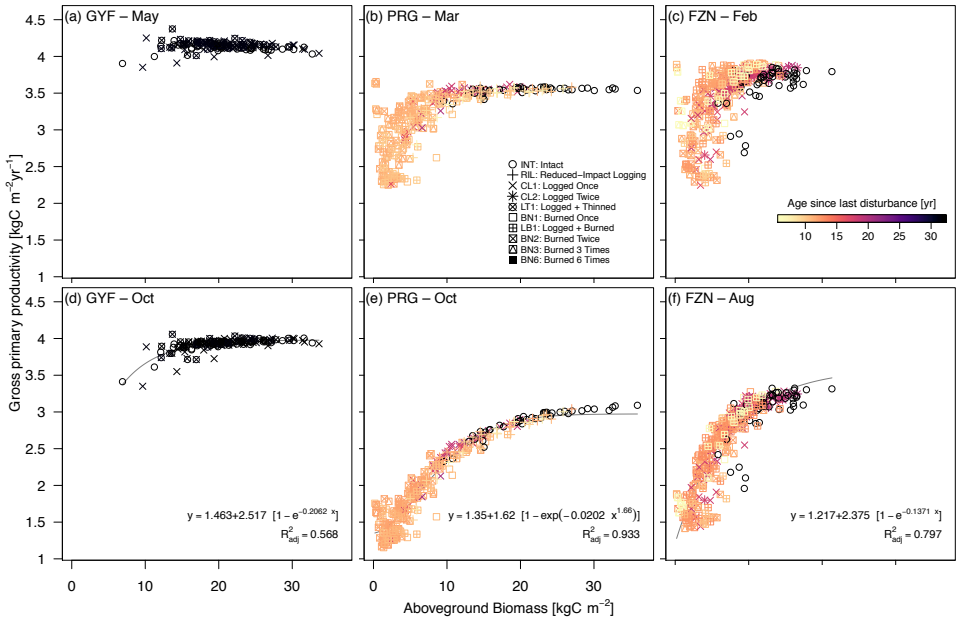

Figure 7. Variability of gross primary productivity (GPP) as a function of local (patch) aboveground biomass (AGB). Scatter plot of AGB (x axis) and GPP (y axis) at sites (a,d) Paracou (GYF), (b,e) Paragominas (PRG), (c,f) Feliz Natal (FZN), for (a-c) the peak of wet season — May (GYF), March (PRG), and February (FZN) — and (d-f) peak of dry season — October (GYF and PRG), and August (FZN). Each point represents the 1980–2016 average GPP of each patch solved by ED-2.2; point shapes correspond to the disturbance history, and point colors represent the time between the last disturbance (undetermined for intact forests) and lidar data acquisition. Curves correspond to non-linear least squares fits of the most parsimonious function, defined from Bayesian Information Criterion (Schwarz, 1978), between shifted exponential or shifted Weibull functions. Only fits that produced $R^2_{adj} > 0.5$ were included.

3.3 Degradation impacts on forest flammability

The impact of forest degradation on ecosystem functioning showed important year-to-year variability, and differences between intact and degraded forests were generally larger during typical years than during extreme droughts. For this section, we calculate the monthly water deficit based on the difference between potential evapotranspiration (calculated following Priestley & Taylor, 1972) and rainfall, and relate the 12-month running averages of multiple response variables with the maximum cumulative water deficit over the previous 12 months, and define drought length as the number of consecutive months in water deficit exceeds 20 mm. Using region PRG as an example, as the region has the

broadest range of recent disturbances and maximum cumulative water deficit, we found that, during typical rainfall periods, evapotranspiration in logged forests and burned forests were 3–6% and 11–22% lower than intact forests, respectively (Figure 8a); this difference was significantly reduced or even reversed during severe droughts, when evapotranspiration of degraded forests were up to 4% higher than in intact forests (Figure 8a). Degraded forests have a lower proportion of shade-tolerant, late-successional trees, and typical stomatal conductance is higher by 19–34% in burned forests and by 5–13% in logged forests (Figure 8b). This result indicates that the reduced typical evapotranspiration results from degraded forests having lower leaf area index relative to intact forests, as local leaf area index is related to local aboveground biomass (Figure S13). In addition, extreme droughts did not substantially reduce the differences in stomatal conductance between degraded and intact forests (Figure 8b). While evapotranspiration was generally lower in degraded forests, total evaporation (from ground and canopy intercepted water) was higher in most degraded forests, with burned forests experiencing 3–26% more evaporation in typical years and 0–14% during severe droughts (Figure 8c). The combination of higher evaporation and relatively shorter canopy (shallower roots) in degraded forests were typically translated into slightly drier near-surface soils (Figure 8d): during typical years, soil water availability at the top 30 cm layers was 1.2–12% lower in burned forests than intact forests, whereas the differences were more modest in logged forests (0.2–3%) and even reversed during extreme droughts (Figure 8d). Carbon and energy fluxes showed similar behavior. Gross primary productivity in intact forests steadily decreased with increased drought severity, and the depletion of productivity caused by degradation is most marked during typical years but is reduced during severe droughts (Figure S14a). While ground temperature is always higher in degraded forests (Figure S14b), differences in sensible heat fluxes and outgoing longwave radiation also diminish during extreme drought conditions (Figure S14c,d).

Degraded forests show drier near-surface soils (Figure 8d) and warmer surface temperatures (Figure S14) than intact forests for most years, yet the interannual variability of climate also modulates the differences in water, carbon, and energy cycles between degraded and intact forests (Figures 8 and S14). Therefore, both degradation and climate may influence the flammability of forests. The average flammable area predicted by ED-2.2 (Section 2.4) shows large variation across regions, ranging from nearly zero at GYF forests (the wettest region) to over 25% yr^{-1} at some of the forests in TAN (the

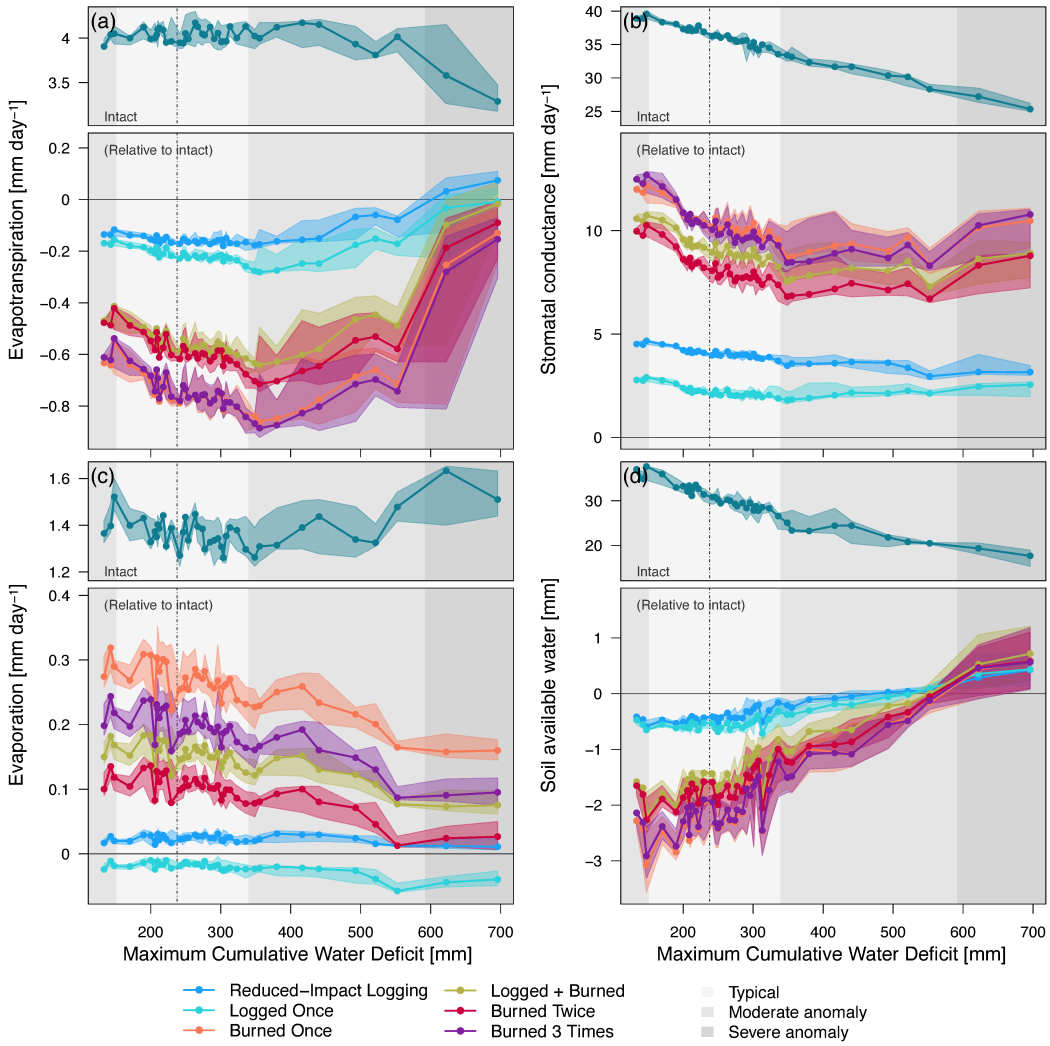

Figure 8. Response of the water cycle components across a forest degradation gradient and drought severity in Paragominas (PRG). Selected components: (a) Total water vapor flux, (b) stomatal conductance, averaged by leaf area, (c) evaporation, and (d) soil available water (i.e. in excess of permanent wilting point) of the top 30 cm. Points correspond to the median value of 12-month running averages, aggregated into 40 quantiles along the range of maximum cumulative water deficit (MCWD). Bands around the points correspond to the 95% range within each MCWD bin. Top panels are the absolute value for intact forests, and bottom panels are the absolute difference between degraded and intact forests. Background shades denote the MCWD anomaly: light gray – 68% range around the median (dot-dash vertical line); intermediate gray – 95% range; dark gray – anomalies exceeding the 95% range.

driest region) (Figure 9a). Within each region (i.e. under the same prescribed climate), the model generally predicted higher flammability for the shortest forests ($< 10\,\mathrm{m}$), although predictions also indicate large within-region variability of flammable area for forests with intermediate canopy height (10–25 m) (Figure 9a). For most forests, flammable conditions were predicted mostly during moderate or severe droughts, regardless of the degradation history, as exemplified by region PRG (Figure 9b). While the time series of flammable area were synchronized across degradation types, ED-2.2 predictions of flammable area were generally higher for burned forests than intact or lightly logged forests (Figures 9b and S15). The one exception was the driest region (TAN), where forests that burned multiple times experienced lower flammability than intact forests (Figure S15d); at TAN, even intact forests were relatively short (Figure 9a), which caused ED-2.2 to predict limited access to deeper soils and increased desiccation.

4 Discussion

4.1 Initialization of forest structure from remote sensing

Our method to derive the vertical structure of the canopy from high-resolution airborne lidar successfully characterized the diversity of forest structures of the Amazon, captured differences in forest structure variability along a precipitation gradient, and described the within-region variability in forest structure caused by forest degradation (Figures 3 and S2-S3). Previous studies have used forest structure derived from remote-sensing data to initialize vegetation demography models in tropical forests (e.g., Hurtt et al., 2004; Antonarakis et al., 2011; Rödig et al., 2018). However, these studies often assume a relationship between forest structure and canopy height with stand age. While this assumption has been successfully applied to intact and second-growth tropical forests (Hurtt et al., 2004; Antonarakis et al., 2011), the association between forest structure and succession is unlikely to be preserved in degraded forests. For example, understory fires proportionally kill more smaller trees than large trees (Uhl & Kauffman, 1990; Brando et al., 2012; Silva et al., 2018), and selectively logging creates complex mosaics of forest structure, with substantial losses of large trees from harvesting, and extensive damage to smaller trees in skid trails (Feldpausch et al., 2005). In contrast, our approach accounts for the entire vertical profile at local (50-m) scale, similarly to Antonarakis et al. (2014), which does not require any assumption on the successional stage of the forest. Importantly, our approach requires only the vertical distribution of returns, and could be adapted to large-

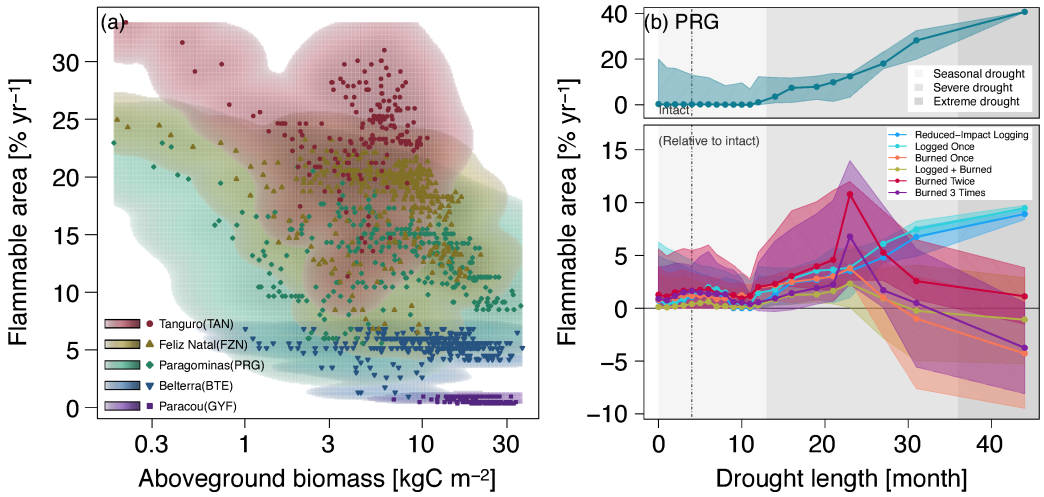

Figure 9. Average flammability as functions of degradation and climate variability. (a) Scatter plot shows the average flammable area (1980–2016) for each simulated patch across all regions, as a function of canopy height. Density cloud (background color) was produced through a bi-dimensional kernel density estimator; points are the averages used to generate each density cloud. Color ramps (logarithmic) range from 0.1 – 100% of the maximum computed scale. (b) Flammable area at region PRG, as a function of degradation history and drought length (number of consecutive months with water deficit in excess of 20 mm). Points correspond to the median value of 12-month running averages, aggregated into quantiles along the drought length. Bands around the points correspond to the 95% range within each drought length bin. Top panels are the absolute value for intact forests, and bottom panels are the absolute difference between degraded and intact forests. Background shades denote drought-length classes used in the text: seasonal (light gray, less than 12 months); severe (intermediate gray, 12–36 months); extreme (dark grey; more than 36 months). Flammability response to degradation and drought duration for other regions are shown in Figure S15.

footprint, airborne or spaceborne lidar data, including the NASA's Global Ecosystem Dynamics Investigation (GEDI, Hancock et al., 2019).

We demonstrated that the initialization from airborne lidar profiles captures most of the variability across and within regions, yet it has important assumptions and limitations. First, our approach relies on allometric equations to determine both the diameter at breast height (DBH), and the individual leaf area (L_i, Text S3.3). These equations have either large uncertainties (DBH) or limited number of samples (Figure S16).

The use of allometric equations that account for regional variation (e.g., Feldpausch et al., 2011, 2012), and the expansion of open-source databases, such as the Biomass And Allometry Database (BAAD, Falster et al., 2015) used in our study, could further improve the characterization of the vertical structure. In addition, the increased availability of terrestrial laser scanning (TLS) and high-resolution, low-altitude unmanned aerial vehicle lidar could substantially increase the data availability and thus improve the overall quality of allometric equations (Calders et al., 2015; Stovall et al., 2018; Schneider et al., 2019). Alternatively, techniques that extract individual tree crowns from lidar point clouds readily provide highly accurate local stem density and local size-frequency distributions (e.g., tree height or crown size; Ferraz et al., 2016). These distributions can be used to attribute DBH to individuals and generate initial conditions akin to forest inventory to the ED-2.2 model, and data-model fusion techniques that leverage the growing availability of data could reduce uncertainties on many model parameters, including allometry (F. J. Fischer et al., 2019). Finally, ED-2.2 overestimated the seasonality of gross primary productivity and evapotranspiration at the driest region (TAN) (Figures S4 and S6). This result suggests that simulated rooting depth for TAN was underestimated in the model. Rooting profiles in tropical forests remain largely uncertain: some site studies have sought to relate individual tree size with rooting depth using isotopic measurements (e.g., Stahl et al., 2013; Brum et al., 2019), whereas regional studies that provide spatial distribution of rooting depth still show important discrepancies in the tropics (e.g., Yang et al., 2016; Fan et al., 2017). Constraining the below-ground allocation of tropical ecosystems should be a priority in future studies.

In our study we inferred the functional diversity from forest structure obtained from existing forest inventory plots. The functional group attribution captured the general characteristics of functional composition along degradation gradients (Figure S1), including the more frequent occurrence of early-successional individuals in degraded forests, consistent with field-based studies (Both et al., 2019); nonetheless, uncertainties in functional attribution from field measurements are high. The increased availability of coordinated airborne laser scanning (ALS) and airborne imaging spectroscopy (AIS) data in mid-latitudes has lead to opportunities to link structural variability with functional diversity (e.g., Antonarakis et al., 2014; Schneider et al., 2017), and previous studies have successfully integrated ALS and AIS data to attribute functional groups in the ED-2 model (e.g., Antonarakis et al., 2014; Bogan et al., 2019). Overlapping ALS and AIS data over

tropical forests are becoming increasingly common (Asner et al., 2014; de Almeida et al., 2019; Laybros et al., 2019) and could provide new opportunities to reduce uncertainties in functional attribution in future studies. Likewise, ongoing and upcoming spaceborne missions at the International Space Station such as GEDI (Hancock et al., 2019), and the Hyperspectral Imaging Suite (HISUI, Matsunaga et al., 2017) will allow for large-scale characterization of structure and function of ecosystems at global scale (Stavros et al., 2017; Schimel et al., 2019).

4.2 Degradation impacts on ecosystem functioning

In addition to carbon losses and structural changes, degradation has substantial impacts on energy and water cycles in Amazonian forests, especially in severely degraded forests with marked dry season. According to the ED-2.2 simulations, ground temperature of logged forests ranged from nearly-identical to intact forests (low-impact logging or old logging disturbances) to 0.7°C warmer (recently logged forests), whereas severely burned forests experienced daytime near-surface temperatures increases of as much as 4°C (Figure S10), and differences between the lowest and highest biomass patches exceeded 9°C (Figure 6). Observed differences in understory temperatures show large variability, but they generally agree with the ED-2.2 results. For example, results of temperature differences between logged and intact areas in the wet forests of Sabah, Malaysia, ranged from negligible to 1.2°C for average maximum temperature (Senior et al., 2018; Jucker et al., 2018). The predicted warmer daytime understory temperatures at recurrently burned forests also yielded drier near-surface conditions: daytime ground vapor pressure deficit was on average 15–25 hPa greater than in intact forests (equivalent to 5–15% reduction in relative humidity), which is within the range observed after the most damaging experimental fire at TAN in 2007 (Brando et al., 2014), and similar to differences in understory relative humidity reported in the dry season between open-canopy seasonally flooded forests and closed-canopy upland forests in the Central Amazon (de Resende et al., 2014).

ED-2.2 showed various degrees of agreement with the few existing observational studies comparing changes in evapotranspiration due to degradation. Evapotranspiration response to reduced-impact logging was minor (−1.9% reduction relative to intact in BTE), consistent with eddy covariance tower estimates in a logging experiment in the same region (−3.7% reduction after accounting for site differences and interannual vari-

ability, S. D. Miller et al., 2011). The model results for the experimental fire at TAN, however, suggested similar wet-season ET between burned and intact forests ($\Delta\mathrm{ET} = \mathrm{ET_{Brn}} - \mathrm{ET_{Int}} = 0.002\,\mathrm{mm\,day^{-1}}$), with stronger depletion of ET in burned forests during the dry season ($\Delta\mathrm{ET} = -0.31\,\mathrm{mm\,day^{-1}}$) (Figures 5 and S6). In contrast, Brando, Silvério, et al. (2019) found higher ET in burned forests over a period of 4 years, albeit ΔET also showed significant interannual variability. A few other studies suggest that the significant decline in dry-season ET in burned forests may be expected in some areas: for example, Hirano et al. (2015) found that evapotranspiration of drained and burned peatlands with second-growth vegetation in Central Kalimantan (Indonesia) was $0.43\,\mathrm{mm\,day^{-1}}$ lower than drained forests; Quesada et al. (2004) inferred ET changes from soil water budget in savannas and found significant reductions following fires in a savanna site in Central Brazil. The advent of high-resolution remote sensing products that quantify energy, water, and carbon fluxes, such as the ECOsystem Spaceborne Thermal Radiometer Experiment on Space Station (ECOSTRESS) and the Orbiting Carbon Observatory 3 (OCO-3), will provide new opportunities to quantify the role of tropical forest degradation on ecosystem functioning at regional scale (Schimel et al., 2019), as well as to provide new benchmark data for ecosystem models.

Our model results indicate that severe degradation substantially alters the magnitude and seasonality of energy, water, and carbon fluxes (Figures 5-7 and S10-S12). In our study, we disabled the vegetation dynamics in ED-2.2 to ensure that predicted differences in ecosystem functioning could be unequivocally attributed to structural diversity, but the differences in ecosystem functioning between degraded and intact forests may diminish over time as the forest recovers from previous disturbance. This pathway is consistent with the relatively small differences in ET and surface temperature (Figures 5-6) observed at logged forests at GYF (25 years since last disturbance) and burned forests at BTE (15 years since last disturbance). However, the recovery trajectory is one out of multiple possible pathways: degraded forests may be more prone to subsequent disturbances (Silvério et al., 2019; Hérault & Piponiot, 2018); the recovery dynamics can be long or not attainable if multiple stable states exist or if succession is arrested (Mesquita et al., 2015; Ghazoul & Chazdon, 2017), potentially prolonging the impacts of forest degradation on energy and water cycles; and feedbacks on precipitation caused by degradation could affect the spatial distribution of rainfall similarly to the effect observed with

deforestation (Spracklen et al., 2018), although to our knowledge this impact has not yet been quantified for degraded forests.

4.3 Interactions between forest degradation and climate variability

The predicted reductions in evapotranspiration (ET) in the most degraded areas during the dry season suggest that land-use change impacts on the water cycle may be more widespread and pervasive than indicated by earlier studies. Previous model-based studies showed that biome-wide deforestation could cause ET to decrease by 25–40% relative to intact forests in the Amazon during the dry season (e.g., von Randow et al., 2004; Zemp et al., 2017). These reductions are comparable to the ET reductions predicted by ED-2.2 at the most degraded forests (21–32%, Figure 5). Because tropical forest degradation affects an area comparable to deforestation in the Amazon (Tyukavina et al., 2017), it may further reduce the strength of the Amazon water vapor source to the atmosphere. In our study, we focused on understanding how climate and structure variability impacts the water and energy fluxes, but degradation-driven changes in these fluxes are likely to feed back into the atmosphere. For example, changes in evapotranspiration and sensible heat flux associated with deforestation are known to either redistribute or reduce total rainfall in tropical forests (Spracklen et al., 2018, and references therein), and a substantial fraction of South American precipitation water comes from evapotranspiration from Amazonian forests (van der Ent et al., 2010). Recent estimates of ET for the Amazon Basin from the Gravity Recovery and Climate Experiment (GRACE) suggest that the basin-wide ET (including intact forests) has decreased by 1.7% between 2002 and 2015 (Swann & Koven, 2017). In addition, several studies suggest that the dry season in the Amazon is becoming longer (Fu et al., 2013; Sena et al., 2018), and land use change is one of the main drivers of the drying trend (Barkhordarian et al., 2018). The role of forest degradation on ongoing and future changes in climate across the Amazon remains uncertain and deserves further investigation, potentially with coupled biosphere-atmosphere models that represent heterogeneity in forest structure and functioning (Swann et al., 2015; Knox et al., 2015; Wu et al., 2017).

Our results show that structural changes resulting from forest degradation make the forest surface drier and warmer (Figures 5-8 and S10). Drier and warmer conditions near the surface increase flammability (Brando, Paolucci, et al., 2019, and references therein), and it has been long suggested that forest degradation and canopy opening make forests

more likely to burn (e.g., Uhl & Buschbacher, 1985; Cochrane et al., 1999; Ray et al., 2005; A. A. C. Alencar et al., 2015). The ED-2.2 simulations indeed predicted higher flammability in degraded (more open-canopy) forests on any given year (Figures 9 and S15). However, our results also suggest that climate strongly drives the variability of flammable area across most of our study regions (Figures 9b and S15), which is consistent with the significant increases in forest fires in the Amazon during extreme drought years (Morton et al., 2013; Aragão et al., 2018). Moreover, our results indicate that differences in flammable area between intact and degraded forests are reduced or even reversed during extreme droughts, which indicates that under extreme conditions, the level of degradation is less critical to create flammable conditions. This effect was predicted for most years at TAN, which typically experiences severe and longer dry seasons compared to the other study regions (Figure S15).

Previous studies suggest that parts of the Eastern Amazon could become drier by the end of the century and experience more extreme events, including droughts (IPCC, 2014; Duffy et al., 2015), and thus potentially more susceptible to future fires (De Faria et al., 2017; Brando et al., 2020). However, how tropical forest flammability will respond in the long-term to ongoing changes in climate and land use is still uncertain, and recent studies have shown that either climate (Le Page et al., 2017) or land use (Fonseca et al., 2019) could be dominant on predicted shifts in fire regime. Importantly, while our analysis focused on flammability, and ED-2.2 fire model captures the general patterns of fire disturbance across the Amazon (Longo, Knox, Levine, et al., 2019), it does not represent many mechanisms and processes that are critical to describe fire dynamics in tropical forests, such as anthropogenic ignitions, diurnal cycle of fire intensity, and fire termination, therefore we could not quantify the effects of fire on further forest degradation. The use of process-based fire disturbance models within the ED-2.2 (e.g., Thonicke et al., 2010; Le Page et al., 2015) framework could contribute to further improve our understanding of interactions between forest degradation, climate, and flammability across the Amazon.

5 Conclusion

Our study showed that tropical forest degradation can markedly modify the ecosystem functioning in the Amazon, with substantial reductions in evapotranspiration (ET) and gross primary productivity (GPP), and increase in surface temperature (Figures 5-

8). Within the regions included in our study, the effects of degradation on energy, water, and carbon cycles were the strongest in the Eastern and Southern Amazon, where the dry season is more pronounced. Notably, in areas where severe forest degradation resulted in substantial changes in forest structure, reductions in dry-season evapotranspiration are similar to those found in deforested areas (Figure 5; von Randow et al., 2004). The area of the Amazon forest impacted by degradation is comparable to the deforested area (Asner et al., 2005; Morton et al., 2013; Souza Jr. et al., 2013; Tyukavina et al., 2017), and thus degradation-driven changes in water, energy, and carbon cycles are potentially important. However, the extent to which degradation affects the biophysical and biogeochemical cycles at regional scale ultimately depends on (1) annual degradation rates; (2) recovery time of degraded forests; and (3) the likelihood that degraded forests are cleared. For example, (Brando, Silvério, et al., 2019) found that ET in burned forests was indistinguishable from intact forests 7 years after the last fire. While their result suggests fast recovery of degraded forests, the impacts of degradation on ET can still be regionally relevant if degradation rates are sufficiently high to maintain low average age since last disturbance in degraded forests. Moreover, we found that the impacts of tropical forest degradation on energy, water, and carbon cycles and on flammability are more pronounced during typical years than during extreme droughts (when all forests become flammable), which highlights the complex interactions between climate and forest structure. To understand and reduce uncertainties of climate-structure interactions, it would be valuable to leverage the recent advances in remote sensing of forest structure, including the recently launched GEDI mission (Hancock et al., 2019), and terrestrial biosphere models that can represent complex and heterogeneous ecosystems (Fisher et al., 2018). Our study, while focusing on airborne lidar data, has demonstrated the opportunities to integrate remote sensing and terrestrial biosphere models even in regions with complex forest structure such as degraded forests.

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nently stored at Longo et al. (2020). Trait data are available at the TRY initiative on plant traits (`http://www.try-db.org`), request 2751; at Gu et al. (2016); or as supporting information from the cited references (I. J. Wright et al., 2004; Santiago & Wright, 2007; Bahar et al., 2017).

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Supporting Information for \Impacts of Degradation on Water, Energy, and Carbon Cycling of the Amazon Tropical Forests"

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Additional Supporting Information (Files uploaded separately)

1. Captions for Dataset S1

Introduction

This supporting material provides additional information on the study sites, methodology, and results in the main text. Text S1 contains additional information on the airborne lidar and forest inventory plot data used in this study. Text S2 summarizes changes in the ED-2.2 model to improve the representation of forest structure and ecosystem functioning. Text S3 describes in detail the steps needed to obtain ED-2.2 initial conditions from airborne lidar.

Figure S1, S2 and S3 provide additional evaluation of the airborne lidar initialization, speci cally the distribution of functional groups, the vertical leaf area index pro le, and the evaluation of plots a ected by reduced-impact logging in region BTE. Figure S4-S9 complement the ED-2.2 model evaluation against eddy covariance towers, comparing

fortnightly averages for multiple energy, water, and carbon cycle variables. Figure S10 shows the di erences in the average seasonal cycle of daytime ground temperature for all the regions simulated by ED-2.2, as functions of the degradation history. Figure S11 shows the ED-2.2 predictions of average seasonal cycle of gross primary productivity as functions of local (patch) aboveground biomass for all focus regions. Figure S12 shows the distribution of evapotranspiration as function of local (patch) biomass and age since last disturbance, during the wet and dry seasons, for three selected regions across the precipitation gradient. Figure S13 shows the local (patch) distribution of leaf area index as a function of aboveground biomass for all the focus regions. Figure S14 shows the drought severity response of intact and degraded forests in region PRG, for multiple carbon and energy variables. Figure S15 complements Figure 9 shows how forest ammability varies as a function of drought length across degradation gradients at additional regions. Figure S16 is part of Text S2 and shows the tted allometric models relating height, diameter at breast height, and individual leaf area, which are used by both the model initialization and model simulations. Figure S17 and S18 are also part of Text S2 and show multiple trait relationships derived from multiple data sets and implemented in the ED-2.2 model. Figure S19 is part of Text S3 and shows an example of how the vertical distribution of lidar returns is processed to obtain cohorts that are provided to the ED-2.2 model. Figure S19 is also part of Text S3 and shows the results of cross-validation of airborne lidar initialization using aggregated forest inventory plot metrics as benchmarks. Figure S21 is also part of Text S3 and summarizes the distribution of scaling factors to adjust the non-dimensional leaf area density pro les.

Table S1 shows a selection of metrics to assess the ED-2.2 model performance against multiple energy, water, and carbon cycle variables obtained from the eddy covariance towers. Table S2 is part of Text S1 and provides additional information of data used for the ve focus regions and the ancillary regions. Table S3 is part of Text S2 and provides detailed information on ED-2.2 model settings. Table S4 is part of Text S3 and lists multiple goodness-of- t statistics for the tted models that relate airborne lidar metrics and aggregated, area-based forest properties.

S1. Additional information on airborne lidar and forest inventory plots

Some of the study regions comprised multiple sites, for which airborne lidar data and disturbance history data were available. Many of these sites also contained forest inventory plots, and have been previously used in studies that quanti ed carbon losses due to degradation in the Amazon and plant area index estimation (Longo et al., 2016; Vincent et al., 2017; Rappaport et al., 2018). Table S2 provides additional information on each speci c site. Further information on plots can be found in Gourlet-Fleury, Ferry, Molino, Petronelli, and Schmitt (2004) (site PRC), Bonal et al. (2008) (site GFE), Brando et al. (2012) (site TGE), and Longo et al. (2016), Sustainable Landscapes Brazil (2019) and dos-Santos, Keller, and Morton (2019) (other sites). To reduce the di erences among plots regarding size and sampling e ort, we considered only living individuals (trees, lianas, and palms) with diameter at breast height $D \geq 10$ cm, and split larger plots ($0.5 \leq 6.25$ ha) into sub-plots that were as close to 0.25 ha as possible. The location of all inventories in Brazil were geo-registered with sub-meter accuracy using di erential Global Navigation Satellite Systems (GeoXH6000); forest inventories in French Guiana were geo-referenced with handheld Global Positioning System, with nominal accuracy of 2 m.

For the study areas in Brazil, airborne lidar data were collected between 2012 and 2017, and surveys used Optech ALTM instruments onboard an aircraft ying at average height of 850m above ground; the sensor scan angle was restricted to 15° -nadir and an average swath sidelap between ight lines of 65% (Longo et al., 2016); the point cloud data are publicly available (Sustainable Landscapes Brazil, 2019). Airborne lidar data at GYF were collected in 2013; the aircraft ew at a height of 550m above ground carrying a Riegl LMSQ560; the scan angle was capped in 20° -nadir, and the ight line sidelap was near 60% (Vincent et al., 2017). To ensure that the terrain elevation was well characterized, ights had to meet a minimum return density of 4 m ^{2} of 99.5% of the area (except water bodies and pastures), following previous recommendations for tropical forests (Leitold et al., 2015).

Some of the regions were only used to assist the calibration of the statistical models (Section S3.2), but not used in the simulations. Because our goal was to characterize the impacts of degradation on forest structure and ecosystem functioning, we did not include simulations from MAO, where all surveyed forests were intact, nor did we include JAM and FST, where all forests were logged (albeit using reduced-impact techniques). Forests in SFX were not included because the disturbance history based on Landsat analysis was uncertain due to widespread presence of vines. Finally, at RBR, none of the surveyed forests could be considered intact or logged using reduced-impact techniques, which precluded us to have a minimally-disturbed forest as reference.

S2. Additional ED-2.2 developments

S2.1. Allometric relations

To obtain an allometric equation for diameter at breast height (D, cm) as a function of tree height (H, m), we used all individual tree measurements from the plots included in steps 1 and 2 that were from living trees (excluding lianas and palms), and had field measurements of both D and H ($n = 15865$). Because the sampling effort was not even across tree sizes, and to reduce the effects of variability in tree measurements of height along the D range on local biases, we followed the approach by Jucker et al. (2017) and binned the data into 50 evenly spaced $\log_e(D)$ classes between $D = 5$ and $D = 200$ cm (the range of D measurements). The binned data were fitted using standardized major axis regression. This choice ensures that the arithmetic inverse relationship (i.e. height as a function of D) could be also used in the ED-2.2 model:

$$\log_e(D) = (\underbrace{2.01 \pm 0.25}_{\log_e(d_1)}) + (\underbrace{1.68 \pm 0.08}_{d_2}) \log_e(H); \qquad \text{(S1)}$$

where H should be in m, and D should be in cm. The model fit is shown in Figure S16a.

We did not have any measurement of individual leaf area (L, m^2_{Leaf} plant^{-1}) at the study sites, therefore we developed an allometric equation based on the Biomass And Allometry Database (BAAD; Falster et al., 2015). Similar to many allometric equations for aboveground and leaf biomass (e.g., Chave et al., 2014), we used D^2H as the predictor. Because we did not seek a reversible equation, we fitted the model using minimum least squares with heteroskedastic distribution of residuals (Mascaro et al., 2011; Longo et al.,

2016). The tted model was:

$$L_i = (0.234 \pm 0.012)\ D^2 H^{0.641 \pm 0.011} + E_N^{h} = 0; \quad = 0.241 \quad 0.026 L_i^{1.001 \quad 0.056^{i}};$$

(S2)

where coe cients are presented in the form Expected Value Standard Error; units for the empirical equation should be: D in cm, H in m, and L_i in m^2_{Leaf} plant ^{1}. The model t is shown in Figure S16b.

In ED-2.2, the carbon stocks (kgC plant^{1}) of di erent tissues | leaves (C_L), ne roots (C_R), sapwood (C_S), bark (C_B) and heartwood (C_H) | are de ned through allometric equations. Leaf biomass (C_L) is obtained from Equation (S2):

$$C_L = \frac{L_i}{SLA}; \tag{S3}$$

where SLA (m^2_{Leaf} kgC ^{1}) is the individual plant's speci c leaf area. Fine-root biomass and sapwood biomass are derived from leaf biomass, using the same relationships described in Moorcroft, Hurtt, and Pacala (2001). Bark biomass followed a parameterization similar to sapwood:

$$C_R = \alpha_R C_L; \tag{S4}$$

$$C_S = \alpha_S H C_L; \tag{S5}$$

$$C_B = \alpha_B H C_L; \tag{S6}$$

where $\alpha_R = 1$ for all plant functional types, following Moorcroft et al. (2001). The leaf-to-sapwood (α_S) and leaf-to-bark (α_B) scaling factors (m ^{1}) are determined using the same formulation as Falster, FitzJohn, Brännström, Dieckmann, and Westoby (2016):

$$\alpha_S = \frac{{}_c SLA \quad {}_W 1000}{A_{L:S}}; \tag{S7}$$

$$q_B = \frac{{}_c SLA \; {}_B \; 1000}{A_{L:B}} \qquad \text{(S8)}$$

where ${}_c$ is an empirical shape parameter based on Falster et al. (2016) parameterization for broadleaf trees; $A_{L:S}$ and $A_{L:B}$ ($m^2_{Leaf}\, m^2_{Bark}$) are the leaf:sapwood and leaf:bark area ratios, respectively; ${}_W$ and ${}_B$ ($g\,cm^{-3}$) are the wood and bark densities, respectively; $= 2:0\,kg\,kgC^{-1}$ is the oven-dry:carbon biomass ratio; and the factor 1000 is included for unit conversion. Values of these parameters are shown in Table S3.

The allometric equation for heartwood biomass (C_H) was obtained using both the pantropical allometric equation for aboveground biomass (C_{AG}, $kgC\,plant^{-1}$; Chave et al., 2014), and that total aboveground biomass is the sum of the biomass of the following tissues:

$$C_{AG} = \frac{1}{-}\,0:0673 \quad {}_W\, D^2 H^{0:976} \qquad \text{(from Chave et al., 2014)} \qquad \text{(S9)}$$

$$C_{AG} = C_L + f_{AG}\,(C_S + C_B + C_H)\,; \qquad \text{(S10)}$$

where f_{AG} is the fraction of biomass above ground; $= 2:0\,kg\,kgC^{-1}$ is the oven-dry:carbon biomass ratio; and units for S9 should be: ${}_W$ in $g\,cm^{-3}$, D in cm, H in m, and C_{AG} in $kgC\,plant^{-1}$. To simplify the implementation of C_H in ED-2.2, we used Equations (S9), (S10) and (S1) to nd C_H at $D = 10\,cm$ (typical minimum diameter measured in inventories) and at $H = 46\,m$ (maximum height allowed for tropical trees) and derive a function for C_H with the same form and units as Equation (S9):

$$C_H = \frac{1}{-}\,0:0608 \quad {}_W\, D^2 H^{1:004}: \qquad \text{(S11)}$$

S2.2. Changes in the photosynthesis module

The photosynthesis module in ED-2.2 has been previously described in detail in (Longo, Knox, Medvigy, et al., 2019); here we show only a brief overview and highlight the

main modi cations. Similarly to previous versions, the net CO_2 assimilation rate (A, mol CO_2 m ^{2} s ^{1}) for C_3 plants is de ned as:

$$A = V_c \quad \frac{1}{2}V_o \quad R; \tag{S12}$$

$$V_o = \frac{2}{c_i} V_c; \tag{S13}$$

$$= \frac{o}{2}; \tag{S14}$$

where V_c, V_o, and R (mol CO_2 m ^{2} s ^{1}) are the carboxylation, oxygenation (photorespiration) and day respiration rates, respectively; (mol CO_2 mol ^{1}) is the CO_2 compensation point; (mol CO_2 mol ^{1}) is the intercellular o = 0:209 mol O_2 mol ^{1} is the oxygen mixing ratio; and is the carboxylase:oxygenase ratio. The terms R, , and are calculated the same way as in (Longo, Knox, Medvigy, et al., 2019). The carboxylation rate V_c depends on environmental constraints, which ultimately limits the net assimilation rate A.

The maximum carboxylation rate given temperature (V_c^{max}) is de ned as in Longo, Knox, Medvigy, et al. (2019):

$$V_c^{max} = \frac{V_{c15}^{max} Q_V^{\frac{T \quad T_{15}}{10}}}{f\,1 + \exp[\quad f\ (T \quad T_c)]g\ f\,1 + \exp[+f\ (T \quad T_h)]g}; \tag{S15}$$

where V_{c15}^{max} (mol m ^{2} s ^{1}) is V_c^{max} at temperature T_{15} = 288:15 K (15 C); T (K) is the leaf temperature; Q_V determines the steepness of the temperature dependence of V_c^{max}; f , T_c, and T_h are phenomenological parameters that reduce V_c^{max} at extreme temperatures, following the same formulation used in previous ED versions (Moorcroft et al., 2001; Longo, Knox, Medvigy, et al., 2019).

The maximum carboxylation rate can never be achieved because CO_2 inhibits oxygenation, and O_2 inhibits carboxylation (von Caemmerer, 2000). The carboxylation rate at

saturated Ribulose-1,5-Biphosphate (RuBP) conditions (V_c^{RuBP}) is determined as:

$$V_c^{RuBP} = V_c^{max} \frac{c_i}{c_i + K_c \left(1 + \frac{o}{K_o}\right)}; \tag{S16}$$

where K_c (mol CO_2 mol^{-1}) and K_o (mol O_2 mol^{-1}) are the Michaelis constants for carboxylation and oxygenation, respectively, and are also calculated as in (Longo, Knox, Medvigy, et al., 2019). Equation (S16) is the same described in (Longo, Knox, Medvigy, et al., 2019).

The RuBP regeneration depends on the electric transport rate (J (mol m^{-2} s^{-1}), which in turns depends on the absorbed irradiance (I (mol m^{-2} s^{-1}). If I is relatively low, then RuBP pools may decline, limiting the carboxylation rate. The RuBP-limited (also known as light-limited) carboxylation rate (V_c^{PAR}) is de ned as in von Caemmerer (2000):

$$V_c^{PAR} = \frac{J}{4 + 8\frac{c_i}{}}; \tag{S17}$$

and J is determined from an empirical quadratic equation (von Caemmerer, 2000; Oleson et al., 2013):

$$J = \frac{(I_{PSII} + J^{max}) - \left[(I_{PSII} + J^{max})^2 - 4\,'\,I_{PSII}\,J^{max}\right]^{\frac{1}{2}}}{2\,'} \tag{S18}$$

$$J^{max} = \frac{J_{15}^{max}\,Q_J^{\frac{T - T_{15}}{10}}}{\{1 + \exp[-f_c\,(T - T_c)]\}\{1 + \exp[+f_h\,(T - T_h)]\}} \tag{S19}$$

$$I_{PSII} = \frac{1}{2}\,{}_{PSII}\,I \tag{S20}$$

where J^{max} (mol m^{-2} s^{-1}) is the temperature-dependent maximum electron transport rate; J_{15}^{max} and Q_J are the equivalent of V_{c15}^{max} and Q_V for the electron transport rate, respectively; I_{PSII} (mol m^{-2} s^{-1}) is the light e ectively used by the photosystem II; $' = 0.7$ is an empirical curvature parameter (von Caemmerer, 2000; Oleson et al., 2013); ${}_{PSII} = 0.85$ is the quantum yield of the photosystem II (von Caemmerer, 2000; Oleson et al., 2013);

and T_c, T_h, f_c, and f_h are empirical parameters to downscale photosynthetic activity at extreme temperatures (Table S3). Unlike the original implementation of V_c^{PAR} (Moorcroft et al., 2001; Longo, Knox, Medvigy, et al., 2019) the explicit representation on electron transport rate is advantageous because it accounts for the di erences in temperature dependence of J^{max} and V_c^{max} (von Caemmerer, 2000), and the saturation behavior of J as I becomes non-limiting.

In addition to light limitation, carboxylation rates may be limited by the triose phosphate utilization (TPU) for synthesizing sugars and starch (von Caemmerer, 2000). The TPU limitation typically occurs when both CO_2 mixing ratio and irradiance are high, or when temperature is low (von Caemmerer, 2000; Lombardozzi et al., 2018), and is expected to become more important as atmospheric CO_2 increases (Lombardozzi et al., 2018). The TPU-limited carboxylation rate (V_c^{TPU}) is de ned as:

$$V_c^{TPU} = 3\,E_{TP}\,\frac{c_i}{c_i}; \tag{S21}$$

where E_{TP} (mol m ^{2} s ^{1}) is the export rate of triose phosphate from chloroplasts, and is normally parameterized as a function of V_c^{max} ($E_{TP} = "_E\,V_c^{max}$; von Caemmerer, 2000; Oleson et al., 2013; Lombardozzi et al., 2018).

Similar to previous versions of ED-2, the net assimilation rate is determined through a law of minimum:

$$A = \min\ A^{RuBP}; A^{PAR}; A^{TPU} \tag{S22}$$

where each of the cases on the right-hand side are calculated from Equations (S12) and (S13), by replacing V_c with each of the cases (Equations (S16), (S17), and (S21)), and using the algorithm described in Longo, Knox, Medvigy, et al. (2019).

Both J_{15}^{max} and E_{TP} are assumed to be proportional to V_{c15}^{max}. To obtain the proportionality ratios, we used the data collected at multiple sites in Panama (Gu et al., 2016; Norby et al., 2017). Even though the Norby et al. (2017) provided ts relating these quantities, we re tted the functions to eliminate the intercept, and corrected for the fact that Norby et al. (2017) provides values at 25°C and ED-2.2 needs the reference at 15°C:

$$V_c^{max} \; (J_{15}^{max} = \varepsilon_J \, V_{c15}^{max})$$

The values of ε_J and ε_E are determined from the data collected at multiple sites in Panama and described in Norby et al. (2017). Although Norby et al. (2017) provided empirical ts relating V_c^{max}, J^{max} and E_{TP}, we obtained the relationships using standardized major axis (SMA) to account for the variability on both variables, and corrected for the fact that Norby et al. (2017) values use a di erent reference temperature (25°C):

$$\varepsilon_J = \frac{J_{25}^{max}}{V_{c25}^{max}} \frac{Q_V}{Q_J}; \qquad \text{(S23)}$$

$$\varepsilon_E = \frac{E_{TP}}{V_{c25}^{max}}; \qquad \text{(S24)}$$

where J_{25}^{max} and V_{c25}^{max} are the values at 25°C, obtained directly from Gu et al. (2016). The SMA line, coe cients ε_J^0 and ε_E and the R^2 are shown in Figure S17.

S2.3. Updated trait and trade-o relationships

In ED-2.2, we represent the functional diversity within ecosystems by de ning multiple plant functional types (PFTs). PFTs are de ned by both morphological characteristics (e.g. tree or grass) and by a set of traits that determine a variety of life strategies within the ecosystems. Many traits and trade-o s of tropical forest PFTs had not been changed since the original ED-1.0 release (Moorcroft et al., 2001), despite the increase in data availability for the tropics. Here, we aggregated data from multiple trait-based studies

and trait data bases such as GLOPNET and TRY (Wright et al., 2004; Santiago & Wright, 2007; Chave et al., 2009; Kattge et al., 2009, 2011, 2020; Baraloto et al., 2010; Powers & Ti n, 2010; Bahar et al., 2017; Norby et al., 2017), to revise the values associated with each PFT. To remove confounding factors such as canopy position, we only used data for sun leaves, or individuals that were either emergent or canopy trees.

Wood density was the most widely available trait in our data base, and also the indicative trait used to de ne PFTs in ED-1.0 (Moorcroft et al., 2001). To re-de ne the PFTs, we used the data from all forest inventory plots available, attributed wood density for each individual using the wood density data base compiled by Chave et al. (2009). We then calculated the probability distribution function of wood density (weighted by basal area), and split the distribution based on quantiles (the lower, middle, and upper 33% of the distribution associated with early-successional, mid-successional, and late-succesional trees, respectively). The expected values of wood density for each PFT was assumed to be the mid-point within each quantile (i.e. 16.67%, 50%, and 83.33% quantiles, respectively).

To determine the trade-o axes between traits, we tted standardized major axes (SMA). Because most wood density data came from the Chave et al. (2009) compilation (only wood density data were available), we aggregated data to species to seek relationships between wood density and other traits. Most traits were not correlated with wood density: leaf turnover rate showed the most signi cant, yet weak correlation with wood density (Figure S18a). For leaf traits, we were able to obtain large number of paired observations (i.e. two trait measurements from the same individual) between speci c leaf area (SLA) and the other traits, and thus we tted the standardized major axes using SLA as one of the variables (Figure S18b, S18c, and S18d).

The revised trait values for the plant functional types used in these simulations are shown in Table S3.

S3. ED-2.2 initial conditions using airborne lidar

The approach to obtain initial conditions for ED-2 using airborne lidar data is summarized in three steps: (1) derivation of unscaled vertical pro les of leaf area density from the vertical distribution of returns, and the height-dependent proportion of leaf area density allocated to each plant functional type; (2) estimation of plot-level properties of the forest (biomass, basal area, and individual's stem density) from airborne lidar; (3) optimization of scaling factors to obtain absolute leaf area density pro les and the initial conditions for ED-2. This approach requires only representative, geo-referenced forest inventory plots for calibration, and small-footprint, discrete-return airborne lidar point cloud data with high density of returns, in addition to knowledge of individual-based allometric equations that relate diameter at breast height (D) to tree height, above-ground biomass and leaf biomass.

S3.1. Vertical foliage pro les

To obtain vertical pro les of leaf area density (Figure 2, Box 1) across the areas surveyed by airborne lidar, we rst clipped the full point cloud domain into 50 50 m columns. For each column, we simulated a pseudo-waveform from the discrete point clouds to create a continuous and smooth distribution of return energy in the vertical (see one example in Figure S19a). Our simulated waveform function $E(\ )$ is based on the algorithm described by Popescu, Zhao, Neuenschwander, and Lin (2011) and Hancock et al. (2019):

$$E(h_i) = X(h) \quad Z(h; h_i); \tag{S25}$$

$$X(h) = \sum_{n=1}^{N} \begin{cases} 1 & \text{if } h_n \in \left[h - \frac{h}{2}; h + \frac{h}{2} \right] \\ 0 & \text{otherwise} \end{cases} ; \tag{S26}$$

$$Z(h; h_i) = \frac{1}{\sigma_h \sqrt{2\pi}} \exp\left[\frac{(h - h_i)^2}{2\sigma_h^2} \right] ; \tag{S27}$$

where h_i is the mean elevation of each bin; $h = 10$ cm is the thickness of each bin layer; $X(h)$ is the energy distribution function across the laser beam trajectory (horizontal); $Z(h)$ is the energy distribution function in the vertical (i.e. along the laser beam trajectory); σ_z is the pulse width in the vertical, which controls the smoothness of the simulated waveform; and $\otimes$ is the convolution operator. Similar to Hancock et al. (2019), we binned the return counts before applying the convolution to improve computational efficiency. When the goal is to simulate the signal of large-footprint waveform lidar (e.g. GLAS or GEDI), the energy distribution function across the laser beam trajectory is frequently assumed Gaussian (Blair & Hofton, 1999; Popescu et al., 2011; Hancock et al., 2019). In our case, however, we sought to characterize the average vegetation profile for the entire column and assumed a uniform (rectangular) distribution across the entire column area instead (Eq. S26). In addition, as we will discuss in later in this text, it is important that the waveform is not excessively noisy to obtain realistic leaf area index, yet it should retain sufficient features to ensure the vegetation structure is not overly aggregated (Figure S19a). We defined $\sigma_h = 50$ cm which resulted in a good compromise in preliminary tests. Finally, following Hancock et al. (2019), we calculated the waveform functions for vegetation (E_v) and ground (E_g) returns separately, in order to obtain the integrated return energy (R_v and R_g):

$$R_v(h_i) = \sum_{j=i}^{N_l} E_v(h_j) ; \tag{S28}$$

$$R_g = \sum_{j=1}^{N_l} E_g(h_j); \tag{S29}$$

where N_l is the total number of layers. In our case, we de ned layers up to $h_T = 70$ m to ensure that the tallest sampled trees would be completely characterized.

To obtain the relative vertical distribution of leaf area density ((h); m^2_{Leaf} m^{-2}), we applied the Beer-Lambert light extinction approach, following the approach originally developed by MacArthur and Horn (1969) and adapted for lidar pro les (e.g., Ni-Meister et al., 2001; Stark et al., 2012; Antonarakis et al., 2014). In this approach, (h) is a function of the gap probability (P, non-dimensional):

$$(h) = \frac{\cos'}{G(h;')} \frac{1}{P(h;')} \frac{@P(h;')}{@h}; \tag{S30}$$

where h is the height, ' is the angle of incident light, and G (h;) is the leaf area projection factor. For most lidar surveys used in this study, the maximum o -nadir scan angle was 5:5 (Longo et al., 2016); the only exception was Paracou (GYF), where the o -nadir angle was 20 (Vincent et al., 2017). As a rst approximation, we assumed 0, and thus P (h; ') P (h), but we acknowledge that this introduces an error (5 8% for 10% of the points at GYF). The leaf area projection factor is dependent upon the mean leaf orientation. For simplicity, we assumed isotropic (random) orientation, i.e. G (h; ') = 0:5 (Ni-Meister et al., 2001; Vincent et al., 2017).

Following Ni-Meister et al. (2001), the vertical pro le of gap probability can be described by the integral of the lidar return energy [$R_v(h)$] between height h and the top canopy height (h_T):

$$\frac{dR_v(h)}{dh} = J_0 r_v \frac{dP(h)}{dh}; \tag{S31}$$

where J_0 is the irradiance emitted by the lidar sensor and r_v is the canopy re ectivity. Using the boundary conditions at the top canopy [$R_v(h_T) = 0$; $P(h_T) = 1$] and that the total energy re ected by the ground is proportional to the total gap fraction, we obtain:

$$R_v(h_i) = J_0 r_v [1 \quad P(h_i)] ; \tag{S32}$$

$$R_{v0} = J_0 r_v [1 \quad P(h = 0)] ; \tag{S33}$$

$$R_g = J_0 r_g P(h = 0) ; \tag{S34}$$

where r_g is the soil re ectivity and $R_{v0} = R_v(h = 0)$. The irradiance emitted by the sensor (J_0) is not provided in the data set, however it is possible to combine Equations (S32)-(S34) to suppress J_0 from the de nition of $P(h)$:

$$P(h_i) = 1 \quad \frac{R_v(h_i)}{R_{v0} + k_r R_g}; \tag{S35}$$

where $k_r = \frac{r_v}{r_g}$, the ratio between vegetation and ground re ectivities. By substituting Equations (S31), (S33), and (S35) into Equation (S30) for the $\theta = 0$; $G = 0.5$ case, we obtain:

$$(h) = 2 \frac{d}{dh} \ln [R_{v0} + k_r R_g \quad R_v(h)]: \tag{S36}$$

It is possible to determine k_r from airborne lidar surveys that have re ectance data (Antonarakis et al., 2014), or from optimization using independent local measurements of leaf area index (Stark et al., 2012). Neither information is easily obtained for large areas, and thus we assumed $k_r = 1.03$, following Tang and Dubayah (2017). We found that the results are not sensitive to small variations in k_r, particularly when the gap fraction is low. On the other hand, the approximation of return counts is only a proxy to the return energy, and therefore, we assumed that the pro le obtained from Equation (S36) was considered unscaled, and will be referred as $\hat{s}(h)$. Following Shao, Stark, de Almeida,

and Smith (2019), we excluded the profile below 5 m, as estimates of leaf area density near the surface often show large uncertainty due to the limited fraction of returns near the surface in denser canopies.

Cohorts in ED-2 are defined as discrete groups of individuals with similar size and same life strategy (plant functional type; PFT). To separate the vertical profile into discrete layers of similar size, we assumed that the layers with the most significant population can be identified by local maxima, or by local saddle points when the layers are not completely separated, as shown in Figure S19b. The boundary between consecutive layers is defined as either the local minima or inflection points that are not saddle points (Figure S19b). These features were automatically determined based on the function `peaks` (package `RSEIS`; Lees, 2017), which was modified to capture inflection points and local minima.

The last stage of step 1 was to attribute the fraction of each plant functional type in each vertical layer, which was used to define the cohorts (Figure S19c). Because the airborne lidar data was from a single band, we could not use spectral mixture analyses (e.g., Antonarakis et al., 2014). To overcome this limitation, we also simulated waveforms for all plots that had complete overlap with airborne lidar data in all of the study sites, and complemented with data from the Sustainable Landscapes Brazil project (Longo et al., 2016; Sustainable Landscapes Brazil, 2019; dos-Santos et al., 2019) (total of 817 0.25 ha plots). For each plot, we determined the expected relative proportion of each PFT p (early-successional, ETR; mid-successional, MTR; and late-successional, LTR) as a function of height ($q_p(h)$) and the associated profile of return heights and built a look-up table. The normalized profile of each column was compared with the normalized profile of all plots in the look-up table using the Kolmogorov-Smirnov test, and the least dissimilar

pro le found in the look-up table was used to determine the relative proportion of PFTs in the column of interest (Figure S19c).

S3.2. Statistical models for plot-level properties

For the second step (Figure 2, Box 2), we developed parametric statistical models that related summary metrics describing the distribution of return heights with four plot-level properties (D 10 cm): aboveground biomass carbon density (ABCD, kg C m^{-2}), basal area (BA, cm^2 m^{-2}), (maximum, allometry-based) leaf area index (LAI, m$^2_{Leaf}$ m^{-2}), and stem number density (ND, m^{-2}). Similar to Step 1 (Section S3.1), we considered again all plots that were entirely within the areas surveyed by airborne lidar (total of 817:25 ha plots, Section 3). For each plot-level property, we selected the most informative yet simple model using the subset selection of regression method method (Miller, 1984). Additionally, we only considered models that did not show strong signs of multicollinearity, quanti ed by the variance in ation factor (VIF < 4). The selected model was tted assuming heteroskedastic distribution of residuals (Mascaro et al., 2011; Longo et al., 2016). Field inventory above-ground biomass was determined using the same models as in Longo et al. (2016). Individual-based maximum leaf area was determined using an allometric model derived from the Biomass And Allometry Database (BAAD; Falster et al., 2015) and presented in Section S3.3.

We obtained the following models:

$$\mathrm{ABCD}_{\mathrm{ALS}} = 0{:}132^{+0{:}072}_{0{:}045}\ h^{1{:}59^{+0{:}14}_{0{:}14}} + E_N \qquad = 0; \quad = 0{:}95^{+0{:}35}_{0{:}25}\ \mathrm{ABCD}_{\mathrm{ALS}}^{0{:}49^{+0{:}15}_{0{:}13}}; \tag{S37}$$

$$\mathrm{BA}_{\mathrm{ALS}} = 1{:}81^{+1{:}19}_{0{:}65}\ \exp^{h}\ 5{:}77^{+1{:}19}_{0{:}94}\ f_{1\ 2{:}5}^{\ i}\ h_{75}^{0{:}85^{+0{:}12}_{0{:}15}}$$

$$+ E_N \quad = 0; \quad = 1.45^{+1.54}_{0.39} \; BA_{ALS}^{0.39^{+0.16}_{0.26}} \; ; \tag{S38}$$

$$LAI_{ALS} = 0.37^{+0.33}_{0.13} \; \exp^{h} \; 5.8^{+1.7}_{2.0} \; f_{1\ 2.5} \; {}^{i}_{h} \; 0.91^{+0.12}_{0.20}$$

$$+ E_N \quad = 0; \quad = 0.462^{+0.141}_{0.045} \; LAI_{ALS}^{0.49^{+0.14}_{0.22}} \; ; \tag{S39}$$

$$ND_{ALS} = 0.0337^{+0.0053}_{0.0083} \; \exp^{h} \; 8.5^{+2.0}_{1.8} \; f_{1\ 2.5} + 0.77^{+0.31}_{0.17} F_{7.5}^{\ i}$$

$$+ E_N \quad = 0; \quad = 0.038^{+0.069}_{0.027} \; ND_{ALS}^{0.37^{+0.26}_{0.40}} \; ; \tag{S40}$$

where $f_{1\ 2.5}$ is the fraction (range 0.00 – 1.0) of returns coming from the layer between 1 and 2.5 m; $F_{7.5}$ is the fraction (range 0.00 – 1.0) of returns from above 7.5 m; h_{75} is the third quartile of the distribution of return heights; and $_h$ is the mean of the distribution of return heights. Numbers after the coe cients are the 68% range (equivalent to 1 if the distribution was Gaussian) of 1000 replicates using a nested bootstrap sampling. We separated the plots by study regions, then for each replicate, we rst randomly selected which study regions to include in the model tting stage, then randomly selected plots from the these regions. Plots from regions excluded from the model tting stage were used for cross-validation.

The tted models for ABCD, BA, and LAI showed similar-quality ts, and both explained over 70% of the inventory-plot variance (Table S4), whereas the model for ND explained 64% of the observed variance (Figure S20c; Table S4). Cross-validation assessment show that all tted models are robust: models show similar fraction of unexplained variance, and none of them are signi cantly biased (Figure S20; Table S4).

S3.3. Plot-speci c scaling factors and absolute cohort demography

For the third step of this approach (Figure 2, box 3), the unscaled pro les obtained in step 1 were calibrated using the stem number density (ND), basal area (BA) and above-

ground biomass carbon density (ABCD) estimated from the parametric models developed in step 2. First, we obtain the unscaled leaf area index of each cohort layer ($_i^?$):

$$_i^? = \int_{h_i}^{h_i^+} {}^?(h)\, dh; \tag{S41}$$

where h_i ; h_i^+ are the lower and upper bounds of the discrete layer associated with cohort i (Figure S19). We then estimated the unscaled stem number density of cohort i ($n_i^?$, m ^{2}) following the same approach by Antonarakis et al. (2014), which assumes that the leaf area index is directly proportional to $n_i^?$, and individual leaf area (L_i, m^2_{Leaf} plant ^{1}), assumed to be a function of the tree size:

$$n_i^? = \frac{1}{L_i\,(D_i\,;\,H_{t_i})}\;\; {}_i^?; \tag{S42}$$

where D_i (cm) is the diameter at breast height, and H (m) is the tree height. Neither L_i nor D_i can be directly retrieved by airborne lidar, therefore we developed allometric equations based on available data. To be consistent with the ED-2.2 simulations, we used the allometric equations for height and individual leaf area described in Supplement S2.1.

The unscaled stem number density of each cohort ($n_i^?$) is obtained by substituting Equations (S2) and (S1) into Equation (S42):

$$n_i^? = \;\; {}_1 H^{\;2} \;\; {}_i^?; \tag{S43}$$

$$_1 = \frac{1}{`_1 d_1^{2\,`_2}}; \tag{S44}$$

$$_2 = \;\; (2\,d_2 + 1)\;\; `_2: \tag{S45}$$

Once all $n_i^?$ values are determined, it is possible to derive unscaled, column-aggregated values of aboveground biomass carbon density (ABCD$^?$), basal area (BA$^?$) and stem

number density ($ND^{?}$):

$$ABCD^{?} = \sum_{i=1}^{I} n_i^{?} f_C a_1 \rho_{p(i)} [D(H)]^2 H^{a_2} ; \quad \text{(S46)}$$

$$BA^{?} = \sum_{i=1}^{I} n_i^{?} \frac{\pi}{4} [D(H)]^2 ; \quad \text{(S47)}$$

$$LAI^{?} = \sum_{i=1}^{I} f n_i^{?} \; {}_i^{?} g; \quad \text{(S48)}$$

$$ND^{?} = \sum_{i=1}^{I} n_i^{?}; \quad \text{(S49)}$$

where I is the total number of cohorts in the analyzed column, $(\rho_{ETR}; \rho_{MTR}; \rho_{LTR}) = (0.450; 0.615; 0.790)$ g cm^{-3} are the wood density values for each PFT $p(i)$, and $(a_1; a_2) = (0.0673; 0.976)$ are the empirical coefficients from the pantropical allometric equation developed by Chave et al. (2014). The unscaled values are compared with the properties estimated using the statistical model using airborne-lidar metrics (Section S3.2), denoted by ND; BA; LAI; $ABCD$:

$$e_A = \frac{ABCD}{ABCD^{?}}; \quad \text{(S50)}$$

$$e_B = \frac{BA}{BA^{?}}; \quad \text{(S51)}$$

$$e_L = \frac{LAI}{LAI^{?}}; \quad \text{(S52)}$$

$$e_N = \frac{ND}{ND^{?}}; \quad \text{(S53)}$$

where $(e_A; e_B; e_L; e_N)$ are the scaling factor that would match the estimates from the third step with estimates from the first step. The minimum overall error when taking all variables into account can be determined from the global minimum of function S based on the weighted least squares:

$$S(e) = \frac{w_A (e - e_A)^2 + w_B (e - e_B)^2 + w_L (e - e_L)^2 + w_N (e - e_N)^2}{w_A + w_B + w_L + w_N}; \quad \text{(S54)}$$

where $(w_A; w_B; w_L; w_N) = (0.279; 0.251; 0.292; 0.177)$ are the weights of ABCD, BA, LAI, and ND, respectively, and are proportional to the inverse of the fraction of unexplained variance for the full model (Table S4). The scaling factor e that minimizes can be determined analytically:

$$e = \frac{w_A e_A + w_B e_B + w_L e_L + w_N e_N}{w_A + w_B + w_L + w_N}; \tag{S55}$$

which is equivalent to the weighted average of the scaling factors. The scaled number density of each cohort i is then assumed to be $n_i = e\, n_i^?$.

S3.4. General scaling factor

The scaling factor in step 3 (Equation S55) could be obtained for any airborne lidar column, as it only relies on the local vertical pro le of returns (Section S3.1) and statistical models based on airborne lidar metrics (Equations S37{S40). However, the statistical models (Equations S37{S40) are based on plots with $D \geq 10$ cm, which is relatively high for the most degraded forests. Consequently, the statistical models cannot fully constrain the leaf area density pro les at the most degraded forests, because the return energy above 11 m (equivalent to $D \geq 10$ cm) may represent a small fraction of the return energy. To overcome this limitation introduced by the lack of small trees in our forest inventory data set, we sought to de ne a characteristic scaling factor that could be applied to all lidar scenes. To do so, we used the results from the regional cross validation at all sites (Table S2) to analyze the distribution of scaling factors e. The distribution of factors from all the plots are shown in Figure S21. The distribution has a well-de ned peak, and the mode of the global distribution is close to the median value $e_{50} = 1.357$. Although

the distribution of factors vary by each site (Figure S21b), for simplicity we used a single factor equivalent to the median at all sites.

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Figure S1. Assessment of basal area by plant functional types (PFTs), for di erent study regions and degradation levels. Plant functional types are early-successional tropical tree (ETR), mid-successional tropical tree (MTR) and late-successional tropical tree (LTR). Grey bars are obtained from forest inventory plots, and blue bars are obtained from the airborne lidar initialization using a 612-fold regional cross-validation (i.e. excluding all plots from region in the calibration stage). Whiskers correspond to the standard deviation either across all plots in the same category (inventory) or across all plots and replicates (lidar). Sites: GYF { Paracou, PRG { Paragominas, FZN { Feliz Natal, TAN { Tanguro. Disturbance classes: BNx { Burned twice or more, CL1 { conventional logging (once), LB1 { logged and burned once, LTH { logged and thinned, RIL { reduced-impact logging, INT { intact.

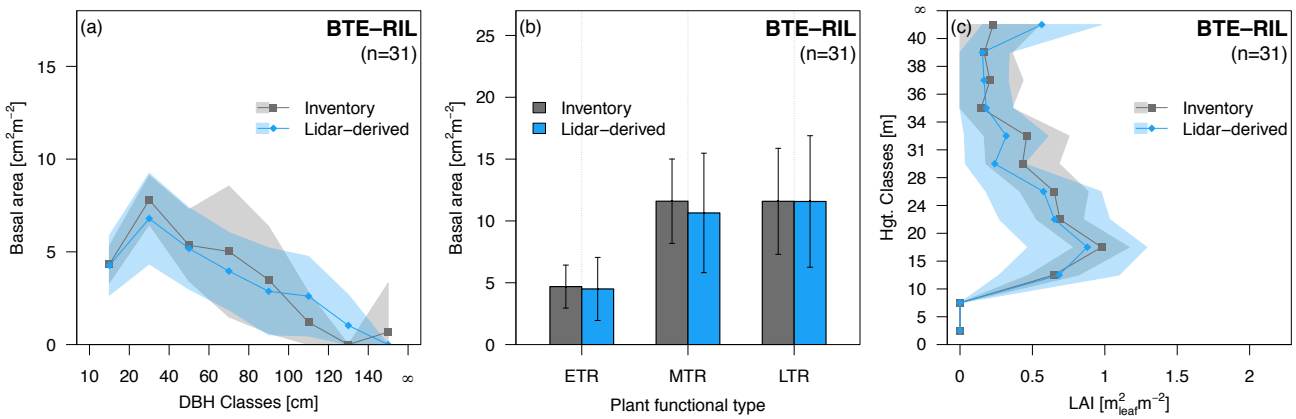

Figure S3. Assessment of airborne lidar initialization for Belterra (BTE). Comparison of (a) basal area distribution across diameter of breast height (DBH) classes, (b) basal area distribution among plant functional types (PFTs), and (c) leaf area index distribution as a function of height, for reduced-impact logging (RIL, the only disturbance type with $n > 20$ plots in BTE). Plant functional types are early-successional tropical tree (ETR), mid-successional tropical tree (MTR) and late-successional tropical tree (LTR). Grey points and bars are obtained from forest inventory plots, and blue points and bars are obtained from the airborne lidar initialization using a 612-fold regional cross-validation (i.e. excluding all plots from region in the calibration stage). Bands around points and whiskers correspond to the standard deviation either across all plots in the same category (inventory) or across all plots and replicates (lidar).

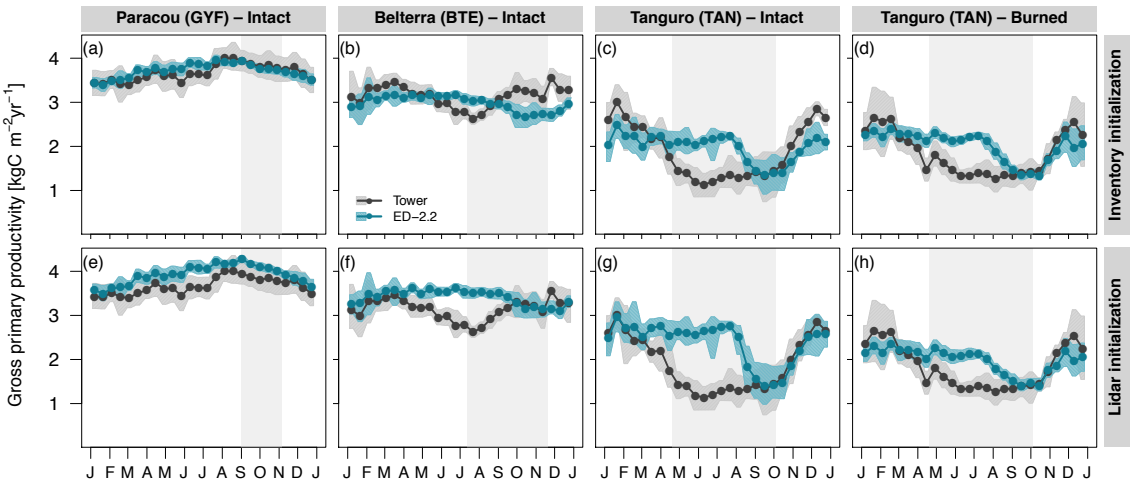

Figure S4. Model assessment of gross primary productivity. Fortnightly averages of gross primary productivity at (a,e) Paracou (GYF), intact forest; (b,f) Belterra (BTE), intact forests; (c,g) Tanguro (TAN), intact forests; (d,h) Tanguro (TAN), burned forests, initialized with (a-d) forest inventory plots and (e-h) airborne lidar. Fortnightly averages for both ED-2.2 and tower estimates were calculated using only hours with available data from the tower, and were integrated by obtaining the mean diurnal cycle then averaging the mean diurnal cycle to avoid biases due to data gaps. Bands around the averages correspond to the 95% con dence interval of the means, obtained through bootstrap. The grey rectangle in the background corresponds to the average dry season.

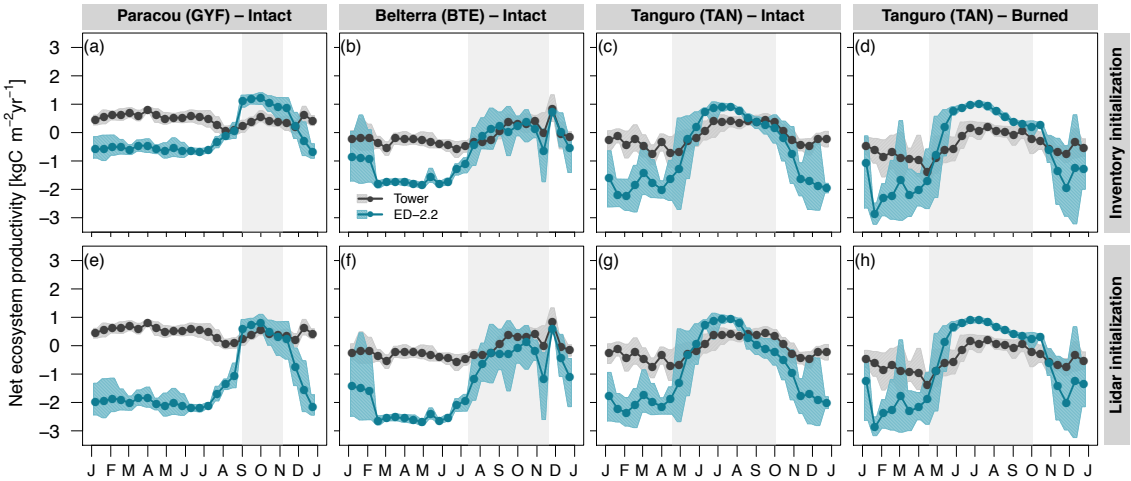

Figure S5. Model assessment of net ecosystem productivity. Fortnightly averages of net ecosystem productivity at (a,e) Paracou (GYF), intact forest; (b,f) Belterra (BTE), intact forests; (c,g) Tanguro (TAN), intact forests; (d,h) Tanguro (TAN), burned forests, initialized with (a-d) forest inventory plots and (e-h) airborne lidar. Positive uxes mean net uptake. Fortnightly averages for both ED-2.2 and tower estimates were calculated using only hours with available data from the tower, and were integrated by obtaining the mean diurnal cycle then averaging the mean diurnal cycle to avoid biases due to data gaps. Bands around the averages correspond to the 95% con dence interval of the means, obtained through bootstrap. The grey rectangle in the background corresponds to the average dry season.

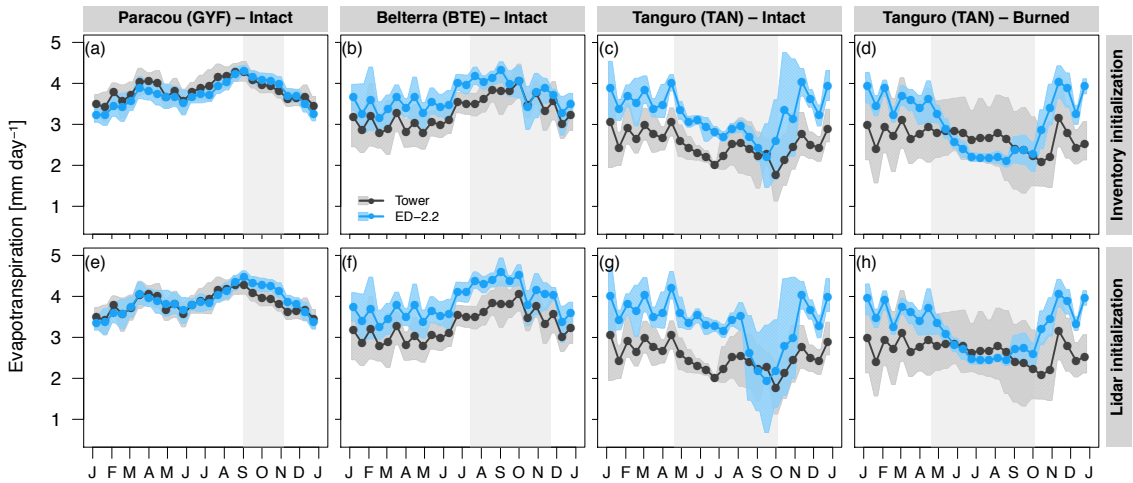

Figure S6. Model assessment of evapotranspiration. Fortnightly averages of water heat ux at (a,e) Paracou (GYF), intact forest; (b,f) Belterra (BTE), intact forests; (c,g) Tanguro (TAN), intact forests; (d,h) Tanguro (TAN), burned forests, initialized with (a-d) forest inventory plots and (e-h) airborne lidar. Fortnightly averages for both ED-2.2 estimates and tower measurements were calculated using only hours with available data from the tower, and were integrated by obtaining the mean diurnal cycle then averaging the mean diurnal cycle to avoid biases due to data gaps. Bands around the averages correspond to the 95% con dence interval of the means, obtained through bootstrap. The grey rectangle in the background corresponds to the average dry season.

Figure S7. Model assessment of sensible heat ux. Fortnightly averages of sensible heat ux at (a,e) Paracou (GYF), intact forest; (b,f) Belterra (BTE), intact forests; (c,g) Tanguro (TAN), intact forests; (d,h) Tanguro (TAN), burned forests, initialized with (a-d) forest inventory plots and (e-h) airborne lidar. Fortnightly averages for both ED-2.2 estimates and tower measurements were calculated using only hours with available data from the tower, and were integrated by obtaining the mean diurnal cycle then averaging the mean diurnal cycle to avoid biases due to data gaps. Bands around the averages correspond to the 95% con dence interval of the means, obtained through bootstrap. The grey rectangle in the background corresponds to the average dry season.

Figure S12. Variability of evapotranspiration (ET) as a function of local (patch) aboveground biomass (AGB). Scatter plot of AGB (x axis) and water ux (y axis) at sites (a,d) Paracou (GYF), (b,e) Paragominas (PRG), (c,f) Feliz Natal (FZN), for (a-c) the peak of wet season | May (GYF), March (PRG), and February (FZN) | and (d-f) peak of dry season | October (GYF and PRG), and August (FZN). Each point represents the 1980{2016 average ET of each patch solved by ED-2.2; point shapes correspond to the disturbance history, and point colors represent the time between the last disturbance (undetermined for intact forests) and lidar data acquisition. Curves correspond to non-linear least squares ts of the most parsimonious function, de ned from Bayesian Information Criterion (Schwarz, 1978), between shifted exponential or shifted Weibull functions.

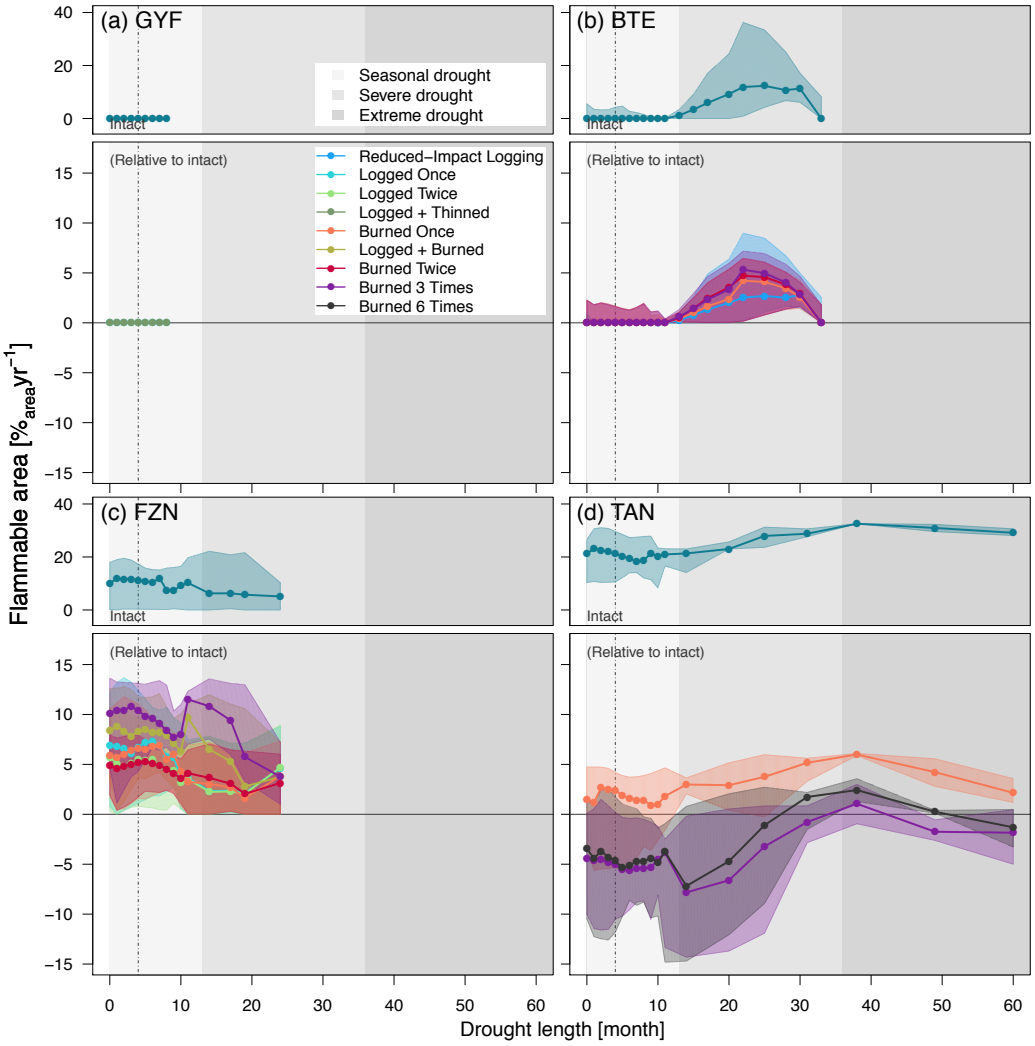

Figure S15. Flammable area as a function of degradation history and drought length (number of consecutive months with water de cit in excess of 20 mm) for regions (a) Paracou (GYF), (b) Belterra (BTE), (c) Feliz Natal (FZN), and (d) Tanguro (TAN). Points correspond to the median value of 12-month running averages, aggregated into quantiles along the drought length. Bands around the points correspond to the 95% range within each drought length bin. Top panels are the absolute value for intact forests, and bottom panels are the absolute di erence between degraded and intact forests. Background shades denote drought-length classes used in the text: seasonal (light gray, less than 12 months); severe (intermediate gray, 12{36 months); extreme (dark grey; more than 36 months).

Figure S16. Fit of the allometric equations developed for the airborne lidar initialization and for ED-2.2 simulations. (a) Diameter at breast height (D) as a function of tree height (H); line corresponds to the standardized major axis equation de ned by Equation (S1). (b) Individual leaf area (L) as a function of size (D^2H). Shaded background corresponds to the density of observed points. The results of the binned sampling with the lowest root mean square error are also shown: blue dots correspond to the binned sampled points used for the model tting, black lines are the tted model, and the goodness-of- t metrics for the cross validation are shown for reference.

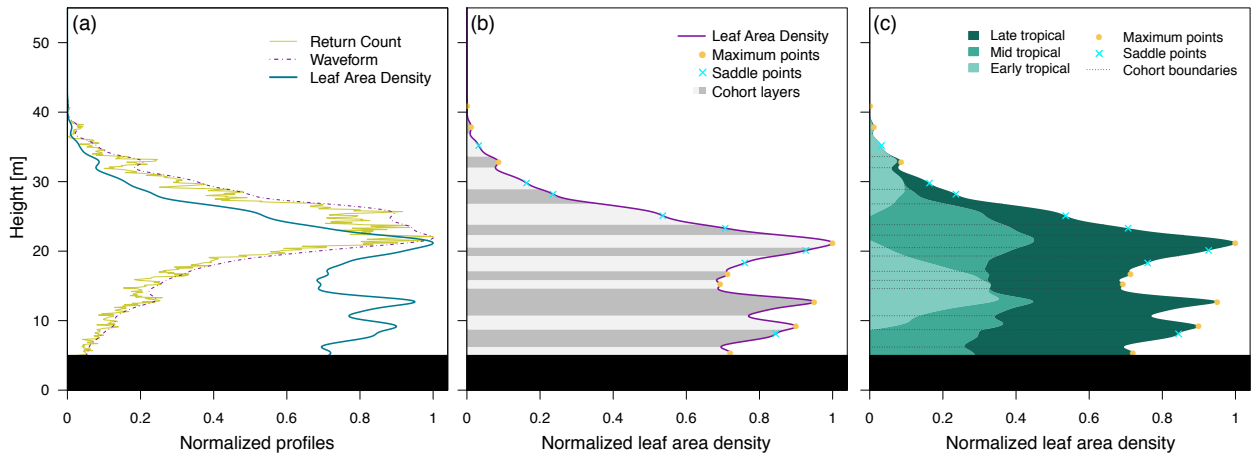

Figure S19. Example of how cohorts are obtained from the vertical distribution of returns, from one 50 50 m column at Paracou (GYF). (a) Thin lines: vertical pro les of return counts (X_v; Eq. S26); dot-dashed lines: waveform function $E(_v$; Eq. S25); thick lines: leaf area density (?; Eq. S30). (b) Discrete layers based on the curve features of leaf area density (thick line); Circles are the local maximum points and crosses are the saddle points. Discrete cohort layers are shown in alternate background shades. (c) Plant functional type (PFT) and cohort attribution. Cohorts are de ned by the cohort layers, and further split by the existing PFTs in each layer. The unscaled leaf area index of each cohort is de ned by the integral of the curve between each discrete layer and within each plant functional group. Black rectangles near ground are the bottom layer that is excluded from the cohort attribution.

Figure S20. Comparison between forest inventory and airborne-lidar estimates of plot-level properties. (a) aboveground biomass carbon density (ABCD), (b) Basal area (BA), (c) (maximum, allometry-based) leaf area index and (d) stem number density (ND). For the airborne-lidar estimates, we show the average results from cross-validation: for each plot, we averaged all replicates which did not include the plot region in the model training step. Bars correspond to the 95% range of cross-validation predictions. Median bias, root mean square error (RMSE) and adjusted coe cient of determination (R^2_{adj}) for cross-validation predictions are shown for reference.