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Degradation and deforestation increase the sensitivity of the
Amazon Forest to climate extremes

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Abstract

About 40% of the Brazilian Amazon has been deforested or suffered changes in forest structure through degradation (selective logging, fires, and fragmentation). The impact of forest degradation on the forest's sensitivity to climate extremes has not been fully explored because of a lack of data and the complex interplay of forest structure and climate drivers. Here, we combined forest structure data from 545 airborne lidar transects (375 ha each) across the Brazilian Amazon with the Ecosystem Demography Model (ED2). We explore the forest's functional response to near-present (1981–2019) climate extremes under observed forest structure from lidar (*Control*) and two forest structure change scenarios: (1) forest recovery by excluding all future deforestation and degradation (*Recovery*) and (2) expansion of selective logging and deforestation (*Degradation*). Using the *Control* simulation, we found a close and positive association between local forest aboveground biomass and the predicted gross primary productivity (GPP) and evapotranspiration (ET). Moreover, both GPP and ET respond negatively to extremes in vapor pressure deficit and downwelling shortwave irradiance in degraded forests in Eastern and Southern Amazon, indicating high sensitivity to droughts. Locally high-biomass forest patches showed little or no negative response of GPP and ET to extreme drought conditions whereas low-biomass forest patches in the same locations—typically degraded forest canopies—responded negatively to higher moisture stress. The results from the *Recovery* scenario showed similar results to simulations with observed structure; however, under the *Degradation* scenario, low-biomass forest patches became more abundant, resulting in more regions where GPP and ET are negatively impacted by hot drought

conditions according to the ED2 model. Our results suggest that local forest structure is a critical determinant of an ecosystem's response to climate variability, and that the loss of canopy trees in the Amazon through forest degradation could increase and expand forest vulnerability to droughts.

1. Introduction

Future climate predictions indicate that most parts of the Amazon will likely experience more frequent extreme and hot droughts [1–3]. Under continuing high carbon emissions, increasingly hot conditions will increase air vapor pressure deficit¹⁵ and intensify soil desiccation, even if rainfall does not change [4–6]. Increases in air vapor pressure deficit are predicted to compromise long-term carbon storage in a future climate [7].

Ecosystem response functions, such as gross primary productivity (GPP) and evapotranspiration (ET), typically increase during the dry season [8–12], consistent with light being the most limiting resource [13]. However, this pattern is disrupted during severe droughts. During the 2015–2016 El Niño event, increases in air vapor pressure deficit and declines in soil moisture were sufficiently strong to make water the main limiting factor for GPP and ET [14–19]. More frequent hot droughts could persistently reduce ET and GPP, amplify carbon losses [20–22], and increase hydraulic failure mortality [23–25].

Nearly 20% of the Amazon has been cleared for pastures and croplands [26, 27]. In addition, selective logging, human-ignited forest fires, and fragmentation are pervasive across the Amazon: these different forms of forest degradation severely reduce canopy cover, canopy height, biomass, and biodiversity (figure S1) [28–32], and collectively have impacted a further 20% of the Brazilian Amazon (figure 1) [26, 33–41].

Forest degradation also alters ecosystem functioning. At the local scale, forest degradation has been associated with decreased GPP and ET, and increased sensible heat flux, land surface temperature and flammability of degraded forests [47–53]. The pervasiveness of tropical forest degradation suggests that its impacts on energy, water, and carbon cycles are also significant at regional and global scales. The combination of climate change, deforestation, and forest degradation is potentially reducing the resilience of Amazon forests' carbon stocks, biodiversity, and ecosystem response function to further changes [21, 54–57].

Understanding how current conditions and future deforestation- and degradation-driven changes in canopy structure may impact the functioning of Amazon forests relies on ecosystem

model predictions. Terrestrial biosphere models have been incorporating dynamic vegetation demography (e.g. growth, mortality and disturbances) and the representation of vertical and horizontal heterogeneity of canopies [58–60]. One such model, the Ecosystem Demography Model (ED2), has been used for investigating the role of structural and functional diversity of forest canopies on ecosystem response function and on the forest's sensitivity to climate extremes [50, 61–65]. However, for the model to realistically represent the feedback between forest structure and biogeophysical cycles, the model must be initialized with the actual spatial distribution of forest structure [66].

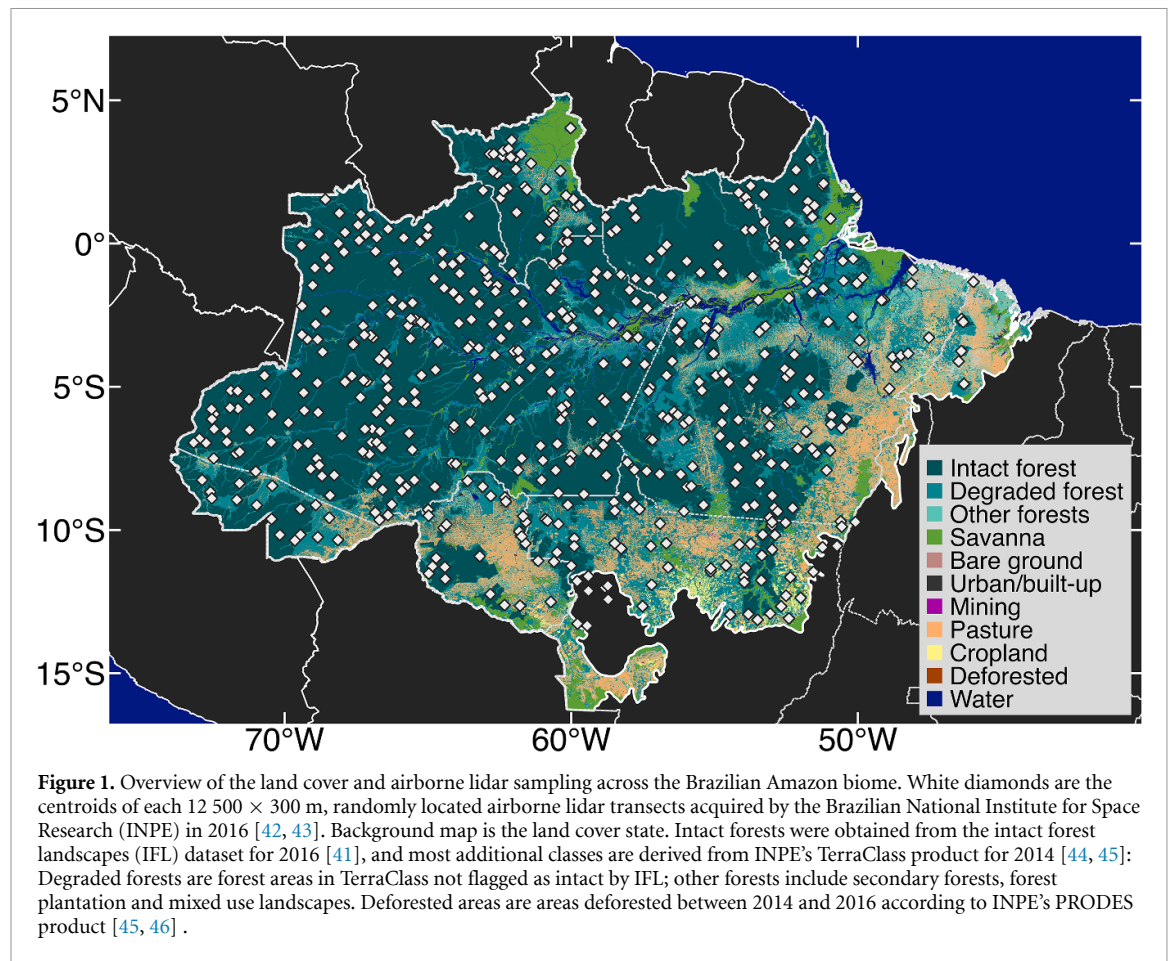
This is now possible due to new active remote sensing techniques such as the light detection and ranging system (lidar), which uses the time between the emission of laser pulses and the detection of reflected light to obtain the distance to targeted objects [67–69]. By surveying large forest areas with high-density sampling flight plans, airborne lidar datasets have been successfully employed to detect and quantify the spatial heterogeneity in tropical forest canopy structure at both local and regional scales, as well as canopy changes due to forest disturbances [30, 70–75]. Importantly, sub-orbital lidar surveys with high density of returns and narrow off-nadir angle of view reliably characterize forest structure [76, 77] and avoid shadow-associated biases typically found in greenness-based remote sensing [78, 79].

Here, we integrate the most extensive airborne lidar survey across the entire Brazilian Amazon to date [42, 43] with the ED2 model to investigate the following scientific questions:

1. How does current forest structure in the Amazon mediate the relationships between climate variability and ecosystem functioning at local and regional scales?
2. How would potential expansions of deforestation, forest degradation, and forest regrowth affect the forest's response to extreme climate across the Brazilian Amazon?

We leverage previous work [50] to generate the ED2 model initial forest structure state from airborne lidar for the entire Brazilian Amazon, and conduct multidecadal simulations to identify and attribute the role of forest structure and forest structure changes on the forest's sensitivity to typical and extreme climate conditions. We then explore how tropical

¹⁵ A brief description of quantities used in this study is available in the supporting information (table S1).



forests in the Amazon change sensitivity to climate extremes under scenarios of forest recovery and further disturbances.

2. Methods

2.1. ED2

The ED2 is a process-based model that represents the horizontal and vertical variability of canopies across landscapes [80–82]. Each grid cell (working spatial resolution) is subdivided into a series of *sites*, which are used to represent landscape-scale heterogeneity in edaphic conditions (e.g. soil texture and depth); *patches*, which describe disturbance-driven variation in local forest community structure; and *cohorts*, which represent the vertical structure and diversity of the plant canopy specified in terms of the abundance of individuals with similar plant size and plant functional type. The ED2 model has a biogeophysical and biogeochemical core that accounts for the above-ground and below-ground heterogeneity of forest structure, by solving the energy, water (including plant hydrodynamics), and carbon cycles for each patch and each cohort independently [80, 83]. For this study, we implemented a soil hydraulic model based on van Genuchten [84] and pedotransfer functions based on Amazonian soils [85–87]. Cohort-specific GPP and transpiration are modulated by both

light and water availability specific to the local micro-environment: small cohorts in dense forest patches may be light-limited, whereas similar-sized cohorts in a neighboring gap may be sufficiently illuminated but experience higher water stress due to high evaporative demand due to lower air vapor pressure deficit. Likewise, similar patches of forests may experience different water stress conditions under the same climate, due to varying soil hydraulic conditions. The ED2 model predictions have been extensively benchmarked and successfully applied across tropical South America [50, 88, 89], and the ED2 model code used for this study (tag v2.2.1-BrAmazALS2) is archived [90] and available on GitHub [91].

2.2. Regional characterization of current forest structure

We split the Brazilian Amazon domain into 350 grid cells ($1 \times 1^\circ$ each), to account for spatial climate variability without incurring an excessive computational burden. To characterize the soil heterogeneity, we combined soil depth data [92] with additional characteristics—texture (clay, silt and sand fractions), acidity (pH), cation exchange capacity, bulk density and organic carbon concentration—from SoilGrids250m v2.0 [93]. Soils were assigned to a combination of one of the 15 broad texture-based soil categories in the ED2 model [80] and the index of the

deepest soil depth grid layer above bedrock. We split each grid cell into up to four classes, which became sites, based on the most abundant combinations of texture and depth.

To obtain initial patches and cohorts, we used 545 small-footprint airborne lidar transects ($12\,500 \times 300$ m each) collected during the 2016 campaign of the *Amazon Biomass Estimation Project* (EBA2016) [42, 43, 94] and available online [95–98]. EBA2016 was led by Brazil's National Institute for Space Research (INPE), and randomly sampled the remaining forests across the Amazon (figure 1; figure S1). Forested areas were obtained from INPE's TerraClass 2014 product [44, 45], with post-2014 deforestation masked using INPE's PRODES deforestation product [45, 46, 99].

We converted airborne lidar data into forest structure distributions across the domain, by applying the same algorithm from an earlier study [50]. This approach consists of: (1) splitting the airborne lidar point cloud from all transects into 1310478 columns (50×50 m each), (2) deriving an initial guess for leaf area density profile of each column, and (3) using lidar-based statistical models of aggregated properties of forests plots including their aboveground biomass, basal area, leaf area index, and stem number density, calibrated with forest inventory data to correct and reduce uncertainty of the leaf area density profiles. Each corrected leaf area density profile is then partitioned into cohorts using a feature-based segmentation, and assumed to be a forest patch. An overview of the approach is available in appendix S1, and described in detail in the previous study [50]. This approach captures both the regional variation in forest structure across the Amazon, and the local heterogeneity due to different disturbance histories (figure S2) [50]. We used the geographic location of each lidar column to assign patches to grid cells and sites. The initial conditions for ED2 are archived and openly available [100].

Because the airborne lidar data acquisition excluded deforested regions [43], for each site we added the appropriate amount of deforested area according to TerraClass and PRODES. Since $\sim 88\%$ of the deforested area in the Brazilian Amazon is pasture (figure 1) [101], the deforested area within each site was represented as a single pasture patch within each site that was comprised of C4 grasses, with a prescribed a leaf area index of $2\text{ m}^2\text{ m}^{-2}$ based on typical values in Amazon pastures [102].

2.3. Simulating impacts of forest structure change on ecosystem response function

For all the ED2 model simulations, we used hourly meteorological data from the bias-corrected *Fifth generation of atmospheric reanalysis from the European Centre for Medium-Range Weather Forecasts* (WFDE5) reanalysis data [103] for a 38 year period (1981–2018). For precipitation, we replaced

WFDE5 data with *Climate Hazards Group InfraRed Precipitation with Station* (CHIRPS) data [104], because CHIRPS agrees better with observations at seasonal scales [105].

To attribute the impact of forest structure changes on the ecosystem response to extreme climate conditions, we conducted three regional simulations:

1. **Control.** In this simulation, we initialized the ED2 model with airborne lidar (section 2.2), and carried out the simulation for one full cycle of meteorological conditions (38 years), disabling dynamic vegetation, so the forest structure remained constant.
2. **Recovery.** In this simulation, we initialized the ED2 model as in *Control*, and ran the model for one full cycle of meteorological conditions (38 years) with vegetation dynamics, allowing only natural disturbances (tree fall) to occur, and thus representing an initial recovery of the forest from current degradation. The forest structure at the end of the recovery period was used as initial conditions for an additional simulation for one full cycle of meteorological conditions (38 years) in which vegetation dynamics was disabled. Only the last 38 year period was analyzed.
3. **Degradation.** In this simulation, we initialized the ED2 model as in *Control*, and ran the model for one full cycle of meteorological conditions (38 years), with vegetation dynamics allowing both natural and anthropogenic disturbances. To drive anthropogenic disturbances (appendix S2), we used the results of a scenario describing the regional expansion of timber harvesting and deforestation between 2010 and 2039 (figure S3) [106]. The forest structure at the end of the degradation expansion period was held constant for an additional simulation for one full cycle of meteorological conditions (38 years), and only the last 38 year period was analyzed.

We note that the intent of using 38 years of meteorological data is to provide the ED2 model with a range of contemporaneous climatological conditions that includes both typical and extreme conditions, without attempting to link recovery and degradation events with specific climate events. Therefore, except for benchmarking purposes (section 2.4), our analyses do not focus on specific meteorological years. The following archived datasets provide the boundary conditions [107], configuration files [108] and the output for selected variables [109] for the ED2 model simulations.

2.4. Regional-scale assessment of the ED2 model

We assessed initial conditions and predictions regionally for the ED2 model, by pooling datasets based on field measurements and remote sensing. To assess

the initial conditions (*Control* simulations), we compared aboveground biomass and leaf area index with annual averages from 2016, or the closest year available, from gridded datasets [110–112]. For evaluations of GPP, ET and sensible heat flux, we compared monthly averages (*Control* simulations) for overlapping years between 2013 and 2018 of multiple gridded products [16, 113–119]. We restricted the comparisons to 2013–2018 to reduce confounding effects from forest dynamics and land use change in the reference datasets. Additional details on the reference data are available in table S2.

2.5. Regional-scale ecosystem response function sensitivity to climate extremes

To calculate sensitivity metrics of ecosystem response function to climate at each grid cell x , we computed averages at monthly time intervals (t) for both environmental drivers ($W_{x,t}$) and ecosystem response functions ($E_{x,t}$). Environmental drivers included incoming solar irradiance, air vapor pressure deficit and soil moisture content in the top 50 cm of the soil column (hereafter top-soil moisture content), whereas GPP and ET are ecosystem response functions. We pooled the averages for all month-years and related the environmental drivers with the ecosystem response function through a local fitting, by using function *loess* [120] and setting the smoothing factor (span) to 1.0. The sensitivity of ecosystem response function E to a specific value of environmental driver W was defined as:

$$S(E_x, W_x) = \frac{\hat{E}_x(W_x + \Delta W_x) - \hat{E}_x(W_x - \Delta W_x)}{2 \Delta W_x}, \quad (1)$$

where $\hat{E}_x$ is the fitted ecosystem response function at any given value of W_x , and ΔW_x is a small change in the value of W_x , defined as 1‰ of the total range of W_x . To assess the simulated sensitivity of ecosystem response function at median and extreme conditions, we computed $S(E_x, W_x)$ for the 5th, 50th, and 95th percentiles of W_x . Percentiles were defined for each grid cell, to account for the regional effects on seasonal and inter-annual variability.

2.6. Effect of local forest structure heterogeneity on ecosystem response function

To quantify the local effects of forest structure on ecosystem response function, we assigned grid cells into sub-regions across the Brazilian Amazon, according to previous classification [121] (figure S4), then grouped all patches across each sub-region according to their aboveground biomass, using the thresholds of 1, 2.25, 4, 6.25, 9, 12.25, 16, 20.25 and 25 kgC m⁻². By choosing thresholds based on the square of aboveground biomass, we highlighted the variability at low-aboveground biomass patches, which are more representative of recently disturbed forests [30, 122]. For

each group of patches (same aboveground biomass level), we binned monthly averages of the ecosystem response functions by monthly averages of environmental drivers, using 21 equally spaced quantiles (q) as thresholds ($q \in 0, 0.05, 0.10, \dots, 0.95, 1$). All the scripts and notebooks used to generate the analyses presented in this manuscript are available in open archives [123, 124].

3. Results

3.1. Regional variation in forest structure and ecosystem response function

The initial conditions generated from airborne lidar (*Control* simulation) were well correlated with reference datasets, albeit with consistently higher values (figures S5–S8). In contrast, each ecosystem response function reference dataset yielded markedly different comparisons with *Control*, both in magnitude and in correlation. The domain-averaged predictions showed averaged differences between *Control* and references that ranged between 1.8–4.1 gC m⁻² d⁻¹ (GPP), 0.3–0.8 mm d⁻¹ (ET) and –2.7–10 W m⁻² (sensible heat flux), depending on the reference dataset (figure S7). Likewise, correlation coefficients between *Control* and references varied between –0.28 and 0.72 for GPP, 0.25 and 0.86 for ET, and 0.66 and 0.88 for sensible heat flux (figures S7 and S8), indicating important differences not only between the ED2 model and the references, but amongst the references themselves.

Long-term (38 years) averages of ecosystem response functions in *Control* varied markedly across the Amazon. The predicted GPP average was 10.7 gC m⁻² d⁻¹, with the lowest values (5.9 gC m⁻² d⁻¹) along the arc of deforestation in the Southern and Southeastern regions (figure 2(a)). The regional distribution of long-term average ET is similar to GPP, although the relative difference between the regional average (4.0 mm d⁻¹) and the lowest regions along the Eastern part of the arc of deforestation (2.9 mm d⁻¹) is relatively smaller (figure 2(b)). The areas with the highest long-term average ground temperature (29.7 °C), in the deforested areas in Maranhão, were more than 3 °C warmer than the regional long-term average (26.3 °C) (figure 2(c)).

3.2. Regional variation in forest sensitivity

Under the *Control* simulation, the sensitivity of GPP to environmental drivers, as defined in section 2.5, varied substantially across the Brazilian Amazon. At the lowest percentiles of incoming solar irradiance (figure 3(a)), GPP sensitivity to incoming solar irradiance was generally positive across the Amazon, indicating light limitation during extreme overcast conditions. Under median conditions, the GPP sensitivity decreased, with degraded forests in Mato Grosso, SE Pará and Maranhão showing negative sensitivity (figure 3(b)). At high incoming solar irradiance

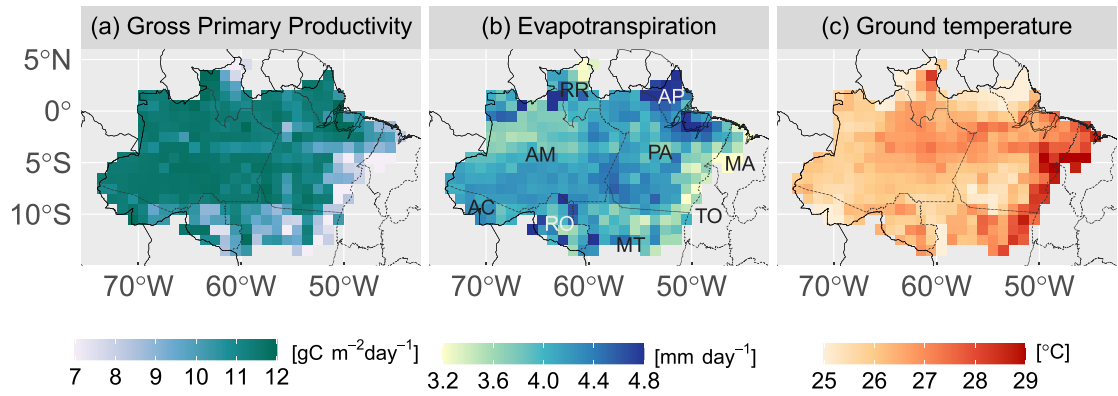


Figure 2. Long-term average of ecosystem response functions for the *Control* simulation. Maps of long-term average (1981–2018) average of (a) gross primary productivity (GPP), (b) evapotranspiration (ET) and (c) ground temperature (T_g). Brazilian states overlapping with the Amazon biome indicated in panel (b): Acre (AC), Amapá (AP), Amazonas (AM), Maranhão (MA), Mato Grosso (MT), Pará (PA), Rondônia (RO), Roraima (RR), Tocantins (TO).

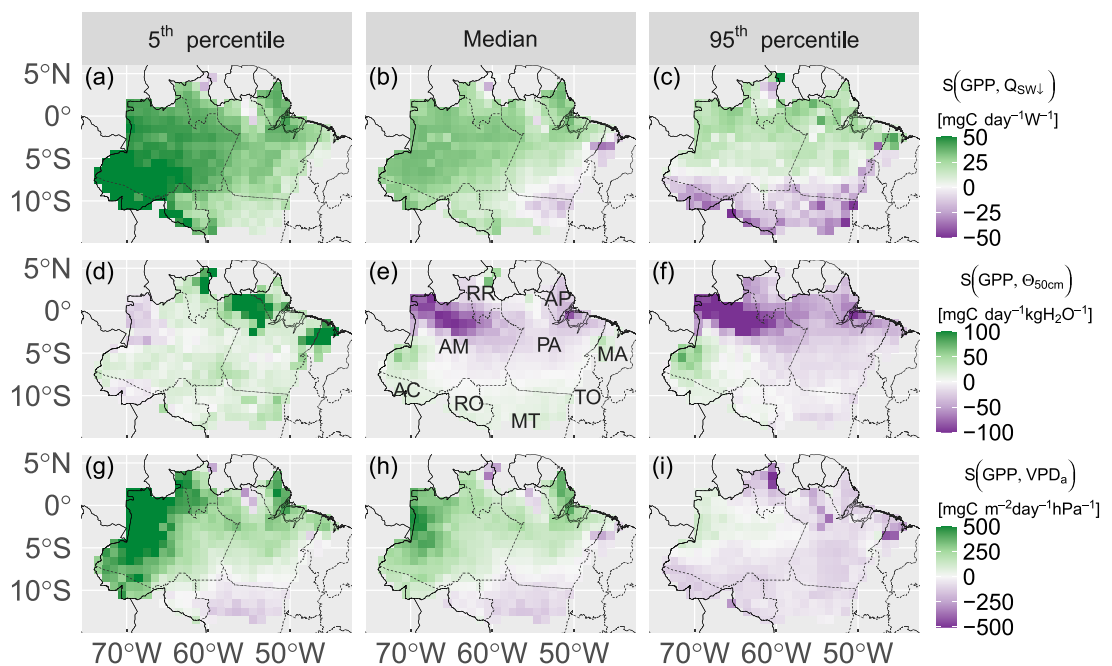
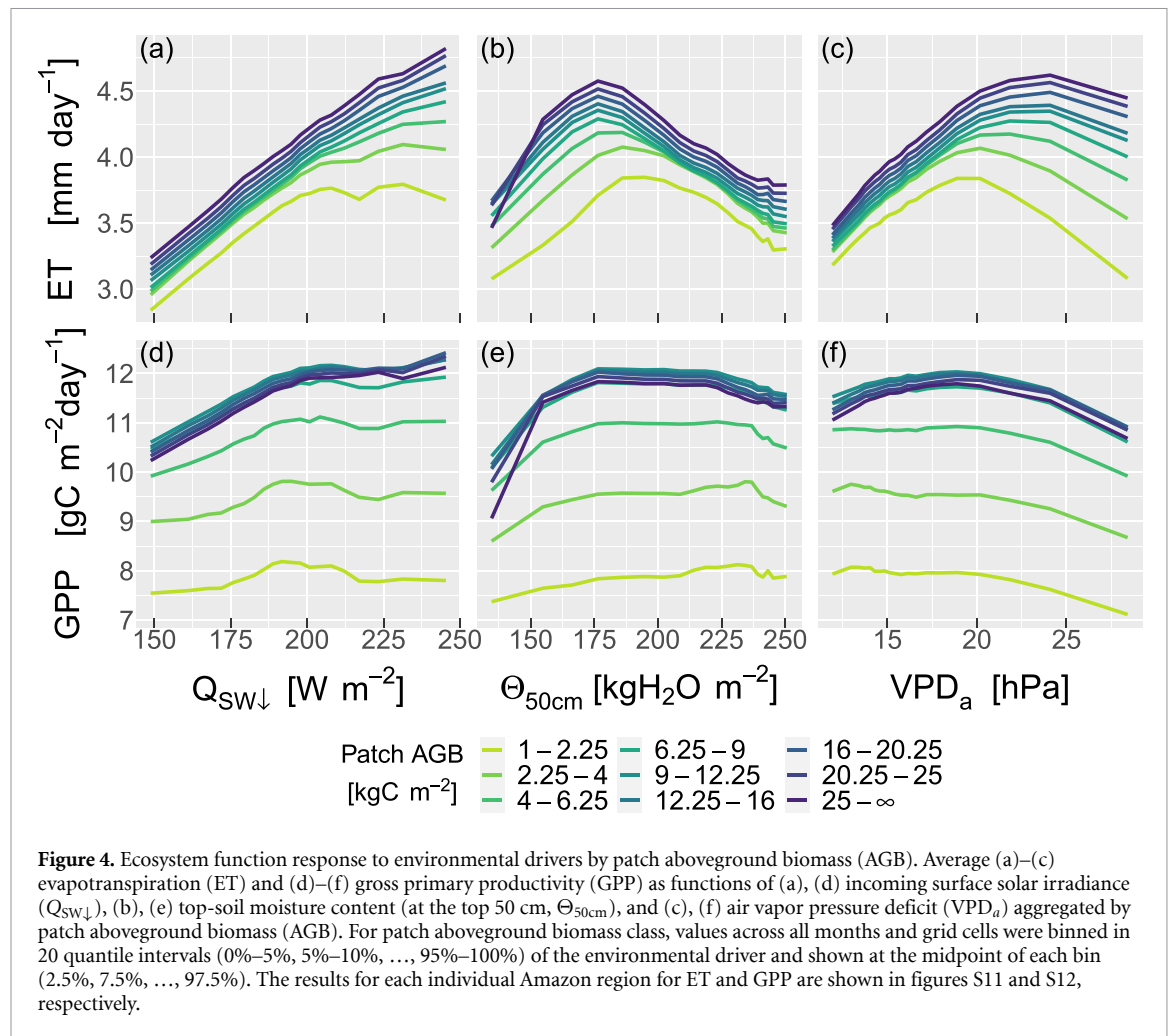


Figure 3. Impacts of environmental drivers on gross primary productivity (GPP) under extreme and typical conditions. Maps of GPP sensitivity to (a–c) incoming surface solar irradiance ($Q_{sw\downarrow}$), (d–f) top-soil moisture content (at the top 50 cm, θ_{50cm}), and (g–i) air vapor pressure deficit (VPD_a) for the (a), (d), (g) 5th percentile, (b), (e), (h) 50th percentile, and (c), (f), (i) 95th percentile of the environmental drivers at each grid cell under simulation *Control*. Positive values of sensitivity indicate that GPP typically increases with increasing environmental driver when the driver monthly average is near the percentile value. Brazilian states overlapping with the Amazon biome indicated in panel (e): Acre (AC), Amapá (AP), Amazonas (AM), Maranhão (MA), Mato Grosso (MT), Pará (PA), Rondônia (RO), Roraima (RR), Tocantins (TO).

percentiles, the GPP sensitivity remained positive across the central Amazon, but negative sensitivities expanded over the southern states, suggesting that other drivers associated with high incoming solar irradiance were causing stress-related GPP declines (figure 3(c)).

To investigate other stress factors, we computed the GPP sensitivity to top-soil moisture content and air vapor pressure deficit. Under extremely low soil moisture conditions, the GPP sensitivity to top-soil moisture content was positive across the biome (figure 3(d)), which implies widespread

water-limitation of GPP during extreme droughts. The most positive sensitivities occurred in the savanna enclave in Northeastern Roraima, and in forests in Northern Pará and Northwestern Maranhão (figure 3(d)). Further analysis shows that this is due to a combination of low precipitation (lower water supply), shallow soil depths (restricted soil water storage) and high fractions of clay (strong root water extraction resistance) (figure S9). In contrast, under median and high soil water content, GPP sensitivity to top-soil moisture content was typically zero or negative, with the most negative values occurring



in Northwest Amazonas (figures 3(e) and (f)), the area with the highest total annual precipitation in the domain (figure S9). The simulated GPP sensitivity to air vapor pressure deficit was consistent with the sensitivity to top-soil moisture content: under low and median air vapor pressure deficit conditions, the domain experienced widespread positive sensitivity (figures 3(g) and (h)), whereas under high air vapor pressure deficit, most of the domain experienced negative sensitivity (figure 3(i)). The patterns of simulated ET sensitivity to incoming solar irradiance, top-soil moisture content and air vapor pressure deficit generally followed the patterns observed for GPP (figure S10).

3.3. Effects of local heterogeneity of forest structure on ecosystem response function

The structural heterogeneity of forests also affected the sensitivity of ecosystem response functions to environmental drivers. The simulated ET typically increased for high-aboveground-biomass patches across all regions and ranges of environmental drivers (figures 4(a)–(c); figure S11). Moreover, ET consistently increased with incoming solar irradiance for intermediate- (6.25–12.25 kgC m^{-2}) and high-aboveground-biomass patches ($\geq 16 \text{ kgC m}^{-2}$).

Conversely, for low-aboveground-biomass patches (1–4 kgC m^{-2}), the response of ET to increasing incoming solar irradiance reaches a plateau or a maximum for incoming solar irradiance $\geq 220 \text{ W m}^{-2}$ (figure 4(a)). Similarly, low-aboveground-biomass patches experience their maximum monthly ET at higher values of top-soil moisture content (190–200 $\text{kgH}_2\text{O m}^{-2}$) than high-aboveground-biomass patches (176 $\text{kgH}_2\text{O m}^{-2}$), suggesting that low-aboveground-biomass forests became water-limited more often than high-aboveground-biomass forests (figure 4(b)). The impacts of air vapor pressure deficit on ET were similar to top-soil moisture content, with ET for low-aboveground-biomass patches peaking at lower air vapor pressure deficit ($\sim 19 \text{ hPa}$) than intermediate- and high-aboveground-biomass patches ($\sim 24 \text{ hPa}$) (figure 4(c)). The effect of environmental drivers on GPP was qualitatively similar to those on ET; however, the relative declines past the maximum were less pronounced (figures 4(d)–(f); figure S12).

3.4. Impacts of forest dynamic scenarios

The simulation scenarios markedly shifted forest structures across the Brazilian Amazon. On average, aboveground biomass under the *Recovery* scenario

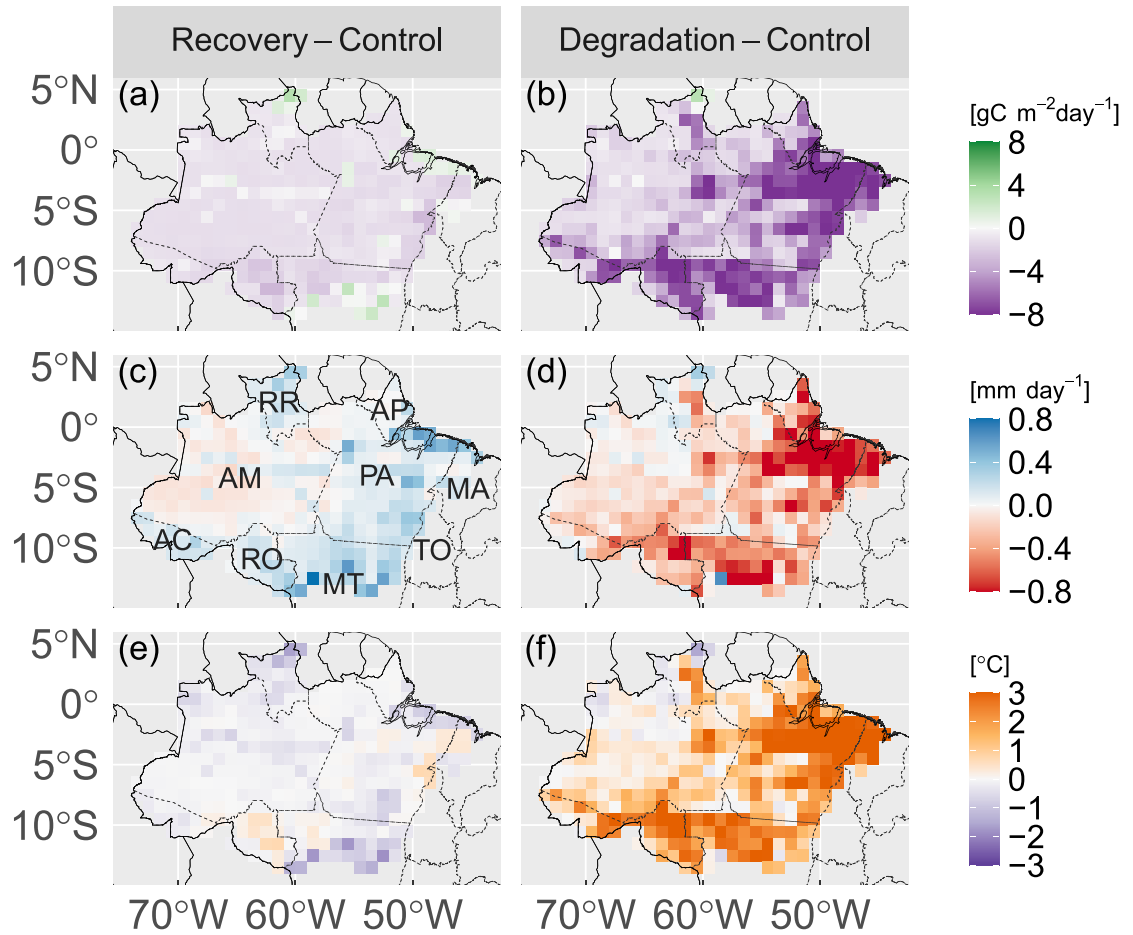


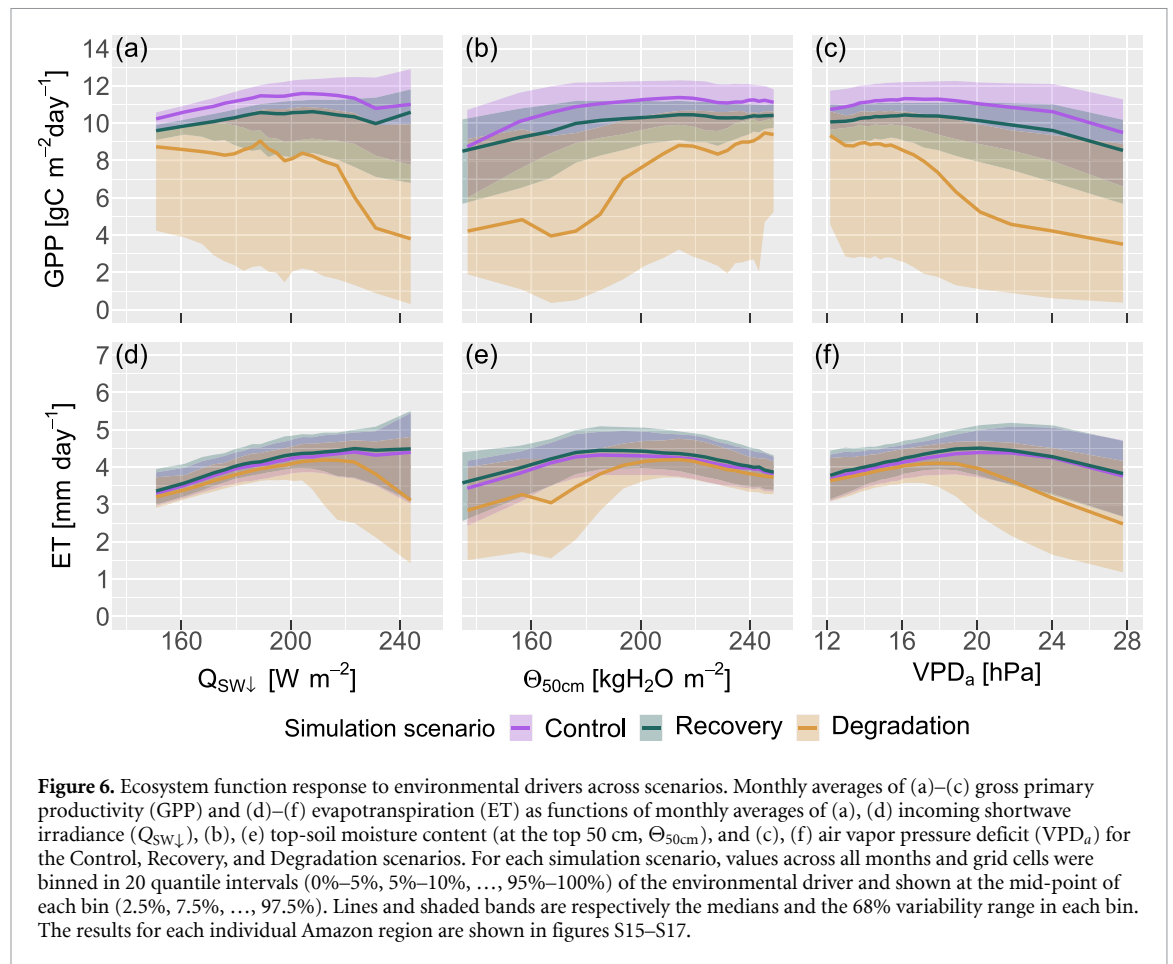
Figure 5. Impact of experiment simulation sets on the long-term average of ecosystem response functions. Maps of the differences between (a), (c), (e) Recovery or (b), (d), (f) Degradation simulation sets and Control, for (a), (b) gross primary productivity (GPP), (c), (d) evapotranspiration (ET), and ground temperature (T_g). Brazilian states overlapping with the Amazon biome indicated in panel (c): Acre (AC), Amapá (AP), Amazonas (AM), Maranhão (MA), Mato Grosso (MT), Pará (PA), Rondônia (RO), Roraima (RR), Tocantins (TO). Absolute values of all simulation sets are shown in figure S14.

increased by 1.2 kgC m^{-2} . The largest aboveground biomass gains occurred in the Southeast, which were partially offset by losses in the tall, high-biomass forests of the Northeast (figures S13(a) and (b)). In contrast, aboveground biomass declined under *Degradation* nearly everywhere (average change of -5.5 kgC m^{-2}), with losses in the Northeast driven by deforestation, and losses in the Central and Northwestern regions largely due to logging (figure S3; figure S13(c)). Both *Recovery* and *Degradation* resulted in leaf area index reductions (figures S13(d)–(f)), although losses in *Recovery* happened where leaf area index was high under *Control*, compared to ubiquitous declines in *Degradation* (figures S13(d)–(f)).

Consistent with the leaf area index changes relative to *Control*, both scenarios predicted declines in GPP, with average changes of $-0.9 \text{ gC m}^{-2} \text{ d}^{-1}$ (*Recovery*) and $-4.0 \text{ gC m}^{-2} \text{ d}^{-1}$ (*Degradation*) relative to *Control* (figures 5(a) and (b)). The declines in GPP under *Recovery* showed small regional variability (figure 5(a)), whereas the largest declines under *Degradation* occurred predominantly in the Southeast and the South (up to $-11.6 \text{ gC m}^{-2} \text{ d}^{-1}$),

where most forests were either cleared or logged (figure 5(b)). Under *Recovery*, long-term averages of ET and ground temperature were only slightly different from *Control*, with the largest shifts towards higher ET and lower ground temperature in the Southeast (figures 5(c) and (e)). Under *Degradation*, the largest decreases in ET (-1.3 mm d^{-1}) and increases in ground temperature (4.7 °C) occurred in the deforestation-dominated East, however, logging-impacted areas such as the Central Amazon experienced marked changes too (average changes of -0.3 mm d^{-1} and 1.1 °C) (figures 5(d) and (f)).

Changes in forest structure affected the predicted forest response to environmental drivers. The median responses of GPP and ET to incoming solar irradiance were similar between *Control* and *Recovery*, with minor decreases of GPP (6%–7% relative to maximum median) at high incoming solar irradiance (figures 6(a) and (d)). In contrast, under *Degradation*, median GPP and ET respectively declined by 58% and 26% at the highest incoming solar irradiance (figures 6(a) and (d)). The response of GPP to top-soil moisture content variability intensified in



Degradation, with median GPP increasing by 52% when top-soil moisture content increased from 176 to 214 $\text{kgH}_2\text{O m}^{-2}$ (figure 6(b)). Moreover, the top-soil moisture content associated with maximum median ET increased from 185 $\text{kgH}_2\text{O m}^{-2}$ (*Control* and *Recovery*) to 214 $\text{kgH}_2\text{O m}^{-2}$ (*Degradation*) (figure 6(e)). The simulated GPP and ET declined with high air vapor pressure deficit for all scenarios (figures 6(c) and (f)). However, under *Degradation*, GPP decreased rapidly when air vapor pressure deficit exceeded 14.0 hPa, with 62% reduction at the highest air vapor pressure deficit relative to the median maximum GPP (figure 6(c)). The declines of ET at upper extremes of air vapor pressure deficit relative to the median maximum were also stronger in *Degradation* (40%) than in *Control* (14%) or *Recovery* (15%) (figure 6(f)). Differences in ET and GPP between *Degradation* and *Control* were noteworthy across most of the Amazon, and occurred both at regions where logging (Northwest) and deforestation (South and Southeast) were the dominant land cover change (figures S15–S17).

4. Discussion

Our results highlight that the Amazon Forest sensitivity to climate extremes emerges from both regional and local drivers. The ED2 model estimates of GPP

and ET are consistently higher than the reference datasets used in this study (figures S7 and S8); however, there was low agreement in the magnitude and seasonality of GPP and ET among the reference datasets themselves that made the estimates of bias and uncertainty in the ED2 model predictions difficult to assess, and highly dependent on the choice of reference dataset (figures S7 and S8). This may be partly due to the higher estimates of aboveground biomass and leaf area index based on airborne compared to satellite remote sensing estimates (figures S5 and S6). Some of the largest differences occurred where airborne lidar data were not available, such as the area bordering Suriname (figure S1), where the nearest airborne lidar data were representative of much taller and denser forests. Moreover, the initialization approach was calibrated with limited field inventory data. Although we had tested the approach for spatial transferability [50], the lack of calibration data from tall-tree dominated forests [42, 94], white sand forests and scrublands [125, 126] and other unique forest landscapes may have impacted accuracy and precision of forest structure estimates. Together, these results indicate that uncertainties and biases may exist on both the ED2 model predictions and the reference datasets, and that there is an important need for calibration datasets that characterize the heterogeneity of tropical forests.

For much of the Western and Central part of the Amazon, the ED2 model predicted positive responses in GPP and ET to drier and sunnier conditions when conditions are near average (figure 3; figure S10), consistent to previous work using solar-induced chlorophyll fluorescence measurements as proxies for GPP [8]. In contrast, both GPP and ET across the Southern and the Eastern Brazilian Amazon responded negatively to the intensification of conditions typical of severe droughts—dry air, dry soil and sunny conditions (figure 3; figure S10)—indicating that these regions are more vulnerable to drought stress both through soil moisture and air vapor pressure deficit, which can lead to higher risk of mortality-driven carbon losses [15, 127]. Increasing atmospheric CO₂ could partially mitigate this risk, although the magnitude of the CO₂ fertilization effect in tropical forests remains unconstrained by observations [128] and highly variable across models [129, 130].

Local heterogeneity of forest canopy structure within grid cells ($1 \times 1^\circ$) had a marked effect on the model predictions across the Brazilian Amazon. Forests with locally low above-ground biomass (aboveground biomass $<6.25 \text{ kgC m}^{-2}$) typically showed lower ET and GPP than those with high aboveground biomass ($>9 \text{ kgC m}^{-2}$) (figure 4; figures S11 and S12). This is expected because these forests are more open and also have lower leaf area index; however, the predicted functional response of low-aboveground-biomass to either low soil moisture or high air vapor pressure deficit is often decoupled from the high-aboveground-biomass forest responses, with ET in low-aboveground-biomass forests peaking at higher soil moisture and lower air vapor pressure deficit, and sustaining more substantial depletions in ET and GPP under extremely water limiting conditions (figure 4; figures S11 and S12). Considering that the maximum ET and GPP occur at lower levels of drought and the depletion is more pronounced in these forests, the simulation results indicate that low-aboveground-biomass forest patches experience water stress more frequently than high-aboveground-biomass forest patches. Nevertheless, the results indicate that once forests reach intermediate levels of aboveground biomass, their response to environmental variability becomes nearly independent of forest structure, behaving similarly to very-high-aboveground-biomass forests ($\sim 25 \text{ kgC m}^{-2}$), which are typical of old-growth conditions. These results are consistent with observations of eddy covariance flux measurements and remotely sensed estimates of fluxes in the Amazon, which found that lightly degraded forests experienced only minor changes in energy, water and carbon fluxes, but forests that burnt multiple times had noticeable differences in GPP and ET for up to 7 years and potentially longer when fire disturbance becomes severe [51, 53, 131, 132].

The ED2 model simulations indicate that the recovery of currently degraded forests will have only a modest impact on the forest sensitivity to climate extremes (figures 5(c) and (e); figure 6). In contrast, the ED2 simulations indicated that degraded forests across the Amazon will likely experience substantially more water and heat stress than intact forests, potentially impacting the ecosystem resilience of degraded forests to extreme events (figures 5(d) and (f); figure 6). Direct impacts of forest degradation include the reduction in forests' aboveground biomass and leaf area index and the increase in canopy openness [29, 71, 133–135], which result in more light penetrating through the canopy. The reduction in leaf area index, combined with the increased radiation reaching the ground, causes both surface desiccation and reduction in transpiration rates, resulting in long-term averages of surface temperature to increase by more than 4°C and long-term ET to decrease by 12% (figure 5; figure S14). Faster drying in degraded or fragmented tropical forests has been observed both in terms of increased near-surface air vapor pressure deficit [136, 137] and decreased near-surface soil moisture [138]. These conditions extend the period in which degraded forests are under water stress, which may increase their vulnerability to extreme droughts, in line with evidence from the changes in canopy water content and greenness indices to the extreme 2015–2016 El Niño drought [139]. In the ED2 model, the results indicate that a potential expansion of deforestation and forest degradation towards the west would expose new areas of the Amazon to more frequent heat and water stress (figure 6; figure S15–S17), even though the simulation sets were carried out without any changes in climate. However, the results from the *Degradation* scenario should be considered a conservative estimate of changes in forest sensitivity to climate extreme, as many parts of the Amazon, including the western regions, are predicted to experience more frequent hot droughts in the future [1], which could further reduce the resilience of newly degraded and fragmented forests in the west to climate extremes [140, 141]. The combination of large-scale heat with the hotter and drier microenvironments associated with deforestation and forest degradation could cause large areas of the Amazon to approach temperatures in which photosynthesis function can no longer be sustained [142], and thus increasing the risk of such forests to reach critical transitions to permanently low canopy cover conditions [143].

The idealized regional ED2 model simulations in this study focused on assessing the direct impacts of forest structure changes on energy, water and carbon fluxes and the responses of these fluxes to climate extremes (figures 5 and 6). In reality, the combination of forest structure changes with climate extremes will likely generate important feedbacks that may accelerate ecosystem transitions to alternative states. For

example, the results from the *Recovery* scenario indicated that savanna enclaves in our domain, such as those in Northeastern Roraima, may experience significant increases in biomass and tree cover if fires are completely suppressed (figures S13(b) and (e)), consistent with previous research highlighting the risk of rapid forest encroachment in the Cerrado savannas-Amazon ecotones [144]. In contrast, other studies have shown that previously degraded tropical forests were more susceptible to drought-, fire-, and wind-driven mortality than intact forests [74, 145]. Likewise, the hotter and drier microenvironments of degraded forests increases forest flammability [53, 136–138], which can be further exacerbated through grass establishment in the typically more open canopies of degraded forests [146]. These positive feedbacks will likely intensify the fire regime across the Amazon [147], and should be explored in future studies using process-based vegetation demography models that can account for realistic representation of fire disturbances [148].

5. Conclusion

By integrating ED2, a terrestrial biosphere model, with a large airborne lidar collection across the Brazilian Amazon, we found that shorter and sparser forests, typical of degraded areas, are more vulnerable to extreme climate conditions than intact forests. Moreover, a potential expansion of forest degradation could expand this vulnerability to areas currently resistant to droughts (e.g. Western and the Northwestern Brazilian Amazon). The feedbacks between forest degradation and higher vulnerability to climate extremes are likely to amplify as climate continues to change, consequently increasing the risk of persistent shifts of these forests towards low canopy cover and reduced carbon stocks. Our study also showed the highly-promising potential to integrate remotely-sensed data and models at continental scales to understand the emergent relationships between forest structure and carbon, water, and energy fluxes. The expansion of airborne and spaceborne lidar datasets, most notably through NASA's Global Ecosystem Dynamics Investigation [149], is allowing better understanding of the role of forest structure on biogeophysical and biogeochemical cycles at larger scales [150], especially when combined with models that represent climate variability across multiple spatial and temporal scales.

Data availability statement

The data that support the findings of this study are openly available at the following URL/DOI: [https://dx.doi.org/10.1038/s41597-023-](https://dx.doi.org/10.1038/s41597-023-02575-4)

[02575-4](https://dx.doi.org/10.1038/s41597-023-02575-4) [43]; <https://dx.doi.org/10.5281/zenodo.7689908> [96]; <https://dx.doi.org/10.5281/zenodo.7689209> [95]; <https://dx.doi.org/10.5281/zenodo.7636453> [98]; <https://dx.doi.org/10.5281/zenodo.7689692> [97]; <https://github.com/mpaiao/ED2/releases/tag/BrAmzALS2> [91]; <https://dx.doi.org/10.3334/ORNLDAAAC/2412> [100]; <https://dx.doi.org/10.15485/2526256> [109]; <https://dx.doi.org/10.5281/zenodo.14773328> [107]; <https://dx.doi.org/10.5281/zenodo.14736560> [108]; <https://dx.doi.org/10.5281/zenodo.14775423> [123]; <https://dx.doi.org/10.5281/zenodo.14775866> [124].

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Conflict of interest

The authors have no competing interests to declare.

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References

- [1] Alves L M, Firpo M Á F, Bettolli M L, Hasson S U, Guerron O V C, Añazco A A and Llopart M P 2024 Projected changes in the frequency of compound hot and dry events over Tropical Brazil in CORDEX-CORE simulations *Clim. Dyn.* **62** 10203–16
- [2] Castellanos E et al 2022 *Climate Change 2022: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* ed H O Pörtner et al (Cambridge University Press) pp 1689–816
- [3] Marengo J A, Espinoza J C, Fu R, Jimenez Muñoz J C, Alves L M, da Rocha H R and Schöngart J 2021 Long-term variability, extremes and changes in temperature and hydro meteorology in the Amazon region *Amazon Assessment Report* ed C Nobre (United Nations Sustainable Development Solutions Network) pp 1–33
- [4] Barkhordarian A, Saatchi S S, Behrangi A, Loikith P C and Mechoso C R 2019 A recent systematic increase in vapor pressure deficit over tropical South America *Sci. Rep.* **9** 15331
- [5] Ukkola A M, De Kauwe M G, Roderick M L, Abramowitz G and Pitman A J 2020 Robust future changes in meteorological drought in CMIP6 projections despite uncertainty in precipitation *Geophys. Res. Lett.* **47** e2020GL087820
- [6] Vogel M M, Hauser M and Seneviratne S I 2020 Projected changes in hot, dry and wet extreme events' clusters in CMIP6 multi-model ensemble *Environ. Res. Lett.* **15** 094021
- [7] Barkhordarian A, Bowman K W, Cressie N, Jewell J and Liu J 2021 Emergent constraints on tropical atmospheric aridity—carbon feedbacks and the future of carbon sequestration *Environ. Res. Lett.* **16** 114008
- [8] Green J K, Berry J, Ciais P, Zhang Y and Gentile P 2020 Amazon rainforest photosynthesis increases in response to atmospheric dryness *Sci. Adv.* **6** eabb7232
- [9] Hasler N and Avissar R 2007 What controls evapotranspiration in the Amazon Basin? *J. Hydrometeorol.* **8** 380–95
- [10] Maeda E E, Ma X, Wagner F H, Kim H, Oki T, Eamus D and Huete A 2017 Evapotranspiration seasonality across the Amazon Basin *Earth Syst. Dyn.* **8** 439–54
- [11] Restrepo-Coupe N et al 2017 Do dynamic global vegetation models capture the seasonality of carbon fluxes in the Amazon basin? A data-model intercomparison *Glob. Change Biol.* **23** 191–208
- [12] Restrepo-Coupe N et al 2021 Understanding water and energy fluxes in the Amazonia: lessons from an observation-model intercomparison *Glob. Change Biol.* **27** 1802–19
- [13] Nemani R R, Keeling C D, Hashimoto H, Jolly W M, Piper S C, Tucker C J, Myneni R B and Running S W 2003 Climate-driven increases in global terrestrial net primary production from 1982 to 1999 *Science* **300** 1560–3
- [14] Li X, Xiao J and He B 2018 Higher absorbed solar radiation partly offset the negative effects of water stress on the photosynthesis of Amazon forests during the 2015 drought *Environ. Res. Lett.* **13** 044005
- [15] Liu J et al 2024 Enhanced carbon flux response to atmospheric aridity and water storage deficit during the 2015–2016 El Niño compromised carbon balance recovery in tropical South America *AGU Adv.* **5** e2024AV001187
- [16] Madani N et al 2020 Recent amplified global gross primary productivity due to temperature increase is offset by reduced productivity due to water constraints *AGU Adv.* **1** e2020AV000180
- [17] Meng L et al 2022 Soil moisture thresholds explain a shift from light-limited to water-limited sap velocity in the Central Amazon during the 2015–16 El Niño drought *Environ. Res. Lett.* **17** 064023
- [18] Restrepo-Coupe N et al 2024 Contrasting carbon cycle responses to dry (2015 El Niño) and wet (2008 La Niña) extreme events at an Amazon tropical forest *Agric. For. Meteorol.* **353** 110037
- [19] Yan H, Wang S-Q, Huete A and Shugart H H 2019 Effects of light component and water stress on photosynthesis of Amazon rainforests during the 2015/2016 El Niño drought *J. Geophys. Res.* **124** 1574–90
- [20] Longo M et al 2018 Ecosystem heterogeneity and diversity mitigate Amazon forest resilience to frequent extreme droughts *New Phytol.* **219** 914–31
- [21] Staal A, Flores B M, Aguiar A P D, Bosmans J H C, Fetzter I and Tuinenburg O A 2020 Feedback between drought and deforestation in the Amazon *Environ. Res. Lett.* **15** 044024
- [22] Zemp D C, Schleussner C-F, Barbosa H M J, Hirota M, Montade V, Sampaio G, Staal A, Wang-Erlandsson L and Rammig A 2017 Self-amplified Amazon forest loss due to vegetation-atmosphere feedbacks *Nat. Commun.* **8** 14681
- [23] Feldpausch T R et al 2016 Amazon forest response to repeated droughts *Glob. Biogeochem. Cycles* **30** 964–82
- [24] Meir P, Wood T E, Galbraith D R, Brando P M, da Costa A C L, Rowland L and Ferreira L V 2015 Threshold responses to soil moisture deficit by trees and soil in

- tropical rain forests: insights from field experiments *BioScience* **65** 882–92
- [25] Rowland L *et al* 2015 Death from drought in tropical forests is triggered by hydraulics not carbon starvation *Nature* **528** 119–22
- [26] Berenguer E *et al* 2021 Drivers and ecological impacts of deforestation and forest degradation *Amazon Assessment Report* ed C Nobre *et al* (United Nations Sustainable Development Solutions Network) pp 1–40
- [27] Vancutsem C, Achard F, Pekel J F, Vieilledent G, Carboni S, Simonetti D, Gallego J, Aragão L E O C and Nasi R 2021 Long-term (1990–2019) monitoring of forest cover changes in the humid tropics *Sci. Adv.* **7** eabe1603
- [28] Barlow J *et al* 2016 Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation *Nature* **535** 144–7
- [29] Bourgoin C *et al* 2020 UAV-based canopy textures assess changes in forest structure from long-term degradation *Ecol. Indic.* **115** 106386
- [30] Rappaport D, Morton D, Longo M, Keller M, Dubayah R and dos-Santos M N 2018 Quantifying long-term changes in carbon stocks and forest structure from Amazon forest degradation *Environ. Res. Lett.* **13** 065013
- [31] Silvério D V *et al* 2022 Intensification of fire regimes and forest loss in the Território Indígena do Xingu *Environ. Res. Lett.* **17** 045012
- [32] Valle D, Silva C A, Longo M and Brando P 2022 Mapping forest degradation using the Latent Dirichlet allocation model applied to airborne LiDAR data: a case study on the effect of forest fragmentation and fire in the Amazon region *Methods Ecol. Evol.* **13** 1329–42
- [33] Brinck K, Fischer R, Groeneveld J, Lehmann S, de Paula M D, Pütz S, Sexton J O, Song D and Huth A 2017 High resolution analysis of tropical forest fragmentation and its impact on the global carbon cycle *Nat. Commun.* **8** 14855
- [34] Bullock E L, Woodcock C E, Souza C Jr and Olofsson P 2020 Satellite-based estimates reveal widespread forest degradation in the Amazon *Glob. Change Biol.* **26** 2956–69
- [35] Lapola D M *et al* 2023 The drivers and impacts of Amazon forest degradation *Science* **379** eabp8622
- [36] Matricardi E A T, Skole D L, Costa O B, Pedlowski M A, Samek J H and Miguel E P 2020 Long-term forest degradation surpasses deforestation in the Brazilian Amazon *Science* **369** 1378–82
- [37] Montibeller B, Kmoch A, Virro H, Mander Ü and Uuemaa E 2020 Increasing fragmentation of forest cover in Brazil's legal Amazon from 2001 to 2017 *Sci. Rep.* **10** 5803
- [38] Nepstad D C *et al* 1999 Large-scale impoverishment of Amazonian forests by logging and fire *Nature* **398** 505–8
- [39] Qin Y *et al* 2021 Carbon loss from forest degradation exceeds that from deforestation in the Brazilian Amazon *Nat. Clim. Change* **11** 442–8
- [40] Tyukavina A, Hansen M C, Potapov P V, Stehman S V, Smith-Rodriguez K, Okpa C and Aguilar R 2017 Types and rates of forest disturbance in Brazilian legal Amazon, 2000–2013 *Sci. Adv.* **3** e1601047
- [41] Potapov P *et al* 2017 The last frontiers of wilderness: tracking loss of intact forest landscapes from 2000 to 2013 *Sci. Adv.* **3** e1600821
- [42] Gorgens E B *et al* 2021 Resource availability and disturbance shape maximum tree height across the Amazon *Glob. Change Biol.* **27** 177–89
- [43] Ometto J, Gorgens E B, Pereira F R D S, Sato L, de Assis M L R, Cantinho R, Longo M, Jacon A D and Keller M 2023 A biomass map of the Brazilian Amazon from multisource remote sensing *Sci. Data* **10** 668
- [44] Almeida C A, Coutinho A C, Esquerdo J C D M, Adami M, Venturieri A, Diniz C G, Dessay N, Durieux L and Gomes A R 2016 High spatial resolution land use and land cover mapping of the Brazilian legal Amazon in 2008 using Landsat-5/TM and MODIS data *Acta Amaz.* **46** 291–302
- [45] Terrabrasilis 2025 Terrabrasilis – Geographic Data Platform (available at: <https://terrabrasilis.dpi.inpe.br/en/home-page/>) (Accessed 26 March 2025)
- [46] Shimabukuro Y E, Dos Santos J R, Formaggio A R, Duarte V and Rudorff B F T 2012 The Brazilian Amazon monitoring program: PRODES and DETER projects *Global Forest Monitoring from Earth Observation* ed F Achard and M C Hansen (CRC Press) pp 153–69
- [47] Flack-Prain S, Meir P, Malhi Y, Smallman T L and Williams M 2019 The importance of physiological, structural and trait responses to drought stress in driving spatial and temporal variation in GPP across Amazon forests *Biogeosciences* **16** 4463–84
- [48] Huang M, Xu Y, Longo M, Keller M, Knox R, Koven C and Fisher R 2020 Assessing impacts of selective logging on water, energy, and carbon budgets and ecosystem dynamics in Amazon forests using the functionally assembled terrestrial ecosystem simulator *Biogeosciences* **17** 4999–5023
- [49] Jucker T *et al* 2018 Estimating aboveground carbon density and its uncertainty in Borneo's structurally complex tropical forests using airborne laser scanning *Biogeosciences* **15** 3811–30
- [50] Longo M *et al* 2020 Impacts of degradation on water, energy, and carbon cycling of the Amazon tropical forests *J. Geophys. Res.* **125** e2020JG005677
- [51] de Oliveira G, Brunsell N A, Chen J M, Shimabukuro Y E, Mataveli G A V, Dos Santos C A C, Stark S C, de Lima A and Aragão L E O C 2021 Legacy effects following fire on surface energy, water and carbon fluxes in mature Amazonian forests *J. Geophys. Res.* **126** e2020JG005833
- [52] Rangel Pinagé E *et al* 2022 Forest structure and solar-induced fluorescence across intact and degraded forests in the Amazon *Remote Sens. Environ.* **274** 112998
- [53] Rangel Pinagé E, Bell D M, Longo M, Silva C A, Csillik O and Huete A 2023 Surface energy dynamics and canopy structural properties in intact and disturbed forests in the Southern Amazon *J. Geophys. Res.* **128** e2023JG007465
- [54] Leite-Filho A T, Soares-Filho B S, Davis J L, Abrahão G M and Börner J 2021 Deforestation reduces rainfall and agricultural revenues in the Brazilian Amazon *Nat. Commun.* **12** 2591
- [55] Saatchi S *et al* 2021 Detecting vulnerability of humid tropical forests to multiple stressors *One Earth* **4** 988–1003
- [56] Staal A, Fetzer I, Wang-Erlandsson L, Bosmans J H C, Dekker S C, van Nes E H, Rockström J and Tuinenburg O A 2020 Hysteresis of tropical forests in the 21st century *Nat. Commun.* **11** 4978
- [57] Trumbore S, Brando P and Hartmann H 2015 Forest health and global change *Science* **349** 814–8
- [58] Bonan G B *et al* 2024 Reimagining Earth in the Earth system *J. Adv. Model. Earth Syst.* **16** e2023MS004017
- [59] Fisher R A *et al* 2018 Vegetation demographics in Earth system models: a review of progress and priorities *Glob. Change Biol.* **24** 35–54
- [60] Fisher R A and Koven C D 2020 Perspectives on the future of land surface models and the challenges of representing complex terrestrial systems *J. Adv. Model. Earth Syst.* **12** e2018MS001453
- [61] Antonarakis A S, Bogan S A, Goulden M L and Moorcroft P R 2022 Impacts of the 2012–2015 Californian drought on carbon, water and energy fluxes in the Californian Sierras: results from an imaging spectrometry-constrained terrestrial biosphere model *Glob. Change Biol.* **28** 1823–52
- [62] Levine N M *et al* 2016 Ecosystem heterogeneity determines the resilience of the Amazon to climate change *Proc. Natl Acad. Sci. USA* **113** 793–7
- [63] Powell T L *et al* 2018 Variation in hydroclimate sustains tropical forest biomass and promotes functional diversity *New Phytol.* **219** 932–46
- [64] Schneider F D *et al* 2023 Remote sensing-based forest modeling reveals positive effects of functional diversity on

- productivity at local spatial scale *J. Geophys. Res.* **128** e2023JG007421
- [65] Meunier F *et al* 2021 Unraveling the relative role of light and water competition between lianas and trees in tropical forests: a vegetation model analysis *J. Ecol.* **109** 519–40
- [66] Antonarakis A S 2014 Uncertainty in initial forest structure and composition when predicting carbon dynamics in a temperate forest *Ecol. Modelling* **291** 134–41
- [67] Ni-Meister W, Jupp D L B and Dubayah R 2001 Modeling lidar waveforms in heterogeneous and discrete canopies *IEEE Trans. Geosci. Remote Sens.* **39** 1943–58
- [68] Drake J B, Dubayah R O, Clark D B, Knox R G, Blair J B, Hofton M A, Chazdon R L, Weishampel J F and Prince S 2002 Estimation of tropical forest structural characteristics using large-footprint lidar *Remote Sens. Environ.* **79** 305–19
- [69] Reutebuch S E, Andersen H-E and McGaughey R J 2005 Light detection and ranging (LIDAR): an emerging tool for multiple resource inventory *J. For.* **103** 286–92
- [70] Andersen H-E, Reutebuch S E, McGaughey R J, d'Oliveira M V N and Keller M 2014 Monitoring selective logging in western Amazonia with repeat lidar flights *Remote Sens. Environ.* **151** 157–65
- [71] Csillik O *et al* 2024 A large net carbon loss attributed to anthropogenic and natural disturbances in the Amazon arc of deforestation *Proc. Natl Acad. Sci. USA* **121** e2310157121
- [72] Longo M *et al* 2016 Aboveground biomass variability across intact and degraded forests in the Brazilian Amazon *Glob. Biogeochem. Cycles* **30** 1639–60
- [73] Rangel Pinag  E, Keller M, Duffy P, Longo M, dos-Santos M N and Morton D C 2019 Long-term impacts of selective logging on Amazon forest dynamics from multi-temporal airborne LiDAR *Remote Sens.* **11** 709
- [74] Silv rio D V, Brando P M, Bustamante M M C, Putz F E, Marra D M, Levick S R and Trumbore S E 2019 Fire, fragmentation, and windstorms: a recipe for tropical forest degradation *J. Ecol.* **107** 656–67
- [75] Wedeux B, Dalponte M, Schlund M, Hagen S, Cochrane M, Graham L, Usup A, Thomas A and Coomes D 2020 Dynamics of a human-modified tropical peat swamp forest revealed by repeat lidar surveys *Glob. Change Biol.* **26** 3947–64
- [76] Yang W, Ni-Meister W and Lee S 2011 Assessment of the impacts of surface topography, off-nadir pointing and vegetation structure on vegetation lidar waveforms using an extended geometric optical and radiative transfer model *Remote Sens. Environ.* **115** 2810–22
- [77] Leitold V, Keller M, Morton D, Cook B and Shimabukuro Y 2015 Airborne lidar-based estimates of tropical forest structure in complex terrain: opportunities and trade-offs for REDD+ *Carbon Balance Manage.* **103** 1–12
- [78] Hilker T *et al* 2008 A modeling approach for upscaling gross ecosystem production to the landscape scale using remote sensing data *J. Geophys. Res.* **113** G03006
- [79] Zeng Y *et al* 2023 Structural complexity biases vegetation greenness measures *Nat. Ecol. Evol.* **7** 1790–8
- [80] Longo M *et al* 2019 The biophysics, ecology, and biogeochemistry of functionally diverse, vertically and horizontally heterogeneous ecosystems: the ecosystem demography model, version 2.2—Part 1: model description *Geosci. Model Dev.* **12** 4309–46
- [81] Medvigy D M, Wofsy S C, Munger J W, Hollinger D Y and Moorcroft P R 2009 Mechanistic scaling of ecosystem function and dynamics in space and time: ecosystem demography model version 2 *J. Geophys. Res.* **114** G01002
- [82] Moorcroft P R, Hurtt G C and Pacala S W 2001 A method for scaling vegetation dynamics: the ecosystem demography model (ED) *Ecol. Monogr.* **71** 557–86
- [83] Xu X, Medvigy D, Powers J S, Becknell J M and Guan K 2016 Diversity in plant hydraulic traits explains seasonal and inter-annual variations of vegetation dynamics in seasonally dry tropical forests *New Phytol.* **212** 80–95
- [84] van Genuchten M T 1980 A closed-form equation for predicting the hydraulic conductivity of unsaturated soils *Soil Sci. Soc. Am. J.* **44** 892–8
- [85] Tomasella J and Hodnett M 2004 Pedotransfer functions for tropical soils *Development of Pedotransfer Functions in Soil Hydrology* ed Y A Pachepsky and W J Rawls (Elsevier) pp 415–29
- [86] Hodnett M G and Tomasella J 2002 Marked differences between van Genuchten soil water-retention parameters for temperate and tropical soils: a new water-retention pedo-transfer functions developed for tropical soils *Geoderma* **108** 155–80
- [87] Marthews T R, Quesada C A, Galbraith D R, Malhi Y, Mullins C E, Hodnett M G and Dharssi I 2014 High-resolution hydraulic parameter maps for surface soils in tropical South America *Geosci. Model Dev.* **7** 711–23
- [88] Longo M *et al* 2019 The biophysics, ecology, and biogeochemistry of functionally diverse, vertically and horizontally heterogeneous ecosystems: the ecosystem demography model, version 2.2—Part 2: model evaluation for tropical South America *Geosci. Model Dev.* **12** 4347–74
- [89] Xu X, Konings A G, Longo M, Feldman A, Xu L, Saatchi S, Wu D, Wu J and Moorcroft P 2021 Leaf surface water, not plant water stress, drives diurnal variation in tropical forest canopy water content *New Phytol.* **231** 122–36
- [90] Longo M *et al* 2025 Ecosystem Demography Model, Tag v2.2.1-BrAmazALS2 (<https://doi.org/10.5281/zenodo.14736060>)
- [91] Longo M *et al* (GitHub) 2025 Ecosystem Demography Model, v2.2.1-BrAmazALS2 (available at: <https://github.com/mpaiao/ED2/releases/tag/BrAmzALS2>) (Accessed 26 March 2025)
- [92] Pelletier J D, Broxton P D, Hazenberg P, Zeng X, Troch P A, Niu G-Y, Williams Z, Brunke M A and Gochis D 2016 A gridded global data set of soil, intact regolith, and sedimentary deposit thicknesses for regional and global land surface modeling *J. Adv. Model. Earth Syst.* **8** 41–65
- [93] Poggio L, de Sousa L M, Batjes N H, Heuvelink G B M, Kempen B, Ribeiro E and Rossiter D 2021 SoilGrids 2.0: producing soil information for the globe with quantified spatial uncertainty *Soil* **7** 217–40
- [94] Gorgens E B, Motta A Z, Assis M, Nunes M H, Jackson T, Coomes D, Rosette J, Oliveira L E, Arag o C and Ometto J P 2019 The giant trees of the Amazon basin *Front. Ecol. Environ.* **17** 373–4
- [95] Ometto J *et al* 2023 L1A - Discrete airborne LiDAR transects collected by EBA in the Brazilian Amazon (Maranh o e Tocantins) *Zenodo* (<https://doi.org/10.5281/zenodo.7689210>)
- [96] Ometto J *et al* 2023 L1A - Discrete airborne LiDAR transects collected by EBA in the Brazilian Amazon (Acre e Rond nia) *Zenodo* (<https://doi.org/10.5281/zenodo.7689909>)
- [97] Ometto J *et al* 2023 L1A - Discrete airborne LiDAR transects collected by EBA in the Brazilian Amazon (Roraima e Amap ) *Zenodo* (<https://doi.org/10.5281/zenodo.7689693>)
- [98] Ometto J *et al* 2023 L1A - Discrete airborne LiDAR transects collected by EBA in the Brazilian Amazon (Mato Grosso, Amazonas e Par ) *Zenodo* (<https://doi.org/10.5281/zenodo.7636454>)
- [99] de Almeida C A *et al* 2021 Methodology for forest monitoring used in PRODES and DETER projects (Instituto Nacional de Pesquisas Espaciais) (available at: <http://urlib.net/8JMKD3MGP3W34R/443H3RE>)
- [100] Longo M *et al* 2025 Amazon forest structure from airborne Lidar, ED2 initial condition files, 2016 ORNL Distributed Active Archive Center (<https://doi.org/10.3334/ORNLDAAC/2412>)
- [101] MapBiomass 2023 Interactive land cover map of Brazilian biomes (MapBiomass v.8.0) (available at: <https://plataforma.brasil.mapbiomas.org>)

- [102] Zanchi F B, Waterloo M J, Aguiar L J G, von Randow C, Kruijt B, Cardoso F L and Manzi A O 2009 Estimate of the leaf area index (LAI) and biomass in pasture in the state of Rondônia—Brazil *Acta Amz.* **39** 335–48
- [103] Cucchi M, Weedon G P, Amici A, Bellouin N, Lange S, Müller Schmied H, Hersbach H and Buontempo C 2020 WFDE5: bias-adjusted ERA5 reanalysis data for impact studies *Earth Syst. Sci. Data* **12** 2097–120
- [104] Funk C *et al* 2015 The climate hazards infrared precipitation with stations—a new environmental record for monitoring extremes *Sci. Data* **2** 150066
- [105] Sapucci C R, Mayta V C and Silva Dias P L 2022 Evaluation of diverse-based precipitation data over the Amazon region *Theor. Appl. Climatol.* **149** 1167–93
- [106] Merry F, Soares-Filho B, Nepstad D, Amacher G and Rodrigues H 2009 Balancing conservation and economic sustainability: the future of the Amazon timber industry *Environ. Manage.* **44** 395–407
- [107] Longo M *et al* 2025 Boundary conditions for ED2 simulations for the Brazilian Amazon, initialised with airborne laser scanning Zenodo (<https://doi.org/10.5281/zenodo.14773328>)
- [108] Longo M *et al* 2025 Configuration files for the ED2 simulations for the Brazilian Amazon, initialised with airborne lidar Zenodo (<https://doi.org/10.5281/zenodo.14736560>)
- [109] Longo M *et al* 2025 Monthly averages of ED2 model simulations initialized with airborne lidar structure, Jan 1981-Dec 2018, Brazilian Amazon Next-Generation Ecosystem Experiments (NGEE) Tropics, ESS-DIVE Repository (<https://doi.org/10.15485/2526256>)
- [110] Burns P, Hakkenberg C R and Goetz S J 2024 Multi-resolution gridded maps of vegetation structure from GEDI *Sci. Data* **11** 881
- [111] Xu L *et al* 2021 Changes in global terrestrial live biomass over the 21st century *Sci. Adv.* **7** eabe9829
- [112] Yan K, Wang J, Peng R, Yang K, Chen X, Yin G, Dong J, Weiss M, Pu J and Myneni R B 2024 HiQ-LAI: a high-quality reprocessed MODIS leaf area index dataset with better spatiotemporal consistency from 2000 to 2022 *Earth Syst. Sci. Data* **16** 1601–22
- [113] Fisher J B, Tu K P and Baldocchi D D 2008 Global estimates of the land-atmosphere water flux based on monthly AVHRR and ISLSCP-II data, validated at 16 FLUXNET sites *Remote Sens. Environ.* **112** 901–19
- [114] Joiner J, Yoshida Y, Zhang Y, Duveiller G, Jung M, Lyapustin A, Wang Y and Tucker C J 2018 Estimation of terrestrial global gross primary production (GPP) with satellite data-driven models and eddy covariance flux data *Remote Sens.* **10** 1346
- [115] Jung M *et al* 2019 The FLUXCOM ensemble of global land-atmosphere energy fluxes *Sci. Data* **6** 74
- [116] Li X and Xiao J 2019 A global, 0.05-degree product of solar-induced chlorophyll fluorescence derived from OCO-2, MODIS, and reanalysis data *Remote Sens.* **11** 517
- [117] Miralles D G, Holmes T R H, De Jeu R A M, Gash J H, Meesters A G C A and Dolman A J 2011 Global land-surface evaporation estimated from satellite-based observations *Hydrol. Earth Syst. Sci.* **15** 453–69
- [118] Miralles D G *et al* 2025 GLEAM4: global land evaporation and soil moisture dataset at 0.1 resolution from 1980 to near present *Sci. Data* **12** 416
- [119] Purdy A J, Fisher J B, Goulden M L, Colliander A, Halverson G, Tu K and Famiglietti J S 2018 SMAP soil moisture improves global evapotranspiration *Remote Sens. Environ.* **219** 1–14
- [120] R Core Team 2023 R: a language and environment for statistical computing (R Foundation for Statistical Computing) (available at: www.R-project.org/)
- [121] Xu L, Saatchi S S, Yang Y, Myneni R B, Frankenberg C, Chowdhury D and Bi J 2015 Satellite observation of tropical forest seasonality: spatial patterns of carbon exchange in Amazonia *Environ. Res. Lett.* **10** 084005
- [122] Rutishauser E *et al* 2015 Rapid tree carbon stock recovery in managed Amazonian forests *Curr. Biol.* **25** R787–R8
- [123] Longo M *et al* 2025 Post-processing workflow for ED2 simulations for the Brazilian Amazon, initialised with airborne lidar (Part 1) Zenodo (<https://doi.org/10.5281/zenodo.14775423>)
- [124] Longo M *et al* 2025 Post-processing workflow for ED2 simulations for the Brazilian Amazon, initialised with airborne lidar (Part 2) Zenodo (<https://doi.org/10.5281/zenodo.14775866>)
- [125] Anderson A B 1981 White-sand vegetation of Brazilian Amazonia *Biotropica* **13** 199–210
- [126] Adeney J M, Christensen N L, Vicentini A and Cohn-Haft M 2016 White-sand ecosystems in Amazonia *Biotropica* **48** 7–23
- [127] Bennett A C *et al* 2023 Sensitivity of South American tropical forests to an extreme climate anomaly *Nat. Clim. Change* **13** 967–74
- [128] Norby R J *et al* 2016 Model-data synthesis for the next generation of forest free-air CO₂ enrichment (FACE) experiments *New Phytol.* **209** 17–28
- [129] Castanho A D A, Galbraith D, Zhang K, Coe M T, Costa M H and Moorcroft P 2016 Changing Amazon biomass and the role of atmospheric CO₂ concentration, climate and land use *Glob. Biogeochem. Cycles* **30** 18–39
- [130] Holm J A *et al* 2020 The Central Amazon biomass sink under current and future atmospheric CO₂: predictions from big-leaf and demographic vegetation models *J. Geophys. Res.* **125** e2019JG005500
- [131] Brando P M *et al* 2019 Prolonged tropical forest degradation due to compounding disturbances: implications for CO₂ and H₂O fluxes of an experimental forest *Glob. Change Biol.* **25** 2855–68
- [132] Miller S D, Goulden M L, Hutrya L R, Keller M, Saleska S R, Wofsy S C, Silva Figueira A M, da Rocha H R and de Camargo P B 2011 Reduced impact logging minimally alters tropical rainforest carbon and energy exchange *Proc. Natl Acad. Sci. USA* **108** 19431–5
- [133] Assis T O, de Aguiar A P D, von Randow C, Gomes D M D P, Kury J N, Ometto J and Nobre C A 2020 CO₂ emissions from forest degradation in Brazilian Amazonia *Environ. Res. Lett.* **15** 104035
- [134] Berenguer E *et al* 2014 A large-scale field assessment of carbon stocks in human-modified tropical forests *Glob. Change Biol.* **20** 3713–26
- [135] Guitet S, Pithon S, Brunaux O, Jubelin G and Gond V 2012 Impacts of logging on the canopy and the consequences for forest management in French Guiana *For. Ecol. Manage.* **277** 124–31
- [136] Brando P M *et al* 2014 Abrupt increases in Amazonian tree mortality due to drought–fire interactions *Proc. Natl Acad. Sci. USA* **111** 6347–52
- [137] Jucker T, Hardwick S R, Both S, Elias D M O, Ewers R M, Milodowski D T, Swinfield T and Coomes D A 2018 Canopy structure and topography jointly constrain the microclimate of human-modified tropical landscapes *Glob. Change Biol.* **24** 5243–58
- [138] Nunes M H *et al* 2022 Forest fragmentation impacts the seasonality of Amazonian evergreen canopies *Nat. Commun.* **13** 917
- [139] Chen S *et al* 2024 Amazon forest biogeography predicts resilience and vulnerability to drought *Nature* **631** 111–7
- [140] Staal A, Dekker S C, Hirota M and van Nes E H 2015 Synergistic effects of drought and deforestation on the resilience of the south-eastern Amazon rainforest *Ecol. Complex.* **22** 65–75
- [141] Wang H *et al* 2024 Anthropogenic disturbance exacerbates resilience loss in the Amazon rainforests *Glob. Change Biol.* **30** e17006

- [142] Doughty C E *et al* 2023 Tropical forests are approaching critical temperature thresholds *Nature* **621** 105–11
- [143] Flores B M *et al* 2024 Critical transitions in the Amazon forest system *Nature* **626** 555–64
- [144] Passos F B *et al* 2018 Savanna turning into forest: concerted vegetation change at the ecotone between the Amazon and “Cerrado” biomes *Braz. J. Bot.* **41** 611–9
- [145] Berenguer E *et al* 2021 Tracking the impacts of El Niño drought and fire in human-modified Amazonian forests *Proc. Natl Acad. Sci. USA* **118** e2019377118
- [146] Silvério D V, Brando P M, Balch J K, Putz F E, Nepstad D C, Oliveira-Santos C and Bustamante M M C 2013 Testing the Amazon savannization hypothesis: fire effects on invasion of a neotropical forest by native cerrado and exotic pasture grasses *Phil. Trans. R. Soc. B* **368** 20120427
- [147] Brando P M *et al* 2020 The gathering firestorm in southern Amazonia *Sci. Adv.* **6** eaay1632
- [148] Shuman J K, Fisher R A, Koven C D, Knox R G, Kueppers L M and Xu C 2024 Dynamic ecosystem assembly and escaping the “fire-trap” in the tropics: insights from FATES_15.0.0 *Geosci. Model Dev.* **17** 4643–71
- [149] Dubayah R *et al* 2022 GEDI launches a new era of biomass inference from space *Environ. Res. Lett.* **17** 095001
- [150] Ma L *et al* 2023 Spatial heterogeneity of global forest aboveground carbon stocks and fluxes constrained by spaceborne lidar data and mechanistic modeling *Glob. Change Biol.* **29** 3378–94