Dear Dr. Müller,

Thank you and the two reviewers for the comprehensive assessment and constructive comments on our first version of the manuscript "*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*" (gmd-2019-71, original title: "*The biophysics, ecology, and biogeochemistry of functionally diverse, vertically- and horizontally-heterogeneous ecosystems: the Ecosystem Demography Model, version 2.2 --- Part 2: Model evaluation*").

Below we include the detailed, point-by-point response to each comment and question raised by each referee. In our responses, line and page numbers correspond to the enclosed annotated manuscript and annotated supporting information. In the annotated files, blue text was added, and ~~crossed text~~ was removed.

We used track changes along with GMD's LaTeX template, and we noticed that the line numbers on the left side of the text were incorrect in some pages. We tried to make the references consistent with the numbers shown in the margin whenever possible. We apologize for this inconvenience.

Sincerely,
Marcos Longo

Responses to Referee 1

R1 Comment 01: The manuscript by Marcos Longo and colleagues performs a detailed evaluation of the ED-2.2 model (described in an accompanying discussion manuscript) for two sites in the Amazon and for the regional patterns simulated for the northern part of South America. The results are mostly presented in a comprehensive way and evaluate many different aspects of the model, both with regard to the short-term behaviour as "land surface scheme" and carbon cycle model and with regard to the long-term vegetation dynamics. It is hard to approach completeness in such an evaluation with all different properties and processes simulated by a model of this complexity, but I think that the authors have presented a nice selection of results in which the most important processes as well as different types of processes are addressed.

These results, while not providing scientific novelties in themselves, provide a thorough evaluation of the model presented in the accompanying manuscript and provide good insight in the strengths and weaknesses of the current model implementation, and I think that these are presented in a balanced manner. I have some remarks about the way of describing and presenting some parts of the results that I would recommend the authors to address. With these adjustments, I expect the manuscript to be acceptable for publication in GMD.

I describe my remarks in more detail below, with some major issues and a list of smaller suggestions for edits and clarifications.

Response: We thank the Reviewer for their encouraging feedback. Our goal in this manuscript was indeed to focus on evaluating multiple processes solved by ED-2.2 to provide a more comprehensive picture of which biophysical and ecological processes are well represented by the model, and which processes still need improvements in future developments.

Major remarks:

R1 Comment 02: Evaluation of ED-2.2 is undertaken for the tropical forest in the Amazon in this study. Such a regional focus is understandable (and enough to be published separately), but as such the evaluation provided in the manuscript is for these tropical conditions specifically. The title of the manuscript could reflect the Amazon focus of this work. Also, it would be good to stress (p. 22, l. 21) that the model was evaluated for Amazon conditions specifically. E.g., this tests indeed "multiple biophysical and biogeochemical mechanisms", but also leaves many "mechanisms" that are typical for non-tropical conditions (e.g. those related to temperature-induced phenological changes or interactions with snow cover) unevaluated. I miss this aspect in the discussion and conclusion of the manuscript. The authors highlight that earlier versions of ED have been tested for other ecosystems as well (p. 21, l. 30ff), but do not discuss to what extent the current version of the model is expected to behave in a similar way or not.

Response: We agree with the Reviewer that we should make it clear in the title and abstract that the model evaluation is presented for tropical ecosystems. We appended "for tropical South America" in the title, and we modified the text in the *Conclusions* (p. 27, l. 27 of the annotated manuscript).

We also included a sentence in the discussion that highlights the need to further evaluate ED-2.2 in non-tropical biomes (p. 27, l. 5–9 of the annotated manuscript).

R1 Comment 03: For the comparison of light extinction in the canopy (p. 3, l. 32; Fig. 2), it seems crucial that atmospheric conditions (e.g. the ratio of direct and diffuse light) are comparable to the average of the simulation period if you do not use the same days. Has this been tested? Even without detailed meteorological information for the time of measurements of the profile, I expect that there is some basic characterization of the weather conditions for those days that could be tested.

Response: Following the Reviewer's suggestion, we included a new Supplemental Information figure (Figure S1) that shows box-and-whisker plots of the daily averages of temperature, humidity, and net radiation from the nearest ABRACOS sites with such information, and the days we used to drive the ED-2.2 model. The range of temperature and humidity were similar between ABRACOS and LBA-MIP; for net radiation, daily averages are consistently higher during the LBA-MIP period, although the days we used from ED-2.2 predictions encompassed the entire range of values observed during the ABRACOS campaigns. For the diffuse-light only comparison (panels c and d), the characterization of weather conditions is not necessary: we are not comparing the absolute light extinction, but rather the normalized canopy radiation profile (i.e. divided by the incoming radiation measured immediately above the canopy), and we restrict the times from both the observations and simulations to be 100% diffuse light.

We updated the text in the Methods section to clarify the differences, the rationale for including the comparison under 100% diffuse radiation conditions, and point to the new SI figure (p. 5, l. 2–8 of the annotated manuscript).

R1 Comment 04: It is unclear how the sensitivity of the model was tested (using average conditions from different forcing data sets, p. 4, l. 17), and how this relates to the regional simulations mentioned earlier. Are these separate simulations? Or are these meteorological drivers merely used to compute statistics to separate grid cells for determining relationships? In the case of the former, the description should be extended to describe the simulations properly, in the case of the latter, I am unsure why the authors have not used the existing model forcing to perform that separation?

Response: Neither CERES-EBAF nor TMPA-3B43 were used to drive simulations. These products are monthly averages, and ED-2.2 requires drivers with time resolution of the order of hours. We opted to use the remote-sensing data sets to make a completely independent assessment of the ED-2.2 simulations.

We addressed the Reviewer's comment (i) by clarifying that CERES-EBAF and TMPA-3B43 were used only to compute statistics, and (ii) by providing similar statistics based on the PGMF meteorological data that were used to drive the simulations as an additional figure in the Supplemental Information. We changed the text in the Methods Section (p. 6, l. 3–11 of the annotated manuscript).

R1 Comment 05: p. 5, l. 4: Yes, net radiation is partly determined by the incoming radiation (which is an input), but so is outgoing radiation of course. I expect the seasonality shown in Fig. 1 to be primarily determined by the seasonality of incoming radiation, and absolute deviations (in both outgoing and net radiation) are probably more informative for understanding model biases than the model's ability to represent the seasonal cycle.

Response: We assumed that the Reviewer was referring to p. 5, l. 14. We agree that the seasonality of outgoing radiation will also be modulated by the seasonality of incoming radiation, and we modified the text to include this important caveat (p. 8, l. 3–5 of the annotated manuscript).

R1 Comment 06: Fig. 2: Shading (confidence interval) appears to be missing in the figure.

Response: We will update the figure. In reality, the original figure had the confidence interval of the mean, which was nearly invisible because we are sampling from many days. However, we think it makes more sense to show the range of the daily averages instead, so the bands of the updated figure will show the 95% range around the mean for all days considered. In the case of diffuse radiation, the model does not predict variability because all PFTs are assumed to have the same optical properties, and we are showing the normalized profile. We updated the Figure 2 caption to include these clarifications, and also address Reviewer 2's suggestion (*R2 Comment 14*).

R1 Comment 07: I like the summaries of functional relationships provided in Fig. 8 and 9. They are very informative to express the model's ability to represent spatial variations for the wider Amazon area.

Response: We are glad that the Reviewer finds Figures 8 and 9 (Figures 9 and 10 in the annotated manuscript) interesting and informative about the model's regional-scale performance.

R1 Comment 08: p. 22, l. 16: The ability of ED-2.2 to represent fine-scale heterogeneity is an interesting aspect, but was not evaluated in this study. Remarks to this would fit better in the accompanying "Part 1" paper than in this one.

Response: As suggested, we removed the sentences regarding fine-scale heterogeneity from "Part 2" (p. 27, l. 17–20 of the annotated manuscript). Similar sentences are present in Part 1.

Minor remarks:

R1 Comment 09: p. 1, l. 4: "excellent" could be removed here: You have verified the conservation of energy and other properties, not its excellency. In general, there is a tendency in the manuscript to describe this conservation as an "excellent" property of the model – I trust that the authors are glad with that result, but conservation of properties is typically considered a technical prerequisite rather than a scientific breakthrough in model development.

Response: We agree with the Reviewer that conservation of properties is a necessary condition and will revise the text to incorporate this statement. As suggested, we removed the word "excellent" from both the *Abstract* and the *Conclusions* (p.1, l.4 and p. 27, l. 21 of the annotated manuscript); However, we believe that the high degree of conservation exhibited by the model is an achievement that is worth noting given the findings of a previous analysis suggesting a lack of energy conservation in several terrestrial biosphere models (Loew et al. 2014) and given that the model is simulating the dynamics of diverse, spatially and horizontally heterogeneous, and temporally varying plant canopies over long timescales.

R1 Comment 10: p. 3, l. 5: does "variability" here refer to spatial variability, temporal variability, or both?

Response: We are referring to both, and we clarified this in the text (p. 3, l.6 of the annotated manuscript).

R1 Comment 11: p. 3, l. 19: remove "the" in front of "each"

Response: We corrected the text as suggested (p. 4, l. 11–12 of the annotated manuscript).

R1 Comment 12: p. 3, l. 19: Please clarify this sentence. I guess that GPP and Reco are "modelled statistically" from observed NEE, right? And have you tried to use NEE as well (next to the evaluations of GPP and Reco)? This is not clear to me at this point in the manuscript (it becomes more obvious when the results are presented).

Response: The Reviewer is correct, and we modified the text accordingly. Also, our original sentence incorrectly referred to NEE as net ecosystem productivity rather than

net ecosystem exchange. Please see the revised text (p. 4. l. 11–14 of the annotated manuscript).

R1 Comment 13: p. 4, l. 16: What was the spatial extent and spatial resolution of the regional simulation?

Response: The regional simulation was run over tropical South America (83°W–33°W; 18°S–13°N) at 1° spatial resolution. We will include this information in the revised manuscript, and replace "Amazon ecoregion" with "tropical South America" as the domain includes areas outside the Amazon ecoregion. We revised the text, which also incorporates suggestions from Reviewer 2 (*R2 Comment 03*, *R2 Comment 10*, and *R2 Comment 17*) (p. 5, l. 14–23 of the annotated manuscript).

R1 Comment 14: p. 4, l. 29: The text is hard to follow here. Remove "the" in "the three remote sensing estimates," they are only introduced in the next sentence. And then, it seems that there are only two estimates introduced, whereas the third one (from the two sites only) cannot provide information on the spatial relationship. How was this used?

Response: We removed the "the" from this sentence. The confusion in this sentence was because the references to the remote sensing products were missing from the original sentence. We were referring to Saatchi et al. (2011), Baccini et al. (2012), and Avitabile et al. (2016). We included these references in the revised manuscript (p. 6, l. 28–29 of the annotated manuscript).

R1 Comment 15: p. 5, l. 4: The description of this sensitivity test is hard to follow – sensitivity to what is tested here, and what is the rationale of testing these different settings of the model?

Response: We tested the sensitivity to factors that may affect the simulated dynamics yet are uncertain, but we agree that the text was not clear. We rewrote this part (p. 7, l. 19–26 of the annotated manuscript).

R1 Comment 16: p. 5, l. 31: Apart from canopy air temperature, it would be interesting to learn whether surface temperature of the canopy is in agreement with observations (if those exist), to investigate whether the overestimated sensible heat fluxes are caused by too high temperatures.

Response: We are not aware of long-term measurements of canopy temperature at the study sites. In the absence of canopy temperature measurements, we evaluated the outgoing longwave radiation ($Q_{LW}\uparrow$; Fig. S2), which should be closely related to canopy temperature in dense forests. As we pointed out in the original text (p. 10, l. 3–5 of the annotated manuscript), the model indeed overestimates $Q_{LW}\uparrow$ at both sites, especially during the afternoon, which suggests that canopy temperature may be overestimated (p. 10, l. 5–6 of the annotated manuscript).

R1 Comment 17: p. 12, l. 11: add "estimates of" between "remote sensing" and "biomass"

Response: We corrected the text as suggested (p. 16, l. 8 of the annotated manuscript).

R1 Comment 18: p. 13, l. 5: Estimates of AGB from ED-2.2 appear to deviate substantially from observed ones, and the cloud of black points in Fig. 9a does not provide any confidence in

ED-2.2 to accurately predict AGB for different sites within the tropical forest. "Generally well characterized" seems a bit too optimistic for this.

> Response: We revised the text to address the Reviewer's remarks (p. 17, l. 10–13 of the annotated manuscript).

R1 Comment 19: p. 20, l. 9: Sentence should probably read ". . . is accounted for for energy, water and carbon dioxide".

> Response: We rewrote the sentence accordingly (p. 24, l. 21 of the annotated manuscript).

R1 Comment 20: p. 20, l. 10: remove "may"

> Response: As suggested, we removed "may" from the sentence (p. 24, l. 22 of the annotated manuscript).

R1 Comment 21: p. 21, l. 7: remove "significant"

> Response: As suggested, we removed "significant" from the sentence (p. 25, l. 21 of the annotated manuscript).

R1 Comment 22: p. 22, l. 10: Correct "ecosystems"

> Response: As suggested, we corrected this typographical error (p. 27, l. 12 of the annotated manuscript).

R1 Comment 23: Fig. S3: remove "based on" from figure caption

> Response: As suggested, we removed "based on" from the sentence (Caption Fig. S4 of the annotated manuscript).

Responses to Referee 2

R2 Comment 01: The authors present an interesting model evaluation of a new version of the Ecosystem Demography Model (version 2.2) for the Amazon region. They show strengths and weaknesses of the modelling approach and identify priorities for further model development. For the model evaluation, the authors use observational data from four specific sites, inventories and remote sensing and nicely present the comparison with the simulation results. Below, I have some comments and remarks that will hopefully help to improve the manuscript.

> Response: We thank the Reviewer for the positive feedback. Our goal in this manuscript was indeed to show both the strengths and weaknesses of the current version and to guide which processes in the model should be prioritised in future model developments.

General comments:

R2 Comment 02: Title: The model evaluation has been done for the Amazon region, please state this in the title.

Response: We agree that the title should make it clear that it was a regional evaluation and accordingly we included "for tropical South America" in the title of the revised manuscript.

R2 Comment 03: The Methods section could profit from more structure and detail. First, although the manuscript has a companion paper that provides a detailed model description, I would recommend to give a summary of the model and a short overview over the relevant processes that are evaluated, in the beginning of the methods section. Additionally, it is to my opinion not fully clear, which datasets are used as forcing data and which are used for model evaluation (e.g. p.4, l.18ff).

Response: In line with the Reviewer's suggestion, we included two paragraphs describing the model structure in the *Methods* section (p. 3, l. 10–31 of the annotated manuscript).

Regarding the data sets used as forcing data and for model evaluation, the input data sets are described in the first paragraph of section 2.2, and the evaluation data sets are described in the second paragraph of this section. To remove ambiguity, we changed the wording in the text to clearly separate input drivers from evaluation data (p. 5, l. 14–23 of the annotated manuscript).

R2 Comment 04: In the Methods section (p. 4, l. 17ff and p.5, l. 4) it is not clearly described how the model sensitivity was evaluated. Did you systematically vary different parameters or driver data?

Response: Regarding p. 4 l. 17, we assessed how the regional variation of biomass predicted by ED-2.2 was related to environmental drivers such as precipitation and radiation. We did not run multiple simulations. We rewrote the sentence to eliminate this ambiguity (p. 6, l. 3–11 of the annotated manuscript).

For p. 5, l. 4, we ran all the combinations of initial time, soil texture, and leaf phenology described in the text (48 simulations per site), but otherwise the simulations used the same parameters. We updated the text following our response to Reviewer 1 (p. 7, l. 19–26 of the annotated manuscript), and also included the total number of simulations per site in the revised manuscript (p. 7, l. 26 of the annotated manuscript)..

R2 Comment 05: The assessment of forest function and structure is interesting and it is nice to see that the model can reproduce the functional relations (Fig. 9). I think it would be important to explain the reader that the mortality rate and wood density (e.g. Fig. 9b,c) are simulated by the model and not prescribed parameters, probably this could be done in the model summary in the methods section as suggested above.

Response: The Reviewer is correct in pointing out that the community-level wood density and mortality are not prescribed parameters. We rewrote the text in the methods section to clarify this important point (p. 7, l. 8–15 of the annotated manuscript).

R2 Comment 06: Regarding the unexplained bias in simulated mortality rates and wood density, it would also be interesting to see the relation between productivity (NPP) and mortality, which are probably the two dominant drivers for AGB. When looking at Fig. 5, it seems that (at plot level) GPP is underestimated and respiration is overestimated (Fig. 6), thus, NPP might be underestimated. With high mortality rates (Fig. 9) I wonder why biomass is overestimated (Fig. 7)?

Response: The most likely explanation for the underestimated NPP and overestimated biomass is biases in the allocation of NPP to growth, reproduction, and maintenance. From Fig. 9, it is possible to see that ED-2.2 is over-estimating growth rates at the two tested sites, which suggests that the model is underestimating maintenance costs of live tissues (e.g. leaf turnover, fine root turnover), underestimating allocation to reproduction (e.g. flowers, fruits and seeds), or both. As suggested, we included a new panel in Fig. 9 (Fig. 10d in the annotated manuscript) that compares the net primary productivity and mortality rates for a limited number of sites for which we had simulations and were able to find estimates of both quantities. We also included text analysing the results shown in Fig. 10d (p. 17, l. 19–24 of the annotated manuscript).

Regarding the issues regarding underprediction of GPP, over-prediction of respiration and over-estimation of AGB, we agree with the Reviewer that reconciling these findings is important, and we updated the discussion to highlight the need to reduce uncertainties in carbon allocation (p. 25, l. 28–34 of the annotated manuscript).

Specific comments:

Section 2.1:

R2 Comment 07: Which climate data were used to drive the model for the assessment of short-term fluxes?

Response: We used the meteorological data from the eddy covariance towers. We modified the text in the first paragraph of Section 2.1 to clarify this point (p. 4, l. 4–7 of the annotated manuscript).

R2 Comment 08: L. 18: What do you mean by "we aggregated the model results to polygon level hourly averages"? Please explain the model setup more clearly (as in section 2.2).

Response: In line with the Reviewer's suggestion, we revised the first sentence of this paragraph as follows to clarify its meaning (p. 4, l. 9–19 of the annotated manuscript)..

R2 Comment 09: L. 19-22: The explanation in these sentences is difficult to understand. Did you compare NEE? Why is it relevant to compare "all times in which the net ecosystem productivity could be estimated. . ."?

Response: Since our goal was to evaluate multiple processes in the model, we presented comparisons for gross primary productivity (GPP) and ecosystem respiration (R_{Eco}) separately . However, neither GPP nor R_{Eco} are directly measured by the towers; instead, they are estimated from net ecosystem exchange (NEE), the difference between GPP and R_{Eco}). We intended to say that we only compared tower estimates of GPP and R_{Eco} with

ED-2.2 simulations for the hours in which NEE data were available. Please see the revised text (p. 4. l. 11–14 of the annotated manuscript).

Response: We rewrote these sentences to clarify the model setup and initialization procedures (p. 5, l. 14–23 of the annotated manuscript): our use of the word "initialization" was confusing in this context, since soil hydraulic and thermal characteristics are assumed to not change over time in ED-2.2.

Response: Our original Equation (1) was incorrect: it should have referred to the cumulative water deficit (CWD), not MCWD. CWD was integrated for each month continuously, i.e. previous water deficit is carried over to the next month, and can only be zero if rain exceeds CWD + ET. For MCWD, we selected the maximum CWD of each calendar year. This approach allows us to account for different precipitation seasonalities and interannual variability of dry-season length.

Regarding the application of our estimates to arid regions, we must clarify a few points. First, MCWD was used only for model assessment: ED-2.2 relies on soil moisture to parameterize ecological changes due to water stress (e.g. drought-induced mortality and fire frequency). Second, we chose to set ET_0 at 100 mm month^{-1} because this value has been frequently used in previous studies as a proxy for water stress in the Amazon region (e.g. Malhi et al. 2009; Lewis et al. 2011; Aragão et al. 2018). We agree with the Reviewer that the actual ET is likely to be lower in arid regions and consequently, actual MCWD is also likely lower than our estimates in these areas. However, our point was to verify that ED2 did not simulate forests in areas where forests should not exist. In this sense, our estimates of MCWD can be thought as MCWD if forests were present in a given location (forest-equivalent MCWD). If values of forest-equivalent MCWD become too high, then this is an indicator that forests should not exist in the place, which is what our analysis shows.

We modified the methods section to clarify the calculation and explain the interpretation of MCWD for non-forested regions (p. 6. l. 11–24 of the annotated manuscript).

Response: We tested the sensitivity to three factors known to be important, but that are uncertain for these two sites, namely, the absence of meteorological data prior to the first inventory, soil texture, and leaf phenology. We rewrote the text to clarify these points (p. 7, l. 19–26 of the annotated manuscript).

: *Page 5 line 13: How was outgoing shortwave radiation calculated by the model? Depending on the method, isn't outgoing-sw a proxy for LAI or FPC for which also site data should be available?*

Response: Outgoing shortwave radiation ($Q_{SW}\uparrow$) is calculated using a multi-layer two-stream model for both photosynthetically active radiation (PAR) and near infrared (NIR) — this implementation is described in detail in part 1. Outgoing shortwave radiation is strongly related to leaf area index, especially in dense canopies such as the Amazon, but the relationship between $Q_{SW}\uparrow$ and leaf area index is modulated by the partition between direct and diffuse radiation, and soil moisture (albeit this effect is very small in dense canopies). Therefore, the translation between LAI and $Q_{SW}\uparrow$ is not direct, but mediated by environmental conditions. We think that the comparison with tower measurements of $Q_{SW}\uparrow$ provides a more direct benchmarking and kept the original comparison.

: *p. 5, l. 19 and Fig. 2: Please define "TAI". The message of Fig. 2 is not clear. Is this related to LAI?*

Response: TAI stands for tree area index (also known as plant area index). TAI is related to LAI but it also accounts for branches and twigs. We included this explanation in the Methods section (p. 5, l. 10–11 of the annotated manuscript), and a reminder in the Results section (p. 9, l. "–1" of the annotated manuscript). We also agree that the caption of Fig. 2 needed clarification and rewrote the text.

: *p. 12, l. 5: Please move this sentence to the methods section and explain how the comparison of MODIS-LAI has been set up (which spatial resolution, for which time period, how did it match with information on deforestation considered in the simulations?)*

Response: Following the Reviewer's suggestion, we moved the data set description to the methods (p. 6, l.29–33 of the annotated manuscript) and included the additional information that was missing. We also modified the text in the *Results* section (p. 14, l.8–9 of the annotated manuscript).

: *Figure 7: The symbols indicating the locations of the focus sites are very hard to see in the map.*

Response: As suggested, we updated the figures to improve visibility of the focus sites (Fig. 7, 8, S4, S5, and S6 of the annotated manuscript).

: *p. 13, l. 7: First time that fire is mentioned, leaving the reader a bit puzzled. It would be good to evaluate the occurrence of fire in more detail and to mention it in the methods section.*

Response: We updated the methods section to inform readers that the regional simulations included fire disturbance (p. 5, l.29–33 of the annotated manuscript).

Also, following the Reviewer's suggestion, we included an evaluation of the fire model with the Global Fire Emission Database (GFED4.1), which has annual burned area rates. We added this information in the Methods section (p. 7, l.0–5 of the annotated

manuscript). We also included a new Figure 8 in the main text that compares the predicted regional distribution of fire regime with GFED4.1, a new Supplemental Information Figure that shows the differences (new Figure S6). Moreover, we added text describing the comparison in the Results section (p. 14. l.11–p. 16 l.1 of the annotated manuscript). Finally, we updated the text in the Discussion that highlights the need to improve the representation of fires in the model, to link with the results of the new Figure 8 (p. 25, l.10–12 of the annotated manuscript).

R2 Comment 18: Page 17, figure 17: ED2 shows (almost) constant mortality; density-independed and dependent. Why is it constant? Was there only background mortality occurring throughout the simulation period? What about the effects of the drought years (e.g. 2005 and 2010)? I would expect to see an effect in the model results.

Response: We assumed the Reviewer was referring to Figure 11. Indeed, during the period of forest inventory measurements (2004—2013 for GYF, and 1999—2011 for TNF), ED-2.2 simulations did not show any significant mortality, which was dominated by background mortality. We included additional text in the discussion, for clarification (p. 26, l.14–27 of the annotated manuscript).

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

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Abstract. The Ecosystem Demography Model version 2.2 (ED-2.2) is a terrestrial biosphere model that simulates the biophysical and biogeochemical cycles of dynamic ecosystems while considering the role of vertical structure of plant communities and the heterogeneity of such structures across the landscape. In a companion paper, we described in detail how the model solves the energy, water, and carbon cycles, and verified the ~~excellent~~high degree of conservation of ~~such~~these properties in long-term ~~simulation~~simulations that include vegetation dynamics. Here, we present a ~~thorough~~detailed assessment of the model's ability to represent multiple processes associated with the biophysical and biogeochemical cycles, with focus on the Amazon forest. We used multiple measurements from eddy covariance towers, forest inventory plots and regional remote-sensing products to assess the model's ability to represent biophysical, physiological, and ecological processes at multiple time scales ranging from sub-daily to century-long. The ED-2.2 model accurately describes the vertical distribution of light, water fluxes and the storage of water, energy and carbon in the canopy air space, the regional distribution of

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biomass in tropical South America, and the variability of biomass as a function of environmental drivers. In addition, ED-2.2 also simulates emerging properties of the ecosystem found in observations, such as the relationship between biomass and mortality rates and wood density, although the relationships predicted by the model were biased. We also ~~identified some of the model~~identify several limitations, ~~such as~~including the model's tendency to overestimate the magnitude and seasonality

5 of heterotrophic respiration, and to overestimate growth rates in a nutrient-poor tropical site. The evaluation presented here highlights the potential of incorporating structural and functional heterogeneity within biomes in ESMs, to realistically represent the role of forest structure and composition on energy, water, and carbon cycles, as well as the priority areas for further model development.

1 Introduction

10 Terrestrial ecosystems are fundamental components of the earth system. Current estimates suggest that net terrestrial biosphere carbon uptake is near $3.2\,\mathrm{GtC\,yr^{-1}}$ (equivalent to 30% of fossil fuel carbon emissions), albeit this sink is partially offset by land use change ($1.5\,\mathrm{GtC\,yr^{-1}}$), or 16% of fossil fuel carbon emissions (Le Quéré et al., 2018). Climate change, land use change, and increase in atmospheric CO_2 are likely to alter the ability of terrestrial ecosystems to accumulate carbon, yet the magnitude and even the persistence of terrestrial biosphere sink, as predicted by dynamic global vegetation models

15 (DGVMs) remains highly uncertain (Friedlingstein et al., 2006, 2014; Krause et al., 2018). The response of tropical forests to global change is of particular interest, because these ecosystems store nearly 40% of the total terrestrial biomass (Erb et al., 2018), and their simulated response to climate change is strongly dominated by vegetation dynamics (Ahlström et al., 2015).

Most DGVMs have thorough and mechanistic representation of biophysical and biogeochemical cycles, and have greatly evolved over the past decades (Fisher et al., 2018). However, two important factors limit the ability of reducing the

20 uncertainties of DGVMs. First, observations of key biophysical and ecological variables (e.g. forest inventory plots and eddy covariance towers) are not evenly distributed, and tropical ecosystems are considerably under-sampled (Schimel et al., 2015). Second, DGVMs tend to describe ecosystems based on very simple characteristics, often from average properties of the ecosystem as a whole, which precludes a proper representation of the heterogeneous environment in which individuals live. In reality, the dynamics of an ecosystem is the emerging property that integrates the contribution of a system of individuals

25 with different strategies and ability to access resources needed for their growth, survival, and reproduction (Moorcroft, 2003, 2006; Evans, 2012; Fisher et al., 2018).

In a companion paper (Longo et al., 2019), we described the Ecosystem Demography Model version 2.2 (ED-2.2). Unlike most DGVMs, the ED-2.2 model is a terrestrial biosphere model that characterizes and represents the vertical and functional structure of plant communities, as well as the horizontal heterogeneity of terrestrial ecosystems. Importantly,

30 ED-2.2 has complete biophysical and biogeochemical cores, which solve the energy, water, and carbon cycles at sub-daily resolution. The biophysical and biogeochemical cores build on previous model developments by other DGVMs; however, in ED-2.2, we also account for the local variability of structure and composition in plant communities.

In this paper, we present a detailed evaluation of the ED-2.2 model, with focus on the multiple processes that comprise the biophysical and biogeochemical cores. Formal optimization of model parameters was beyond the scope of this paper, although it has been previously carried out with earlier versions of ED-2 (e.g. Medvigy et al., 2009; Kim et al., 2012; Fer et al., 2018). Instead, we focused on thoroughly evaluating the model in the Amazon, using two data-rich sites with decadal-long series of measurements that quantify several water, energy, and carbon components fluxes and storage terms predicted by ED-2.2. We also appraised the model ability to represent both the regional distribution of biomass and forest structure and the mechanisms that drive the spatial and temporal variability in carbon stocks and structure, by comparing the model results with independent field measurements and remote-sensing estimates. Together, these analyses aim to verify the model consistency and the potential for the current model to be applied in both short-term and long-term studies.

2 Methods

Since its conception (Moorcroft et al., 2001; Hurtt et al., 2002), the plant community in the Ecosystem Demography model (ED) is represented by a hierarchical structure that accounts for both abiotic (e.g. soil texture and aspect) and biotic (e.g. age since last disturbance and disturbance types) effects on the vertical structure of canopy and the horizontal heterogeneity of such structures across the landscape. To characterize this sub-grid heterogeneity within the areas of interest and the changes of structure over time, ED solves a system of partial differential equations that describe growth, mortality and recruitment of individuals, as well as the changes in the plant community following disturbances. The current version of the model, ED-2.2, which is presented in a companion paper (Longo et al., 2019) builds on the developments by Medvigy et al. (2009) to quantify in detail the biophysical and biogeochemical cycles of energy, water, and carbon that fully accounts for the sub-grid heterogeneity of the above- and below-ground structure of the ecosystem.

In this manuscript, we evaluate a range of short-term (hours to seasons) biophysical and biogeochemical processes and long-term (years to centuries) demographic and ecological processes, with focus in tropical South America. Specifically, for the short-term processes, we used detailed information from eddy covariance tower sites in the Amazon to assess the model's ability to represent the canopy radiation transfer, evapotranspiration, sensible heat flux, temperature and water in sub-canopy pools (e.g. canopy air space and soils), and carbon fluxes (gross primary productivity and respiration). For the long-term processes, we evaluated the model ability to represent the distribution of biomass and leaf area index across tropical South America, and relevant demographic characteristics such as the simulated forest structure and demographic rates (e.g. mortality, growth). Importantly, we also tested the ecosystem response to environmental controls both for short- and long-term processes. Examples of such evaluations for short-term processes include the predicted response of gross primary productivity and respiration to environmental factors such as incoming radiation and soil moisture. For long-term processes, we tested how predicted carbon stocks were modulated by the regional variation of environmental controls such as rainfall and radiation, as well as emergent ecosystem properties such as the average mortality rate and average wood density, both of which are also predicted by the model.

2.1 Assessment of short-term fluxes

For most evaluations of biophysical and biogeochemical cycles, we ran ED-2.2 for two sites in the Amazon where both eddy flux towers and forest inventories were available for a long period: the Guyaflux tower ($5°17'$N; $52°55'$W) at Paracou, French Guiana (GYF; Bonal et al., 2008), and the Tapajos National Forest site ($2°51'$S; $54°58'$W), located in central Amazon (TNF; Hutyra et al., 2008; Pyle et al., 2008). Both data sets underwent multiple-stage quality control, in addition, variables used as input for ED-2.2 were gap filled We used the meteorological variables measured at the eddy covariance tower sites to drive these ED-2.2 simulations. These variables included temperature, specific humidity, pressure, wind speed, incoming solar radiation, incoming longwave radiation and precipitation. All meteorological variables used as inputs for ED-2.2 were gap filled, following Longo (2014). Net ecosystem productivity (NEE) was processed using the approach by Hayek et al. (2018b), which corrects flux bias due to lack of turbulence and turbulent-independent divergence of CO_2.

To ensure that model and observations at or near eddy covariance flux towers could be directly compared, and that the observed signal was strongly related to actual environment conditions, we aggregated the model results to polygon-level hourly averages, and only used the model output for the time period when the each variable of interest was measured, we saved model outputs every hour, and only used the model output for the hours when each variable of interest was measured. Gross primary productivity (GPP) and ecosystem respiration ($\dot{R}_{\mathrm{Eco}}$) are not measured but statistically modeled from net ecosystem exchange (NEE), therefore we compared all times in which the net ecosystem productivity (NEE) could be estimated from tower observations. We also required that the 24-hour period preceding any given time had less than 24 gap filled values among all seven driver variables. Finally, in ED-2.2, we solve fluxes for each local plant community (patch) within the area of interest (polygon). Since eddy covariance towers provide flux measurements and estimates that are representative of the entire plant community, to assess ED-2.2 results against the eddy covariance fluxes, we compared the tower estimates with the ED-2.2 polygon averages (i.e. area-weighted average of fluxes for all simulated patches).

To evaluate the in-canopy radiation profile, we compared model results against measured profiles of photosynthetically active radiation at two sites in the Brazilian Amazon: Jaru Biological Reserve (RJA: $10°05'$S; $61°56'$W) near Ji-Paraná, and Adolpho Ducke Forest Reserve (MDK: $2°57'$S; $59°55'$W), near Manaus (Cabral et al., 1996; Tomasella et al., 2008). At RJA, data were collected during two measurements campaigns as part of the Anglo-Brazilian Climate Observation Study (ABRACOS; Gash et al., 1996) in August–September 1992 and April–June 1993 and measurements were taken at 2.3, 6.1, 11.6, 15.7, 21.3, and 35.0 m above ground; at MDK, the measurement campaign occurred in August–September July–August 1991 and sensors were installed at 5.0, 10.0, 15.0, 20.0, 25.0, and 35.0 m above ground; in both cases two to three sensors were installed in each level either East or West of the tower, and both sites used the same quantum radiation sensors of model SKP 215, skye Instruments Ltd, Powys, UK (Tomasella et al., 2008). To reduce the impact of the towers on the measurements, we only used data from sensors east of the towers in the morning and west of the towers in the afternoon (Mercado et al., 2007). The model was run for the same days of year as the data. However, we simulated different years — 1999-2006 for MDK and 1999-2002 for RJA — using the LBA-MIP Large-Scale Biosphere-Atmosphere Experiment in Amazonia Data Model Intercomparison Project (LBA-MIP) data (de Gonçalves et al., 2013), because we did not have data

from all meteorological variables needed by ED-2.2 during the period when the radiation profile data were collected. Also, because the diurnal cycle of any point measurement within the canopy depends on local heterogeneities can be dramatically affected by the Sun's azimuth and zenith angles (e.g. sun flecks when the sensor is aligned with an opening in the canopy), we only used the average daily radiation relative to the top of canopy to compare with the model results. Although simu-
lated days (LBA-MIP) include the entire range of daily averages of temperature, humidity, and net radiation observed during the ABRACOS campaign, the simulated period had significantly (t-test at 95% confidence) warmer average temperatures at MDK ($0.67°C$) and higher net radiation at both RJA ($13.7\,\mathrm{W\,m^{-2}}$) and MDK ($18.5\,\mathrm{W\,m^{-2}}$) (Fig. S1). Therefore, we also compared the predicted light extinction profile with observations for overcast hours, when the direct radiation (based on Weiss and Norman (1985) model) would be zero, when the model predictions of relative light extinction do not depend on the total incoming radiation (Longo et al., 2019). ~~The tree area index was estimated from published data~~To evaluate the model's ability to represent changes in light environment throughout the canopy, we compare the light profiles of model and observations as a function of the cumulative tree area index (TAI). TAI is defined as the sum of leaf area index (LAI) and the branch wood area index (WAI). TAI profiles were estimated from published data at RJA (Simon et al., 2005) and near MDK (McWilliam et al., 1993).

2.2 Evaluation of long-term dynamics

To evaluate the model's ability to represent the long-term dynamics, we carried out multiple simulations intended to test the model's ability to describe regional variability as well as the structural and functional diversity of ~~ecosytems~~ecosystems in tropical South America.

~~First, to assess the model ability to represent the biome distributions in regional scale, we ran ED-2.2 starting from near-bare-ground conditions and carried out a 500-year simulation across the Amazon ecoregion.~~First, to assess the model's ability to represent the distribution of biomass and leaf area index across tropical South America ($83°W$–$33°W$; $18°S$–$13°N$), we carried out a $1-°$ resolution, 500-year-long regional simulation, starting from near-bare conditions (1400-1900) to produce the simulated potential vegetation. In these simulations, we assumed a constant treefall disturbance rate of $1.4\%\,\mathrm{yr^{-1}}$ (Moorcroft et al., 2001), and allowed the occurrence of fire, using the original ED-1 implementation of fire disturbance model (Moorcroft et al., 2001). We then resumed the simulation in 1900, applying anthropogenic disturbance and ran the model until 2002, using a combination of land use transition matrices from Hurtt et al. (2006), nudged to match the initial conditions from Soares-Filho et al. (2006) in the Amazon. We ~~initialized soils with texture obtained from~~specified the soil texture for each grid cell using data from Quesada et al. (2011) for the Amazon, RADAMBRASIL (de Negreiros et al., 2009) for non-Amazonian areas of Brazil, and IGBP (Tempel et al., 1996) for non-Amazonian areas elsewhere~~, and the meteorological forcing from~~Soil texture characteristics (sand, silt, and clay content) are used to determine the pedotransfer function, hydraulic and thermal conductivities, and heat capacity of soils (Longo et al., 2019). For the meteorological forcing, we used the Princeton University Global Meteorological Forcing Dataset (PGMF, Sheffield et al., 2006) for 1969 to 2008, which was recycled multiple times to simulate a period equivalent to 1500 through 2002.

To estimate the model sensitivity to light and water availability across the region, we used the annual average downwelling shortwave irradiance from the Clouds and the Earth's Radiant Energy System's Energy Balanced And Filled product (CERES-EBAF; Kato et al., 2013) between 2001 and 2017, and the average of annual precipitation from the Tropical Rainfall Measurement Mission's (TRMM) Multi Satellite Precipitation Analysis Product (TMPA-3B43 V7; TRMM, 2011; Liu et al., 2012) between 1998 and 2017. We examined the relationship between regional above-ground biomass (AGB) and light and water availability by comparing the model's AGB predictions against regional observations of these two quantities. Specifically for light availability, we compared the model predictions against two estimates of average annual shortwave radiation: one calculated from the PGMF shortwave measurements and that were used to drive the model simulations and second the annual average downwelling shortwave irradiance from the Clouds and the Earth's Radiant Energy System's Energy Balanced And Filled product (CERES-EBAF; Kato et al., 2013) between 2001 and 2017. Similarly, for rainfall, we compared the model's AGB prediction to annual rainfall estimates calculated from both the PGMF meteorological dataset and the average of annual precipitation calculated from the Tropical Rainfall Measurement Mission's (TRMM) Multi-Satellite Precipitation Analysis Product (TMPA-3B43 V7; TRMM, 2011; Liu et al., 2012) between 1998 and 2017. For maximum cumulative water deficit (MCWD, mm), we assumed a constant monthly evapotranspiration ($ET_0 = 100\,mm\,mo^{-1}$) and monthly precipitation (P, $mm\,month^{-1}$) from TMPA-3B43, following ~~Malhi et al. (2009a)~~previous studies for the Amazon region (Malhi et al., 2009a; Lewis et al., 2011; Aragão et al., 2018). For any month t, we defined the cumulative water deficit (CWD, mm) to be:

$$CWD(t) = \min\{1200, \max[0, CWD(t - \Delta t) + ET_0 - P(t)]\},\tag{1}$$

where $\Delta t = 1\,month$. ~~The maximum of 1200 mm was imposed to avoid run away water deficit at the most arid regions, where precipitation is never sufficient to bring water deficit back to zero because of the high baseline evapotranspiration.~~This integration is continuously carried over the entire time series. For each calendar year, we defined MCWD as the maximum monthly value of CWD. Note that this estimate of MCWD assumes evapotranspiration values that are typical of tropical rainforests (i.e. $ET_0 = 100mm$) and therefore should be regarded as a forest-equivalent MCWD, not an actual measurement. High values of MCWD indicate regions where water losses would be too high to maintain forests. This baseline evapotranspiration is high for arid regions, and consequently we imposed a cap of $1200\,mm$ on CWD to avoid extremely high deficits at the most arid regions, where precipitation is insufficient to bring the water deficit back to zero.

We ~~reprojected~~re-projected the estimates of shortwave irradiance, precipitation, and ~~water deficit~~MCWD to the same grid as ED-2.2 using spatial averaging. For each environmental variable, we divided the grid cells into 20 quantile-based groups $(0 - 0.05; 0.05 - 0.10; \ldots; 0.95 - 1)$, and obtained the average and the 90% quantile range within each bin for the ED-2.2 model and ~~the~~ three remote-sensing estimates of aboveground biomass: Saatchi et al. (2011), Baccini et al. (2012), and Avitabile et al. (2016). We also compared the model's predictions of leaf area index (LAI) with estimates from the Moderate Resolution Imaging Spectroradiometer (MODIS, product MCD15A2H, Collection 6) (Yan et al., 2016). We used all cloud-free, high-quality data from MODIS-MCD15A2H that were available between August 2002 and July 2004.

We selected this period to reduce temporal — and land-use related — differences between the model simulation and MODIS-MCD15A2H, and we aggregated the average LAI to 1° resolution to be consistent with the ED-2.2 simulations. Finally, to evaluate the model's predictions of fire regime across tropical South America, we compared the average fire disturbance rate over predicted by ED-2.2 over one full cycle of the meteorological drivers (last 40 years of the simulation) with the Global Fire Emissions Database, version 4.1 (GFED4.1, Giglio et al., 2013; Randerson et al., 2018). Similarly to aboveground biomass and LAI, we aggregated GFED4.1 relative burned area to 1°; because GFED4.1 data has a short overlapping period with the PGMF drivers, we used all available years (1997–2015) to compute the average fire disturbance rate.

To evaluate the model's ability to predict emergent properties, we used published values of biomass and mortality obtained from the RAINFOR field inventory network in the Amazon (Phillips et al., 2004; Baker et al., 2004a, b) and the results from long-term simulations near the field inventory sites (Levine et al., 2016). Specifically, we investigated the relationship between aboveground biomass and long-term average mortality rates, and community averaged wood density across these sites. In ED-2.2, typical wood density and background mortality rates are prescribed for each cohort, based on their plant functional type (PFT). However, the model allows for coexistence of PFTs that can be modulated by abiotic and biotic factors such as soil texture, climate, and direct competition for limiting resources (e.g. light and water) between PFTs (Moorcroft et al., 2001; Longo et al., 2019). Consequently, mortality rates and community-level wood density are not prescribed parameters; instead, these properties emerge from the population structure comprised by different plant functional types (PFTs).

Finally, we tested both the forest structure predictions and the model's ability to represent variability of demographic rates at the two study sites (GYF and TNF) for which we had long-term forest inventory data. We ran the model from near-bare ground conditions for 500 years for each location, driven by the site-specific meteorological conditions, to obtain the near-steady state of each forest and to evaluate the forest structure predicted by the model at steady state. To evaluate Several factors that are not well constrained for these sites may affect the simulations. For example, at both sites the meteorological drivers were not available for the period before the first inventory (in the case of TNF, meteorological data became available only two years after the first inventory). In addition, soil texture is known to be heterogeneous at local scale (e.g. Epron et al., 2006). Likewise, leaf phenology strategies within the local community can be diverse and heterogeneous (Bonal et al., 2000), and not known for the species included in the forest inventories. ED-2.2 model simulations are known to be modulated by such factors (e.g. Longo et al., 2018); therefore, to evaluate the sensitivity of mortality and the growth rates to these factors, we carried out an ensemble of simulations using all 48 combinations of (1) different initial times, between 5 and 60 years before the first inventory (intervals of 5 years); (2) soil texture, using clayey loam and sandy clay loam for GYF, and clayey sand and clay for TNF following the typical soils found at each site (Nepstad et al., 2002; Bonal et al., 2008); (3) assuming that trees were all evergreen or all drought deciduous. Only cohorts with $\text{DBH} \geq 10\text{cm}$ were considered for the comparison of structure and demographic rates, because this was the minimum size of trees measured at both locations (Pyle et al., 2008; Rowland et al., 2014).
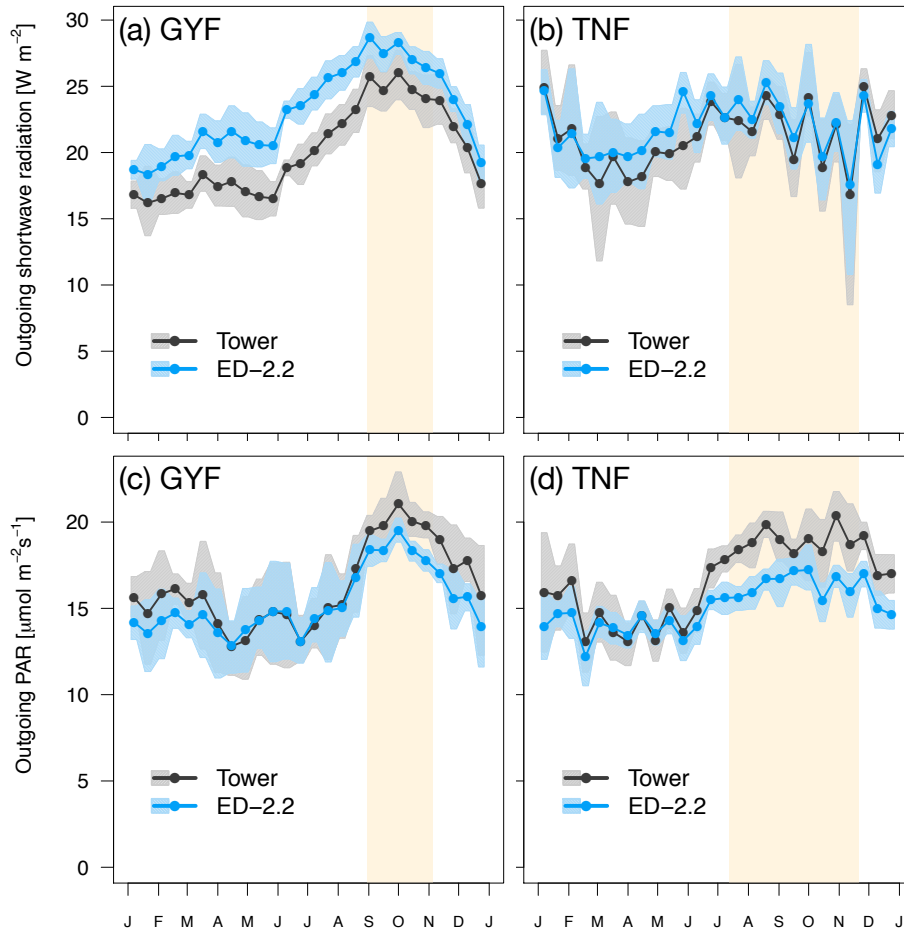
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Figure 1. Mean annual cycle from fortnightly means of (a,b) outgoing shortwave radiation and (c,d) outgoing photosynthetically active radiation for (a,c) GYF and (b,d) TNF. Bands are the 95% confidence interval of means, and rectangles in the background correspond to the site's climatological dry season.

3 Results

3.1 Evaluation of energy and water fluxes

Both GYF and TNF had measurements of outgoing shortwave radiation ($\dot{Q}^{\uparrow}_{\mathrm{SW}}$) and outgoing photosynthetically active radiation ($\dot{Q}^{\uparrow}_{\mathrm{PAR}}$). Here, we compared the outgoing radiation instead of net radiation because net radiation includes incoming radiation, which are input variables for the model. ~~The seasonal variation and the magnitude of both $\dot{Q}^{\uparrow}_{\mathrm{SW}}$ and $\dot{Q}^{\uparrow}_{\mathrm{PAR}}$ are close to observations at both sites:~~ The seasonal variation of both $\dot{Q}^{\uparrow}_{\mathrm{SW}}$ and $\dot{Q}^{\uparrow}_{\mathrm{PAR}}$ is close to observations at both sites (Fig. 1a-d). This result is expected because the seasonality of outgoing radiation is strongly modulated by incoming radiation. Nevertheless, the differences between simulated and observed $\dot{Q}^{\uparrow}_{\mathrm{SW}}$ and $\dot{Q}^{\uparrow}_{\mathrm{PAR}}$ are also small: the bias in the annual average of $\dot{Q}^{\uparrow}_{\mathrm{SW}}$ was $3.0\,\mathrm{W\,m^{-2}}$ (GYF) and $0.6\,\mathrm{W\,m^{-2}}$ (TNF), and the annual average bias of $\dot{Q}^{\uparrow}_{\mathrm{PAR}}$ was $-0.9\,\mathrm{\mu mol\,m^{-2}\,s^{-1}}$ (GYF) and
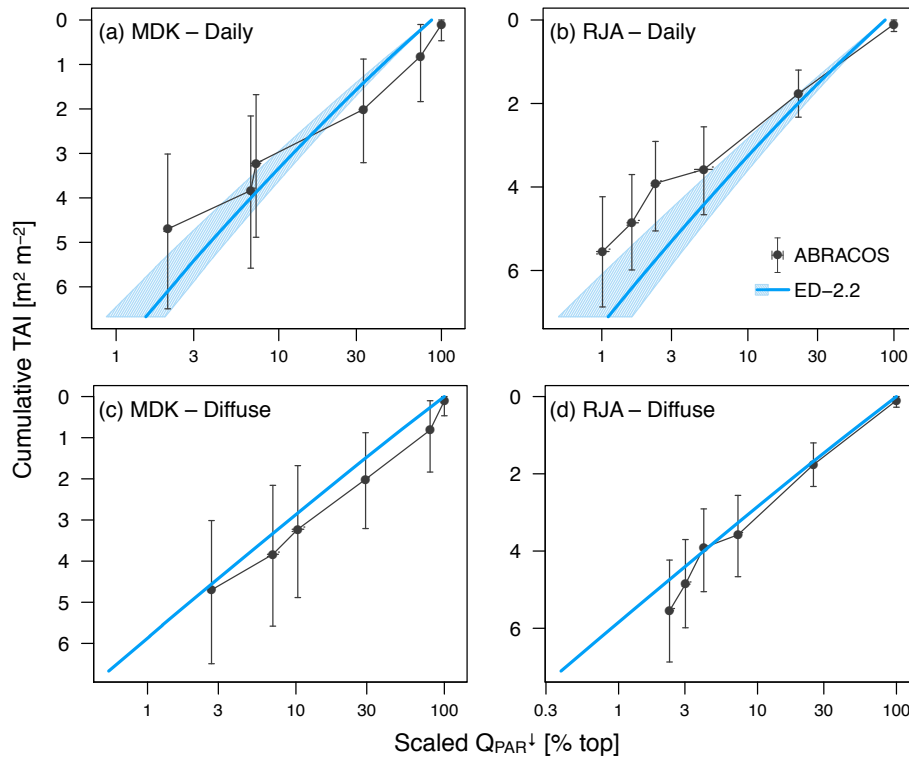
Figure 2. Comparison of downward photosynthetically active radiation ~~profile~~ relative to the top of ~~the~~ canopy. (a,b) Average of daily ~~accumulation~~radiation as a function of cumulative tree area index (TAI); (c,d) average of times with diffuse radiation only for (a,c) Adolpho Ducke (MDK) and (b,d) Jaru (RJA). Shaded areas in the model correspond to the 95% ~~confidence interval, using simple bootstrap of the daily and diffuse hour subsamples, respectively~~range of daily averages. Simulated subsamples for diffuse radiation only do not show variability because all plant functional types are assumed to have the same optical properties.~~.~~. Horizontal whiskers in observed values also correspond to the 95% confidence interval of daily and diffuse subsamples, whereas the vertical whiskers correspond to the 95% confidence interval ~~on leaf area index~~of cumulative TAI at the points of measurement.

$-1.6\,\mu\mathrm{mol}\,\mathrm{m}^{-2}\,\mathrm{s}^{-1}$ (TNF) (Fig. 1a-d). Likewise, the vertical profiles of daily averages of relative incoming PAR are close to the simulations, especially considering the large uncertainties on the observed ~~TAI~~tree area index (TAI) profile and that the simulated years are not the same as the observations (Fig. 2a,b). When we only consider overcast hours (less sensitive to local horizontal heterogeneities), the model shows even better agreement with model predictions, particularly at RJA, where

5   the average profile was measured at the same site as the original observations, albeit at different years. While limited by the observation constrains, this comparison suggests that the model is able to reasonably reproduce typical light profiles.

      Compared to tower observations, the model predicted higher mean sensible heat flux at both sites. At GYF, ED-2.2 captures the seasonal cycle very similarly to the observations, however, the fluxes are on average $19.5\,\mathrm{W}\,\mathrm{m}^{-2}$ higher in ED-2.2 than measured by the tower (Fig. 3a). On the other hand, the model predicts significantly higher values at TNF

10   (average bias $35.9\,\mathrm{W}\,\mathrm{m}^{-2}$), in particular during the dry season (average dry-season bias $44.5\,\mathrm{W}\,\mathrm{m}^{-2}$). The predicted seasonal cycle at TNF is very similar to the model prediction for GYF, whereas the tower measurements suggest much less variation

between wet and dry seasons (Fig. 3b). From the distribution of fluxes by time of the day, we found that ED-2.2 predicted higher than observed sensible fluxes during the afternoon at both sites (Fig. 3c,d). In addition, ED-2.2 was unable to capture events of strong nighttime negative flux as measured at both towers. The predicted canopy air space temperature at GYF is typically $0.5\,^{\circ}$C lower than tower estimates (Fig. S2a), whereas the predicted canopy air space temperate at TNF shows close agreement with tower estimates during the wet season, and ED-2.2 predicts temperatures about $0.5\,^{\circ}$C higher than tower estimates at TNF (Fig. S2b). Comparison with outgoing thermal infrared radiation, which is correlated with the vegetated surface temperature, show that the model typically predicts higher-than-observed values at daily scale (Fig. S3a,b), as a result of the model predicting higher fluxes during the afternoon (Fig. S3c,d). Therefore, the results suggest that the excessive sensible heat flux may be attributable to the model's overestimation of canopy temperature.

Water flux above canopy was well represented at both study sites (Fig. 4). The bias on annual average was $-0.23\,\mathrm{kg_W\,m^{-2}\,day^{-1}}$ for GYF and $+0.28\,\mathrm{kg_W\,m^{-2}\,day^{-1}}$ for TNF. The agreement was even better during the dry season (bias $-0.12,\mathrm{kg_W\,m^{-2}\,day^{-1}}$ for GYF and $+0.12\,\mathrm{kg_W\,m^{-2}\,day^{-1}}$ for TNF). ED-2.2 correctly represents increased water flux during the dry season in TNF (Fig. 4b), and that water flux does not increase during the dry season in GYF (Fig. 4a), although the model underestimates the fluxes during the first wet season (Dec-Feb) in GYF. Likewise, the diurnal cycle of water flux is well characterized at both sites, with median values predicted by the model similar to observations both during the day and during the night (Fig. 4c,d). The mean canopy air space humidity at GYF shows excellent agreement during the wet season and slight underestimation during the dry season (Fig. S2d). In contrast, the model predictions at TNF show slightly lower values during the wet season, consistent with higher water fluxes, and agrees well during the dry season (Fig. S2d).

3.2 Evaluation of productivity and respiration

When we compared gross primary productivity (GPP) with estimates from eddy covariance towers, the model captured the weak seasonality with slightly higher values during the dry season at GYF although the magnitude was consistently lower (Fig. 5a), whereas it captured the magnitude of GPP at TNF but it could not represent the decreased GPP early in the dry season (Fig. 5b).

Ecosystem respiration from ED-2.2 is more seasonal than the tower estimates, and the model predicts the highest respiration rates during the wet season at both sites, whereas tower-based estimates do not show a consistent seasonal pattern. Based on tower estimates, respiration reaches the maximum early in the dry season in GYF (Fig. 6a), whereas the maximum occurs during the wet season in TNF (Fig. 6b). At both sites the model response is largely driven by fluctuations in soil moisture affecting heterotrophic respiration (Fig. 6c,d).

Ecosystem respiration is not directly measured from eddy covariance tower. The magnitude of ecosystem respiration from towers often depend on the choice of the $u^{\star}$ filter (Hayek et al., 2018b), and can be biased because the extrapolation of respiration from nighttime to daytime does not account the light inhibition of daytime leaf respiration known as the Kok effect (Wehr et al., 2016). Therefore, we also compared the model results against results from other studies that focused on measuring or estimating each component of the total respiration. For TNF, we used the respiration components estimated by a bottom-up assessment of the carbon cycle (Malhi et al., 2009b). For GYF, we estimated the respiration terms using previously
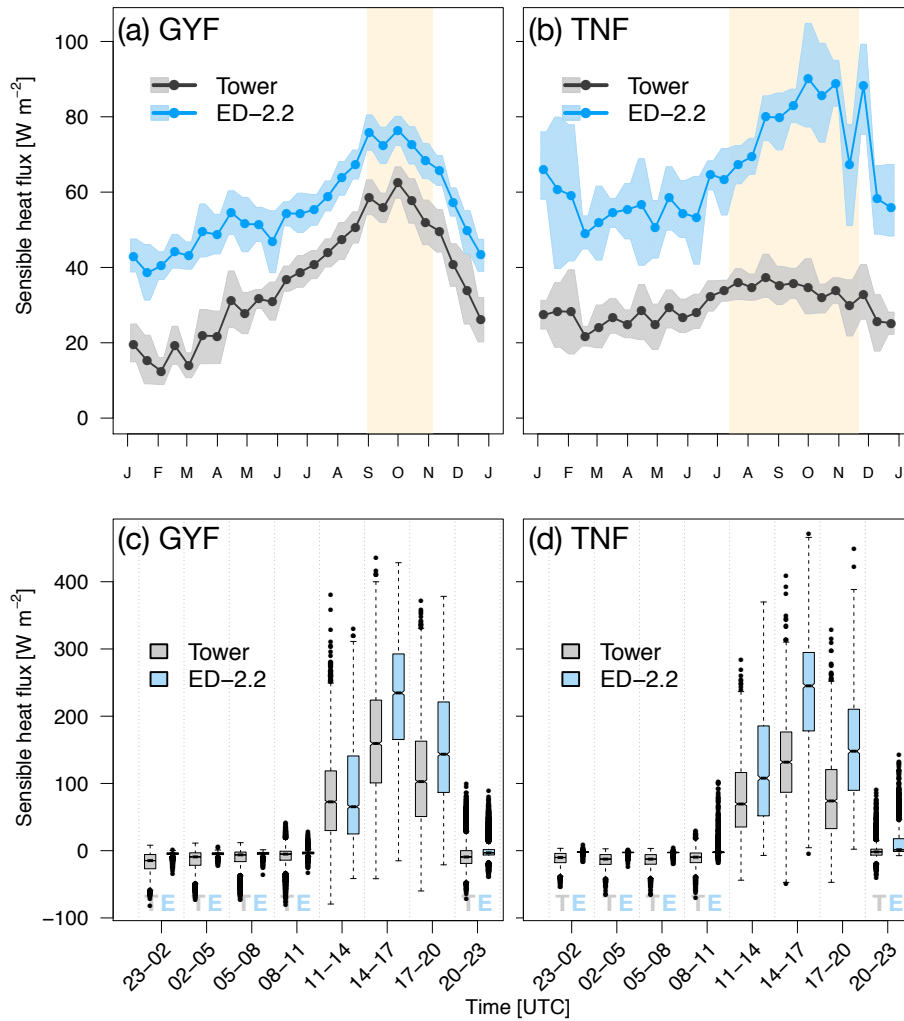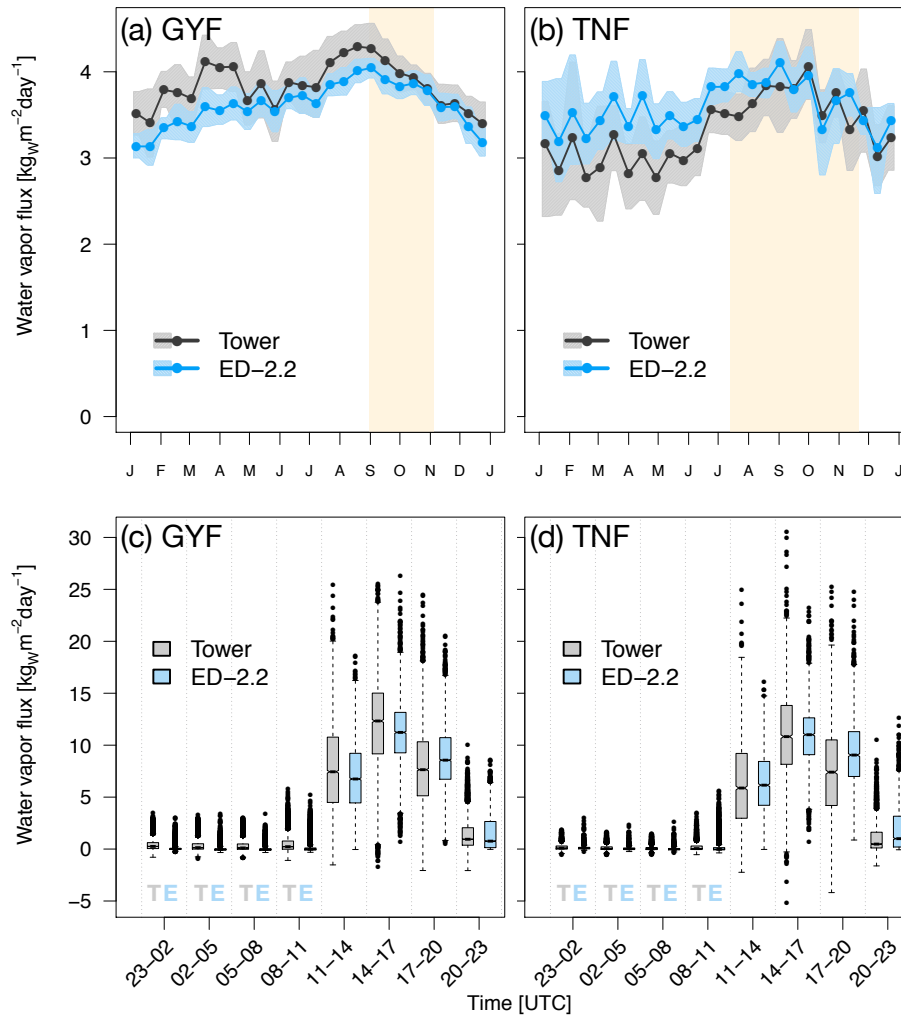
Figure 3. Mean annual cycle from fortnightly means of sensible heat flux for (a) GYF and (b) TNF. Bands are the 95% confidence interval of means, and rectangles in the background correspond to the site's climatological dry season. Box plot of sensible heat fluxes aggregated by time of day for all hours with available data for (c) GYF and (d) TNF.

published results and aggregated the components following Malhi et al. (2009b) (Supplement S1). The mean ecosystem respiration predicted by ED-2.2 overlaps with the 95% confidence interval at both sites (Table 1). In GYF, differences in heterotrophic respiration are the largest and explain most of the difference in the total respiration, whereas in TNF the positive bias in total respiration is due to autotrophic respiration. Within the autotrophic respiration, ED-2.2 predicts stem respiration that is $89 - 134\%$ higher than the bottom-up assessment. In GYF the excessive stem respiration is compensated by leaf and root respiration that are 36% and 19% lower than field estimates, respectively. As a result, the total autotrophic respiration at GYF is within one standard error from the expected rate based on the bottom-up analysis. In TNF, the reference
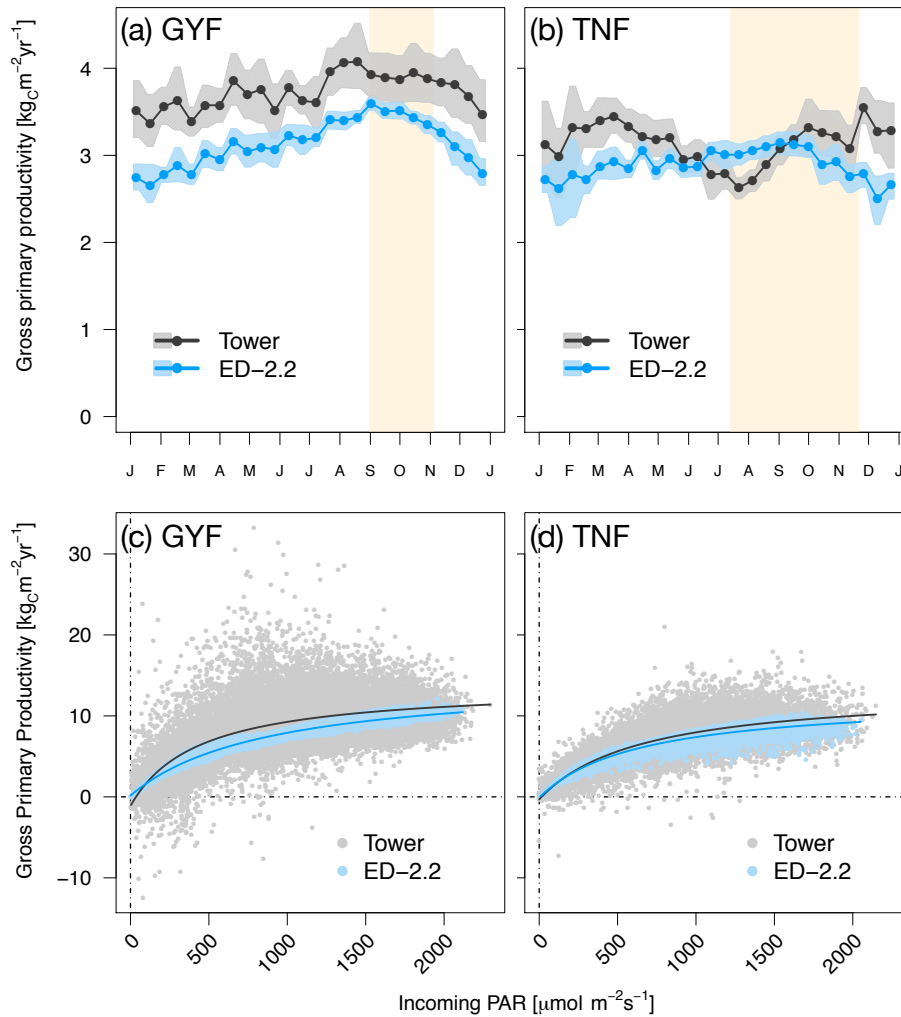
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Figure 4. Mean annual cycle from fortnightly means of water flux for (a) GYF and (b) TNF. Bands are the 95% confidence interval of means, and rectangles in the background correspond to the site's climatological dry season. Box plot of water fluxes aggregated by time of day for all hours with available data for (c) GYF and (d) TNF.

leaf and root respiration are nearly half the magnitude for GYF, and as a result, ED-2.2 autotrophic respiration is 57% higher than the estimates by Malhi et al. (2009b).

3.3 Regional patterns of biomass

The model correctly predicts the extension of the Amazon forest (Fig. 7a), and it also represents the regional distribution of aboveground biomass within the Amazon biome compared to regional biomass maps from Saatchi et al. (2011), Baccini et al. (2012) and Avitabile et al. (2016), the latter being based on the other two maps. For example, ED-2.2 predicts higher aboveground biomass in the Guiana Shield, similar to estimates from Saatchi et al. (2011) and Avitabile et al. (2016) (Fig. 7b,d),
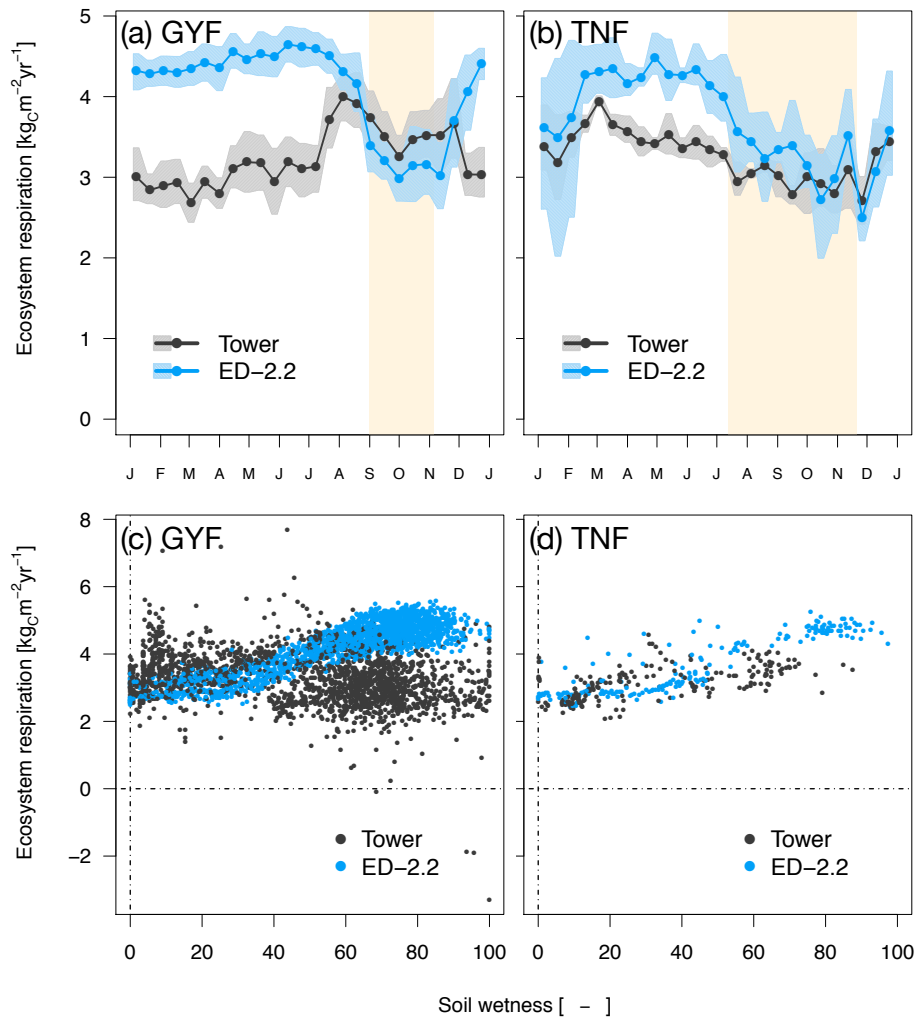
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Figure 5. Mean annual cycle from fortnightly means of GPP for (a) GYF and (b) TNF. Bands are the 95% confidence interval of means, and rectangles in the background correspond to the site's climatological dry season. Hourly averages of GPP as a function of incoming PAR for both model and tower based estimates at (c) GYF and (d) TNF.

the higher biomass near the border between Brazil, Peru, and Colombia, similar to Baccini et al. (2012) and Avitabile et al. (2016) (Fig. 7c,d), and the low biomass, open savanna area near the Brazil-Guyana-Venezuela border. The model generally predicts higher biomass than the three remote-sensing maps for most of the Amazon south of the Guiana Shield, particularly in the Western part of the Amazon (Fig. S4b-d), resulting in a peak in the distribution of biomass at $16.5\,\mathrm{kgC\,m^{-2}}$, whereas

5   the high-biomass peaks ranged between $11.5 - 14.0\,\mathrm{kgC\,m^{-2}}$ for the remotely sensed estimates of aboveground biomass (Fig. 9a). The ED-2.2 model and the remote-sensing estimates consistently predict relatively lower density function for intermediate values of biomass, and a pronounced peak of low biomass, even though the low-biomass peak predicted by ED-2.2 ($0.65\,\mathrm{kgC\,m^{-2}}$) is lower than the remote-sensing estimates ($1.0 - 3.4\,\mathrm{kgC,m^{-2}}$, Fig. 9a). The shift in the low-biomass peak

Figure 6. Mean annual cycle from fortnightly means of ecosystem respiration for (a) GYF and (b) TNF. Bands are the 95% confidence interval of means, and rectangles in the background correspond to the site's climatological dry season. Daily mean ecosystem respiration for (c) GYF and (d) TNF as a function of daily mean relative soil moisture at (c) $20\,cm$ and (d)$50\,cm$, for days with both soil moisture measurements and tower-based estimates of ecosystem respiration.

is mostly driven by ED-2.2 predictions of biomass in the savannas and xeric shrublands of Eastern Brazil, which were consistently lower than the remote-sensing estimates (Fig. S4). ~~We also compared the results of leaf area index (LAI) with estimates from the Moderate Resolution Imaging Spectroradiometer (MODIS, product MCD15A2H, Collection 6) (Yan et al., 2016) and found~~We also found that ED-2.2 predicted a similar extent of LAI over the Amazon region when compared to MODIS estimates (Fig. S5). However, ED-2.2 predicted lower LAI than MODIS for most of the Amazon, in particular along the arc of deforestation, and higher LAI in northwestern Colombia and Central Brazil (Fig. S5c).

The predicted transitions between the Amazon biome and the Cerrado (savanna biome in Central Brazil) and Los Llanos (grassland area in Venezuela) are driven by increased fire activity, consistent with the Global Fire Emission Database

Table 1. Comparison of respiration between ED-2.2 and published values for GYF and TNF ($\overline{X} \pm \mathrm{SE}(\overline{X})$ for any variable X), using a bottom-up approach with published values. Values in parentheses are the standard error of the mean. For ED-2.2 the standard error was estimated from bootstrapping the annual means.

	Paracou (GYF)[a]		Tapajós (TNF)[b]	
	Bottom-up estimates	ED-2.2	Bottom-up estimates	ED-2.2
Ecosystem	3.8 ± 0.5	4.03 ± 0.12	3.0 ± 0.4	3.80 ± 0.10
Heterotrophic	1.10 ± 0.20	1.66 ± 0.03	1.49 ± 0.14	1.432 ± 0.024
Autotrophic	2.8 ± 0.5	2.37 ± 0.10	1.5 ± 0.4	2.36 ± 0.09
Soil+CWD[c]	1.84 ± 0.23	2.20 ± 0.05	1.65 ± 0.13	1.97 ± 0.04
Leaf	1.4 ± 0.4	0.896 ± 0.004	0.7 ± 0.4	0.937 ± 0.005
Stem	0.504 ± 0.019	0.94 ± 0.07	0.38 ± 0.10	0.89 ± 0.06
Root	0.67 ± 0.20	0.542 ± 0.030	0.37 ± 0.08	0.534 ± 0.026

[a] Observed values for GYF are summarized in Supplement S1. Estimates were based on the approach described by Malhi et al. (2009b, c).
[b] Observed values for TNF are from Malhi et al. (2009b, c) and references therein.
[c] ED-2.2 does not have a separate coarse woody debris pool, therefore we compared the sum of both.
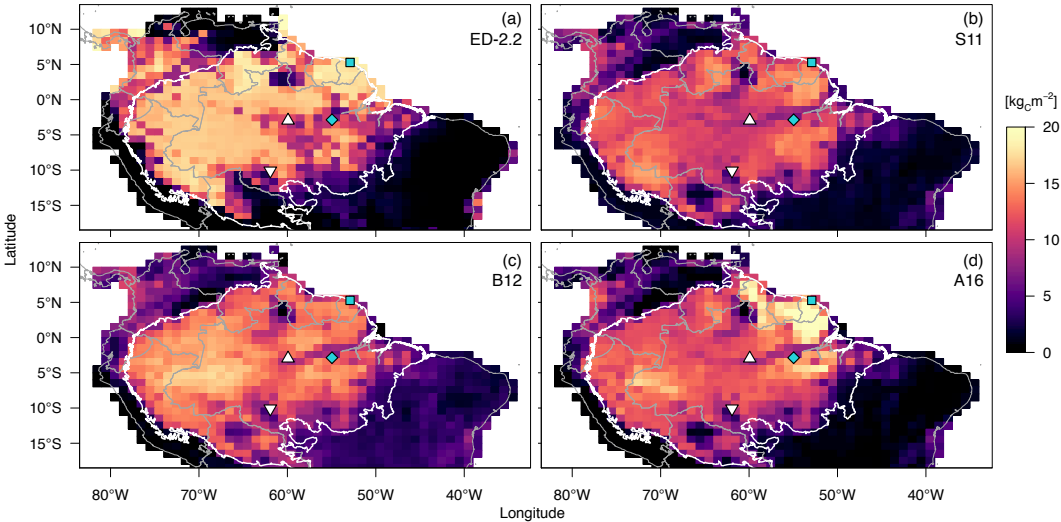
Figure 7. Comparison of aboveground biomass from (a) ED-2.2 and based on remote-sensing estimates from (b) Saatchi et al. (2011), (c) Baccini et al. (2012), and (d) Avitabile et al. (2016). Remote-sensing maps were aggregated to $1°$ resolution. Blue points represent the focus sites of Paracou (GYF, ~~triangle~~□) and Tapajós (TNF, ~~lozenge~~◊). White points represent the sites used for radiation profile evaluation: Ducke (MDK, ~~⋇~~△), and Jaru (RJA, ~~+~~▽). White contour is the domain of the Amazon biome, and grey contours are the political borders. Maps of the differences between ED-2.2 and remote-sensing are shown in Fig. S4. **(Figure was updated, following R2 suggestion.)**

(GFED4.1 Giglio et al., 2013; Randerson et al., 2018) regional distribution of burned area (α; Fig. 8). In addition, ED-2.2 correctly predicted higher burned area in the savanna region at the Brazil-Guyana-Venezuela border and low fire activity over most of the Amazon biome and in the Caatinga (low-biomass, semi-arid region in Northeastern Brazil) (Fig. 8). In contrast, ED-2.2 underestimated fire activity in El Beni (Bolivian savannahs, $\Delta\alpha = \alpha_{\mathrm{ED-2.2}} - \alpha_{\mathrm{GFED4.1}} = -6.8\%\,\mathrm{yr}^{-1}$) in the Colombian Los Llanos ($\Delta\alpha = -9.2\%\,\mathrm{yr}^{-1}$), while it overestimated fire disturbance in forest areas near the border
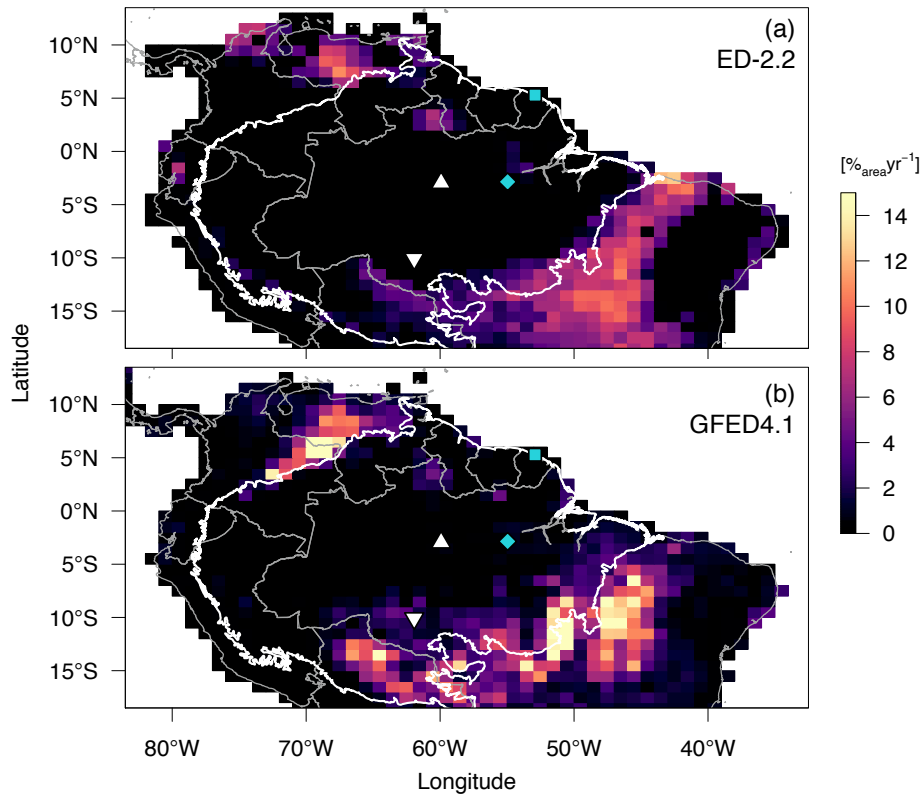
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Figure 8. Comparison of average burned area (a) predicted by ED-2.2 for a 40-year average driven by the Princeton Global Meteorological Forcing (PGMF (1969–2008); Sheffield et al., 2006), and (b) obtained from the Global Fire Emission Database (GFED4.1 (1997–2015); Giglio et al., 2013; Randerson et al., 2018), aggregated to $1°$ resolution. The location of focus sites of Paracou (GYF, $\square$) and Tapajós (TNF, $\lozenge$), and the sites used for radiation profile evaluation: Ducke (MDK, $\triangle$), and Jaru (RJA, $\triangledown$) are shown for reference. Thick contour is the domain of the Amazon biome, and thin contours are the political borders. Maps of the difference between ED-2.2 and GFED is shown in Fig. S6.

of Brazil and Bolivia ($\Delta\alpha = 1.9\%\,\mathrm{yr}^{-1}$), the coastal areas of Brazilian states of Maranhão and Piauí, immediately east of the Amazon biome ($\Delta\alpha = 5.0\%\,\mathrm{yr}^{-1}$), and areas in Eastern Brazil south of $15°$S ($\Delta\alpha = 3.7\%\,\mathrm{yr}^{-1}$) (Fig. 8; S6). Because the original fire model in ED-2.2 does not predict fire ignitions based on human activities (Moorcroft et al., 2001; Longo et al., 2019) ED-2.2 does not predict the burned areas along the arc of deforestation in the Southern and Eastern edges of the Amazon biome (Fig. 8a).

The predicted spatial variability of total carbon stocks in the region also emerged from variation in the environmental conditions such as variability in available light and water (Fig. 9;S7). Both ED-2.2 and the three remote-sensing estimates of biomass consistently showed the highest average biomass ($11.7 - 15.1\,\mathrm{kgC\,m}^{-2}$) at $195\,\mathrm{W\,m}^{-2}$, and the sharpest decline as a function of increased irradiance ($0.53 - 0.77\,\mathrm{kg_C\,W}^{-1}$) near $225\,\mathrm{W\,m}^{-2}$ (Fig. 9b; S7a). Similarly, the relationship between annual precipitation and above-ground biomass was consistent between model and remote-sensing estimates, with the highest changes in average biomass by increase in annual rainfall occurring between 1500 and $2200\,\mathrm{mm\,yr}^{-1}$, and relatively stable

values of above-ground biomass above $2500\,\mathrm{mm}$ (Fig. 9c). Some of the variability of simulated biomass at low ($< 1000\,\mathrm{mm}$) annual rainfall can be attributed to discrepancies between TMPA-3B43 and PGMF, which was used to drive the simulations, as the simulated biomass is consistently low where PGMF estimates of annual rainfall are less than $1000\,\mathrm{mm}$ (Fig. S7b). The increasing dry season severity, summarized by MCWD, has a strong association with decreasing average aboveground

5 biomass in both the model and the remote-sensing estimates when the annual MCWD is less than $500\,\mathrm{mm}$. The strongest declines in average biomass occurred at mean annual MCWD between $300 - 350\,\mathrm{mm}$ in both ED-2.2 and the remote-sensing estimates (Fig. 9d; S7c). It must be noted, however, that the transition between high biomass and low biomass when MCWD $300 - 350\,\mathrm{mm}$ is substantially more pronounced in ED-2.2 ($-0.075\mathrm{kgC\,m^{-2}\,mm^{-1}}$) than in the remote-sensing estimates (between -0.041 and $-0.050\,\mathrm{kgC\,m^{-2}\,mm^{-1}}$) (Fig. 9d).

10 ### 3.4 Assessment of forest function and structure

In addition to the total carbon stocks, the regional variability in forest function and composition at steady state is generally well characterized by ED-2.2. ~~First, the range and the variability of biomass across the network is generally well characterized with the exception of the driest sites located in Bolivia (red dots in Fig. 10a), where the model predicts less biomass than observations because of frequent fires predicted in the model~~The range and variability of biomass across the network are similar

15 to the range and variability observed across most of the network (Fig. 10a). However, the model does not accurately predict the AGB of individual plots at the wettest sites (black dots in Fig. 10a). The model also predicts lower-than-observed biomass than at the drier sites located in Bolivia (red dots in Fig. 10a) because of frequent fires occurring in the model simulation.. Also, both the model and the field measurements show similar negative correlation between biomass and mortality rates (Fig. 10b), and a similar positive correlation between biomass and the mean wood density (Fig. 10c), albeit significant

20 differences exist in biomass for any given value of mortality or wood density (Fig. 10b,c). Both wood density and mortality rates are related to the abundance of pioneers or late successional individuals both in the model (Moorcroft et al., 2001) and in observations (e.g. Chave et al., 2009; Kraft et al., 2010), suggesting that the model characterizes the variability in forest composition within the Amazon region. Fewer sites had estimates of both mortality rates and net primary productivity (NPP). However, the average predicted values at steady state ($1.29\,\mathrm{kgC\,m^{-2}\,yr^{-1}}$) were slightly lower than values reported

25 in the literature ($1.35\,\mathrm{kgC\,m^{-2}\,yr^{-1}}$) for the selected sites (Fig. 10d). Consistent with previous observations in the Amazon (e.g. Quesada et al., 2012), both the ED-2.2 predictions indicate a positive correlation between NPP and mortality. However, this correlation is highly uncertain because of the limited number of plots ($n = 7$) and the large variability in both NPP and mortality across sites (Fig. 10d).

The model captured the general distribution slope of stem demographic density (abundance) at GYF (Fig. 11a),

30 and both the total basal area and the typical distribution of basal area for individuals with DBH between 20 and $50\,\mathrm{cm}$ (Fig. 11b), although the model predicted a lower contribution from trees with DBH $< 20\,\mathrm{cm}$ to both abundance and basal area, and a higher contribution of individuals with DBH $> 50\,\mathrm{cm}$ to basal area (Fig. 11a,b). Model comparison with TNF data also showed that the model reproduced the main characteristics of the forest structure, although the slope of abundance
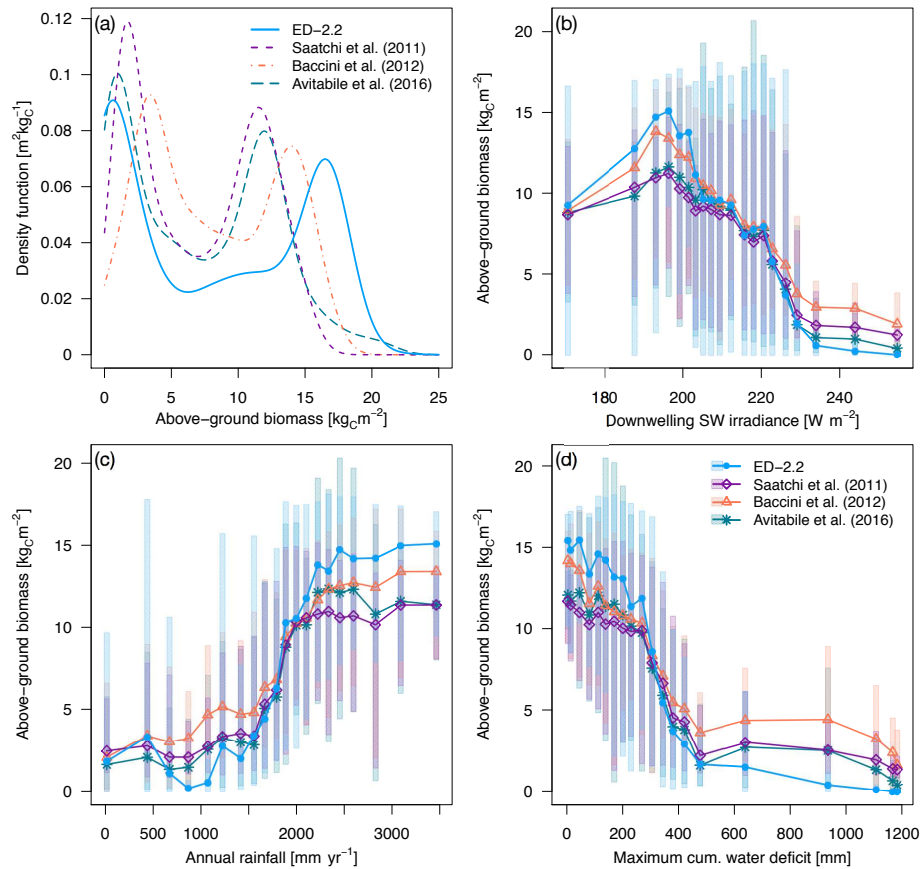
Figure 9. (a) Density functions of aboveground biomass predicted by ED-2.2 and based on remote-sensing estimates from Saatchi et al. (2011), Baccini et al. (2012), and Avitabile et al. (2016); points used to derive the distribution are the same as Fig. 7, and the density functions were calculated using the same bin width across the range of biomass from the model and the remote-sensing based maps. (b-d) Average biomass predicted by ED-2.2 and based on remote-sensing maps, aggregated by annual averages of (b) downwelling shortwave irradiance; (c) mean annual precipitation; (d) maximum cumulative water deficit. For each annual average of environmental properties, grid points were grouped into 20 quantile bins: points represent the average within each bin, and shaded area corresponds to the 90% quantile range within each bin. Data source for annual means: surface downwelling shortwave irradiance data (CERES EBAF-Surface Ed4.0; Kato et al., 2013); precipitation (TMPA-3B43; Liu et al., 2012); maximum cumulative water deficit was based on the same approach as Malhi et al. (2009a), using the TMPA-3B43 precipitation. The distribution of average biomass based on the meteorological drivers used by the ED-2.2 simulation (Sheffield et al., 2006) are shown in Fig. S7.

as a function of size was steeper in the model compared to observations (Fig. 11c). Basal area structure, on the other hand, showed good agreement with field inventory data and total basal area was within 5 % of the observed basal area.

Total mortality rates were generally higher in ED-2.2 simulations than based on the observed rates at both GYF and TNF (Fig. 12a,b), the model shows little variability in mortality between different census intervals. Most of the modeled mortality was due to background mortality, which is a combination of density-independent factors such as aging and treefall mortality, both assumed time-invariant in the model (Moorcroft et al., 2001). While the mortality due to environmental constrains (density-dependent) showed interannual variability, its magnitude was small, never exceeding $0.5\%_{AGB}\,yr^{-1}$.
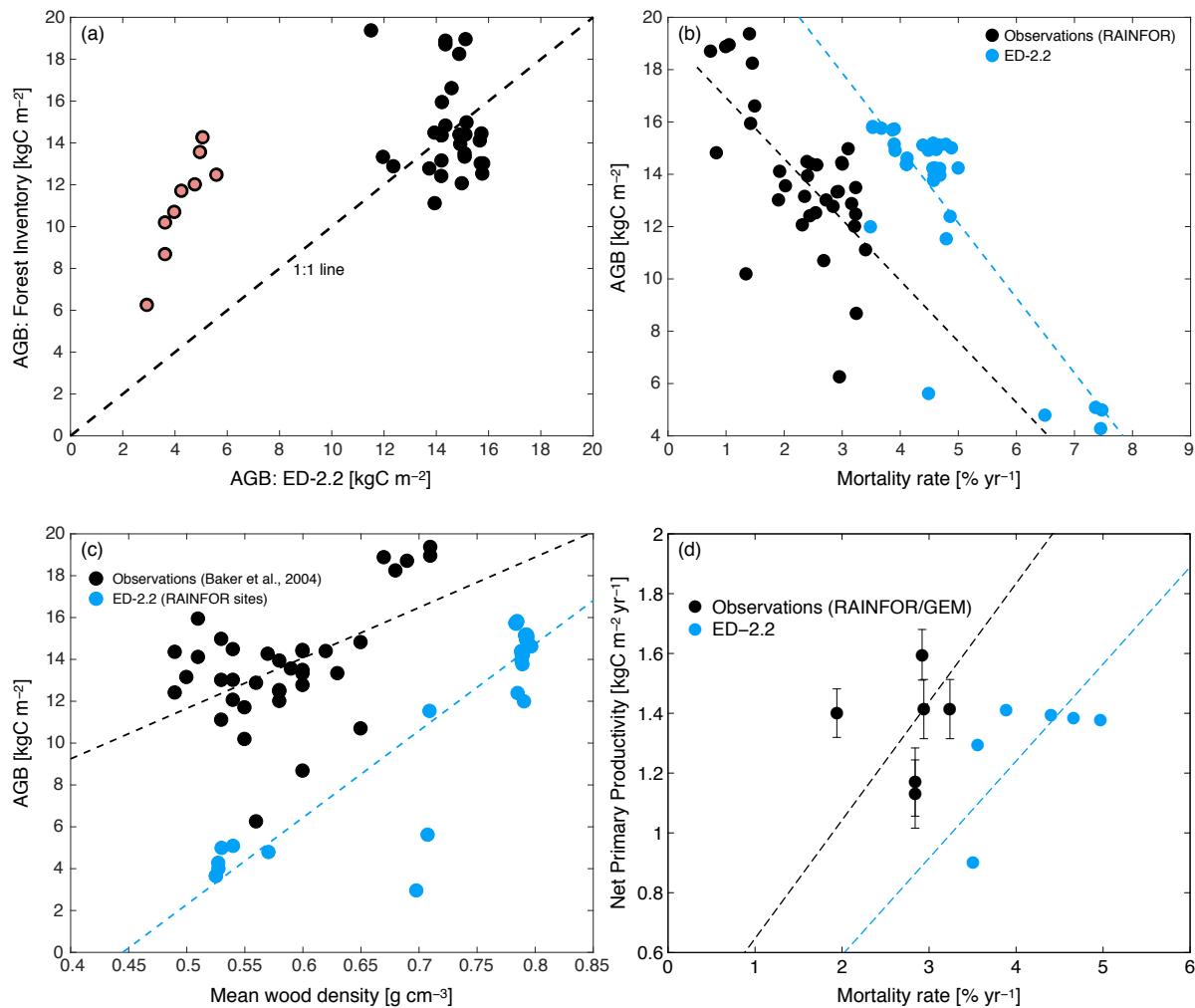
Figure 10. Evaluation of the ED-2.2 biomass and relationship between biomass and productivity and ecosystem function. (a) (Redrawn from Knox et al., 2015) Comparison of ~~model estimated~~ model predictions of mean aboveground biomass (AGB) with field estimates at multiple sites presented in Baker et al. (2004a, b). To be consistent with field measurements, model estimates included only biomass from living individuals with $DBH \geq 10$ cm (diameter at breast height). Points in red are from drier forest sites in Bolivia. (b,c) (Redrawn from Levine et al., 2016). Steady-state aboveground biomass distribution across the Amazon as a function of (b) mortality rates and (c) basal-area weighted mean wood density, for both the ED-2.2 model (blue circles) and based on field observations (black circles). Source of field-based estimates: Phillips et al. (2004); Baker et al. (2004a, b). (d) Steady-state net primary productivity (NPP) as a function of mortality rates, for both the ED-2.2 model (blue circles) and based on field observations (black circles; error bars are the reported standard error). Source of field-based estimates: mortality (Phillips et al., 2004, 2010); NPP (Aragão et al., 2009; Malhi et al., 2015).

The high mortality rates in the model is mostly attributable to early-successional trees, for which the modeled mortality rates was near $7.5\,\%_{AGB}\,yr^{-1}$, or 5-fold higher than late-successional, whereas observations were typically $3.0\,\%_{AGB}\,yr^{-1}$, or 3 times higher than late-successional. Likewise, growth rates were also higher than in observations, particularly at GYF (Fig. 12c), whereas the values were closer to observations for most of the simulated period at TNF (Fig. 12d). Growth rates
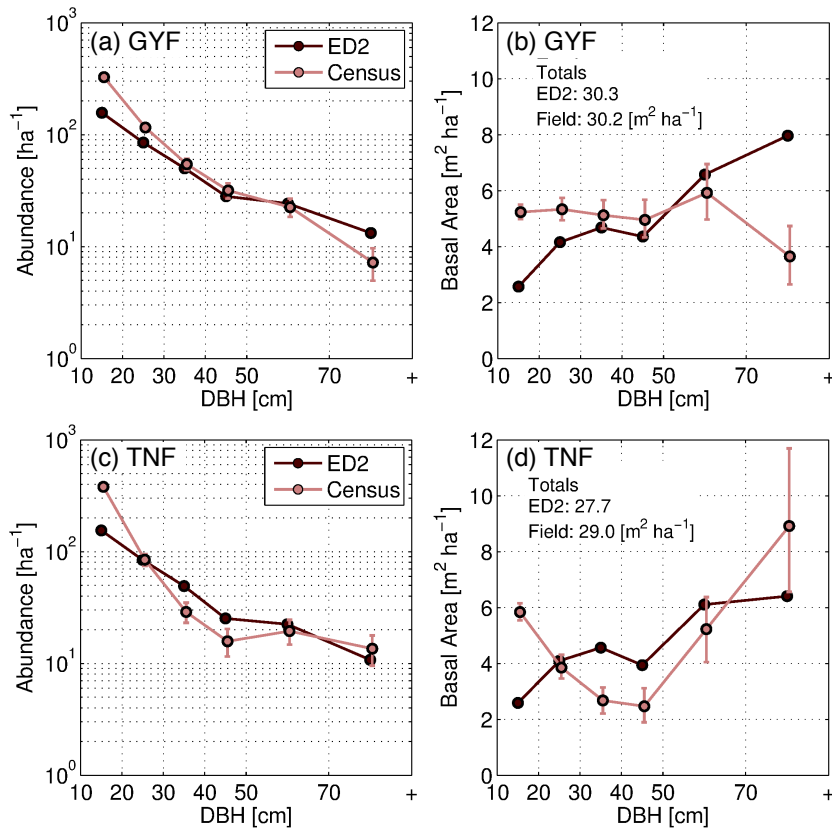
Figure 11. Evaluation of the ED-2.2 estimated size structure at the (a,b) GYF and (c,d) TNF sites, expressed in terms of abundance (a,c) and in terms of basal area (b,d). Confidence intervals on inventory analysis at 95% are shown with error bars. This is the confidence of the inventory sample representing the broader population (representativeness), as measurement error is assumed to be small. The confidence interval on abundance is estimated by a Poisson counting process. The confidence on the basal area is estimated by generating an ensemble of 100 random samples of the inventory, and quantile regression of the basal area sums of those re-samples. Total basal area predicted by ED-2.2 and observed in the census are shown in panels (b,d).

of both sites are significantly different, which could be related to the particularly nutrient-poor soils at GYF (e.g, Baraloto et al., 2005), and that the ED-2.2 does not account for nutrient limitation. Alternatively, higher growth rates may be due to tree allometry and low allocation to living tissues and contributing to high accumulation rates on structural tissues.

4 Discussion

4.1 Water and energy fluxes

The comparisons with eddy covariance towers demonstrated the ability of ED-2.2 to simulate the magnitude and seasonality of both the evapotranspiration fluxes and the water storage in the canopy air space (Fig. 4;S2). The good agreement of evapotranspiration in the tropical sites using ED-2.2 contrasts with previous assessments using ED-2.1 for temperate sites,
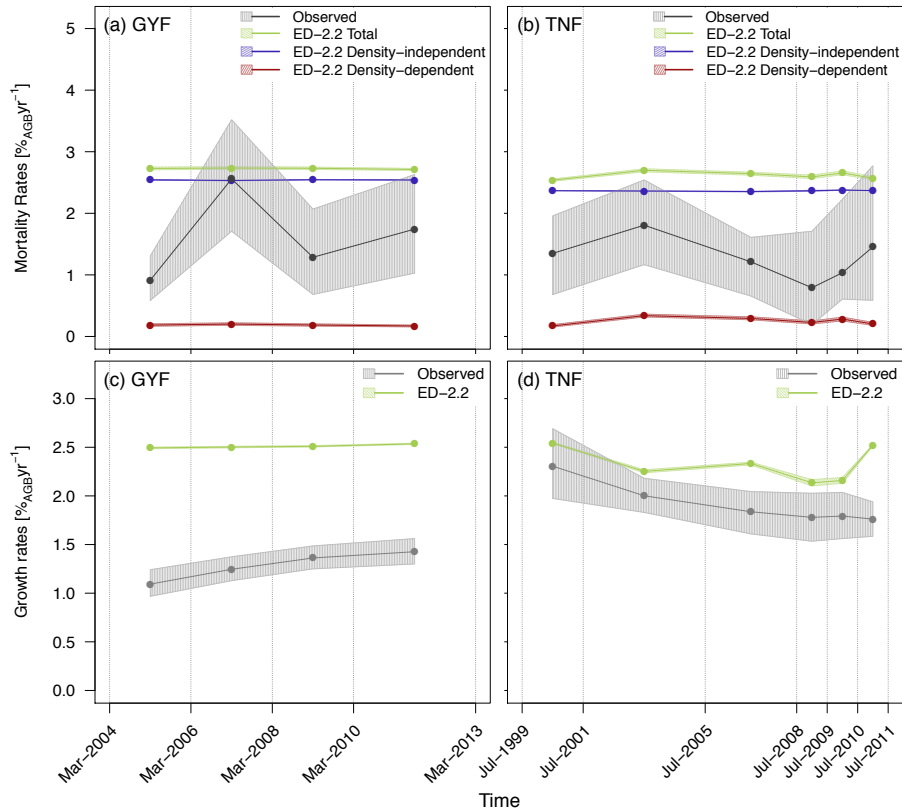
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Figure 12. Comparison of (a,b) mortality rates and (c,d) growth rates obtained from simulations and forest inventories for the (a,c) GYF and (b,d) TNF sites (redrawn from Longo et al. (2018)). Vertical lines are the approximate times of forest inventory surveys, and bands associated with observations correspond to the 95% confidence interval, obtained from bootstrap (see Longo, 2014, for further details), and bands associated with model results are the range of simulations with different soil texture, leaf phenology, and initial time. To be consistent with the field plot protocol, only those cohorts with $DBH \geq 10$ cm (diameter at breast height) were included in the model estimates.

which found significant negative biases in simulated evapotranspiration and attributed the bias to the model overestimating the impacts of water stress on stomatal conductance (Matheny et al., 2014; Walker et al., 2014). The average ratio between canopy evaporation and total rainfall ranged from $7 - 11\%$ at the two forest sites tested here (Guyaflux and Tapajos), which is at the low end but in the same range of values founds in previous studies ($9 - 20\%$; Tobón Marin et al., 2000, and references therein). The hydrological cycle, on the other hand, showed some important deviations in absolute value, particularly near the surface, despite being consistent with observation in relative terms (Fig. S9). Large biases in absolute soil moisture were caused by the mismatches in the soil hydraulic properties that ultimately define the residual moisture and wilting point, field capacity, and porosity, thence the range of possible values of soil moisture. Soil hydraulic properties were derived from texture characteristics previously published for all sites. In ED-2.2 these properties were simplified to a single fraction assumed constant at every patch and throughout the profile, whereas in reality soil properties are known to vary significantly within the same area and with depth (e.g. Epron et al., 2006). Moreover, soils in ED-2.2 are assumed to be mineral, whereas

in reality macropores and soil organic content can substantially affect such properties (Saxton and Rawls, 2006; Fisher et al., 2008).

The model also realistically represented both the net absorption of visible irradiance and the vertical distribution throughout the canopy. The model showed similar magnitude and seasonality of the outgoing shortwave radiation, including photosynthetically active radiation, at the two long-term sites (Fig. 1), and the average light level profiles within the canopy. Agreement was even higher during cloudy conditions (Fig. 2), when the spatial distribution of individual trees has less of an impact on local variability in the light profile (Mercado et al., 2009). Differences were more significant for photosynthetically active radiation than for total shortwave radiation, particularly during the dry season (Fig. 1c,d). These differences may result from two factors. First, leaf optical properties in ED-2.2 are assumed constant for any given PFT, whereas observations indicate that leaf reflectivity depends on leaf age (Toomey et al., 2009; Chavana-Bryant et al., 2017). Second, ED-2.2 represents canopy structure in only one dimension for each patch, the effect of neighboring trees (or their absence) is not represented. A full three-dimensional approach similar to Morton et al. (2016) may not be feasible within the ED-2.2 because of the intensive computational burden and that the model does not represent the actual position of individual trees. Alternatively, the perfect plasticity approach (Purves et al., 2008; Farrior et al., 2013), in which finite-crown individual trees are arranged to maximize light access, has been recently adapted to another cohort-based model, the Functionally-Assembled Terrestrial Ecosystem Simulator (FATES, Fisher et al., 2018). The perfect plasticity approach has the advantage of allowing trees of similar size to experience the same light levels (as opposed to the sequential light interception in ED-2.2), which could contribute to improve the light extinction profile in closed canopy forests. Importantly, while the current representation of vertical light distribution in ED-2.2 may affect light availability of individual cohorts, it does not imply that the simulated understory in ED-2.2 is excessively dark. In fact, when we compared the modeled and observed vertical structure of diffuse light (which is less sensitive to the observed position of trees than direct light) we found that the model slightly overestimates understory light levels (Fig. 2).

The model predictions of canopy air space temperature at TNF generally matches observations well, except for a slight overestimation during the dry season at TNF (Fig. S2). However, the sensible heat flux also tends to be higher than tower estimates, particularly at the drier TNF site (Fig. 3). The better agreement of simulated water fluxes with observations relative to sensible heat flux is very common among land surface models (Best et al., 2015). One possible cause of this disagreement is that observations from eddy flux towers typically contain significant sources and sinks from lateral advection and air drainage that may result in departures from energy closure by as much as 30% (Tóta et al., 2008; da Rocha et al., 2009; Leuning et al., 2012; Stoy et al., 2013). ~~Energy conservation is a requirement in ED-2.2 and conservation of energy is consistently checked every model time step (Longo et al., 2019)~~ Energy conservation is an important requirement for terrestrial biosphere models, particularly in the context of coupled biosphere-atmosphere modelling studies where they need to ensure conservation of energy at the lower boundary of the atmosphere. In ED-2.2, conservation of energy is checked every model time step (Longo et al., 2019).. ~~However,~~Since ED-2.2 does not ~~represent~~incorporate lateral advection or ~~air drainage~~of air within the plant canopy, ~~and~~in situations where significant lateral advective transport of energy occurs within the canopy, the model may compensate ~~such losses~~for the absence of lateral transport through an ~~increase in~~increased or decreased rate of

vertical eddy fluxes. ~~Moreover,~~ Haughton et al. (2016) suggested that parameterization problems, ~~and not~~rather than energy conservation, are the most likely cause for biases in land surface models. ~~In ED-2.2, one possible~~One potential issue in this regard in ED-2.2 is that the heat capacity of branches and leaves could be biased, allowing greater variability of temperature and higher sensible heat fluxes at the expense of reduced storage. To our knowledge, no long-term measurements of leaf or branch temperature exist for the Amazon sites, but differences in outgoing thermal-infrared irradiance (Fig. S3) suggest that the observed vegetation temperature during the afternoon may be lower and less variable than the model predictions. Additional measurements of leaf and wood heat capacity for tropical forests could improve the accuracy of leaf and branch temperatures in the model.

4.2 Carbon fluxes and carbon storage

Comparisons of GPP between the ED-2.2 model and tower-based estimates show that the model captures both the magnitude of GPP and the typical GPP response to light (Fig. 5). In ED-2.2, the seasonality at tropical forest sites is mostly driven by light, thus the maximum productivity often occurs during the dry season (Fig. 5a,b). Estimates of GPP based on eddy covariance towers, however, suggest a more complex pattern, with minimum occurring either during the wet season (GYF) or the transition from wet to dry season (TNF), and modestly increasing productivity during the dry season (Fig. 5a,b; see also Bonal et al., 2008; Restrepo-Coupe et al., 2013, 2017). GPP depends on multiple processes, and thus differences between ED-2.2 and tower estimates may be due to several factors including biases in the seasonality of leaf area and photosynthetic properties of leaves. In particular, empirical studies have shown that the seasonality of GPP in Amazon forests is linked to seasonal variation of photosynthetic capacity and leaf phenology (Wu et al., 2016; Restrepo-Coupe et al., 2017), whereas in the current implementation of ED-2.2 both the leaf turnover rate and the maximum photosynthetic capacity are assumed, for simplicity, to be constant. Work from several modeling studies (Kim et al., 2012; De Weirdt et al., 2012; Medvigy et al., 2013), and a leaf-level carbon optimization model (Xu et al., 2017) have shown that incorporating such seasonality into the dynamics of leaf longevity and photosynthetic capacity significantly improves predictions of the seasonality of carbon fluxes in tropical forests. However, data from multiple sites may be needed to develop a generalizable phenology model for evergreen forests.

The model estimates of ecosystem respiration were generally higher and more seasonal than the expected values either from eddy covariance tower estimates or from a bottom-up assessment, especially at GYF (Fig. 6; Table 1). In the model, the seasonality of ecosystem respiration was nearly exclusively driven by the seasonality in heterotrophic respiration, with a significant decline in the dry season due to lower soil moisture (Fig. 6c,d), whereas eddy covariance tower estimates suggest a dry-season reduction in respiration only at TNF (Fig. 6a,b; Restrepo-Coupe et al., 2017; Aguilos et al., 2018). The ED-2.2 assumption that heterotrophic respiration at lower soil moisture (Longo et al., 2019) is consistent with observations for total respiration at GYF (e.g. Fig. 3 of Aguilos et al., 2018); however, the magnitude of the heterotrophic response to moisture is likely overestimated in the ED-2.2 model.

Total autotrophic respiration estimates from ED-2.2 were within range with independent bottom-up estimates for both sites , albeit only marginally within the 95%-confidence level (2 standard errors) of the bottom-up estimates at TNF

(Table 1). At both sites, the simulated autotrophic respiration was driven by leaf and stem respiration, which contributed with roughly the same proportion to autotrophic respiration. In contrast, the bottom-up estimates at both sites suggest leaf respiration was 2-3 fold higher than stem respiration (Table 1). One possibility is that the allocation of carbon gains to tissue growth was overestimated in ED-2, which is consistent with the overestimated growth rates compared to forest inventory

5   plots (Fig. 12). It must be noted, however, that several terms estimated from observations also carry large uncertainties and assumptions. For example, stem respiration is typically measured near the surface (e.g Chambers et al., 2004; Stahl, 2010), which may introduce biases given that branches may have significantly higher respiration rates (Cavaleri et al., 2006). Furthermore, observed differences of expected values between sites are generally much larger than the differences obtained by the model, and such differences may reflect true differences of plant community functioning between sites, or differences

10   in sampling and techniques (Malhi et al., 2009b). Improved measurements of the different terms of ecosystem respiration would allow for improved constrains on the individual processes driving the total respiration.

       In addition to tropical sites, the model's ability to represent productivity and respiration has been previously assessed for temperate ecosystems. The model showed excellent agreement in magnitude and seasonality of both net ecosystem productivity (NEP) and gross primary productivity (GPP) at three flux tower sites installed at Harvard Forest, in particular

15   when the model was initialized with ground-based or remote-sensing-based data (Antonarakis et al., 2014). In contrast, the model showed significant biases in net primary productive under ambient CO_2 at two Free-air CO_2 Enrichment (FACE) sites in Southeastern United States, overestimating NPP at Duke (evergreen forest) and underestimating at Oak Ridge (deciduous forest) (Walker et al., 2014). Also, a previous model-intercomparison study for eleven North American tower sites also revealed significant negative biases in ED-2.1, although the model inter-annual variability of GPP and ecosystem respiration

20   were within the observed range for both deciduous and evergreen sites (Keenan et al., 2012). In addition, a wavelet analysis of the normalized error across 9 tower sites across North America suggested that the errors in net ecosystem exchange (NEE) are dominated by sub-annual (but longer than daily) time scales (Dietze et al., 2011). Together, these results indicate the need of quantifying which processes and parameters contribute the most to model uncertainties in order to improve the model predictions using ED-2.2, which is currently being pursued (Fer et al., 2018; Raczka et al., 2018).

25   Finally, because ED-2.2 solves the carbon dioxide cycles at sub-hourly scale, it also accounts for changes in storage in the canopy air space. As described in the companion paper (Longo et al., 2019), in ED-2.2, canopy air space storage is accounted for for energy, water, and carbon dioxide. While changes in storage are generally small in the seasonal or multi-annual scale (Fig. S8a,b), they ~~may~~ are not negligible in the sub-daily scale. The relevance of the storage of CO_2 in the canopy air space has been long recognized by the eddy covariance community (e.g. Goulden et al., 1996; Bonal et al., 2008;

30   Hayek et al., 2018b), but only rarely included in biosphere or land surface models. For example, the strong release of carbon dioxide in the early morning hours, resulting from the nighttime accumulation of respired CO_2, is well characterized by the model at both test sites (Fig. S8c,d). Accounting for this time lag between biologically-driven emission or uptake and the emissions to the free atmosphere is particularly important for benchmarking the model with the upcoming column-integrated measurements of CO_2 Orbiting Carbon Observatory-3, which will provide samples at multiple times of the day (Eldering

35   et al., 2017; Stavros et al., 2017).

4.3 Long-term, large-scale ecosystem dynamics

A key feature of the ED-2.2 model is the emergence of long-term, large-scale ecosystem composition, structure and function from spatially-localized, height-structured competition between individuals within the plant canopy. As seen in Fig. 9, the model's large-scale predictions are consistent with remote-sensing estimates of how AGB variability along key climatological gradients of incoming solar irradiance, rainfall, and dry-season severity. In addition, the regional pattern of AGB predicted by ED-2.2 reproduces several notable features present in the remotely-sensed based estimates of AGB (Fig. 7). In particular, the model captures the spatial extent of the Amazon forest, and reproduces two characteristic patterns of spatial variability in forest biomass, namely (i) the high biomass forests found in the Guiana Shield (near GYF) and in the area south of the TNF flux tower, and (ii) the area of lower biomass forest that runs east-to-west spanning the TNF and MDK sites.

The model's predictions of regional AGB also reveal important discrepancies. First, the model estimates are generally lower than the remote-sensing estimates of AGB in the drier savannas and xeric shrublands of central and Northeastern Brazil (Fig. 7-9). The low biomass estimates in drier regions is likely related to the simplified fire model used in the regional simulations . Following Moorcroft et al. (2001), fire occurrence within each climatological grid cell is controlled by a simple fixed soil moisture threshold, the area burned per year increases linearly as a function of the mean AGB within each grid cell, and no plants survive burn events. ~~In reality,~~Although this simplified approach captures many patterns of fire regime in tropical South America (Fig. 8), it has important shortcomings in representing fire ignition mechanisms and the ecosystem's response to fire disturbance. For example, as previous work has shown (e.g. Cardoso et al., 2003; Cochrane, 2003; Andela et al., 2016), fire frequency, burn area, and fire severity are also strongly influenced by environmental factors in addition to soil moisture, such as proximity to roads and deforested areas. Moreover, the model does not account for size-related differences in fire survivorship and plant-functional diversity-related differences in fire survivorship arising from variation in plant traits such as bark-thickness-and re-sprouting ability (Brando et al., 2012; Trugman et al., 2018). Furthermore, the model simulations do not include plant functional types with adaptations for the semi-arid conditions typically observed in Northeastern Brazil. Such adaptations include smaller leaf size; internal water storage; modular, independent and redundant vascular systems; germination synchronized with rainfall; and Crassulacean Acid Metabolism (CAM) photosynthetic pathway (Cushman, 2001; Schenk et al., 2008; De Micco and Aronne, 2012). Incorporating these mechanisms that drive the ecosystem dynamics in drier areas could ~~significant~~ improve the model predictions outside tropical forests.

In the western Amazon, the model's predictions of AGB are generally higher than all three remote-sensing estimates, implying that the model is over-predicting AGB in this region (Fig. 7). ED-2.2 also tends to overestimate the high-biomass peak of the regional distribution of biomass (Fig. 9a). One potential reason for the AGB over-estimation in the Western Amazon is the model's predicted dominance of late-successional plants over most of the Amazon region, whereas field observations indicate that forests in Western Amazon have higher stem turnover rates and lower wood densities than Eastern Amazon (Phillips et al., 2004; ter Steege et al., 2006). This has been linked to the fact that soils in Western Amazon have higher nutrient availability (Quesada et al., 2012), which was not accounted for in ED-2.2. Moreover, the model assessment suggests that ED-2.2 overestimates growth rates (Fig. 12) and AGB (Fig. 9a), despite evidence that ED-2.2 may be under-

estimating net primary productivity (NPP; Fig. 5; Tab. 1; Fig. 10d). This result likely indicates that allocation to growth, maintenance, and reproduction may be biased. Trait and allometric data bases have considerably expanded over the past decade (e.g. Kattge et al., 2011; Falster et al., 2015; Keenan and Niinemets, 2016), with many of them have adopted open-access platforms. Incorporating these databases to develop and constrain allocation and maintenance costs of the functional groups in ED-2.2 could significantly reduce uncertainties in carbon stocks, productivity, and demographic rates. Finally, the regional simulation did not account for all types of anthropogenic disturbances from tropical forest degradation, which could also explain part of the overestimation by ED-2.2 compared to the remote-sensing estimates. Tropical forest degra-dation through selective logging, mining and low-intensity understory fires in the Amazon is pervasive along the arc of deforestation (Fig. 8b; Morton et al., 2013; Asner et al., 2013; Tyukavina et al., 2017) and is known to significantly deplete aboveground biomass (Berenguer et al., 2014; Longo et al., 2016; Rappaport et al., 2018).

The regional model simulation also qualitatively captures two disturbance-mediated relationships between canopy AGB and other tropical forest attributes observed in plot measurements (Fig. 10): the negative correlation between AGB and average stem mortality rates (Phillips et al., 2004; Johnson et al., 2016), and the positive correlation between AGB and average wood density found by Baker et al. (2004b). The fact that the model qualitatively captures the directional trend of both these two relationships is encouraging and suggests that the model's predictions of regional biomass trends are arising from mechanisms similar to those observed in nature. However, the magnitudes of the predicted relationships differ from the observations: for a given value of AGB, the model predicts a higher mean stem mortality rate and a higher mean wood density value than is observed in the plot measurements. The reasons for the differences in the ~~magntidues~~magnitude of these relationships are, at present, unclear. However, in the case of the mean mortality-AGB relationship, the mismatch is likely related to the over-prediction of mortality rates seen in ED-2.2 (Fig. 10; 12). In addition, the predicted mortality rates at the two tropical forest sites showed nearly constant mortality rates during the period in which observed rates were available (Fig. 12). In ED-2.2, density-independent rates are modulated only by changes in functional composition (i.e., relative increase in abundance of pioneer plants), which did not occur in these simulations. Density-dependent mortality is associated with environmental conditions such as droughts and can drive the inter-annual variability of simulated mortality rates, yet these rates also nearly constant during this period. We interpret this result to be consistent, as the droughts of 2005 and 2010 were significant in the southwestern part of the Amazon (Lewis et al., 2011), but not at our study sites. The low sensitivity to 2005 and 2010 droughts is also supported by the observations, which did not show significant increases in mortality after 2005 and 2010 (Fig. 12); the increase in mortality at GYF between 2006 and 2008 is attributable to a substantial treefall event that affected one of the measurement plots in 2007. Nonetheless, the model does show sensitivity to historic droughts such as the 1992 and 1998 events in TNF (Longo et al., 2018) and the model response is consistent with anomalously high coarse woody debris found at the site when field inventory measurements began in 1999 (e.g. Pyle et al., 2008; Hayek et al., 2018a).

In this manuscript, we focused on assessing the model's ability to represent the dynamics of tropical forests, but previous studies have also shown that the model reasonably describes the dynamics of temperate ecosystems. For exam-ple, Medvigy and Moorcroft (2012) demonstrated that the model captures regional variation in both growth and mortality

rates across forests of northeastern North America, especially when using the optimized parameters from Medvigy et al. (2009). Also, Miller et al. (2016) applied ED-2.1 at Duke's Free Air Carbon dioxide Enrichment experiment site (conifer-dominated) and found that the model accurately predicts biomass changes over time for both ambient and elevated CO_2, and realistically characterizes the changes in gross and net primary productivity (NPP) as functions of stand age. This result was consistent with a previous model-intercomparison study, which found good agreement on observed and ED-2.1 modeled CO_2 fertilization effect at Duke, whereas the model predicted response to elevated CO_2 at Oak Ridge (broadleaf-dominated) was overestimated (De Kauwe et al., 2013). In contrast, in a millennium-long model inter-comparison study for Northeastern United States, the model overestimated both the magnitude of NPP and its variability as a function of rainfall and CO_2 when compared to tree-ring estimates (Rollinson et al., 2017), which indicates the need of constraining the model response for environmental conditions outside the current range. While these studies used versions of the model that contained many of the implementations of ED-2.2 described in the companion manuscript (Longo et al., 2019), future work using the ED-2.2 model in temperate ecosystems should critically evaluate processes that could not be assessed in our analysis, such as leaf phenology and processes related to snow dynamics. Such benchmarking efforts should be regarded as priorities in future studies.

5 Conclusions

Results from both observations and experimental studies have shown that plant diversity is an important determinant of terrestrial ecosystem function and how terrestrial ~~eco fsystems~~ecosystems respond to environmental perturbation (Tilman, 1996; Gunderson, 2000; Cadotte et al., 2011; Mori et al., 2013; Hautier et al., 2015; Falster et al., 2017). Terrestrial ecosystem models have advanced significantly towards representing functional diversity over large regions over the past twenty years (Moorcroft et al., 2001; Medvigy and Moorcroft, 2012; Fisher et al., 2015, 2018), however their ability to represent complex, heterogeneous communities also depends on their ability to represent the heterogeneity of the environments where plants live and compete for resources. ~~The ED-2.2 model accounts for this fine-scale heterogeneity by solving the energy, water, and carbon cycles for the different micro-environments in the plant community. The ED-2.2 model integrates biophysical, ecological and biogeochemical terrestrial ecosystem processes of heterogeneous landscapes on timescales ranging from minutes to centuries and on spatial scales ranging from individual plants to continental scales.~~ As we have shown in the companion paper (Longo et al., 2019), the model ~~shows excellent~~exhibits a high degree of conservation of energy, water, and carbon dioxide that is ~~a necessary condition for the model application to longer time scales and for accurate coupling with atmospheric models.~~important in long-term ecosystem simulations, coupled biosphere-atmosphere modeling studies, and earth system model simulations. This is encouraging in light of a previous analysis that suggested a lack of energy conservation in the radiation schemes of several widely-used terrestrial biosphere models (Loew et al., 2014) and in the context of simulating the long-term dynamics of functionally diverse, vertically and horizontally heterogeneous plant canopy.

~~The thorough~~This detailed evaluation of the model performance in tropical South America, including an assessment of the separate components of the energy, water, and carbon cycles demonstrated the model's ability to represent multiple

biophysical and biogeochemical mechanisms. The model dynamics are consistent with observations in most short-term fluxes of shortwave radiation (Fig. 1-2) and water (Fig. 4;S2), and even though ~~it showed~~there was significant overestimation ~~in~~of sensible heat ~~flux~~fluxes, the model correctly characterized the average and the pattern of seasonality of canopy air space temperature (S2). The model represented realistic ~~magnitude~~average magnitudes and light response ~~curve~~curves of gross primary productivity (GPP) at GYF and TNF, albeit it did not capture the pattern of GPP seasonality at TNF (Fig. 5). Respiration showed the highest disagreement, both in terms of magnitude and seasonality, reflecting the uncertainties in representing respiration processes (Fig. 6; Table 1). In addition to the short-term comparisons with eddy covariance towers, ED-2.2 also showed good agreement with independent estimates of aboveground biomass distribution at regional level in the tropics (Figs. 7-10) and the size distribution of the aggregated properties (Fig. 11), and reasonable magnitude of mortality rates and growth rates for TNF, an inland tropical forest site, although it significantly overestimated growth rates at GYF, a particularly nutrient-poor site (Fig. 12).

As pointed out in the companion model description manuscript (Longo et al., 2019), the ED-2.2 model continues to be developed. The ED-2.2 model evaluation presented here highlighted some short- and long-term processes that should be regarded as priorities for future developments. Better constrains in vegetation heat capacity could improve the quantification of energy storage and reduce biases in outgoing long wave radiation and sensible heat flux. Likewise, ecosystem respiration showed significant departures in magnitude and seasonality from site-level estimates. Formal optimization of parameters that control respiration response to temperature and moisture, along with better description of the range of decomposition time scales may be required. Finally, the excessive tree growth rates identified in nutrient-poor sites could be addressed by expanding the representation of biogeochemical cycles in tropical forests by including nitrogen and phosphorus dynamics, which could significant improve the characterization of the carbon cycle.

Code and data availability. The ED-2.2 software and further developments are publicly available. The most up-to-date source code, post-processing R scripts, and an open discussion forum are available on https://github.com/EDmodel/ED2. The code described in this manuscript, along with a wiki-based technical manual, is stored as a release at https://github.com/mpaiao/ED2/releases/tag/rev-85 and permanently stored at https://dx.doi.org/10.5281/zenodo.2579481. Eddy covariance data from GYF and TNF sites are available at https://fluxnet.fluxdata.org. Forest inventory are available upon request to the data PI: GYF – D.B. (damien.bonal@inra.fr); TNF – P.B.d.C (pca-margo@cena.usp.br). The PGMF meteorological data set can be requested at http://hydrology.princeton.edu/data.pgf.php. The Oak Ridge National Laboratory Distributed Active Archive Center provides access to the RADAMBRASIL (https://dx.doi.org/10.3334/ORNLDAAC/941), IGBP (http://dx.doi.org/10.3334/ORNLDAAC/565) and the photosynthetically active radiation (https://dx.doi.org/10.3334/ORNLDAAC/899) data sets. Remote-sensing biomass maps were obtained by contacting the corresponding authors (Saatchi et al., 2011; Baccini et al., 2012), and from http://lucid.wur.nl (Avitabile et al., 2016). CERES EBAF-Surface and TMPA-3B43 products are available at https://ceres.larc.nasa.gov and https://dx.doi.org/10.5067/TRMM/TMPA/MONTH/7, respectively. MODIS Leaf area index product (MCD15A2H, Collection 6) is available at http://doi.org/10.5067/MODIS/MCD15A2H.006.

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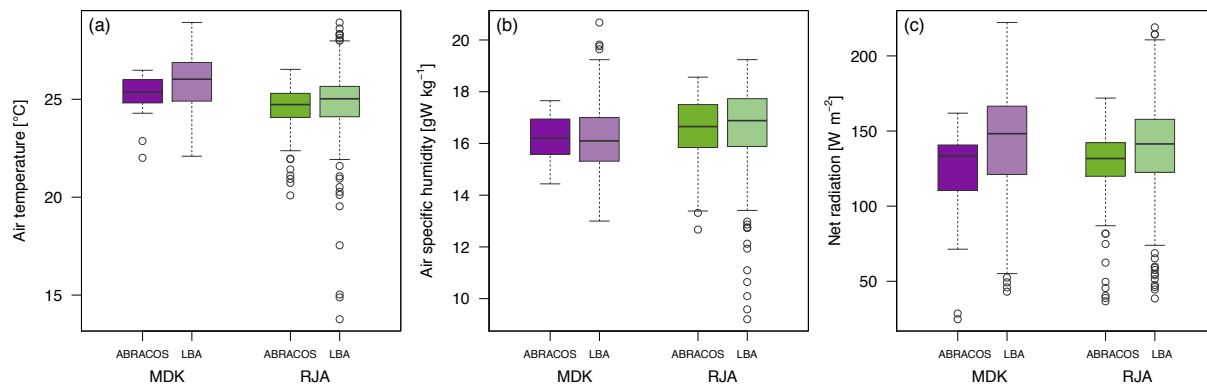
Figure S1: Box-and-whisker plots of the daily averages of (a) temperature, (b) specific humidity, and (c) net radiation of sites Jaru Biological Reserve (RJA) and the nearest sites from Adolpho Ducke Forest Reserve (MDK). The periods of comparison correspond to the Anglo-Brazilian Climate Observation Study (ABRACOS Cabral et al., 1996; Tomasella et al., 2008), and the data from the Large-Scale Biosphere-Atmosphere Experiment in Amazonia Data Model Intercomparison Project (de Gonçalves et al., 2013; de Gonçalves et al., 2013, LBA-MIP). For RJA, we used ABRACOS data from Aug-Sep 1992 and Apr-Jun 1993; for MDK, we used data from Fazenda Dimona (Jul-Aug 1991). For the LBA-MIP, we used the same days of year with ABRACOS measurements, from sites RJA (1999-2002) and K34 (1999-2006). Boxes correspond to the interquartile range, whiskers encompass data within 1.5 times the interquartile range, and the black line in the boxes are the median.
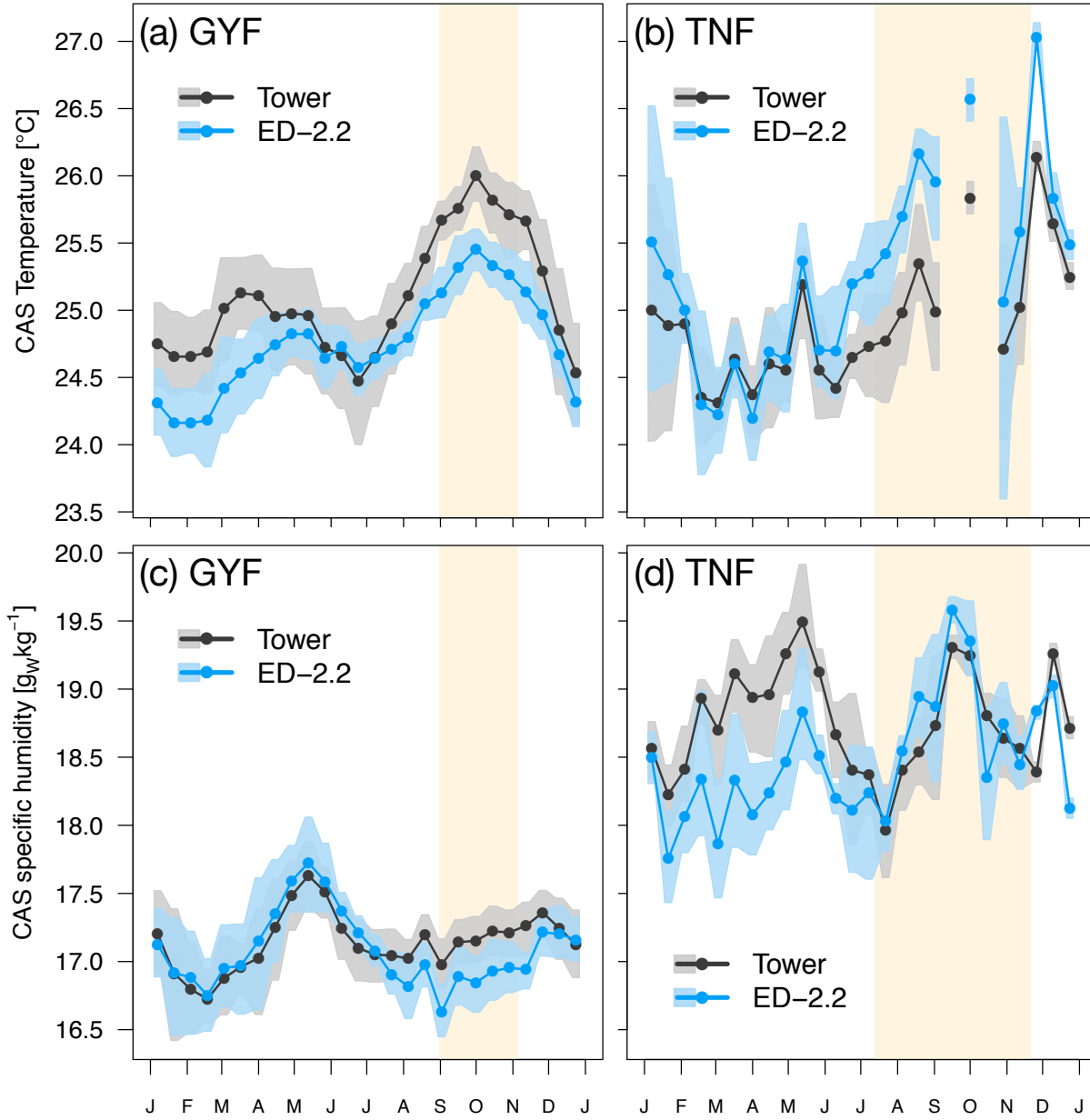
Figure S2: Fortnightly means of the (a,b) mean canopy air space temperature and (c,d) mean canopy air space specific humidity, obtained from the model and from the vertical average of the (a,c) GYF and (b,d) TNF tower measurements. Data for the TNF tower are available between 2002 and 2005 (Hutyra et al., 2008). Bands are the 95% confidence interval of means obtaining from bootstrapping, and rectangles in the background correspond to the site's climatological dry season. The missing periods are due to insufficient data of all times of the day to generate the fortnightly averages.
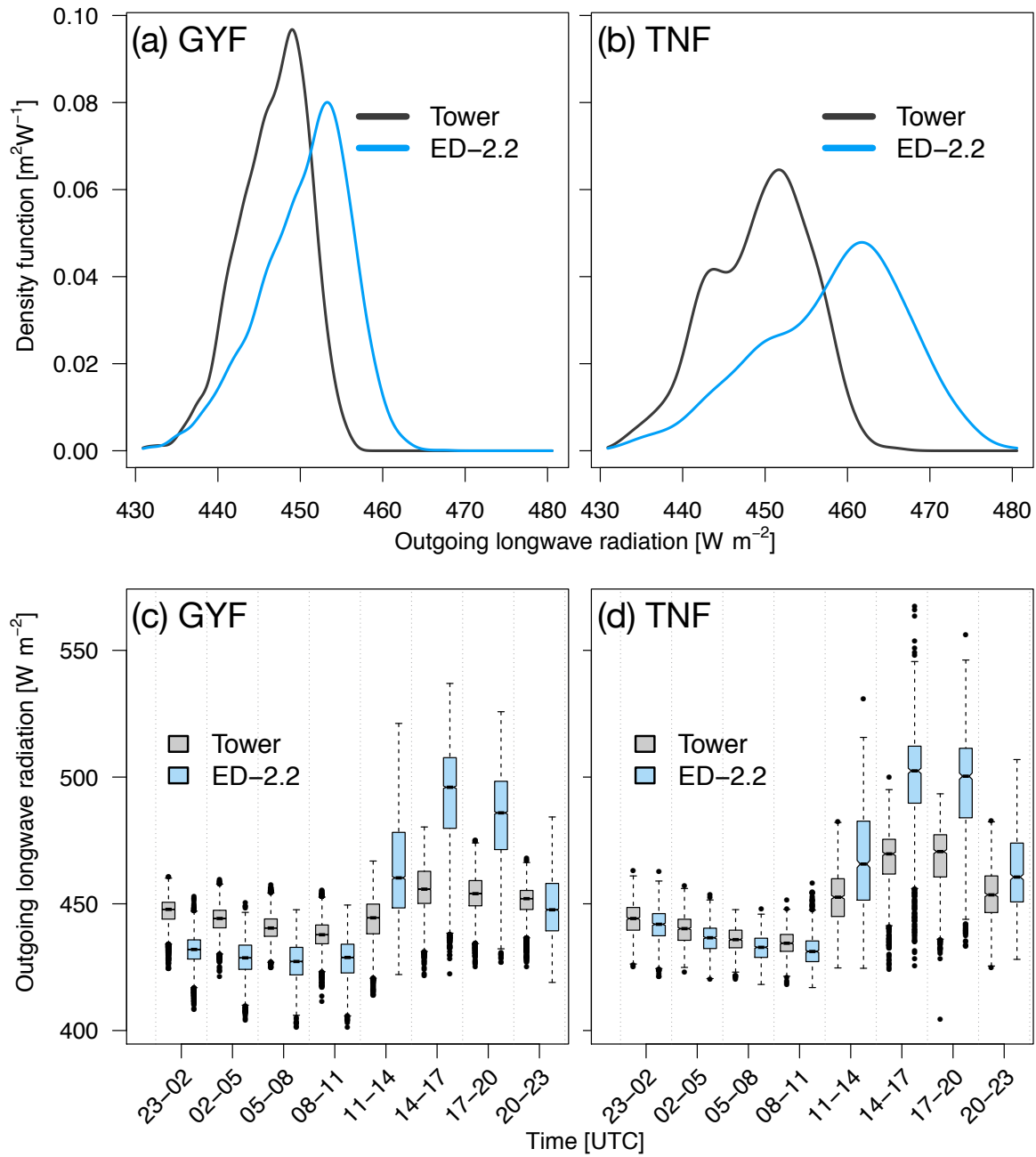
Figure S3: (a-b) Kernel density estimate of daily averages of outgoing thermal infrared (longwave) irradiance predicted by the model and measured at the towers for sites (a) GYF and (b) TNF. Only days with no gaps in observations were used to estimate kernel density for both observations and model. (c-d) Box-and-whisker plot of outgoing thermal infrared irradiance from ED-2.2 and observations, organized by time of day, for sites (c) GYF and (d) TNF. The model distribution includes only the times for which a corresponding observation existed.
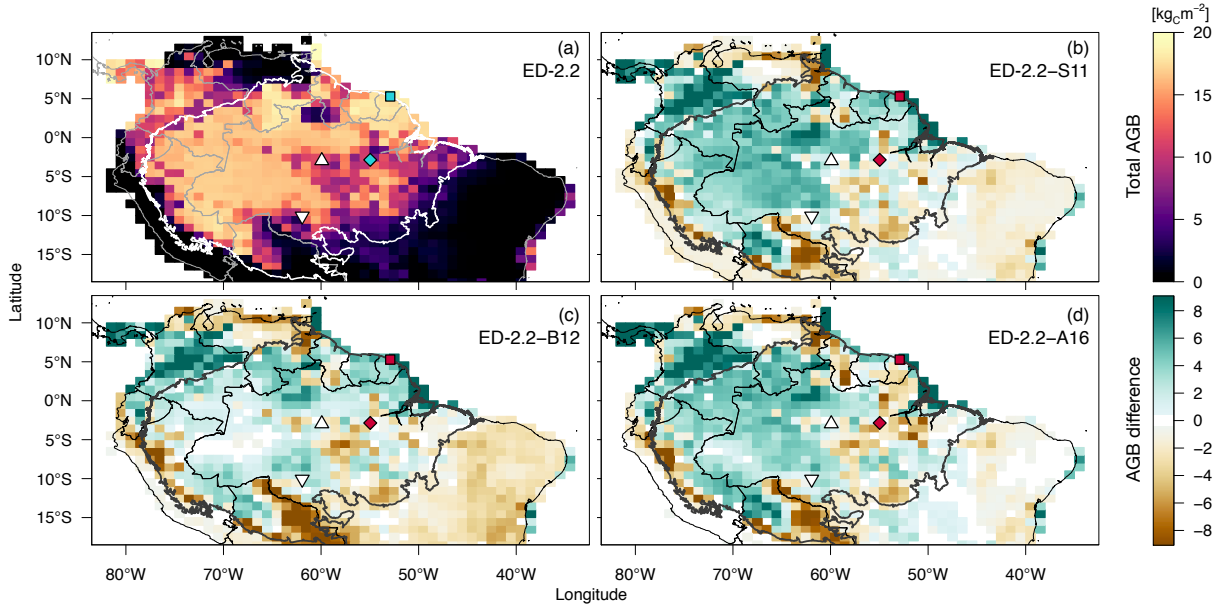
Figure S4: (a) Regional aboveground biomass obtained from ED-2.2, and difference between ED-2.2 and ~~based on~~ remote-sensing estimates from (b) Saatchi et al. (2011), (c) Baccini et al. (2012), and (d) Avitabile et al. (2016). Remote-sensing maps were aggregated to 1° resolution. Positive (negative) values in (b-d) mean that ED-2.2 predicted higher (lower) aboveground biomass than remote sensing estimates. The location of focus sites of Paracou (GYF, ~~triangle~~□) and Tapajós (TNF, ~~lozenge~~◇), and the sites used for radiation profile evaluation: Ducke (MDK, ✳△), and Jaru (RJA, ╋▽) are shown for reference. Thick contour is the domain of the Amazon biome, and thin contours are the political borders. **(Figure was updated, following R2 suggestion.)**
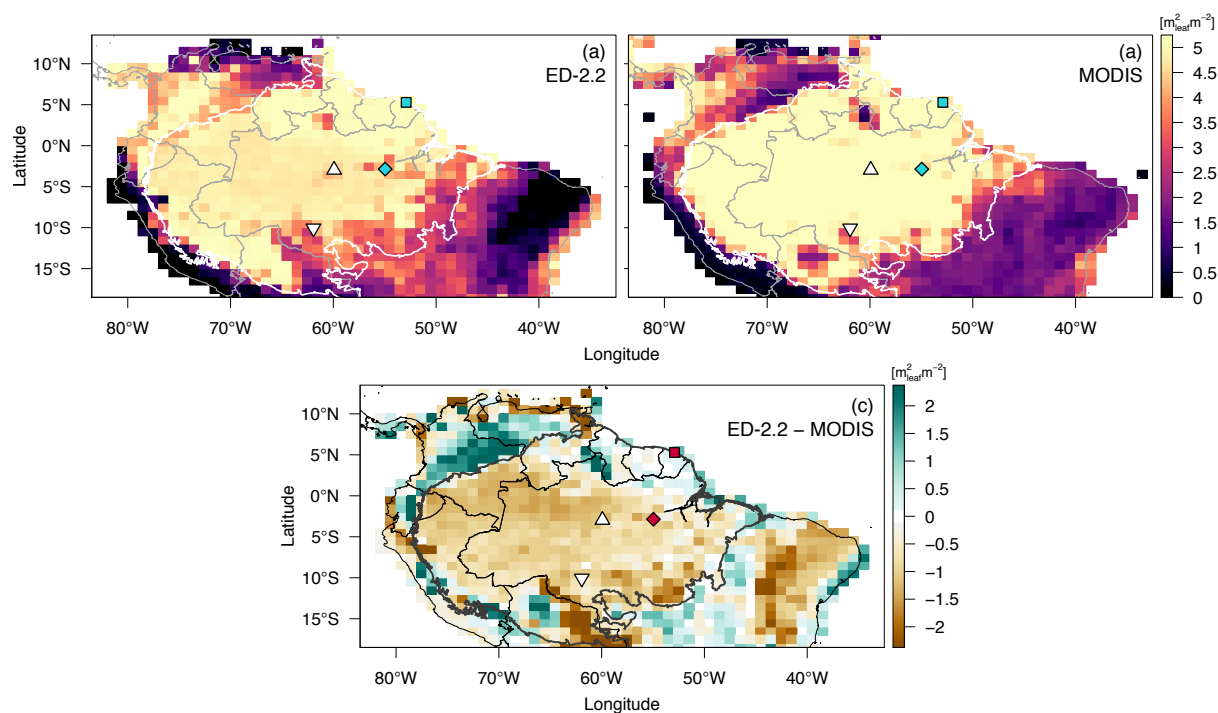
Figure S5: Comparison of leaf area index from (a) ED-2.2, and (b) based on remote-sensing estimates from Moderate Resolution Imaging Spectroradiometer (MODIS), product MCD15A2H, Collection 6 (Yan et al., 2016); (c) Difference between ED-2.2 and the MODIS-MCD15A2H product. Estimates from MODIS-MCD15A2H used all cloud-free, high-quality data available between August 2002 and July 2004. The location of focus sites of Paracou (GYF, ~~triangle~~□) and Tapajós (TNF, ~~lozenge~~◇), and the sites used for radiation profile evaluation: Ducke (MDK, ⨉△), and Jaru (RJA, +▽) are shown for reference. Thick contour is the domain of the Amazon biome, and thin contours are the political borders. **(Figure was updated, following R2 suggestion.)**
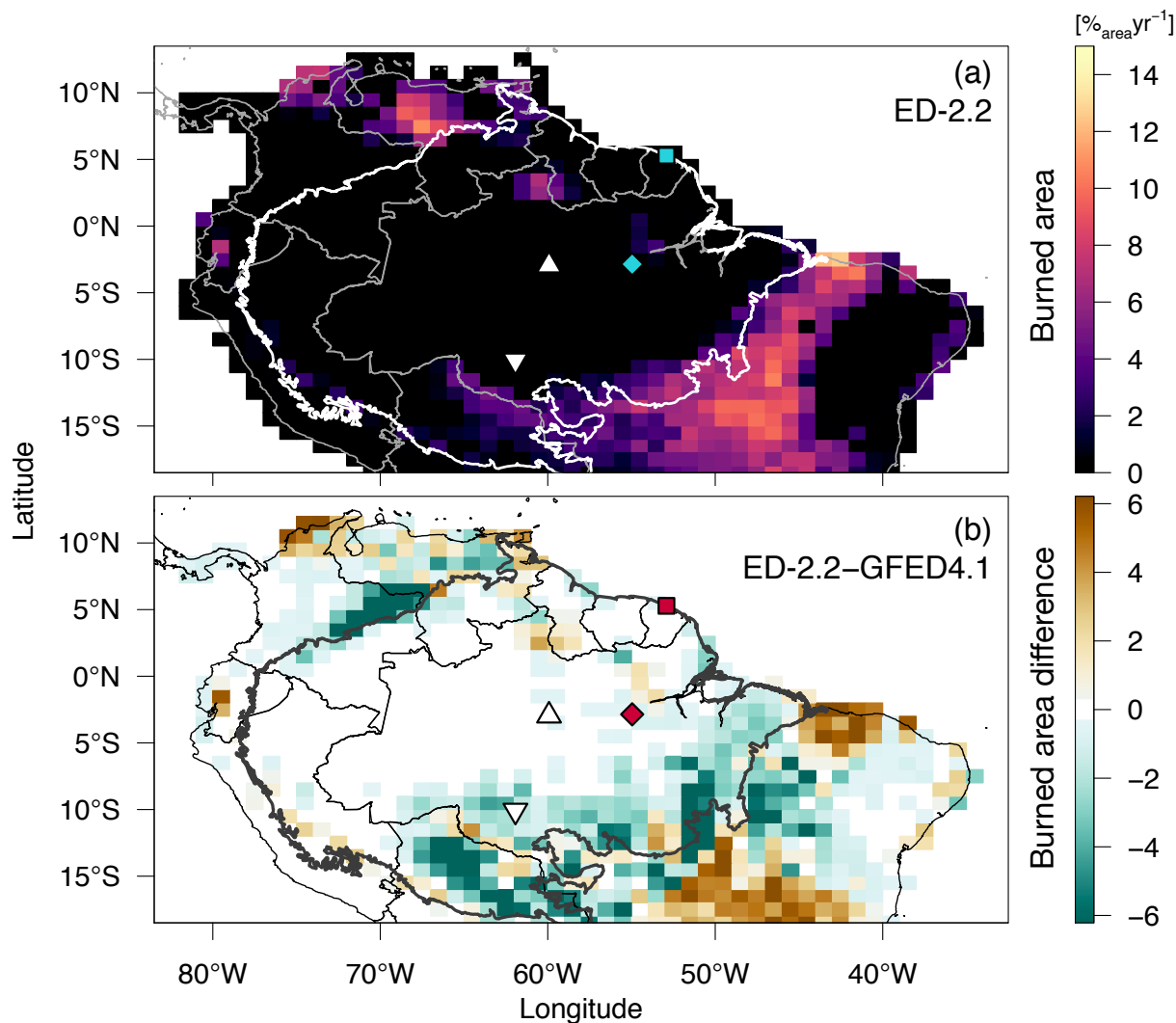
Figure S6: (a) Regional burned area obtained from ED-2.2, and (b) difference between ED-2.2 and the Global Fire Emission database (GFED4.1 Giglio et al., 2013; Randerson et al., 2018) burned area product (1997–2015 average). Remote-sensing maps were aggregated to 1° resolution. Positive (negative) values in (b-d) mean that ED-2.2 predicted higher (lower) aboveground biomass than GFED4.,1 estimates. The location of focus sites of Paracou (GYF, □) and Tapajós (TNF, ◇), and the sites used for radiation profile evaluation: Ducke (MDK, △), and Jaru (RJA, ▽) are shown for reference. Thick contour is the domain of the Amazon biome, and thin contours are the political borders.
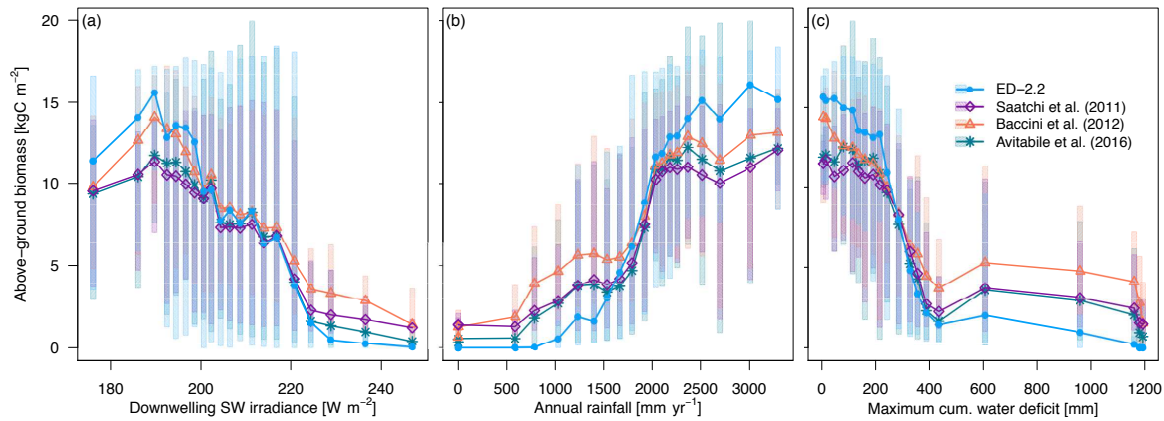
Figure S7: Average biomass predicted by ED-2.2 and based on remote-sensing maps, aggregated by annual averages of (a) downwelling shortwave irradiance; (b) mean annual precipitation; (c) maximum cumulative water deficit. For each annual average of environmental properties, grid points were grouped into 20 quantile bins: points represent the average within each bin, and shaded area corresponds to the 90% quantile range within each bin. Data source for the annual means: downwelling shortwave irradiance and precipitation Princeton Global Meteorological Forcing (PGMF; Sheffield et al., 2006) (1969-2008), which were also used as drivers for the ED-2.2 simulation; maximum cumulative water deficit was based on the same approach as Malhi et al. (2009a), using the PGMF precipitation.
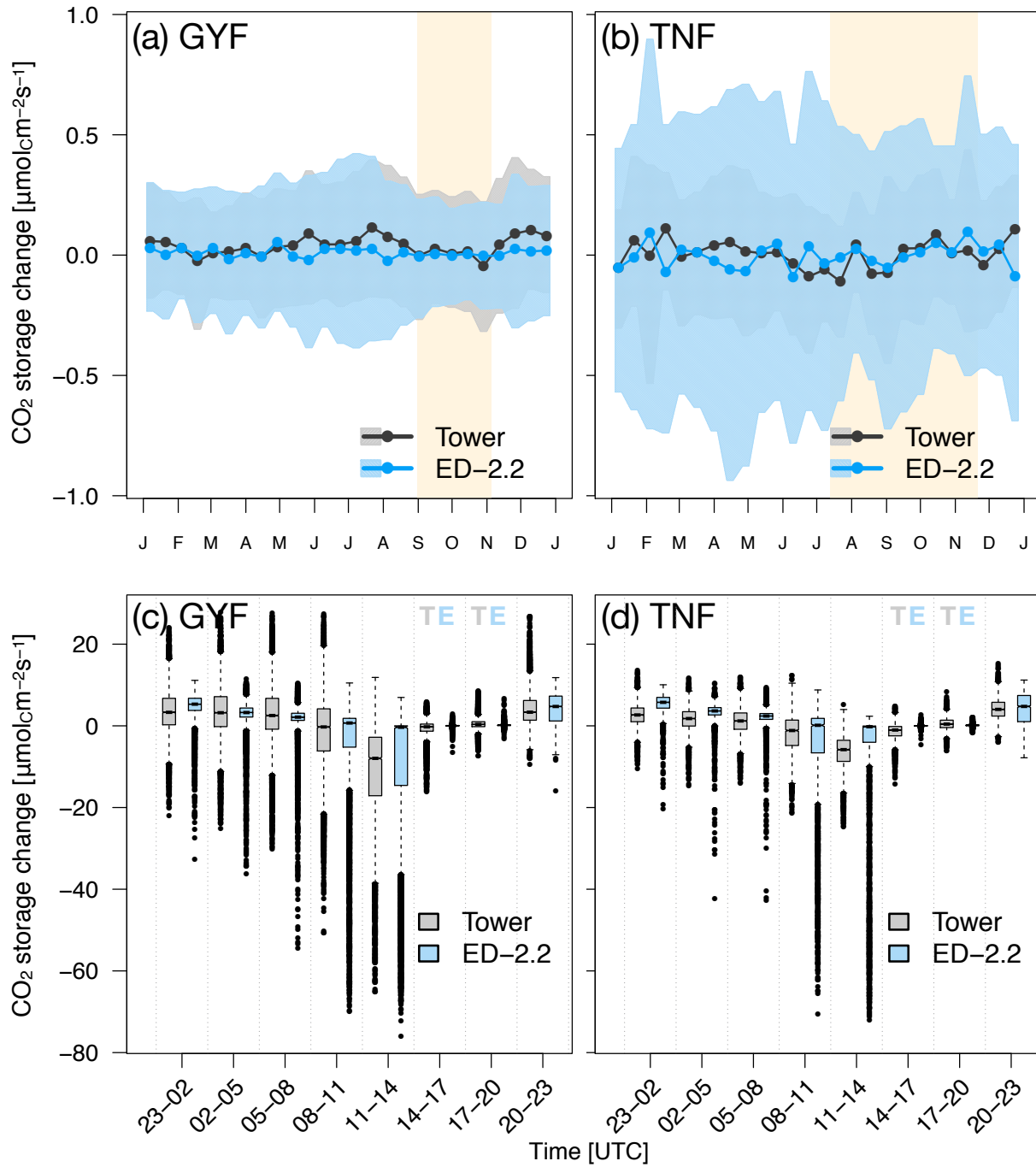
Figure S8: Mean annual cycle from fortnightly means of change in CO_2 storage in the canopy air space for (a) GYF and (b) TNF. Bands are the 95% confidence interval of means, and rectangles in the background correspond to the site's climatological dry season. Box plot of change in CO_2 storage in the canopy air space aggregated by time of day for all hours with available data for (c) GYF and (d) TNF.
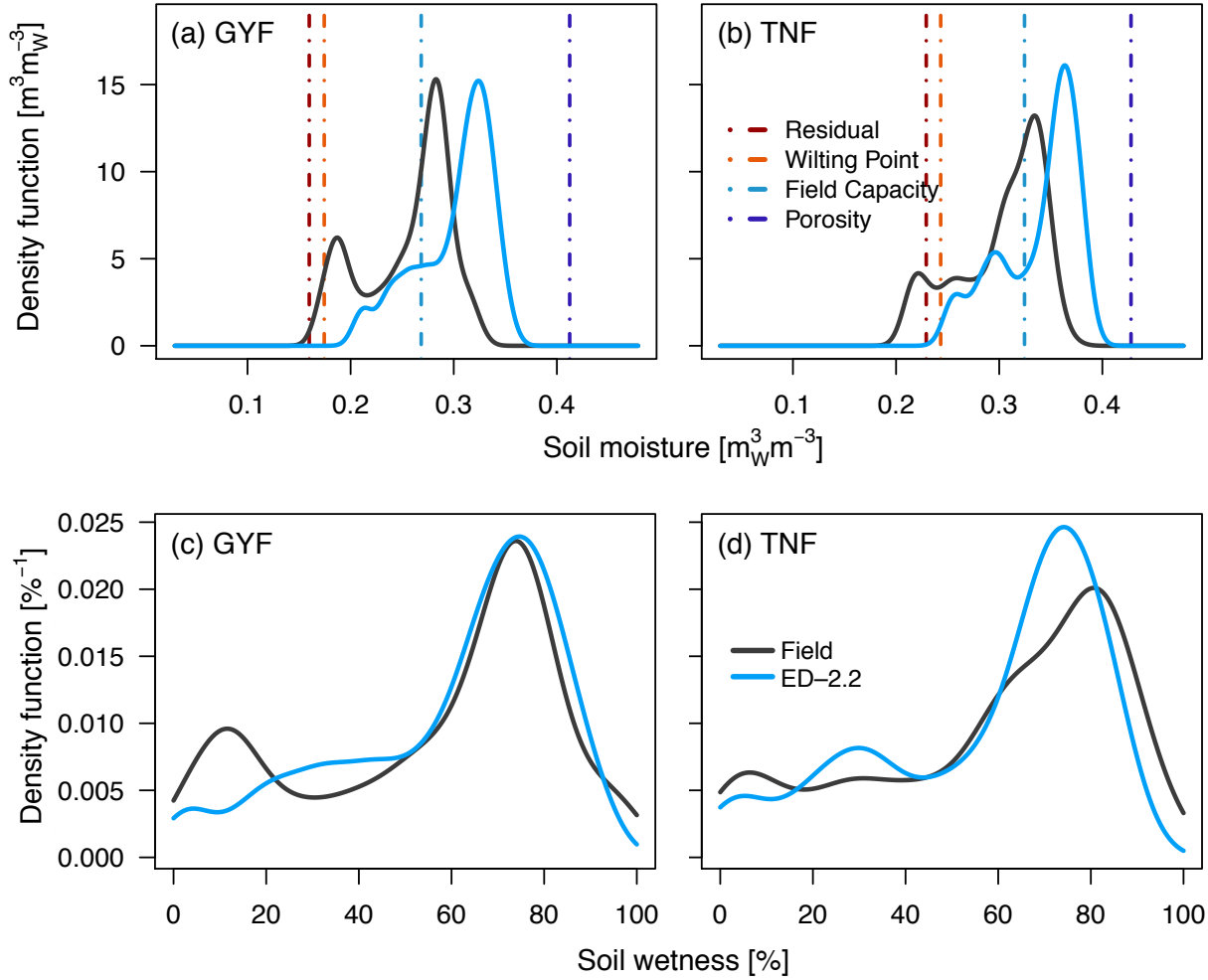
Figure S9: Kernel density estimate of daily averages of (a-b) volumetric soil moisture and (c-d) relative soil moisture at (a,c) GYF (depth 53 cm) and (b,d) TNF (depth 20 cm). Data for GYF were collected at the tower site (2007-2012), and data for TNF were collected at a site located 15 km south of the tower between 2001 and 2003 and available from Miller et al. (2009) and de Gonçalves et al. (2013). Vertical dashed lines in panels (a) and (b) correspond to the residual, permanent wilting point, field capacity and porosity calculated by ED-2.2 using the reference soil texture at each site: (56% sand; 9% silt; 35% clay) for GYF (Bonal et al., 2008), and (39% sand; 2% silt; 59% clay) for TNF .(Nepstad et al., 2002) Soil wetness was defined as the relative water content between residual (0%) and porosity (100%).

S1 Derivation of the respiration estimates at Guyaflux (GYF)

To obtain respiration estimates at Guyaflux (GYF), we follow the same methodology described by Malhi et al. (2009b), and used the same approach to obtain the standard error estimates. Whenever possible, we used published estimates of the different terms of the respiration terms.

- *Leaf respiration*. Individual-level leaf respiration was measured and reported by Stahl (2010). Leaf-level measurements were scaled to ecosystem scale using LAI-2000 measurements also by Stahl (2010). Following Malhi et al. (2009b) and Lloyd et al. (2010), the value was scaled down by 34% to account for diurnal down-regulation of dark respiration.

- *Stem respiration*. Individual-level stem respiration was measured and reported by Stahl (2010); Stahl et al. (2011). Values from both *terra firme* and seasonably flooded forest were included. Wet season and dry season values were weighted by the season length in 2008, also reported by Stahl et al. (2011). Although Stahl et al. (2011) had scaled to stand level, we recalculated their estimate to be consistent with Malhi et al. (2009b), by finding the mean stem area index from the forest inventory, following Chambers et al. (2000, 2004). The stem area index was 1.07 ± 0.03 m^2 m^{-2}.

- *Total soil respiration*. Total soil respiration was reported by Epron et al. (2006) and Bréchet et al. (2011). Following Malhi et al. (2009b), their estimates were averaged using an weighting factor equivalent to the sampling area times the square root of the duration of the measurments.

- *Coarse woody debris respiration*. Coarse woody debris (CWD) respiration was reported by Rowland et al. (2013). Their estimates of coarse woody debris respiration were scaled by soil water content, and thus these estimates are not entirely observed.

- *Soil Heterotrophic respiration*. This term was estimated by Bréchet (2009), using trenching method.

- *Root respiration*. This term was assumed to be the difference between total soil respiration and soil heterotrophic respiration, following Malhi et al. (2009b).

- *Aggregated respiration terms*. Heterotrophic respiration (soil + CWD), autotrophic respiration (leaf + root + stem), and ecosystem respiration (heterotrophic + autotrophic) were defined

as the sum of the terms, as defined above. Uncertainties were assumed independent, and propagated similarly to Malhi et al. (2009b).

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