TROLL 4.0: representing water and carbon fluxes, leaf phenology and intraspecific trait variation in a mixed-species individual-based forest dynamics model – Part 1: Model description

Responses to reviewers

Referee 1:

The manuscript describes a new version of TROLL, which represents 3D variation in canopy heterogeneity and individual-level dynamics that can best match field observations. The main development is to include (1) water fluxes, plant water stress, and some degree of micro-environment variability, (2) random intra-species variation, and (3) more realistic crown shapes.

As a vegetation modeler, I read the manuscript and the companion paper with great interests because representing species-level dynamics and 3D heterogeneity are important yet challenging in predicting tropical forest dynamics. I appreciate the efforts by the authors to push in this direction. At the same time, I feel the organization and presentation can be improved to better highlight the novel development and some of the model assumptions warrant justification and further discussions.

R: we thank the referee for his very constructive and useful comments. They have helped improve the quality of our two manuscripts and we have addressed all of these comments as detailed below.

Overall, I would recommend reporting more key intermediate variables in the new modules (beyond ecosystem-level outputs in Fig. 4), such as predawn water potential, stomatal conductance, evaporation/transpiration partitioning, LAI_opt, etc. These will help the readers understand the behavior of the model and better interpret the other companion paper. Given the unique 3D configuration, it would be cool to show the simulated vertical/horizontal variation of the new processes/variables.

R: The variation of several additional variables (such as evaporation/transpiration partitioning, or individual demographic rates) is now shown in the revised companion paper; this provides a more complete understanding of the model behaviour. The horizontal variation of simulated and observed canopy height is also provided in the companion paper. We agree that a more in-depth exploration of the vertical and horizontal variations of simulated ecosystem functioning and structure would be valuable, and this is a work in progress which we leave for a future contribution.

In addition, the leaf phenology section is tough to read through. Some schematic figures to explain the phenological dynamics would be helpful.

R: following the reviewer's suggestion, we have now added a new figure to clarify this section (see new Figure 4).

Finally, it can be useful to conduct/report some sensitivity tests of key model parameters (e.g. crown area allometry, rooting allometry, vertical temperature/VPD gradient etc.) so that we know how results might change with these parameters qualitatively.

R: we agree, but we believe a detailed sensitivity analysis is out of the scope of our already long manuscripts. The model sensitivity to the calibrated parameters is now illustrated in the revised version of the companion manuscript. The effect of root allometry and micro-climate variation on simulated outputs are currently being explored and a description of this work is left for future contribution.

Below I list my specific comments along the order of the manuscript

Line 52-65, there are some efforts to extend gap models regional to global scales. See the two reviews by H. Shugart

Shugart, H. H., Wang, B., Fischer, R., Ma, J., Fang, J., Yan, X., Huth, A., & Armstrong, A. H. (2018). Gap models and their individual-based relatives in the assessment of the consequences of global change. Environmental Research Letters, 13(3), 033001. https://doi.org/10.1088/1748-9326/aaaacc

Shugart, H. H., Foster, A., Wang, B., Druckenbrod, D., Ma, J., Lerdau, M., Saatchi, S., Yang, X., & Yan, X. (2020). Gap models across micro- to mega-scales of time and space: examples of Tansley's ecosystem concept. Forest Ecosystems, 7(1), 14.

R: thank you for these references. The efforts made to expand the scale of applications of gap models have now been better highlighted l. 58-59.

Line 168-176: Does this radiative transfer scheme consider solar geometry? It seems to me LAI(v) only considers the LAI right above the voxel, which means the model does not consider the diurnal and seasonal changes in solar zenith angle. This seems to be too simplistic to me, which can lead to biases in leaf physiology predictions. In addition, is *k* a fixed global parameter or species-specific?

R: the radiative transfer scheme included in TROLL 4.0 does not consider solar geometry, and light diffusion through the canopy is computed through a vertical only iterative process. While we have shown that this is a reasonable approximation for the model purposes in tropical regions, this may need to be reconsidered to transfer the model to other regions with stronger variation in solar zenith angle. Although the light extinction rate k is indeed expected to vary with zenith angle and species leaf inclination angle, it is here assumed uniform and constant to be consistent with the model representation of light diffusion (we also note that relevant data are largely missing for tropical tree species). This is now better acknowledged l. 166-169 and 177-178.

Line 177-188: this LAI-based extrapolation of temperature and VPD seem problematic to me for at least three reasons. First, this scheme means both canopy and understory have the same diurnal temperature range based on eqn. 4 but understory will just be a few degrees cooler. In reality, canopy temperature has large diurnal variations (due to radiative heating) while understory has smaller variations (more similar to air temperature). One idea is to use radiation/air temperature to estimate crown-level temperature (e.g. following Rey-Sanchez et al. 2016). Second, such empirical extrapolation will likely violate the physical linkage between T and VPD. A better method is to interpolate relative humidity and temperature, then calculate VPD based on RH and T. Third, these empirical relationships might not hold when making future predictions under novel climate regimes. Ideally, energy balance should be tracked but I understand it might be too 'heavy' for a 3D model.

Rey-Sánchez, A. C., Slot, M., Posada, J. M., & Kitajima, K. (2016). Spatial and seasonal variation in leaf temperature within the canopy of a tropical forest. Climate Research, 71(1), 75–89.

R: The simple empirical representation of within-canopy micro-environmental variation in TROLL is indeed imperfect in several regards. Such representation was inherited from the previously published version of TROLL (Maréchaux & Chave 2017), and was in agreement with the few data available at that time, as explained l. 197-201. As data has been accumulated over the past few years, we are currently evaluating alternative empirical representations, such as the ones relying on recent tools (Maclean and Klinges, 2021), to assess the actual cost and benefit of including an explicit energy balance (such as in Ogée et al., 2003). This is now better acknowledged l. 201-203 (in addition to what was already suggested in the discussion l. 1059-1060). However, note that this empirical variation of temperature and VPD are the ones of the air within the canopy, and not the one at the leaf surface as in Rey-Sánchez et al. (2016). The temperature and VPD at the leaf surface are computed from the variables of the surrounding air using an explicit energy balance (see sections 2.5.4 and equations and references therein). Therefore, Eq. (4) and (5) do not necessarily imply a qualitative disagreement with what is shown in Rey-Sánchez et al. (2016).

Line 218-227. It might be better to expand equation 10 into 2, one for top layer one for other sub-surface layer.

R: thanks, we have now added two sub-equations, one for the top soil layer (Eq. (10a)), and one for the other layers (Eq. (10b))(l. 235-241).

Line 254: how is soil temperature calculated?

R: the temperature at soil surface is computed following Eq. (4) at ground level. This is now clarified l. 273. As answered to the reviewer above, while this is a simplification and we are currently exploring more process-based alternatives, we assume this is a reasonable approximation for our first objectives given the low contribution of soil water evaporation in dense forests (Kunert et al., 2017). We don't have an explicit representation of soil temperature.

Line 274: it is good to see van Genuchten equation is used here!

Line 285: it is unclear to me how LA is used in the model. Is it used to calculate LAD of each voxel in the crown? If so, how?

R: Leaf-level area (LA) is used to compute the leaf boundary layer conductance for free and forced convection (see. Eqs. (46) and (47), and l. 600-601). Leaf mass per area (LMA) is used to convert biomass allocation to leaf production into crown-level total leaf area (see Eq. (56)).

Line 296: it seems that there is no light-associated vertical trait gradient (or, light-driven trait plasticity) in the model, but this plasticity has actually become a common feature in many vegetation models. Besides, our work with ED2 model (e.g. the method section in Xu et al. 2021 and a manuscript under review) has shown that light-driven plasticity is critical to model realistic LAD profile in tropical forests. And representing realistic environmental plasticity is recognized as a research priority (Fisher & Koven 2020; Xu & Trugman 2021)

Fisher, R. A., & Koven, C. D. (2020). Perspectives on the Future of Land Surface Models and the Challenges of Representing Complex Terrestrial Systems. Journal of Advances in Modeling Earth Systems, 12(4). https://doi.org/10.1029/2018ms001453

Xu, X., & Trugman, A. T. (2021). Trait-Based Modeling of Terrestrial Ecosystems: Advances and Challenges Under Global Change. Current Climate Change Reports, 7(1), 1–13. https://doi.org/10.1007/s40641-020-00168-6

Xu, X., Konings, A. G., Longo, M., Feldman, A., Xu, L., Saatchi, S., Wu, D., Wu, J., & Moorcroft, P. (2021). Leaf surface water, not plant water stress, drives diurnal variation in tropical forest canopy water content. New Phytologist, 231(1), 122–136. https://doi.org/10.1111/nph.17254

R: we do agree that light-driven trait plasticity is widespread in dense forests and a current front of development in vegetation models. While this was already acknowledged and discussed in the companion paper, this was missing in Part 1 and this is now better developed l. 316-317 and l. 1045-1047, also in agreement with a comment of Reviewer 3. Note however, that, while for a given individual, leaf properties do not vary vertically within the crown, and the variation of leaf properties across individuals within species is not controlled by their position within the canopy, the model still accounts for vertical trait variation across the canopy that results from the co-variation of leaf properties and stature across species.

L 304: If allometry has a random term, how is growth in height tracked in simulations? Wouldn't it cause troubles in carbon conservation when converting NPP to woody and height growth? Or this is only used during initialization?

R: the random term is associated to the individual tree, it is randomly drawn at tree birth, and not independently drawn at each time step. This is noticeable with the subscript "h,j" (and not h_j), and this is now clarified l. 328-329.

L 319: "the treetop grows quicker in height than the outer crown parts" reads confusing to me. How quicker? what functions are used to determine the difference? How is carbon/leaf area balance is maintained in the process? In addition, how is total leaf area calculated for each tree crown? Is any leaf area allometry used? If leaf area allometry is an emerging feature of the model, is it consistent with observations (e.g. the BAAD data base, Falster et al. 2015)

Falster, D. S., Duursma, R. A., Ishihara, M. I., Barneche, D. R., FitzJohn, R. G., Vårhammar, A., Aiba, M., Ando, M., Anten, N., Aspinwall, M. J., Baltzer, J. L., Baraloto, C., Battaglia, M., Battles, J. J., Lamberty, B. B., van Breugel, M., Camac, J., Claveau, Y., Coll, L., … York, R. A. (2015). BAAD: a Biomass And Allometry Database for woody plants. Ecology, 96(5), 1445. https://doi.org/10.1890/14-1889.1

R: We agree that this section may create confusion and we have clarified it (l. 339-348). This section solely refers to the shape of the tree crown, and not its total extent, nor its total leaf area or carbon balance. Total leaf area emerges from the carbon allocation to leaf production, converted to area using the tree LMA, and leaf shedding, described in section 2.6.2, and this now clarified l. 336-337. The growth of the tree top/centre is fully determined by the tree height allometry, and the crown's horizontal extent is fully determined by the crown radius allometry. What is described here is how space between the tree top and crown edge is filled in, i.e., whether and by how much tree height declines towards the outer edges of the crown. For this, various idealized or empirically calibrated shapes can be prescribed (e.g. cylinders, cones). The default shape is an umbrella-like shape as visualized in Schmitt et al. (2023).

L 357: I believe the horizontal extent of the root is usually bigger than crown. You might check Schenk et al. 2002 for some global meta-analysis of lateral root extent

Schenk, H. J., & Jackson, R. B. (2002). Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. Journal of Ecology, 90(3), 480–494. https://doi.org/10.1046/j.1365-2745.2002.00682.x

R: the rare data available on the horizontal extent of tree root distribution indeed suggests it can expand beyond the crown dimension footprint. We thank the reviewer for mentioning this interesting reference we were not aware of. However, Schenk & Jackson (2002) focused their study on water-limited systems, and tropical forests are particularly under-represented relatively to their taxonomic and functional diversity (see Fig. 2 in Cusack et al., 2024, in which, interestingly, horizontal extent of root distribution is even not mentioned). This is now better discussed l. 383-386.

L. 391: Sounds like Ca has vertical gradient in the model? How is the gradient simulated in the model?

R: No, we assumed CO_2 air concentration does not vary vertically within the canopy. This assumption was made on the basis of measurements made at the Paracou site showing that CO_2 concentration was almost constant across the canopy vertical gradient, apart from the few centimetres above the ground (Buchmann et al., 1997) where no gas exchange is simulated within this TROLL version. This could be easily revisited in the future. This is now clarified l. 216-217.

L. 420: internal leaf temperature reads confusing, does the model separates leaf surface temperature and internal temperature?

R: no, this has been corrected l. 450.

L. 426: Isn't photorespiration already accounted for in the Farquhar model? Or do you mean reduction of daytime respiration due to Kok effect?

R: yes, photorespiration is accounted in equation (24). We here described how it is computed, assuming a reduced respiration rate in the light in agreement with observations (Atkin et al., 2000). We now explicitly refer to the different equations to make this crystal clear.

L 479-480: for tropical forests, many recent work by M Slot has evaluated non-stomatal limitation....

R: thanks for the information. However, we were not able to find recent published results from Martijn Slot supporting a dominated effect of non-stomatal limitation under decreased water availability, but look forward to seeing this published if this is on-going.

L 508: In Xu et al. (2016) we applied this limitation at sub-daily scale instead of daily scale in order to better capture midday suppression in photosynthesis and stomata functioning. To be honest, I am not aware of solid physiological support for such subdaily non-stomatal effects. That being said, applying this at daily scale won't have much effects (psi_pd is usuallal much higher than psi_tlp).

R: thanks for your thoughts and feedback on this specific point. As now better discussed in the companion paper, the fact that our representation of gas exchange reduction as water availability decreases relies on leaf predawn water potential (and not on leaf water potential which varies much more within a day) likely explain the overestimated productivity in the dry season. We aim at implementing a more explicit representation of leaf water status within TROLL and compare its outputs with the ones of the current version, but choose this first more parsimonious approach given the low data availability on whole plant conductance and vulnerability to cavitation in such biomes, as discussed l. 968-980. As explained l. 544-545, it is expected that non-stomatal limitations through damage of the photochemical apparatus arise lately, in comparison to the decline of other functions as drought increases

L 531-582: The "leaf energy balance" from Penman-Monteith equation is interesting... I am not sure whether this is actually circular given gs as already been calculated. In my understanding, Tl and VPD are 'inferred' to match Medlyn gs with Penman-Monteith ET... This does not seem right to me. Again, figures of simulated diurnal/seasonal cycle of Tl and VPDs would be helpful.

R: Actually gs and CO2 assimilation rate are re-computed at each iteration with the new Tl and VPD values, using the Medlyn and Farquhar model respectively. The iterative scheme stopped when differences in values between two iterations are below a given threshold, as explained l. 566-571 and as in Medlyn et al. (2007). So, Tl and VPD are not ‘inferred’ to match gs, and there is no circularity.

L 610: what does "conversion factor" mean? convert to what?

R: this has been clarified l. 640-641.

L. 681: great to see woody branch turnover is included in the model! They are important!

L 702-704: interesting way to simulate increasing in new leaves and loss of old leaves in dry season but it still only assumes water is the main driver of phenology? Where does leaf age limitation comes into play in this scheme?

R: The shedding of old leaves is indeed accelerated under decreasing water availability, but leaf senescence also plays a role as the leaf turnover in absence of any decrease in water availability is computed from the maximal leaf lifespan (see equations (56) and (57)). The production of new leaves strongly depends on light availability as it is determined at each timestep by computing the net benefit of producing new leaves accounting for self-shedding and the tree photosynthetic and respiration rates, as explained l. 706-709.

L 706-712: I have a hard time to interpret these parameterizations and how they influence phenology. It would be helpful to plot a diagram of the phenological cycle under different a/b/delta parameters.

R: we have now added a new figure 4 to clarify the effect of $a_{T,o}$ and $b_{T,o}$. The sensitivity to the three parameter values has also been better illustrated in Fig. A5 of the companion paper.

L 739-740: what is the fate of the senescenced NPP? Are they lost to respiration?

R: the fate of this senesced NPP is actually not tracked in this version of the model. As discussed l. 1047-1049, future versions could include improvements to fully close the carbon budget, and we have now highlighted this should include respiration terms.

L 761: what is reproduction opportunity? established 1cm sapling?

R: yes, l. 793-795 did provide an explanation, but this has now been clarified.

Line 879 Fig.4 panel (a) Gross not Growth, panel (d) Psi_TLP is hard to read. In addition to these figures, it would be helpful to show carbon balance at individual tree to ecosystem level (I guess only carbon conservation is tracked?)

R: this has been corrected on the figure (now Figure 5). This figure aims at providing examples of model outputs as requested by the journal guidelines ("Examples of model output should be provided"), and other outputs are discussed and compared to data in the companion paper, while carbon balance is discussed l. 1047-1049.

L 973: how many CPUs (what type of CPU) are used?

R: This referred to a single TROLL simulation on a single CPU. We have added this information l. 1023.

L 1034: I am surprised that the C++ codes are all in a single cpp file for TROLL. From a software engineering perspective, this is not the best practice to organize the codes of 10k+ lines. I would recommend modularization in the future to facilitate model development and sharing....

R: This is a good point. We have been meaning to provide a more modular version of the code, and agree this is a better practice. We leave this improvement for a forthcoming version.

Referee 2:

I think this manuscript should be merged with part2 (TROLL 4.0: representing water and carbon fluxes, leaf phenology, and intraspecific trait variation in a mixed-species individual-based forest dynamics model – Part 2: Model evaluation for two Amazonian sites) instead of acting as an extra paper to be published.

R: the split in two parts was motivated by the length of the manuscripts and the fact that while Part 1 aims to be generic, Part 2 aims to specifically evaluate the model for Amazonian forests, and as suggested in the journal guidelines ("Where evaluation is very extensive, a separate paper focussed solely on this aspect may be submitted"). We leave it to the editor to decide on this point. We do note that previous papers in Geoscientific Model Development have followed this strategy (e.g. Longo et al., 2019a, b)

Here are detailed comments:

1. The introduction part from the beginning to Page 3 Line 90 is too long, while there is too short to introduce current research gaps and your model contributions (from Lines 96-100). I suggest the authors reorganize the paragraph structure to shorten the modeling history and stick out why the community need your model. In you paragraph, I learn that (from Lines 96-100) the finer model may able to address the spatial mismatch problems between model simulations and observations in some degrees. However, there is far away enough, add more to make your readers feel like your model is important.

R: In agreement with other reviewers' comments, we have further developed the model novel contributions in light of the short historical overview of modelling approaches provided at the beginning of the introduction, both in the introduction l.132-134 and in the discussion l. 933-936, 1007-1015.

2. Lines 109-111: I suggested the author can point out how much uncertainties of the previous TROLL in simulating some biochemical processes and structures so that they can let the readers know why their new developed model TROLL 4.0 really matters.

R: what is new to this TROLL version in comparison to previous ones is now better explained in the next paragraph (l. 122-134), which provides a finer description of the model structure and representation of tree- to ecosystem-scale processes.

3. Lines 332-333: I disagree with this agreement that LAI has no relationship with crown extent.

R: We were uncertain whether the referee was referring to the relationship between total leaf area and crown extent, or leaf area index (leaf area per unit crown area) and crown extent. We assume they referred to total leaf area, as this is what lines 332-333 were addressing.

First, we note that, generally, total leaf area has a strong positive relationship with crown extent in TROLL. This is because the total leaf area of crowns in TROLL is limited in two ways: by sapwood area and by self-shading, i.e., leaves are only added to the crown in proportion to conductive stem tissue and if their photosynthesis production exceeds respiration costs. Both limits directly change with tree crown size: (i) sapwood area increases with stem diameter growth in TROLL and thus also with crown growth; (ii) given the same amount of total leaf area, larger crowns experience less self-shading, so they can add more leaves, before reaching the predicted limits of total leaf area.

Second, total leaf area and crown extent are only assumed to be independent in TROLL among individuals when sapwood area is held constant, and only within species. Since sapwood correlates with stem diameter, one could also say that total leaf area and crown extent are only independent for similarly-sized trees of the same species. The idea is that a tree that has more space to grow and can extend its branches further laterally can only exploit this space better for photosynthesis when it simultaneously grows more conductive tissues to support new leaves. We have amended the sentence to make this clearer (l.339-348).

4. Line 335: why ”total fine root biomass is equal to leaf biomass”?

R: Thanks. This assumption is made on the premise that root biomass should track leaf biomass as the former capture resources (water, nutrients) that are critical to sustain the functioning of the latter. As discussed l. 360-361 and l. 1048-1049, while other models make the exact same assumption, a more explicit and plastic allocation to roots could be considered in the future.

5. Line 485: TROLL calculated Vcmax and Jmax based on the LMA and N, have you considered the impact of water stress on LMA and N?

R: this is an interesting suggestion. Non-stomatal limitations of gas exchanges are more related to damage in the photochemical apparatus than to impacts on LMA and nutrient content. Additionally, implementing a drought effect on LMA and N would lead to non-independent effects on other processes such as respiration or carbon allocation to leaves, which would be difficult to represent given the current state of the art.

6. Fig 4. I think figures are not enough to explain TROLL model at all
    1. Figure 4 should showed the results of these two tropical sites seperately and validate the model accuracy with the site level measurements
    2. For all process revised and new incorprated like hydrulics, soil water, photosynthesis, LAI, the authors should plot figures to let readers know what’s the TROLL model’s performance. That’s to say, all processes you listed in the model description should be visulized and validated. Also detailed analysis these results are very necessary.

R: as answered above, this is the aim of the companion paper and we kindly refer the reviewer to this Part 2. This figure here aims at illustrating the type of outputs the model can produce as requested by the journal guidelines (“Examples of model output should be provided”).

7. Lines 901-911: I agree but why you think current TROLL model development is appropriate? what scientific questions new TROLL can answer?

R: Thank you very much again for pointing to the relevance of this work. These has now been better highlighted at the end of the introduction following one of the reviewer’s previous comments, and are also summarized, and now better elaborated, at the beginning of the discussion (l. 933-936).

8. Line 963 What’ s the meaning of data-driven knowledge?

R: this has been rephrased to clarify l. 1007.

9. Lines 983-984: rephrased this sentence, too exaggerated

R: this sentence has been rephrased.

Referee 3:

In this manuscript, the authors present the TROLL 4.0 model, which simulates forest dynamics and processes at the scale of individual trees. Improvements in TROLL 4.0 from the previous version of the model include representation of the water cycle and non-structural carbon storage. In addition, traits can now vary for individuals within a PFT/species – this is an exciting development!

The design of this model seems ideal for parameterizing based on field measurements and for comparing output to field and lidar data. It was a bit unclear to me how the model could help us to improve DGVMs that can be coupled to GCMs, and I would love to see this discussed more explicitly in the text! In addition, it would be helpful to include some figures showing parameter sensitivity.

R: we thank the reviewer for this encouraging comments. We have now better discussed how a model like TROLL could support the improvements of DGVMs as detailed below. Also, sensitivity to some parameters has been better illustrated in the revised version of the companion paper.

Major comments:

Figure 4 – I think this figure should be presented in companion paper instead. In its place, it would be useful to see some figures showing the sensitivity of the model to variations in PFT/species input parameters.

R: Fig. 4 intends to provide an illustration (and not an evaluation) of the type of outputs the model can produced as required for a “model description” manuscript type in Geoscientific Model Development (the guidelines read “Examples of model output should be provided”). We respectfully think that performing a sensitivity analysis in beyond the scope of this description manuscript.

Line 965 – “TROLL 4.0 can help inform the development of DGVMs” – can you explain more about how this model can act as a bridge between observations and DGVMs that can be coupled to GCMs?

R: we have now better developed this point l. 1007-1015. One option would be to use TROLL as an emulator of a DGVM. Another option would be to use it as a DGVM evaluation tool. To give an example with tree demography: the strength of TROLL is that it can represent tree demography in a highly detailed manner – including a realistic range of tree species, their dispersal and interactions in 3D space, as well as intraspecific variation within species. However, it can also represent demography much more coarsely, e.g., by approximating species through a few functional groups or a single species with a continuous trait distribution. The flexibility of TROLL can thus be used to find a compromise between complexity and the level of detail necessary to render vegetation dynamics accurately in DGVMs.

Line 356-8 – “Tree roots are distributed across vertical layers, but do not spread across belowground voxels horizontally. As a result, trees only deplete the water content of the belowground voxels located below their trunk position” – does this mean that trees are not competing for water? Also, I was a bit confused by this in contrast to Figure 1 (right), where it looks like the roots of the large tree illustrated span multiple belowground voxels. Can you clarify if trees are competing for water in the model or if each tree has its own “bucket”?

R: As belowground voxels have a coarser resolution of aboveground voxels (l. 221-222), several trees will typically deplete the same belowground voxels, and compete for water with each other. This is now clarified l. 386-387. Figure 1 has now been modified to avoid confusion.

Minor comments:

Line 92-93 – consider adding a reference for the FATES model:

Koven, C.D., Knox, R.G., Fisher, R.A., Chambers, J.Q., Christoffersen, B.O., Davies, S.J., Detto, M., Dietze, M.C., Faybishenko, B., Holm, J. and Huang, M., 2020. Benchmarking and parameter sensitivity of physiological and vegetation dynamics using the Functionally Assembled Terrestrial Ecosystem Simulator (FATES) at Barro Colorado Island, Panama. Biogeosciences, 17, 3017-3044.

R: reference added.

Line 162 – do you mean that canopy density is recalculated once a day? Does the incident irradiance vary with solar angle throughout the day?

R: yes, canopy density is computed every daily timestep in this version. Variation in solar angle is not accounted for in this version and this is now clarified in the text, as also asked by reviewer 1. 166-169.

Line 294-5 – do leaf properties vary vertically throughout the canopy? E.g.

Lloyd, J., Patiño, S., Paiva, R.Q., Nardoto, G.B., Quesada, C.A., Santos, A.J.B., Baker, T.R., Brand, W.A., Hilke, I., Gielmann, H. and Raessler, M., 2010. Optimisation of photosynthetic carbon gain and within-canopy gradients of associated foliar traits for Amazon forest trees. Biogeosciences, 7, 1833-1859.

Lamour, J., Davidson, K.J., Ely, K.S., Le Moguédec, G., Anderson, J.A., Li, Q., Calderón, O., Koven, C.D., Wright, S.J., Walker, A.P. and Serbin, S.P., 2023. The effect of the vertical gradients of photosynthetic parameters on the CO2 assimilation and transpiration of a Panamanian tropical forest. New Phytologist, 238, 2345-2362.

R: for a given individual, leaf properties do not vary vertically within the crown, and the variation of leaf properties across individuals within species is not controlled by their position within the canopy. This is now clarified and better discussed l. 316-317 and l. 1045-1047, also in agreement with a comment of Reviewer 3. However, it would be interesting to assess the trait vertical variation across the canopy that results from the co-variation of leaf properties and stature across species, which is accounted for in the model.

Line 335 - add reference for this “common assumption”?

R: The sentence has been rephrased and a reference added (l. 360).

Line 722 - should the size of NSC storage vary with species? E.g.

Signori-Müller, C., Oliveira, R.S., Valentim Tavares, J., Carvalho Diniz, F., Gilpin, M., de V. Barros, F., Marca Zevallos, M.J., Salas Yupayccana, C.A., Nina, A., Brum, M. and Baker, T.R., 2022. Variation of non-structural carbohydrates across the fast–slow continuum in Amazon Forest canopy trees. Functional Ecology, 36, 341-355.

R: thanks for the reference. The size of the NSC storage is calculated from the tree AGB (Eq. (59)), which itself depends on the tree wood density and its size (Eq. (60)). It thus varies across species, and its variation is precisely in agreement with the growth-storage trade-off described in Signori-Müller et al. (2022). This interesting point is now highlighted l. 767-769.

Figure 2 – can you use a thicker lineweight and larger font size for this figure?

R: the figure has been modified accordingly.

References:

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