Response to Reviewer 1:

Robust Ecosystem Demography (RED): a parsimonious approach to modelling vegetation dynamics in Earth System Models

Arthur P. K. Argles, Jonathan R. Moore, and Peter M. Cox on behalf of co-authors. (*on behalf of the co-authors*)
24th March 2020

We thank the reviewer for their extremely detailed review. Most of the suggestions were on technicalities within the literature and definitions used within the paper. We address each of the queries raised below. The relevant reviewer comments are written in italics below followed by our responses in plain font with the changes given in blue.

> **Reviewer**:
>
> *In this paper, Argles and co-authors introduce the 'Robust Ecosystem Demographic' (RED) model. RED is introduced as an alternative to cohort-based vegetation demographics models, and its justifications are largely presented as being in opposition to more complex approaches that discretize tree size and age since disturbance. Instead of discretizing age since disturbance and tracking individual cohorts performance, RED makes several simplifying assumptions including:*
>
> 1. *Productivity for each plant size class is not calculated as a function of it's resource availability within a PFT x age class matrix (as for a typical ecosystem-demography based VDM) and instead is assumed to scale with plant size, as per the idealized 'Metabolic Scaling Theory'.*
>
> 2. *Thus, there is no possibility of relative plant size determining competition for light, and hence productivity and growth, and thus all plants of a given PFT are supposed to occupy the same area.*

Response (1):
While it is true that we do not explicitly model light competition (except with respect to the net growth-rate of the recruitment flux), it is not true that plant size has no impact on growth-rate or that all plants of a given PFT occupy the same area. In RED we assume allometric relationships relating tree mass to growth-rate (Equation 2) and crown area (Equation 3). We have clarified these assumptions within a revised model by including forms for class growth and coverage.

Edit:

"Corresponding to the total mass within a class, we can get the total growth, $G_i = N_i g_i$, and coverage, $\nu_i = N_i a_i$, within a given class."

> **Reviewer**:
>
> > *3 The horizontal area is divided into said PFT tiles, and another tile wherein disturbance and seed establishment occur.*

Response (2):
This is an interesting way of viewing RED, but it's not quite how we see it. In fact, PFT-dependent disturbance occurs across the whole of the grid-box, as does seed establishment. The confusion may arise from the fact that the latter is affected by light-competition and therefore depends on the unvegetated fraction of the grid-box. We have clarified these points in a revised model description.

Edit:

"Spreading is homogeneous across the entirety of the grid-box, but only seedlings established within 'unoccupied space' will survive to join the plant cohort.""

Edit:

"Disturbance mortality rates from γ_d can in principle be both PFT-dependent and mass-dependent (e.g. to capture forestry practices) and are thus explicitly applied across mass class and PFT dimensions."

> **Reviewer:**
> *On account of these various simplifications the model can be solved analytically for a given productivity and mortality rate and RED is generally proposed as an alternative method for the simulation of some aspects of vegetation demographics in Earth system models (ESMs). I appreciate the novelty of this approach, and think it is important that a diversity of avenues are taken towards improving the representation of the terrestrial carbon cycle within ESMs.*
>
> *While this is an interesting set of concepts, and potentially an interesting 'middle ground' in complexity of representation of vegetation demographics, there are numerous issues with the presentation, description and validation of the model that I find problematic in this paper.*
>
> *First, in the introduction, there is insufficient explanation of the existing diversity of approaches to the simplification of forest models. A class of models already exists which is much closer conceptually to RED, e.g. the POP (Haverd et al., 2014) and ORCHIDEE-MICT (Yue et al., 2018) models, that also track different size or age cohorts within a single tile devoted to each PFT. While RED additionally provides a DGVM capacity in the form of the competition for seed recruitment, it seems that this class of models certainly requires description at the very least.*

Response (3):
As suggested, we now compare and contrast RED with these other published models, within our revised discussion and introduction.

Edit:

"In a similar vein a few other models have limited the number of cohort dimensions, for example looking at using patch-age while using allometric relationships to capture size scale. Firstly the POP model (Haverd et al., 2014), uses stand-age cohorts as the dimension for population dynamics, every time-step applying crowding and resource limited mortality rates. Another ex- ample is the ORCHIDEE-MICT (Yue et al., 2018), which disaggrates the populations of a PFT into patch

"Cohort" functional types, with transitions between cohorts diagnosed when the average basal diameter passes a threshold."

Edit:

"This is a distinct approach relative to other intermediate complexity DGVMs which are based on patches defined by time since disturbance, such as the POP or ORCHIDEE-MICT models (Haverd et al., 2014; Yue et al., 2018)."

> **Reviewer**:
> *Further, despite the numerous mentions of the PPA approach, the paper does not actually describe this alternative approach to defining 'tractable' solutions to demographic modeling. A comparison of the RED and PPA approaches would be interesting, in particular given the fact that the PPA requires slightly more parameters than RED. This is particularly relevant given that the PPA is also implemented in the GFDL ESM. A comparison of the RED and PPA approaches would be interesting, in particular given the fact that the PPA requires slightly more parameters than RED. This is particularly relevant given that the PPA is also implemented in the GFDL ESM.*

Response (4):
We have included a description on PPA in the discussion and how this relates to the minimum overlap assumption within RED.

Edit:

"Finally, we assume that light-competition is only significant for the lowest 'seedling' mass class. This enables us to capture the impacts of light competition on seedling emergence through a simple 'gap' boundary condition. This represents a significant simplication compared to other approaches involving the Perfect Placisity Assumption (PPA), as used within other DGVMs such as LM3-PPA or CLM(ED) (Fisher et al., 2015; Weng et al., 2015), where canopies are assumed to perfectly fill gaps through photomorphism (Strigul et al., 2008). In LM3-PPA the radiative flux is limited by the available gap fraction in a given crown layer. PPA parallels our gap boundary condition at the lowest mass class (Equation (11)), but in RED the growth of a cohort is purely dictated by the the disaggregation of total growth assimilate assuming metabolic scaling (Equation (16))."

> **Reviewer**:
> *Instead of a description of the relevant literature, the current justification statements in the introduction focus on somewhat vague assertions that full ED-type size-and age structured approximations are too cumbersome. A comparison with more similar models would be helpful, as would a more general depiction of the pro's and cons of the approach used here. The model clearly has some benefits in terms of simplicity and tractability, but also has some drawbacks in terms of reduced ecological fidelity compared to real ecosystems. Given this, it would be good if the paper at some point addresses the questions for which RED would and would not be appropriate.*

Response (5):

As suggested, we have now included a discussion of the pros and cons of RED, and the implications for its applications, within the revised Discussion section. We have also explained where more complex approaches (such as ED) are required.

Edit:

"Our previous work in evaluating demographic equilibrium theory for regional forest inventory datasets in North America (Moore et al., 2018) and using RAINFOR sites for South America (Moore et al., 2020), has provided the theoretical premise for the development of RED. In those studies we found that tree-size distributions within observed forests can be satisfactory understood in terms of demographic equilibrium in the size dimension alone. This is a reduction in complexity compared to other cohort models which are based-on patch age, and yet an improvement in ecological fidelity compared to older phenomenological DGVMs such as TRIFFID (Cox, 2001). The modular design of RED allows for easy coupling into land-surface schemes, merely requiring the per unit PFT total carbon assimilate rate and any additional mortality disturbance rates as inputs for each grid-box (Figure 2). In principle, RED allows scope for more complex tree size-dependent processes, although in this first study we choose to assume size-independent (but spatially varying) mortality rates for each PFT. Our previous work suggest that this is a good assumption (Moore et al., 2018, 2020)."

Edit:

"Currently, RED would not be the most appropriate DGVM to answer important questions regarding the role of biodiversity in ecosystem function (Pavlick et al., 2013; Levine et al., 2016). More sophisticated DGVMs are required to simulate plant diversity, such as individual-based models (Fischer et al., 2016), and DGVMs specifically-designed to capture sub-gridscale patch dynamics (Longo et al., 019a,b). Adapting our 'gap' boundary condition (Equation 12) appears to be a promising way to allow greater PFT diversity in RED, without unduly increasing model complexity. We see this as a key priority for future research.""

> **Reviewer:**
> *Many demographic model development activities, for example, as specifically motivated by a desire to include greater diversity of functional types in ESMs, and to predict their distribution as a function of their plant traits, which in most models primarily impact upon growth. Removing the ability of the model to simulate growth-based competition for light, and indeed, to simulate a diversity of trees within the same class, means that this RED would not be suitable for that problem.*

Response (6):

Agreed. The introduction has been rewritten to explain how in RED we choose to trade model complexity for reduced parameter uncertainty. This trade-off seems to be appropriate for the purposes of modelling large-scale forest demography and carbon storage (Moore et al., 2018, 2020), but it is indeed less appropriate for applications related to forest ecology and diversity.

Reviewer:

Further, the introduction suggests that part of the motivation for resolving tree size is to introduce size-dependant physiological processes, but by introducing the metabolic scaling of productivity from an arbitrary reference size to all of the other classes, RED is also unable to simulate how tree size actually affects physiology - e.g. plant hydraulics, light availability, fire damage, allometry (and thus allocation and demand for nutrients in pools of different stoichiometry), size dependant rooting depth (and thus uptake of water and nutrients) , burial by snow, etc. Many developments of demographics models are specifically motivated by the representation of size, so again, RED could not be used for those types of question.

Response (7):

RED is a demography model which requires net PFT growth rates and disturbance rates as inputs. In the study presented in this paper, net PFT growth-rates were provided by the JULES land-surface scheme. In principle, details on the tree size distribution can be fed back into JULES (or any other land-surface scheme) to enable size-dependent processes to be included (for example to represent size-dependent drought mortality). We include these possible future developments in our new Discussion section.

Edit:

"RED is currently being coupled to the JULES Land Surface Model, replacing TRIFFID as the default DGVM within that framework. In parallel, significant improvements are being made to the representation of physiological processes in JULES, most notably through the representation of non-structural carbohydrate ('SUGAR', Jones et al. (2019)), and through the inclusion of a coupled model of stomatal conductance and hydraulic failure under drought stress ('SOX',Eller et al. (2018, 2020)). Plans are also being made to derive the mortality rates for RED from the INFERNO forest-fire model (Burton et al., 2019). These developments will allow us to simulate the effects of size-dependent tree mortality rates within the near future . "

Reviewer:

As a parallel, RED also does not provide discretization of the time-since-disturbance continuum, and instead really divides the grid cell into various PFT tiles, with resolved height, and one 'gap' tile, where new seedlings compete for space. Many demographic model developments are motivated by the ability to represent how the development along the successional trajectory impacts physiological boundary conditions. Examples of this include simulating the dominance of N fixers in early succession, of the matrix of post-fire disturbance conditions (including the vertical co-existance of grass and trees), representation of variation in light conditions to capture successional composition shift and the horizontal variation of vegetation height in systems which are buried by snow.

Response (8):

As pointed out above (response 2), this picture of RED is not correct. We have clarified this in the revised model description. The other points concerning the age-dependent (rather than size-dependent) processes are covered in our revised introduction and discus-

sion (see our response 3).

Reviewer:
I am also highly skeptical of the authors claim that mortality rates can be backed out from spatial coverage of a particular PFT. Given that only a single not very convincing validation is presented, I remain far from convinced that this is a reasonable model inversion method. While it might be mathematically plausible, given the myriad simplifying assumptions of the model, I'd like to see how robust the mortality estimates are to variations in the seed production rates and minimum size, as well as assumptions on the spatial arrangement of crowns, and indeed, the uncertainties in the estimates of PFT areal coverage.

Response (9):
As requested, we have carried-out a senstivity analysis to show how our estimates of mortality-rates depend on the model parameters (α, m_0) along with the 'observed' PFT areal coverage and UKESM carbon assimilate input. This is included as a new Appendix C.
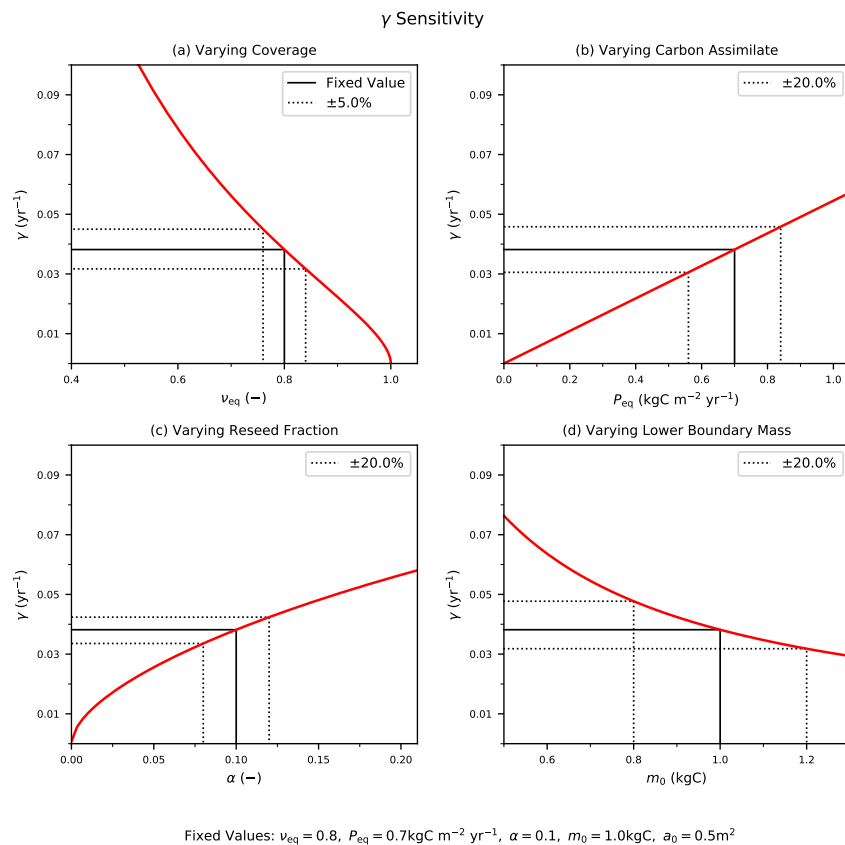
Edit:

Figure 1: " For assumed variables ν_{eq}/coverage (a) and P_{eq}/carbon assimilate (b), along with the model parameters: α/reseed fraction (c) and m_0/lowest mass (d). The solid black line indicates the fixed values with corresponding $\pm 20\%$ or $\pm 5\%$ variation (dotted black lines)."

$$\gamma = \frac{\alpha P_{\text{eq}} a_0}{m_0} \left(\frac{1 - \nu_{\text{eq}}}{\nu_{\text{eq}}} \right) \left[1 + \frac{1}{2\mu_0} + \frac{1}{8\mu_0^2} \right]. \tag{1}$$

Figure 1 demonstrates the fixed sensitivity of the derived mortality rate using the continuous solutions of the equilibrium equations (solving Equation B10 and Eq.(1)). Equation (1) Is found by rearranging for γ in the equilibrium boundary condition.

In panes (a) and (b) we show how the mortality is dependent on firstly the assumed coverages and carbon assimilate, respectfully. We see that when $\nu_{\text{eq}} \to 1$ the mortality rate tends towards 0, as opposed to when the $\nu_{\text{eq}} \to 0$, the mortality rate is asymptotic towards infinity. In (b), the mortality and carbon assimilate have a linear proportionality, if the assimilate rate tends towards zero the mortality rate will compensate to match the same fixed coverage.

In panes (c) and (d) we show how the mortality changes with the key model parameters α and m_0. There are non-linear dependencies with $\alpha \to 1$ and $m_0 \to 0 \, \text{kgC}$ the mortality will approach infinity, this is to compensate for larger recruitment flux arising from the boundary condition (Equation 11). In both instances uncertainty around the chosen values translates into smaller uncertainty within the mortality. "

Reviewer:
Lastly, the paper has some issues with clarity that I have tried to cover in some detail in the following comments. Some of the excessive mathematical details could be moved to the appendix as they rather detract from the flow of the paper. A more informed and nuanced description of how the model fits into existing demographic model literature and of it's strengths and weaknesses would, I think, be more useful for the general readership.

Response (10):
As suggested, we have moved the mathematical details concerning the equilibrium state to Appendix B. The pros and cons of RED are discussed in more detail in our revised Discussion section (as outlined abov in response 5).

Specific Comments

Reviewer:
P1, L21: The statements in these first three sentences all need references.

Response (11):
Done.

Edit:

"A key requirement of Earth System Science is to estimate how much carbon the land surface will take-up in the decades ahead (Ciais et al., 2014). This is an important component of the total carbon budget consistent with avoiding global warming thresholds, such as 2 C (Schleussner et al., 2016). Unfortunately, projections of future land carbon storage still span a wide-range (Brovkin et al., 2013; Friedlingstein et al., 2014; Arora et al., 2019).

Reviewer:
P2, L7: I'm not sure what to take from this assertion that uncertainty 'can be attributed' to CO2 responses and regrowth. It can also be attributed to a lot of other features of LSMs. Is it really necessary to state this so definitively?

Response (12):
Agreed - we have now removed this phrase.

Reviewer:
P2, L9: You didn't really describe or define what a DGVM is yet.

Response (13):
DGVM now defined at the point of use.

Edit:

"The transient representation of plant communities within Earth System Models (ESMs) is achieved through the use of Dynamic Global Vegetation Models (DGVMs)."

Reviewer:
P2, L15: Here it is indicated that 'processes that are dependant on size' is a core motivation for the implementation of this concept, but RED actually ignores that size of all except the reference tree, using an assumption to scale to the other size classes. There are lots of processes that do actually depend on size (hydraulics, allocation, fire mortality, competition for light, wind damage, snow burial, etc.) and so this is a genuine justification for using a size-structured model, but it does not apply to RED. Therefore, a different justification is required.
Further, in ED-type models, the faster regrowth after disturbance is typically predicted on the use of multiple tree types that exist in early, mid and late successional systems (as opposed to an average, slower growing tree).

Response (14):
Please see our responses to points in (1), (2) and (7) above.

Reviewer:
P2, L21: This is true, but you are also going to get lots of different outcomes of climate change from alternative parameterizations of RED - parameters that are absent from the simpler model are really just assumed to be fixed in RED (e.g. the decay coefficient of productivity with size, seed production, competition parameters). Making the parameters either assumed constants or round numbers doesn't make their uncertainties go away. It would be more interesting to investigate these uncertainties and illustrate a succession experiment under a range of model assumptions.

Response (15):
Previous studies testing RED equilibrium profiles against observed forest demography for north and south America (Moore et al., 2018, 2020), suggest that our simplifying

assumptions are sufficient to capture tree size distributions in many locations. However, we agree that it is important to assess the sensitivity of our simulations to the assumed fixed parameters. This is why we have included a new senstivity analysis in Appendix C, as per (9) above.

> **Reviewer**:
> *P2, L24: Cohort models are numerically unwieldy and no-doubt more expensive, but as you attest later in the paper, it is disingenuous to state that they make a new patch every timestep when in fact ED-derived models immediately fuse the newest patch to the next largest one.*

Response (16):
The algorithm used to 'fuse' patches is arguably an arbitrary feature of such models. However, we have toned-down our implied criticism of these alternative approaches in the introduction.

> **Reviewer**:
> *P2, L26: Cohort models can either track tree age or tree size, so adding this here to distinguish RED from a cohort model doesn't really make sense.*

Response (17):
The norm for cohort model is to track both tree age and tree size. As stated within the sentence RED is a "simplified" cohort model, the simplification being not tracking tree size.

> **Reviewer**:
> *P3, L5: The way in which this equation is presented seems overly contrived. Surely it can be presented such that the dn/dt is the sole term on the left hand side?*

Response (18):
We choose to write the equation in this way, because the lhs is essentially the continuity equation for a conserved variable (in this case tree number), while the rhs contains the source and sink terms. This is a standard way to write Fokker-Planck type equations.

> **Reviewer**:
> *Neither g(m) nor lambda(m) appear in the actual equation, so this is again a little hard to get ones head around.*

Response (19):
The terms g and γ (Rather than lambda?) appear in equation 1. We choose not to write these explicitly as functions of mass (e.g. "$g(m)$") for clarity. Again, this is standard practice.

> **Reviewer**:
> *P3, L11: What did Niklas and Spatz find or do, briefly?*

Response (20):

We have edited this sentence to include "...consistent with the meta-analysis of field-based measurements by of Niklas and Spatz (2004).."

> **Reviewer**:
> *P3, L16: I do not understand how the last term translates into fractional area, when it looks like it should just return 'area'. Further, is there no constraint on the area the trees can occupy? That seems strange and needs further discussion.*

Response (21):

This term returns fractional area because of the dimensions of "a" (m^2) and "n" ($number/kgC/m^2$). Integrating over mass-classes therefore yields a unit of (m^2/m^2).

> **Reviewer**:
> *P4, L1: I'm not sure why you need to state that the model conserves carbon three times. All vegetation models must conserve carbon. This isn't very surprising.*

Response (22):

This subsection derives the discrete equations for RED using the conservation of mass as a constraint on the net fluxes of plants moving between the mass classes. We now make this clear at the beginning of the subsection.

Edit:

"We wish to produce a model of vegetation demography that can be updated numerically and which explicitly conserves vegetation carbon, providing a constraint on the number of plants moving between mass classes in the discrete form."

> **Reviewer**:
> *P4, L3-15: I'm not sure what purpose is served by this sequence of equations.*

Response (23):

Please see response (22) above.

> **Reviewer**:
> *P4, L20: This equation would be easier to read if it were split into terms for seed recruitment and growth.*

Response (24):

The equation as written shows that seedling recruitment depends on the fraction of net-assimilate which goes into seedling production (α), the net-assimilate (P), and the fractional gap area (s). We have added a sentence below the equation to make this clearer.

Edit:

"Therefore, the rate of recruitment is given as the ratio of a fraction of the total carbon assimilate,

αP, and m_0, along with being constrained by the effective canopy cover s."

Reviewer:
P4, L23: The PPA assumes minimum overlap of crowns within each layer of the canopy. It distinctly does not assume no overlap of PFTs. It assumes that canopies are arranged into layers and within each layer there is no overlap. Competition for light occurs at the boundary of the layers and is a strong control on ecosystem assembly. In fact, much of RED is highly contradictory to the PPA concept, given the MST rejects the need to different growth parameters as a function of light availability (as demonstrated convincingly for tropical forests by Farrior et al. (2016)). I think it's thus a little disingenuous to cite the PPA here as a justification for this assumption.

Response (25):
Based-on the reviewers' own comments here, it sounds to us like the minimum overlap assumption in RED and PPA are indeed related. However, the potential relationship to PPA is just an aside , so we have removed the reference to PPA here to avoid further concern from the reviewer on this point.

Reviewer:
P4, L25: "injected"? How do trees get injected?

Response (26):
Changed to "recruited".

Reviewer:
Figure 1: I don't find figure 1 particularly informative. It would be better to have a depiction of the actual area available for seeds and to illustrate how the different PFTs might affect the allocation to each PFT. This figure just tells me that shrubs are smaller than trees.

Response (27):
Others who have seen this diagram have found it useful, so we have retained it despite the reviewer's opinion on this point.

Reviewer:
P5, L4: The calculation of the area occupied by each PFT, as it is introduced here, needs a lot more explanation. In the description on L16 of P3, it simply states that the area of all the mass classes is added together, such that there is no overlap between the canopies of the trees in each plant type. This implicitly assumes that all the trees are in the 'canopy' layer, (using PPA terminology) and thus by implication that they should all get the same amount of light. Of course, via use of equation 2, the actual light environment of the plants is divorced from assumptions about their spatial arrangement, but it seems like a strong assumption to me to include no possibility of additional canopy layers. What happens when the total amount of space occupied by the plants exceeds the ground area available?

Response (28):

Our gap boundary condition given by equation 12 ensures that there are no steady-state solutions where the total vegetated fraction exceeds one. We have added a sentence to clarify this point.

Edit:

"This 'gap' boundary condition results in there being no equilibrium solution where the amount of coverage exceeds 1. Doing so would halt the recruitment flux such that mortality processes would bring the fractional coverage back below unity."

> **Reviewer:**
> *P5, L5: It should be noted here that the Cox 2001 paper is at-least inspired by the Lotka-Volterra approach, to better allow connection of this concept to community ecology literature.*

Response (29):

Agreed. Rewritten as "..this is a similar competition regime to the Lotka-inspired TRIF-FID model..."

> **Reviewer:**
> *P5, L7: Later on you state that the coexistence between PFTs of the same type doesn't actually work, so this statement that Eqn 12 allows for coexistence is a little misleading.*

Response (30):

Here we mean by "inter-functional group" we mean tree-shrub-grasses. We make that clearer in a revised sentence.

Edit:

"...allows for the co-existence between inter-functional groups (Tree, Shrubs and Grasses) of PFTs. For instance, a PFT such as broadleaf Deciduous tree can co-exist with a deciduous shrub and C3 grass but not another tree PFT."

> **Reviewer:**
> *P5, L8: This allows succession as you note, but only between the PFT of different classes, not within a given class, unless I'm mistaken? . Figure 3: I'm not really sure what this Figure is supposed to illustrate. What are the red dotted lines in the middle of the triangle? There are three heavy double headed black arrows and not one (as implied by the legend).*

Response (31):

Figure 3 shows that the RED equilibrium state can be determined using observed areal cover plus either growth or mortality rate. We have removed this figure.

> **Reviewer:**
> *Eq 28 and 29: These equations need a bit more explanation and description.*

This section feels like you are making a concerted effort to lose readers. Is it really necessary that everyone understands how the equilibrium solution of the model is derived? Could this go in an appendix?

Response (32):
Equation 28 is important in the derivation of the analytical equilibrium. We have now moved the derivation into the description (Appendix B2) and have included more explanation offer the mathematical expressions.

Reviewer:
P10, L1: As I said above, I am highly skeptical that this is a robust way of estimating turnover, given the uncertainties to do with seed production and spatial extent.

Response (33):
As response (9) and (15) states, we have conducted a sensitivity analysis for the RED equilibrium mortality within the new appendix C.

Reviewer:
P10, L8: So, productivity was derived from JULES using TRIFFID? Were the outputs saved for each month? Is there interannual variability? This needs a bit more detail.

Response (34):
We have appended more detail around the UKESM input:

Edit:

"The UKESM simulation ran on a yearly time-step, and provides NPP and local litterfall per unit PFT. We multiply by PFT fraction to get the grid-box mean values required to drive RED (using ESA landcover data, as explained below)."

Reviewer:
P11, L3: Is this really how succession works in Amazonian forests? I think it's really mostly trees that are present in the formation of small to medium sized gaps.

Response (35):
In typical succession you see the establishment of faster-growing PFTs (C3, Esh), but ultimately slower-growing trees often dominate. We see this sort of successional dynamics in RED transient simulations, as shown in Figure 4.

Reviewer:
P11, L5: Can you illustrate the dependance on alpha and m0?

Response (36):
See responses (9), (15) and (33). This is now done in appendix C.

13

Reviewer:
P12, L11: What are we to take from this illustration of 'succession' in the model? There isn't any comparison with data, nor an illustration that the model fixes the issue of slow recovery from disturbance that was raised in the introduction. What controls the area fractions of the smaller PFTS? Is there always some gap fraction dedicated to them? How is this equilibrium maintained?

Response (37):
Data on forest regrowth is unfortunately difficult to find. However, this successional sequence is broadly consistent with ecological understanding and other DGVMs. We show it here to demonstrate the dynamical nature of the model. Sub-dominant PFTs occupy space left by dominant PFTs (as determined by our gap lower boundary condition - equation 12). For all PFTs the equilibrium is maintained as a balance between mortality and seedling recruitment (which is dependent on net growth-rate and competition through equation 11). We have added text below Figure 4 to clarify.

Appended onto the bottom of the caption on Figure 3:
"The ultimate steady-state is determined by the balance between recruitment and mortality (Equation 11). Intra- and inter-PFT occurs here through the shading of seedlings, which implies that just a fraction of the gridbox (s, 'space' or 'gap' fraction) is available to grow seedlings (Equation (12))."

Reviewer:
Figure 6: The inputs of productivity taken from JULES do not, for example, allow BETs to grow outside of the tropics, and so many of the critical questions related to the prediction of biome boundaries that are asked of DGVMs cannot be addressed in this circular analysis.

Response (38):
In fact JULES does allow BET to grow outside of the tropics. We have revised the colour scale of Figure 6 now (5) to make this clearer. However, we also sense that the reviewer is under a false impresssion about the nature of RED. RED is a model of forest demography that is driven by net growth-rates and mortality rates that can come from land-surface models or observations. In this study we have driven RED with fluxes from the JULES land-surface scheme, but the current paper is not about JULES or even JULES-RED. We clarify this point in our Introduction.

Reviewer:
P14, L1: It seems that reproducing the PFT map should be a trivial matter given the productivity inputs illustrated in Figure 6.

Response (39):
We are simply performing a model inversion to analytically solve for the RED dynamical steady-state. We have not seen this approach from another stand-alone DGVM.

Reviewer:
P 16 L8 This is confusing because the reference to Figure 10 comes before it is

described. The use of the mortality rates in these simulations is not described in this section until now.

Response (40):
We have moved the mortality section so that it is now before the global dynamical plot.

> **Reviewer**:
> *P17, L1: To what does this 'diagnosed mortality rates' refer? Isn't this sentence about diagnosing mortality rates? This adds another layer of confusion onto my previous comment.*

Response (41):
We can see how this might be confusing. Therefore, we have rearranged the sections to be more clearer (Modelling setup → Equilibrium mortality rates → Local simulation → Global simulations).

> **Reviewer**:
> *Figure 9: This color map does not allow one to distinguish between most of the lower turnover areas. You need some sort of logarithmic variation in color with mortality rate.*

Response (42):
As suggested, we have now used a logarithmic color map in Figure 9.

> **Reviewer**:
> *Referee: P17, L8: How influential is the minimum recruit size? This needs to be illustrated.*

Response (43):
As stated in (9), (15), (33) and (36) we have carried out a sensitivity analysis in appendix C which includes the sensitivity to m_0.

> **Reviewer**:
> *P17, L10: The sentence that begins "Under the assumption" isn't a whole sentence. Moreover, what is the aim of defining a 'healthy' environment? You need to state what you are trying to achieve first. . .*

Response (44):
We have rewritten this statement for clarity. The use of 'healthy' is indeed rather vague – so we have clarified this to 'dominant'.

> **Reviewer**:
> *P17, L12: This is a very quick and potentially confusing switch to discussing the growth is as this mortality ratio and not mortality (you should maybe also re-state what is (μ_0??) a non-standard quantity.*

Response (45):

We think reviewer means μ_0 (there appears to be an error in the reviewer document)? We have now defined μ_0 before this sentence (with a pointer to the equilibrium section). μ_0 is the ratio of mortality to growth-rate ($m_0\gamma/g_0$).

> **Reviewer:**
> *P17, L13: This number seems extraordinarily high for the stem turnover rate of tropical forests? Comparison with data is, of course, where this aggregation idea is problematic, as mortality rates have clearly been shown to vary with tree size (Lines et al., 2010; Johnson et al., 2018), and thus the range of tree size with which one can compare these rates is unclear, particularly the lower size boundary.*

Response (46):

The reviewer appears to be confusing μ_0 with γ, we therefore have clarified μ_0 as per response(45). The sensitivity of the lowest boundary and the derived γ see the sensitivity analysis with m_0, (as with previous responses (9), (15), (33) and (36)) see appendix C. Assumptions of size independence of mortality has provided credible fits of size structure of the entire US forest inventory database (Moore et al., 2018) and plots across the tropics (Muller-Landau et al., 2006b; Lima et al., 2016; Moore et al., 2020). Interestingly, within Johnson et al. (2018) (Supplementary Figure 10), the plots have a similar mortality distribution within our papers analysis .

> **Reviewer:**
> *P17, L13: Table 3 contains goodness of fit metrics, and not estimates of mortality.*

Response (47):

A simple typo – we should have referenced Table 4 here. Now corrected.

> **Reviewer:**
> *P17, L15: The 'value within the paper' doesn't state which paper, nor why it needs converting. Thus is very confusing.*

Response (48):

We have made this clearer.

> **Reviewer:**
> *Referee: P18, L1: This text on the differences between the Moore paper value*

and this value (which are indeed extraordinarily close and probably don't need excusing) would be better spent describing first how the Moore method differs from RED. This section assumes the reader is familiar with, for example, the non-discretized nature of the Moore method.

Response (49):
We have outlined the non-discretized form within Appendix B, which we now refer to and have added text to explain the relationship to the Moore et al. (2020) paper.

Edit:

"Furthermore, Moore et al. (2020) used the continuous, rather than discrete forms of the equilibrium equations (Appendix B)."

Reviewer:
P18, L5: "Potentially providing a future constraint on ESM growth rates for PFTs." is not a whole sentence.

Response (50):
We have combined this sentence with the previous one.

Reviewer:
Figure 10: The mortality numbers in figure 10 for tropical forests seem too high. (0.07- 0.08). Again, it's hard to know what mortality rates they can be compared to. In Table 4, the numbers are different from the figure, perhaps because they are area weighted, but this isn't really clear from the text.

Response (51):
This is because of a difference of sampling - "non-zero" grid-box fractions (figure 10) versus top quartile grid-boxes . We now use the same subset for all grid-boxes to calculate the mortality rates in figure 10 (the top quartile of non-zero grid-box fractions) and make it more obvious what we are doing.

Reviewer:
P18, L11: I'm not sure what "within the top 25% of coverages" means, nor what this is trying to achieve. Further, there is no data in figure 10, so I am not sure why one is supposed to conclude that the model captures the data well. Maybe you actually mean figure 11, which reduces the RED estimate, but only down to about double the observations. Given the a doubled mortality rate is approximately equal to a halved biomass, I'm not sure that this provides a very convincing validation. Further, many estimates of mortality are lower than this. Lewis et al. (2004) find mortality rates of tropical forest from 1.5-1.7%, for example.

Response (52):
There are a few things the reviewer raises here – the seemingly arbitrary "top 25%" of coverage and the fitted mortality rates being too high. Firstly, we picked this threshold to identify areas where PFTs have greater coverage – and therefore mortality rates hy-

pothetically closer to an undisturbed baseline. We have included a sensitivity analysis in Appendix C of how the diagnosed mortality rates depend on other model parameters (as stated in our previous responses (9), (15), (32), (34) and (40).

> **Reviewer**:
> *P20, L4: I could not find a definition of DET prior to this usage here.*

Response (53):
We now refer to appendix B and have stated the definition of DET in the introduction.

Edit:

" This paper presents a simplified cohort model (*Robust Ecosystem Demography (RED)*) which updates the number of trees in each mass class, but does not separately track tree-age or patch-age. RED assumes that the tree size-distribution of a forest is determined by how the rates of tree growth and mortality vary with tree size (Kohyama et al., 2003; Coomes et al., 2003; Muller-Landau et al., 2006b; Lima et al., 2016). We follow many other studies in assuming that tree-growth rates vary with the three-quarter power of tree mass ($m^{3/4}$), as suggested by metabolic scaling theory (West et al., 1997). Where tree mortality rate can also be assumed to be approximately independent of tree mass, the demographic equation yields equilibrium tree-size distributions which follow a Wiebull distriubution – this is sometimes termed 'Demographic Equilibrium Theory (DET)' (see Appendix B). These simplifications significantly reduce the number of free parameters in RED, but still enable it to fit forest inventory data in North America (Moore et al., 2018) and South America (Moore et al., 2020). "

> **Reviewer**:
> *P22, L1-10: I'm not sure what to take from this section about fire. The last line seems to suggest that RED overestimates fire mortality, when figures 12 and 13 seem to show the opposite. The logic of this section needs tightening.*

Response (54):
The purpose this section is to investigate if we see a raised mortality rate in regard to areas with fire disturbance and land-use. We have now changed Figure 12 to indicate this more clearly and rewritten the paragraph.

> **Reviewer**:
> *P23, L1-6: This, and the paragraph above, are in need of more references.*

Response (55):
As per the response above (54), We have now included more references.

> **Reviewer**:
> *P23, L6: This statement about patch merging is incorrect in its assertion that patches can only be merged after a certain age in ED-type models. Further, it does not illustrate that this is actually problematic, and simply asserts as such. Fusion criteria are indeed to some extent arbitrary, but that this is a*

genuine problem has not actually been demonstrated.

Response (56):
We have now rewritten the criteria for patch merging within ED. As stated previously (response (5)), we have now sought to discuss both the pros and cons of RED relative to other DGVMs.

> **Reviewer:**
> *P23, L7: Which important features is it designed to capture exactly? This hasn't really been stated.*

Response (57):
We have now more clearly stated the important features of second-generation DGVMs within our updated introduction and discussion sections (as stated in response (5)).

> **Reviewer:**
> *P23, L16: Metabolic scaling theory has been widely debunked by numerous studies comparing its predictions with observations (Muller-Landau et al., 2006a; Russo et al., 2007; Coomes et al., 2011; Rüger and Condit, 2012) in particular where asymmetric competition for light (e.g. in forests) is important.*

Response (58):
The reviewer is perhaps confusing metabolic scaling theory for tree growth-rate as a function of tree mass ($g \propto m^{3/4}$), with an extension of metabolic scaling-theory to simulate forest demography (Brown et al., 2004). Observed tree-size distributions do not seem to be consistent with the latter, but do seem consistent with the former, as discussed in Moore et al. (2020). We have revised the introduction to clarify.

> **Reviewer:**
> *P23, L18: I am not sure how the seed model allows you to capture the effects of light competition. It allows you to represent the impacts of recruitment competition, but seems to me that it explicit does not include light competition.*

Response (59):
Agreed that we do not explicitly represent light competition. We have now removed this statement for the sake of clarity.

> **Reviewer:**
> *P24, L1: It is stated here that equation 12 is a promising method to deal with the problems of coexistence in RED, but equation 12 is already part of RED, thus how can it be the solution? Further, I do not know what 'gap boundary conditions' refers to here.*

Response (60):
Co-existence can be achieved by having competition coefficients less than 1. This model paper is RED version 1, there is always scope for future improvements to the model in

this topic.

> **Reviewer**:
> *P24, L4: I am skeptical, without further much more robust testing and illustration, that these relationships would be meaningful.*

Response (61):
Noted. We hope that future work involving closed-form DET and RED will help provide some illustration. See our responses concerning the sensitivity of this method for determining γ.

> **Reviewer**:
> *P24, L13: I do not think that this model is 'based on' the ideas of the PPA in any meaningful way. The idea of the PPA is primarily concerned with how trees fill space, which is specifically ignored by RED, and also on the division of the canopy into discrete layers, which is definitively at-odds with the metabolic scaling method of disaggregating production solely based on tree size.*

Response (62):
As per response (4) and (25) we have now edited and removed the mentions of PPA from the manuscript.

> **Reviewer**:
> *P24, L16: It apparently can be fitted, but I'd argue that there has been no validation presented to show that this is 'effective'.*

Response (63):
We have also tested for robustness in our new appendix C. (see also response to points (9), (15), (33), (36), (43) and (52)).

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