

Referee 2

We would like to thank Referee 2 for his/her review and supportive comments on our paper. Below we summarise our response to his/her comments (comments in bold, response in normal font).

General Comments:

The authors present a new trait-based and individual-based formulation of terrestrial vegetation. This paper has been fun to read, exciting, and I am looking forward to seeing this model address more science questions in the future. The methodology, as far as I know, is novel. The novel contribution to the modeling community is the method of randomly assigning traits to individuals from a reference stand-sample of traits with limited size. There are also various adaptations of biophysical processes, but the dividing line between new contribution and existing method is not as clear. The strengths of the paper are as follows: appropriate review of literature, novel science, appropriate level of comparison of model performance with observations, acceptable coverage of model mechanics and evaluation of the trait variability space and other emergent properties. The manuscript has modest shortcomings, that can be easily addressed: redundancies in the explanation of the model, the order of which concepts are introduced and explained, amount of emphasis placed on explaining both new and existing model concepts.

Specific Comments:

The most interesting and novel components of the model is the choice of the trait set, and how the sample of traits is generated. The authors also create apparently unique adaptations of water controls and light interception too, but it is less clear. If it is new, you've got bragging rights! Tell us at the beginning of the model description! They need to state out front, other than the trait sampling and generation process, what model mechanics are novel. The model description in the main text should emphasize these points. For instance tessellation is a concept brought up by Purves 2007 (which you acknowledge), but its not so clear if and how your adaptation of tessellation and ultimately light scattering differs. *Note that this is definitely not an issue about giving an acceptable level of credit to prior research, that is fine.

We have modified section "2.1 Model Description" in order to summarise all the unique adaptations made in TFS, as suggested by Referee 2. A full description of these methods is given in the Supplementary Information. Section 2.1 now reads as follow:

“...
“Traits-based Forest Simulator” (TFS) is an individual-based forest model, i.e. it simulates water and carbon fluxes for each tree in a stand. In the current version of the model, stand structure is prescribed in terms of the number of trees and their diameter at breast height (d). This is thus a “snapshot” version of the model, which does not take into account tree recruitment and mortality. In this version of TFS, each individual is first fully described through d , with allometric equations used to estimate other attributes of interest like tree height (H), crown area (C_A), total leaf area (L_A) and tree-level leaf area index (L). Whole tree biomass is then partitioned to leaf (B_L), stem (B_S), coarse root (B_{CR}) and fine root (B_{FR}) biomass using established allometric equations. Allocation of assimilated carbon to different plant components is static, i.e. it does not change with size or resource availability, but rather implements field-derived allocation coefficients (Aragão et al., 2009). The general architecture of the model is presented in Fig. 1.

The functional diversity of the trees in a stand is expressed through four traits (M_a , $N_{L,m}$, $P_{L,m}$, D_w) randomly assigned from local observations, using a data-driven random vector generation algorithm. Leaf photosynthesis is calculated using a modified version of the Farquhar biochemical model (Farquhar et al., 1980), that incorporates leaf chemical and soil moisture effects. The maximum photosynthetic rate is regulated by N_L or P_L through the co-limitation model of Domingues et al. (2010). In contrast to most ecosystem fluxes models, where photosynthetic rates are directly regulated by water availability (Clark et al. 2011), we couple water ‘stress’ to reduction of canopy conductance by estimating a daily fractional available soil water content for each tree in the stand. Carbon fluxes are estimated on an hourly basis and water fluxes with a daily time-step.

Light competition is based on the assumption of a perfect canopy tessellation and flat disc-shaped canopies. The flat-top version of the perfect plasticity model of Purves et al. (2007) has been used in the current version of TFS to characterise canopy and sub-canopy trees, by assuming that all of a tree's foliage is found at the top of its stem (S1, Canopy Architecture and Radiation Environment). A canopy height Z^*

is estimated for a forest stand defining canopy and sub-canopy trees. By summing up the crown area (C_A) of all trees in the stand, Z^* is estimated as the height of the last tree that enters to the sum before the cumulative crown area is equal to the plot area. Canopy trees are absorbing a mean daily amount of shortwave solar radiation equal to the sum of mean beam, diffuse and scattered daily radiation in correspondence to the sun-shade model of de Pury and Farquhar (1997). The direct and diffuse fraction of solar radiation is estimated with the Spitters et al. (1986) approximation. The functional configuration of a tree (i.e. the values of the traits quartet) does not affect its competitive status, as tree height and crown area are not directly regulated by any of the four traits. Future versions of the model will incorporate such effects.

Soil water balance is approximated through a simple bucket model, with soil water content affecting leaf conductance and thus photosynthetic rates. Competition for soil water is approximated through a size hierarchy, i.e. bigger trees, with a more extensive root system are assumed to have access to deeper water (S1, Water Balance Algorithm). By assuming that a tree with a higher leaf biomass (B_L) requires a higher fine root biomass (B_{FR}), we indirectly implement a M_a effect on water competition S1, Definition, Allometry and Stoichiometry of Individual Trees in TFS). In particular, between two trees of the same size, the higher M_a tree will be more competitive in terms of acquiring soil water.

TFS is coded in Java and it is fully described in S1. Model components that are linked with any of the 4 base traits are described in following paragraphs. All statistical analyses and graphs were made with R (R Development Core Team, 2013).

...”

The authors walk through how the methods of light interception, stomatal conductance and water controls are integrated into the model, yet they do not place the same attention on how the method of Taylor and Thompson is specifically applied. I would strongly recommend **giving more treatment to how the Taylor and Thompson method works in this model, paragraph 2.1.1 is helpful but it needs more substance.**

We agree with Referee 2 that the Taylor and Thompson (T&T) method is probably one of the most interesting parts of this paper. For this reason we now place more attention by extending 2.1.1 to further describe it (see paragraph below). An algorithm for the T&T method is readily available as a subroutine in IMSL Fortran Numerical Stat Library (Visual Numerics, 2014) or can be provided on request in Java from the first author of this paper.

To replace section 2.1.1

“... ”

As noted above, TFS employs neither species nor PFT descriptions, but rather continua of the four key functional traits M_a , N_{Lm} , P_{Lm} and D_W used to characterize an individual tree along with a diameter-based allometry. To achieve this, these four functional characters were assigned to individual trees based on the actual values recorded within each plot using a random vector generation algorithm (Taylor and Thompson, 1986). This algorithm, appropriate for generating non-repeated pseudo-observations from a relatively small sample of observations, was originally developed to provide for a realistic probabilistic representation of shrapnel projectile distributions in military battlefield simulations in the face of only a limited amount of available data (due to the cost and difficulty of undertaking the appropriate experiments). The Taylor and Thompson (1986) “ballistic method” is notable in that it was specifically designed to short-circuit the usual step of multivariate density estimation (with the inevitable assumptions regarding the nature of the underlying statistical distributions) in the generation a pseudorandom population with approximately the same moments as the original sample. The ballistic method is readily programmable as follows (with the underlying rationale as discussed in Taylor & Tompson 1986 and Thompson 1989) with the following description based on Visual Numerics (2014):

First take a vector X with n multivariate observations ($x_1 \dots x_n$). To generate a pseudodataset from x , one observation (x_j) is first chosen at random and its nearest m neighbours, x_{j1} , x_{j2} , x_{jm} are then determined and with the mean \bar{x}_j of those nearest neighbours subsequently calculated. Next, a random sample

u_1, u_2, \dots, u_m is generated from a uniform distribution with lower bound $\frac{1}{m} - \sqrt{\frac{3(m-1)}{m^2}}$, and upper bound $\frac{1}{m} + \sqrt{\frac{3(m-1)}{m^2}}$.

The random variate as delivered is then

$$\sum_{l=1}^m u_l (x_{jl} - \bar{x}_j) + \bar{x}_j$$

and the process then repeated as required. Somewhat subjective here is the selection of the appropriate value of the number of nearest neighbours (m) although the nature of the simulations is not strongly dependent upon that value (Taylor & Thompson, 1986) and thus, following their recommendation and as in the Visual Numerics (2014) default, we have taken here $m = 5$.

In our case, coordinated trait suites for each tree in a stand are thus generated based on a smaller trait sample from trees in the same stand without any assumptions having to be made about their underlying statistical distributions. Thus no single functional trait “average stand” value is used (or even required). Further, between-stand differences in the traits distributions and their covariances that may have arisen from either the abiotic or biotic status the stand are also intrinsically taken into account. This is because each stand is characterised by its own multivariate trait sample and size distribution. More fertile plots have an overall lower M_a and higher $N_{L,m}$ and $P_{L,m}$ compared to infertile plots (Fyllas et al., 2009), with this being reflected in the photosynthetic capacity of individual trees, as described in the next paragraph.

...”

The supplemental material is a trove of interesting results and explanation of model mechanics. However, it is not clear why the authors decided to put some description in the body text, and some description in the supplemental material. There is also some redundancy. For instance the "daily fractional available water content" equation is displayed twice, and the leaf photosynthetic capacity equation is displayed twice. The logic behind what model mechanic is explained in the body text must be stated up front. For instance one way to separate the explanation is to only cover direct functional relationships that involve the 4 base traits. Otherwise, condense and combine the explanations of non novel model mechanics from the main text with the supplemental material; then make a concise summary of these modules for the main text.

We would like to thank Referee 2 for his comments and suggestions. Our initial thought was to discuss in the manuscript only parts of model that were new, and have a full model description in the Supplementary Information. However his/her suggestion to cover in the manuscript only functional relationships that include the traits quartet seems reasonable and we believe it will lead to a smoother text. We will thus change the main manuscript accordingly, and keep S1 in its original form.

It would be really interesting to see a diagram showing how the 4 traits tie into the model mechanics of the stand, although I think the manuscript is fine without. Some commentary in the discussion, or even a sensitivity analysis could be made, regarding how the size of the trait sampling space impacts model response and validation with observation. I am on the fence whether this type of analysis is really necessary. Although, I think it would be very useful.

The way the four traits affect different parts of the model mechanics has now been specifically discussed in Section 2.1. The size of the trait sampling does not seem to affect the behavior of the model. As shown in the “Randomisation Exercise” that has been now added in the manuscript (see response to Referee 1), applying meaningful constraints and trait-environment interactions is more important than the size of the trait sample distribution. We feel that the response given through the “Randomization Exercise” to Referee 1 also covers this comment from Referee 2.

The introduction gives a background on the four traits, but I would recommend that the discussion address other traits that were considered and rejected. The authors acknowledge works of Scheiter and Higgins, and Falster et al. 2011 and explain the differences in the three modeling schemes. For instance though, why was a trait such as seed size not included? A perfectly acceptable reason would be that you simply wanted to keep the trait set small or lack of data, but the decision making process would also be interesting and informative.

The following paragraph on the choice of functional traits used in TFS has been added.

“... ”

The four functional traits used in the current version of TFS, i.e. leaf dry mass per area, leaf nitrogen and phosphorous concentrations and wood density, are directly related to the rates of tree photosynthesis and respiration. For that reason they provide a stable basis that should allow alternative ecological strategies based on well known trade-offs such as the “growth vs. survival” to be implemented in trait-based vegetation dynamics models. These four traits have been extensively studied around 70 plots in the Amazon and their patterns of variation and inter-correlation have been analysed (Baker et al., 2009; Fyllas et al., 2009; Patiño et al., 2009; Patiño et al., 2012). For the purpose of this study, it is important to know the within stand variation of the functional traits used, i.e. the trait values at the individual level across different plots. Additional functional traits that were considered but not included as base traits in this version of TFS were the seed size and the leaf area to sapwood area ratio. Seed size is an important functional trait that expresses a tolerance vs. fecundity trade-off, with seed size trading-off with seed number and with larger seed species being more tolerant at more stressful places (Muller-Landau, 2010). However data on seed size are usually available at the species level, i.e. intraspecific variation is not usually recorded, and thus this kind of data cannot be included in the current version of TFS. The leaf area to sapwood area ratio, Φ_{LS} , is an important trait that can be used to constrain the hydraulic architecture of trees (Meinzer et al., 2008). Here Φ_{LS} is expressed as a function of D_w and H (equation 7) and it is not used as an independent (base) trait. Future version of TFS will include this aspect of functional variability, but for this first study we have selected just a small set of key traits in order to maintain a relative simple model structure.

...”

Technical comments:

This list of technical comments, apologetically, is definitely not complete. While the paper read smoothly in general, there were some awkward phrases here and there, and some overly verbose deliveries of concept. These are things that will smooth out with a few re-reads and the normal word smithing.

L26 1418: It is unclear what "functional dimensions" means here.

Changed to: “Two axes of functional variation/strategy”

L28 1418: change "leaf N and P dry mass concentration" to "leaf nitrogen and phosphorous dry mass concentration"

Changed

L5 1419: awkward sentence "Co-varying ..."

Changed to: “Low M_a and high nutrient content leaves are associated with comparably short longevity and usually have high (mass-based) gas exchange rates.”

L10 1419: awkward sentence "The fourth trait..."

Changed to: “The fourth trait, D_w , is used to represent a tree architectural axis with denser wood species supporting an overall higher aboveground biomass and thus having a higher maintenance respiration.”

L19 1433: cite Moorcroft et al. 2001 along with Fisher et al. 2010, capitalize Ecosystem Demography

Done

The font sizes in the figures need to be en-biggered in some places: figure 1 is not even close to readable, figure 4 axis tick labels are just barely readable, S1.1 is a mirror of figure 1 and enlarged but some axis are still completely unreadable, the axis ticks and labels in the lower panel of S1.5 are also too small.

All fixed

New References

Thompson, J. R.: Empirical Model Building, John Wiley & Sons., 1989.

Meinzer, F. C., Campanello, P. I., Domec, J.-C., Gatti, M. G., Goldstein, G., Villalobos-Vega, R. and Woodruff, D. R.: Constraints on physiological function associated with branch architecture and wood density in tropical forest trees, *Tree Physiology*, 28(11), 1609–1617, 2008.

Muller-Landau, H. C.: The tolerance–fecundity trade-off and the maintenance of diversity in seed size, *Proceedings of the National Academy of Sciences*, 107(9), 4242–4247, 2010.

Spitters, C. J. T.: Separating the diffuse and direct component of global radiation and its implications for modeling canopy photosynthesis Part II. Calculation of canopy photosynthesis, *Agricultural and Forest meteorology*, 38(1), 231–242, 1986.

Thompson, J. R.: Empirical Model Building, John Wiley & Sons., 1989.

Visual Numerics Fortran Numerical Stat Library, 2014 (available at <http://www.roguewave.com/portals/0/products/imsi-numeric-libraries/fortran-library/docs/7.0/stat/stat.htm>)