

Referee 1

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

The general topic of this paper is highly relevant and I appreciate the model development, which facilitates accounting for detailed biodiversity data in the context of a forest model.

Nevertheless, I think it would be useful to provide a more thorough comparison of the TFS concept to existing individual based vegetation models (e.g., LPJ-GUESS, FORMIND, Scheiter et al. 2013) and ongoing developments to improve the representation of PFTs in DGVMs (e.g., Verheijen et al. 2013, Wang et al. 2012, Pavlick et al. 2012) to better demonstrate the differences and novelty of TFS compared to existing models and concepts.

We modified and expanded the first two paragraphs of section “4.2 Practical Implications” to better discuss and compare TFS with the individual-based models and recent advances in DGVMs suggested by referee 1. (See also next comment response for descriptions of new sensitivity studies).

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The modelling of tropical forest carbon fluxes and stand dynamics has traditionally involved approaches aimed at a balance between simplicity, computational economy, and complexity. On one hand, the enormous biological and biogeochemical heterogeneity of tropical forests (Townsend et al., 2008) places special importance on how modelers prioritise both the amount and the detail of processes that should be included to capture the main controls and feedbacks. On the other hand, the finding that Amazonia is dominated by just 227 tree species (ter Steege et al., 2013) implies that most biogeochemical cycling in the world’s largest tropical forest is performed by a tiny sliver of its diversity. At one end of the complexity spectrum are individual-based models which are able to properly simulate population dynamics and thus lags due to demography. Individual-based models of tropical forests have traditionally focused on realistically representing the light environment (TROLL - Chave, 1999) or grouping tree species on the basis of their different responses to environmental resources as suggested by field observations (FORMIND - Kohler & Huth, 1998, LPJ-GUESS – Helly et al., 2006). At the other end of the complexity spectrum are DGVMs which simulate population dynamics more simplistically (but see Moorcroft et al., 2001; Scheiter & Higgins, 2009). Using a DGVM model Verheijen et al. (2013) allowed for within-PFT climate-driven trait variation to occur and achieved an improvement of the predicted vegetative biomass and PFT distribution patterns. A similar rationale was followed in Wang et al. (2012) where it was shown that the inclusion of multi-trait covariance in DGVM can be used to constrain model parameters and reduce uncertainties in simulated ecosystem productivity. Fisher et al. (2010) applied the individual-based Ecosystem Demography model (Moorcroft et al., 2001), and showed that by varying traits related to demographic processes, forest and biomass dynamics exhibited a wide range of responses to climate forcing.

Most of the above approaches have used discrete PFTs to represent tree species and functional diversity. These studies suggest that by allowing for within PFT trait variability a more plastic and realistic response to the relevant environmental drivers is observed. In contrast to the above, TFS replaces the use of PFTs with traits distributions, following a different model philosophy and architecture using the concept of multidimensional trait continua. In particular, considering functional diversity to be expressed by a multidimensional trait space, the use of PFTs selects a number of clusters where the central vector defines the average trait values of each PFT (Fyllas et al., 2012). Recent studies (Verheijen et al., 2013; Wang et al., 2012) allow for the average trait values to be shifted based on empirical climatic and/or trait inter-correlation functions. In contrast the use of trait continua does not cluster the multidimensional trait space but rather allows any potential trait combination to happen. Successful trait combinations under given environmental conditions are then expected to emerge as a by-product of model dynamics (Higgins et al., 2014). A similar to TFS representation of functional diversity is implemented in the aDGVM model (Scheiter & Higgins, 2009; Scheiter et al., 2013) where the importance of including trait-variability in simulations of vegetation dynamics has also been highlighted. In TFS, variable-trait ($R^2=0.42$) simulations led to a better model performance compared to fixed-trait ($R^2=0.29$) simulations (Fig. 6). Thus including functional diversity in simulations of vegetation dynamics is expected not only to suggest less vulnerable communities under changing climatic conditions (Fauset et al., 2012; Scheiter et al., 2013) but also, it seems, to better describe the current patterns of key ecosystem properties like aboveground productivity.

A few modelling studies that implement a similar traits continua approach have recently been published. Scheiter & Higgins (2009) were the first to develop an individual-based framework that eschews the use of PFTs and allows for plants to allocate carbon as a function of local environmental conditions. Falster and colleagues (2011) presented a model where they used leaf economic strategy, height, wood density and seed size to scale-up from individual scale processes to landscape predictions. Pavlick et al.

(2013) applied an interesting approach where they used 15 traits to incorporate trait diversity within plant community in a DGVM. The rationale of the above models is that they allow different plant functional strategies to be available in a specific location with given environmental conditions (for example a grid cell), and that by setting up a set of functional trade-offs they “filter out” poorly adapted trait combinations from the community. This is effectively an implementation of ideas arising from the environmental filtering/community assembly theory to predict an optimum plant community at a given location (Keddy, 1992; Scheiter et al., 2013; Fortunel et al., 2014). By contrast, drawing on recent findings on the processes controlling Amazonian forest dynamics, we have here attempted to incorporate within TFS the relevant observed associations between functional trait diversity, stand-structure and soil physical and chemical properties (Fyllas et al., 2009, Quesada et al., 2012). Although there are similarities with some of the more recent models discussed above to our knowledge this is the first time all these linkages have been represented in a single modelling framework. Our approach has been made possible (and thus differs from others) because of the type and quantity of observational constraints used. For example in any given plot we do not force the model to select some “optimum” trait combination based on the prevailing environmental conditions, but we rather assume that the observed trait distribution reflects that of the evolutionary stable community structure occurring at each site. Similarly we don’t require the model to predict what the optimum tree-size class distribution would be. Rather, we initialize simulations with what is observed. We have here employed this implementation as our primary aim was to validate the predictive ability of the model at some extensively monitored Amazonian plots.

Even with these prescribed constraints, the trait randomization exercise yielded some interesting outputs regarding the importance of trait variability in simulations of forest dynamics. As already discussed the default variable-trait (*var-tr*) simulations gave the best TFS performance in terms of predicting patterns of aboveground production at the 40 permanent measurement plots with fixed trait (*fix-tr*) TFS simulations showing a lower predictive ability and an overall higher mean Π_{AN} . This pattern of trait variability reducing above-ground biomass is in contrast with a similar simulation from Scheiter et al. (2013), where variable trait simulations gave rise to a higher mean biomass because of an increased chance of selecting a trait combination allowing trees to grow larger. This difference arises from the photosynthesis NP co-limitation constraint hardwired into the current version of TFS as the use of the Amazon wide mean N_L and P_L values, leads inevitably to universally P -limited estimates of V_{cmax} and J_{max} that reduce the overall predictive ability of the model. And when the NP co-limitation is removed, the variable trait simulations (*rand-tr-N*) do indeed yield the highest Π_{AN} estimates. Finally the random variable trait setup (*rand-tr*) resulted again in a similarly poor TFS behavior ($R^2=0.29$), emphasizing the importance of potential environment – trait interactions in accounting for between-stand structural differences. In other words trait distributions cannot be used without a consideration of how they may be shifted by the local growing conditions when modelling tropical forest dynamics.
 ...”

The main result of the current application of the TFS model (Page 1415 abstract: ...measures of stand level productivity were positively related to annual precipitation and soil fertility) could probably be directly derived from observed climate, soil and inventory data of the 40 RAINFOR permanent measurement plots, which in the context of this paper had been used to validate the model. However, the motivation of TFS development was an insufficient representation of biodiversity within PFTs in the context of current DGVMs. Given these two aspects it would be interesting to analyse the impact of the more detailed representation of biodiversity on model results, e.g., to which extent is the representation of biodiversity necessary to reproduce the observed pattern of stand level productivity?

I think it would be useful to represent in the model results the (additional) uncertainty introduced by the high degree of modelled detail, which on the other hand is to some extent constrained by observations.

We agree with this point and in order to respond we have set up a randomization exercise with TFS that highlights the importance of accounting for functional diversity and including known constraints when simulating Amazonian forest dynamics. This exercise consists of four alternative TFS simulations (described below – see also Fig 6) along the 40 permanent RAINFOR measurement plots. Results from these simulations show that:

1. when functional tree diversity is not included in the model (an equivalent of having just a single PFT) the predictive ability of the model is reduced,
2. when site-trait interactions are not included in the model, expressed here by the observed stand-level (in contrast to the regional level) trait distribution the predictive ability of the model is reduced,
3. when known biochemical constraints (in our case the NP co-limitation of photosynthetic capacity) are not included in the model, its predictive capacity is reduced.

This exercise is described in the next paragraphs and will be added in the revised manuscript.

To be added in the “2.2 Study Sites & Simulations Set-up” section

“...

2.2.4 Randomisation Exercise

In order to explore a) the importance of including trait variability and thus functional diversity in our simulations and b) the importance of including constraints that are known to control the large scale patterns of Amazonian forest dynamics, we conducted a randomisation exercise with the model being run under four alternative set-ups at the 40 permanent RAINFOR plots. The first set-up denoted as *var-tr* is the variable-trait simulation with trait initialization based on the observed stand-level trait distribution as described in the previous paragraphs (default set-up). The second set-up, denoted as *fix-tr*, is a fixed-trait simulation with all trees having the same (dataset mean) values for each trait: This thus representing a single PFT's case. The third set-up (*rand-tr*) is a variable-trait simulation with trait initialization based on random values of the traits quartet as recorded in any individual along the 40 permanent plots. This setup thus ignores any potential patterns of functional trait biogeography, i.e. traits are not related to the environmental conditions a tree is growing under. The fourth setup (*rand-tr-N*) is a variable trait simulation where the photosynthetic capacity of an individual is only defined by its leaf N content and thus the NP co-limitation constraint is removed. These alternative set-ups were compared by considering both the slope and the R^2 of SMA regressions between the predicted and the observed $\Pi_{N,S}$.

...”

To be added in the “3 Results” section

“...

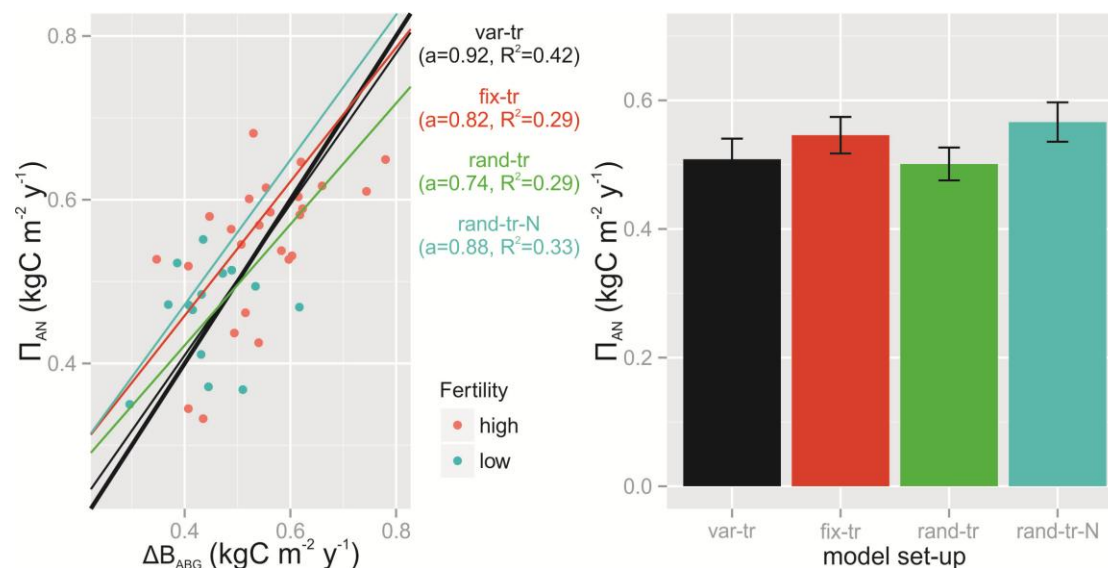
3.4 Randomisation Exercise Simulations

Results from the randomisation exercise (Fig. 6) found the fully constrained default set-up (*var-tr*) to have the best predictive performance ($R^2=0.42$ with a SMA slope $a=0.92$). This is as compared to the fixed trait simulations (*fix-tr*) single PFT parameterization with a decreased predictive ability of TFS ($R^2=0.29$, $a=0.82$) and an overall higher mean predicted aboveground productivity. Not accounting for the site specific distribution of the traits quartet, i.e. bypassing potential biogeographic patterns of functional diversity and/or environmental-trait interactions (*rand-tr*) also reduced the predictive ability of the model ($R^2=0.29$, $a=0.74$). Finally the random trait no NP co-limitation set-up (*rand-tr-N*) similarly lead to an inferior model performance ($R^2=0.33$, $a=0.88$) and with the highest mean simulated aboveground productivity.

This paper seems to be the first presentation of TFS. Therefore I am surprised that not the whole concept of TFS seems to be presented (e.g., page 1420: “snapshot version”, page 1430: “reported here on the core components”) and that it is highlighted that TFS is work in progress (page 1434: “..., TFS represents work in progress”).

With this version of TFS we wanted to create a tool that 1) takes full advantage of inventory data gathered following protocols similar to the RAINFOR network and 2) validate its behavior with very detailed tree by tree data at short time scales; this being an essential first step required before extrapolating TFS output to longer time scales. Thus the “snapshot version of TFS “ uses tree by tree diameter data and functional traits distribution measured at a specific plot to test whether a model like TFS can be used to upscale from the individual to stand level properties, for relatively short timescales (a few years). We did not want to present a recruitment and a mortality sub-model here, as including traits distribution in these processes is not trivial especially under changing abiotic (e.g. climate change) and biotic (e.g. succession) conditions. This is our next effort with TFS, but before moving there we wanted to be sure that the model performs well in short-term “stable” conditions.

Figure 6: Summary of the randomisation exercise simulations. a) Simulated stand-level aboveground net primary productivity (Π_{AN}) against observed stand-level aboveground biomass growth (ΔB_{ABG}) for the four different set-ups. The slope of the SMA (a) and the adjusted R^2 are given in the parentheses for each set-up. Different colors indicate different setups b) Simulated Amazon-wide aboveground net primary productivity (Π_{AN}) for the four different set-ups.



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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 constrains 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

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