

## 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  $\Pi_{AN}$ . 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  $\Pi_{AN}$  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.  
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**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

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#### 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  $\Pi_{N,S}$ .

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To be added in the “3 Results” section

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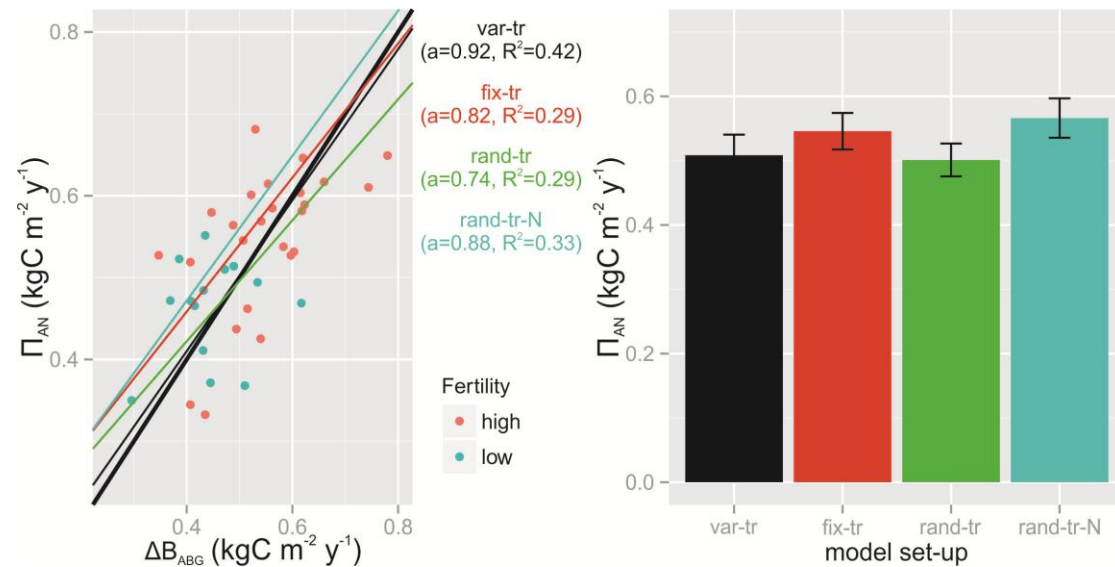
#### 3.4 Randomisation Exercise Simulations

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 ( $\Pi_{AN}$ ) against observed stand-level aboveground biomass growth ( $\Delta B_{ABG}$ ) 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 ( $\Pi_{AN}$ ) for the four different set-ups.



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