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Interactive comment on "Predicting biomass of hyperdiverse and structurally complex Central Amazon forests – a virtual approach using extensive field data" *by* D. Magnabosco Marra et al.

D. Magnabosco Marra et al.

dmarra@bgc-jena.mpg.de

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Response to Referees

General comments

We acknowledge Dr Ronald E. McRoberts and Dr Jochen Schöngart for reviewing our manuscript with great care and competence. Answering the points they raised significantly improved our revised manuscript. In particular, we would like to thank Dr McRoberts for his explanation on possible sources of uncertainty that could affect

the accuracy and precision of our landscape biomass estimates. We address this and other general comments below. We also provide a point-by-point response to 'technical' and 'minor' comments, which is given as the last part of this response.

The major general comment from Dr McRoberts referred to the treatment of uncertainty, in particular in being more accurate in describing sources of uncertainty and how we dealt with them. We aimed to parameterize biomass estimation models applicable across species and capable of producing accurate ad precise landscape biomass predictions in complex Central Amazon terra firme forests that include a range of successional stages (Chambers et al., 2009, 2013; Marra et al., 2014). Specifically, we sampled areas that represent our target forest and applied data from 727 trees from more than 100 species, contributing to reduce the uncertainty around parameter estimation. To deal with the residual uncertainty associated with model predictions, we applied different modeling approaches and finally tested our models against virtual forest-scenarios.

Parameter uncertainty (i.e. uncertainties in the data from which models were parameterized)

To our knowledge, our dataset is one of the largest allometric datasets from the same single extensive forest site. It is worth mentioning that these data were collected by the same work-team, which was trained over decades (LMF/INPA). Many biomass estimation models in the literature have been parameterized using datasets collected by different groups, under different conditions and using different methods (Wirth et al., 2004). In contrast, ours used a robust and self-consistent dataset containing a wide/complete range of predictors (i.e. DBH, H, SG and WD). By using a representative (i.e. Central Amazon terra firme forest) and reliable dataset on the parameterization of our models, we attenuated in the best possible way the uncertainty associated to the parameters estimation. Thus, we assume our 727 observations to be sufficient to assume non-negligible effects of parameter uncertainty.

Uncertainty associated with model structure

The model structure is directly related to the quality of the fit and comprises another important source of uncertainty. Addressing this residual uncertainty was our main motivation to fit and test models parameterized from different approaches. Our MOV approach produced better results than typically used approaches such as the NLS and the OLS (Sileshi, 2014). In our study, we did not use any conversion factor (e.g. tree volume to tree biomass), surely another important source of uncertainty.

Uncertainty associated with variability within a population

Another possible source of uncertainty pointed out by Dr McRoberts relates to the 'manner in which population variability is accommodated'. To address this issue we improved the explanations (sections 2.1 and 2.2) of site selection, sampling design and harvesting method (Chambers et al., 2001; Higuchi et al., 1998b; Lima et al., 2012). Our study site (EEST, Fig. 1) is a well known area (Braga, 1979; Guillaumet, 1987; Higuchi et al., 1998a; Ranzani, 1980; Teixeira et al., 2007) mainly covered with old-growth terra firme forest. The terra firme is the predominant forest type in the Amazon basin (Braga, 1979; Higuchi et al., 2004). Although landscape differences in floristic composition and forest structure exist at the regional scale (Phillips et al., 2004; Vieira et al., 2004), at the local-scale such differences become less relevant and small variations in forest attributes are mainly related to soil properties (Castilho et al., 2006), topography (Carneiro, 2004; Ribeiro et al., 1999) and vertical distance from drainage (Schietti et al., 2013). Our plot selection method accounted for variations in topography (i.e. sampled from plateaus and valleys) and successional stages (i.e. old-growth and secondary forests at different successional stage). Plots were sampled from previously surveyed, homogeneous and representative areas. For our secondary forests contiguous to our old-growth forest, we knew the time since disturbance, disturbance intensity and use-history (Lima et al., 2007; Santos, 1996; Silva, 2007). As described in section 2.2 and 2.3, the structural and floristic variability found in the secondary forests were added with the goal of increasing our capacity of sampling all possible combinations of

predictors (Tab. S1 and S2; Fig. S4 and S5).

Improvements/changes related to general comments

Dr McRoberts suggested that we assess 'the lack of accuracy in the context of uncertainty'. To address this, we present a new version of Fig. 6 (attached), which shows the overall performance of our tested models along the six virtual forest-scenarios. In this new version, both RMSE and bias are presented in terms of biomass (Mg). None of our best models (i.e. M33 and M23) had magnitudes of deviations substantially greater than the uncertainty of predictions (Fig. 6). The deviation of the modeled biomass from the real biomass was smaller, both in absolute (Mg) and relative (%) magnitude (as presented in the 1st version), than the uncertainty assigned to the prediction (based on the errors in the goodness-of-fit of the biomass model to the training data set).

As pointed by Dr McRoberts, techniques for propagating sources of individual uncertainty through landscape estimates are not trivial and thus, not often used. Assessing this uncertainty was the main focus of many different studies, which have used information from remote sensing (Chen et al., 2015) to Taylor series (Berger et al., 2014) and Monte Carlo simulations (Breidenbach et al., 2014; McRoberts and Westfall, 2015). All these methods are premised on detecting and quantifying the uncertainty associated with error propagation when going from individual to landscape-level biomass estimates. We parameterized our models in WinBUGS, which would have allowed us to easily run error propagation using Markov chain Monte Carlo (MCMC) code. Instead, our study focused on more relevant and unknown sources of uncertainty associated with biomass estimates in a landscape that is a mosaic of forest successional stages (Asner, 2013; Chambers et al., 2013), and therefore varying in forest structure and species composition, something not yet explored in hyperdiverse tropical forests. Nonetheless, we agree with the second point raised by Dr McRoberts and, where applicable, we calculated the r2 coefficient of determination and present it together with the R2adj adjusted coefficient of determination in the revised manuscript.

Our modeling approaches and 'internal evaluation' with virtual forest-scenarios produced consistent and robust scenarios. As argued by both Referees, we believe that our study fully addressed our proposed questions and sheds new light on this important topic. We hope that our revised manuscript will be accepted for final publication in Biogeosciences.

Point-by-point answer to 'minor' and 'technical comments'

Dr Ronald E. McRoberts

p. 15539, line 28: Destructive sampling is not always necessary (Westfall & Scott, 2010).

While we agree, the data set also includes belowground biomass (not reported in this study) (Santos, 1996; Silva, 2007), which is still not possible to measure without destructive sampling. Nonetheless, since here we focused on aboveground biomass, the word 'destructive' was removed. The sentence is rewritten to say: 'Reliable biomass assessments for the Amazon basin still depend on the collection of allometry data at the local/regional scale and forest inventories including species-specific attributes, which are often unavailable or estimated imprecisely in most regions.' p. 15539, lines 10, 11, and throughout the paper: Avoid use of subjective terms such as "good", "poor", "better", etc whose criteria are not defined.

We revised the whole manuscript and removed seven of these terms. In few cases were they were used, a criterion/reference was given.

p. 15541, line 10, and throughout the paper: In statistics, unbiasedness or biasedness is a property of a statistical estimator (a formula), not estimates, not predictions, not models, and not samples. Formally, an assessment of unbiasedness or biasedness entails a comparison between the true value of a parameter and the expected value over all possible samples that could have been obtained using the sampling design. Thus, a bias assessment requires knowledge of the true value and at least a very large

number of samples. Unless a very large number of samples (sets of observations, not individual observations) are used, predictions should not be characterized as "biased." Rather, something related to "predictions that deviate from their observations" could be used.

We thank Dr McRoberts for providing this explanation. We rewrote several sentences in response:

Lines 80-86: 'Unfortunately, transferring such species-, size-, ontogeny- and site-specific biomass estimation models to other contexts - other species, other size ranges, other life-stages, other sites or successional stages - typically leads to predictions that deviate strongly from observations, especially when the sampling design does not allow the selection of relevant data for proper estimation of the parameters of interest (Gregoire et al., 2016) or when predictor ranges are limited or neglected (Clark and Kellner, 2012; Sileshi, 2014) .'

Lines 645-647: 'As observed in our (Tab. 2) and other allometry datasets (Sileshi, 2014), the high collinearity between DBH and H can distort coefficient values, inflate standard errors and lead to unreliable estimates.'

Lines 475-477: 'This explains why the models fit with these approaches produced more reliable (i.e. smaller differences between predictions and observations) AGB estimates as compared to those fit with the NLS approach.'

Lines 100-102: 'The design matrix should ideally cover all possible real-world combinations of predictor values in order to avoid error-prone extrapolations and unreliable predictions.'

p. 15541, line 23, elsewhere: The term "coefficient" is only appropriate if the model is linear; check any good dictionary. A generic term that includes both linear and nonlinear models is "parameter."

We thank Dr. McRoberts for pointing this out and have corrected the whole manuscript (i.e. tables and figures) for this issue.

p. 15442, line 1: The term “multivariate” refers to multiple response or dependent variables. When the model is linear and multiple predictor or independent variables are used, then the term “multiple regression model” is often used.

The sentences in which we have used this term were corrected to read: Lines 91-93: ‘Instead, the challenge is to develop generic local or regional formulations that generalize also across species (Higuchi et al., 1998b; Lima et al., 2012; Nelson et al., 1999; Saldarriaga et al., 1998).’

Lines 102-103: ‘However, in multiple regression models, this precondition is rarely met, not even by large design matrices.’

Lines 106-107: ‘The larger the variation of predictor values within a stand, the higher is the likelihood that extrapolation errors occur.’

p.15443, line 17: Is there any assurance that these simulated plots represent actual plots on the landscape?

To our knowledge, our study includes the largest destructive allometric dataset for one single site in the Amazon. This dataset includes 727 trees from 101 genera and at least 135 species. By including this large number of trees and species, we assume that our data set satisfactorily represents the local landscape variation in tree architecture and allometry. Our scenarios were designed to span a successional gradient created by natural disturbances in which the interaction of tree mortality intensity and species vulnerability and resilience produce complex communities varying in species composition and size-distribution of trees (Chambers et al., 2009, 2013; Marra et al., 2014). As mentioned in the ‘Introduction’ and ‘Material and Methods’ sections, our scenarios of simulated 100 1-ha forest plots included variations in (1) floristic composition (i.e. specific proportions of pioneer, mid- and late-succession species) and (2) size distributions (i.e. specific proportions of large and small trees). For assembling

our scenarios, we defined thresholds of tree density and basal area (see details in section 2.4.2) that were based on empirical observations and data from a network of permanent plots in the same overall study site, including an old-growth forest (LMF unpublished data [1996-2012 census] and Silva et al., 2002), a four year-old blowdown (Marra et al., 2014), a seven year-old blowdown (LMF unpublished data), a 14 year-old blowdown (LMF unpublished data), a 17 year-old blowdown (LMF unpublished data), a 24 year-old blowdown (LMF unpublished data), a 27 year-old blowdown (LMF unpublished data), a 14 year-old slash and burn secondary forest, and a 23 year-old clear cut secondary forest (Lima et al., 2007;âĂÍ Silva, 2007). Thus the parameters of the simulated 100 ha plots did have a basis in reality, in that they were constrained by empirical observations but represent real scenarios recovering from windthrow disturbance (Fig. 2).

p. 15443, line 26: The term “bias” is incorrect here. A preferable term would be “mean deviation.”

We corrected the sentence as follows:

Lines 154-157: ‘We expected that the best model, the one reducing both mean deviation and error of single and landscape-level biomass prediction, would require species-specific variables as well as an additional parameter allowing the modeling of heteroscedastic variance.’

p.15545, line 8: Although issues of cost and access are acknowledged, observations for trees on the same plot should not be considered independent when constructing models because they are all affected by the same site, competition, and other factors, i.e, these observations are surely correlated.

Although individuals in the same plot might be expected to be ‘related’ (compared to those more distant from each other), our plot-based method has several advantages. Biomass estimation models were fit at the individual-level. Our sample unit was individual trees. The applied plot-based method (Chambers et al., 2001; Higuchi et al., 1998b; Lima et al., 2012; Silva, 2007) relied on a random selection of plots from a homogeneous forest. This method, besides than ensuring a random selection of trees, allows for a valid representation of the size-distribution of the target forest. Since all the biomass of each plot is harvested, this method also allow for a landscape validation of the parameterized models. It is also appropriate for assessing the biomass partitioning among different life forms (trees, palms, lianas, epiphytes, etc.) and strata (seedlings, saplings and trees), which were among the main goals of the studies for which the data was collected (Santos, 1996; Silva, 2007). In total, we harvested trees from 21 plots (5,100 m2). As previously mentioned, our plots do cover the various landscape elements present in both old-growth and secondary forests.

p. 15547, line 12: How is the categorical variable "successional group" used as a predictor variable? Predictor variables are usually assumed to be continuous?

We used the successional group (SG) assignment as a factor, thereby representing functional diversity along a main axis of tree successional strategies, functional and architectural variation. Depending on the model-type parameters of the continuous variables were allowed to vary to capture the successional aspects of functional diversity. We consider the grouping factor SG as integral part of the model. Fitting all SGs in one model in an MCMC context is different from fitting separate models because the joint model also absorbs the covariance structure of the parameters across groups, especially in models were not all parameters are allowed to vary between SG. Whether in this context we are allowed to call it a predictor, we are not exactly sure. We therefore propose to use the term 'categorical predictor' whenever we address SG in particular.

p. 15548, line 21: Change "equation" to "model" as in the rest of the paper. Despite widespread erroneous usage in the applied literature, the two terms are not synonymous.

The mistake was corrected. Now it reads: 'In contrast to prior approaches, we did not test models based on compound. . .'

p. 15549, line 21: The measure expressed in Eq. (3) is highly questionable when there is heteroscedasticity.

There is indeed heteroscedascity in our data (as in fact in all tree allometry data relating linear to volume-proportional data), which is why we applied our MOV approach. We agree with you that the relative standard error Syx% is not an appropriate measure in this case. This is why we did not use it as model selection criterion. We calculated it only to allow for the comparisons of different model structures/approaches, as this measure is commonly reported (Lima et al., 2012; Ribeiro et al., 2014; Sileshi, 2014). However, we understand that our writing my suggest otherwise. We therefore reformulated the paragraph preceding Eq. (3) and also placed the caveat you were pointing us to herein.

p. 15550, line 13: Are 100 replications sufficient? The general understanding is that replications should continue until the statistic of interest stabilizes. Note that Efron and Tibshirani (1994) who wrote the bible on bootstrapping recommend at least 200 replications.

Our main idea in testing models with the different scenarios was to assess their overall performance once subjected to the gradient of successional stages typical of Central Amazon terra firme forests (i.e. strong variations in species composition and size-distribution). In producing scenarios, we also considered local and regional logistic-economic aspects. We assembled 1-ha plots because this is the regular size of permanent plots used in assessments of forest dynamics (i.e. biomass and carbon) in tropical forests. Most of the forest inventories in the Amazon have a total sampled area of less than 5 ha. When taking into account that our evaluation (this is not a model validation per se) is based on the joint performance of the different models over all six different scenarios we simulated (Figs. 3-6), each model is actually tested against 600 replications of 1-ha plots. More to the point, our 100 replications of each scenario produced robust and representative results compared to several other tests we carried out using a greater (up to 1000) and fewer number of replications. The suitability of our

100 1-ha plots on representing the proposed scenarios with their respective variations in floristic composition and size-distribution is also shown in Fig. 2.

p. 15551, line 19: Because the actual parameter estimates have been included, in Eq. (5), place a caret (ËĘ) over "logAGB" to indicate that it is a prediction.

The character was added.

Dr Jochen Schöngart

Abstract: L. 24: Indicate the meaning of AGB the first time used in the text.

We could not track/identify this error in the line 24 of the 'Abstract'. Nonetheless, we have checked the entire manuscript to assure that all acronyms, when used for the first time, were followed by their respective meaning.

Introduction: L. 72/73: I suggest some studies on wood anatomy and also tree-ring analysis (for instance, Worbes, Brienen).

We added two extra references on wood density and growth from tree ring analysis. The sentence was rephrased as following: 'In addition, there is large variation in growth rate (the speed at which a certain space is filled) and consequently in wood anatomy among species (Bowman et al., 2013; Silva et al., 2002; Worbes et al., 2003).'

Material and methods L. 164/165: Indicate the period of the observed annual average temperature and total annual rainfall.

We have included the period of measurement and respective references. The sentences now read as follows: Lines 168-171: 'Averaged annual temperature in Manaus was 26.7 °C for the 1910-1983 period (Chambers et al., 2004). Averaged annual precipitation ca. 50 km east of our study site was 2610 mm for the 1980-2000 period (Silva et al., 2003) with annual peaks of up to 3450 mm (Silva et al., 2002).'

L. 167-170: The sandy soils on the slope bottoms (baixios) are subject to seasonal flooding during the rainy season, however, in contrast to the floodplains (igapó and

várzea) along the huge Amazonian rivers with a monomodal and predictable flood-pulse, the baixios are characterized by a polymodal and not predictable flood-pulse patterns with many, sporadic and short inundations (Junk et al., 2011). This should be better described.

The reference was incorporated to the paragraph, which was rephrased as following: Lines: 173-179: 'Soils on upland plateaus and the upper portions of slopes have high clay content (Oxisols), while soils on slope bottoms and valleys have high sand content (Spodosols) and are subject to seasonal flooding (Telles et al., 2003). In contrast to floodplains (i.e. igapó and várzea) associated with large Amazon rivers (e.g. Rio Negro and Rio Amazonas), valleys associated with streams and low-order rivers can be affected by local rain events and thus have a polymodal and not predictable flood-pulse pattern with many short and sporadic inundations (Junk et al., 2011).'

L. 172-173: There is no doubt that terra firme forests are the predominant forest type in the Amazon basin. However, many of the terra firme forests in the Western Amazon basin are paleovárzeas with lower C-stocks in AGB, but a higher AGB productivity (Quesada, et al. 2012). Junk et al. (2011) estimate that wetlands cover approximately 30% of the Amazon basin.

We rephrased the sentence as following: 'The terra firme forests are among the predominant forest types in the Brazilian Amazon (Braga, 1979; Higuchi et al., 2004) and c. 93% of the total plant biomass is stored in trees with DBH $\geq$ 5 cm (Lima et al., 2012; Silva, 2007).'

L. 227: Should it not be "species" instead of "studies"?

In this sentence, we referred to the variation in wood density values from different studies (methodological differences) (Williamson and Wiemann, 2010) for a same species. In order to make our point clear, we rephrased the sentence as following: Lines 248-251: 'Since reported WD wood density values for the same species or genera can vary strongly among different studies (Chave et al., 2006) and sites (Muller-Landau, 2004), we compiled WD values mainly from studies carried out in the Brazilian Amazon (Chave et al., 2009; Fearnside, 1997; Laurance et al., 2006; Nogueira et al., 2005, 2007).'

L. 247: variables (plural form).

The plural form was added.

Discussion: L. 431/432: I think you should add "one" after "either".

We have checked this sentence and decided to do not change it.

L. 492-494: Avoid using three times the word "dataset" in the same sentence".

The sentence was changed to: Lines 522-525: 'Observed differences on the relationship between predictor variables (DBH and WD) and AGB of trees from our dataset and that used in the pantropical model highlight part of the variation in tree allometry and architecture that was not represented in the pantropical dataset (Fig. S4).'

L. 583-588: Not all of these indicated methods allow the measurement of wood density in live trees. X-densitometry and high-frequency densitometry are performed in laboratories as they require the preparation of the wood samples to perform the analyses which require a sophisticated infrastructure.

Here we wanted to say that the improvement of available methods, which still might not be fully applicable, could reduce costs and provide greater autonomy/capacity of collecting data. We rewrote the sentence as following: Lines 618-622: 'This requires improvement of available methods and tools (e.g. resistography, X-ray, ultrasonic tomography, near-infrared-spectroscopy, acoustic/ultrasonic wave propagation and high-frequency densitometry) (Isik and Li, 2003; Lin et al., 2008; Schinker et al., 2003) that in the future may allow the measurement of WD in live trees from hyperdiverse tropical forests (thousands of species).'

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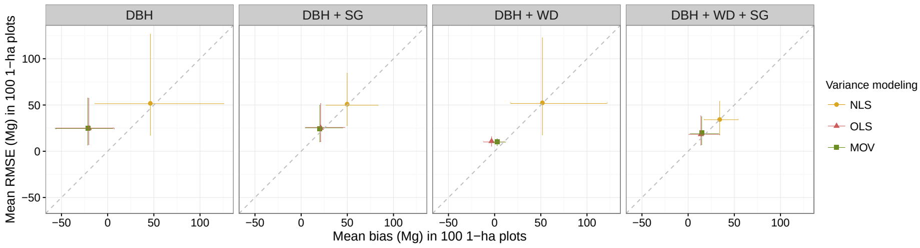

DBH
DBH + SG
DBH + WD
DBH + WD + SG
Mean RMSE (Mg) in 100 1−ha plots
Mean bias (Mg) in 100 1−ha plots
100
50
0
−50
−50
0
50
100
Variance modeling
NLS
OLS
MOV

Fig. 1.