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Title: Selecting allometric equations to estimate forest biomass from plot- rather than individual-level predictive performance

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We thank the two Reviewers for their helpful suggestions and comments that hopefully permitted to improve the manuscript. We were encouraged by the positive review of the reviewers.

All changes in the revised manuscript are highlighted using blue text. Unless otherwise indicated, line numbers refer to the previous version of the manuscript.

Response to Reviewer #1's comments

Methodology:

1. *“Although the study focuses on the giant Congo rainforest, the study employs a detailed approach to estimate biomass in tropical forests using different plot size strategies. Is the methodology used to calibrate and validate the models robust enough for possible different types of tropical forests? How do these methodologies deal with the heterogeneity of tropical forests, which can vary significantly in terms of structure and species composition?”*

Because it partitions the prediction error between bias, plot variability and coefficient variability, we believe that the method we propose is particularly relevant to study how biomass allometry varies when scaling up across different forest types. If we fit an allometric equation to a local forest type and then applies it to another forest with a different structure and species composition, we expect the bias component of MSS to be important (see our response to comment #2 below). However, when dealing with the heterogeneity of tropical forests, the central question remains to know whether it is worth to address it by introducing in allometric equations additional covariates that explain this heterogeneity, or whether it is enough to leave it as a random noise that will cancel off if the plot is large enough. This question is a question of trade-off between bias and variance. Our dataset provides an example of such a trade-off linked to species composition. When looking at the tree-level, the model with the best predictive performance is model (4) that fits a different allometry for each species genus. It confirms that different tree genera have different biomass allometries. However, at the scale of the forest where the species composition is not exactly the same as in the calibration dataset, model (4) is also the one that results in the highest bias and the weakest overall predictive performance. The conclusion for this example is that, even there are differences in allometry between tree genera, if our objective is to predict the biomass of large plots, it is statistically more efficient to leave the heterogeneity in species composition as a random noise. We cannot say that this conclusion is general because it is based on our particular dataset. Nevertheless, the methods we provide will allow other people to address such questions in other contexts.

We rewrote the beginning of each paragraph in the Results section to better convey the main messages, which allowed us to remove some parts of the Discussion (lines 280-285). Instead, we developed the ideas given above (lines 261-268 in the revised manuscript).

2. “*Considering that field data collection is essential for model calibration, how was the potential bias from limited or non-representative sampling of different forest areas addressed? Can this be addressed in the manuscript?*”

We can address the question of the bias arising from the non-representativeness of the sample of trees by using a different dataset. To be more precise, we can fit the allometric equations using a dataset and assess their predictive performance using another dataset. This computation corresponds to the validation case that we discussed in Section 4.2 of the manuscript. To exemplify this bias, we fitted the allometric equation using the dataset of Fayolle et al. (2018) and assessed its predictive performance using the subset of the dataset of Chave et al. (2014) corresponding to the Amazon (with trees coming from Brazil, Colombia, French Guiana and Peru). We may expect indeed central African forests not be representative of Amazonian forests. We complemented Fig. 4 with a panel showing the partition of MSS when the model is fitted to central African trees and MSS computed using Amazonian. The coefficient variability and the plot variability were of the same order for Amazonian forests as for central African forests. However, the bias component was about 30 times bigger for Amazonian forests than for central African forests. This was not a surprise since the allometric equations were fitted using central African trees. Therefore, assessing the predictive performance of the allometric equations on a dataset that is not representative of the forest where the equations were fitted inflates the role of bias in the overall performance. We added these elements in Section 4.2 of the manuscript.

Results, broader implications, and limitations of the study:

1. “*How do the authors interpret the results found regarding spatial and temporal variability of biomass in the studied forests? Is there any indication of changes in biomass stock over time that could be correlated with environmental or anthropogenic factors?*” 2. “*Is biomass quantification in line with estimates from similar studies? Can you provide data showing or not showing discrepancies, and what might explain them?*” 3. “*The results indicate that tropical forests have a significant capacity to store biomass. What are the implications of these findings for conservation and climate change mitigation policies? How do these results contribute to the global understanding of the role of tropical forests as carbon sinks?*”

These three questions are indeed very important, but we are afraid these questions make sense at geographical scales beyond the forest (landscape, region, country, continent...). Our study deals with the scales between the tree and the forest. The overall objective of our study is to improve the strategy in developing allometric equations, by changing its target. The target of this strategy used to be the minimization of the prediction error at the tree level. Our proposal is to set it as the minimization of the prediction at the plot level. We expect our results to contribute to a better efficiency in the estimation of biomass stocks, but we are not providing actual estimates of biomass stocks. This latter objective would require forest inventory data. Such forest inventory data do exist, but it is out of the scope of our study.

For instance, there is no temporal dimension in our study, for the mere reason that biomass allometry is assumed to be a timeless characteristic of trees, deriving from their biological char-

acteristics only. Changes in forest biomass stocks over time basically result from (1) changes in forest areas, and (2) changes in biomass density. Based on the FAO definition of forests that mainly refer to land use, the former changes (the so-called “activity data” in IPCC’s terminology) are driven by human factors. The latter changes may result from changes in forest structure and composition over time. To address this component of change, we would need forest inventory data at different dates.

This being said, we acknowledge that the objective of our study was not clearly stated in the introduction. We modified the introduction to better explain it (lines 69-70 of the revised manuscript).

4. *“To what extent does this study advance knowledge on the quantification of biomass and carbon in tropical forests? How does it contribute to the development of new methodologies or the improvement of existing methodologies?”*

Our study shows that minimizing the prediction error at the tree level may not be the most efficient strategy to develop allometric equations when the objective is to assess forest biomass stocks at a large scale (at the forest scale and beyond). As a consequence, introducing additional covariates in the models, with additional measurements costs incurred, may not be needed. Our results may thus contribute to save efforts in measuring tree biomass for the future development of allometric equations. However, the development of allometric equations may be motivated by other objectives than the estimation of forest biomass stocks at large scales. For instance, there may be a theoretical interest in understanding the biological basis of biomass allometry. In that case, the focus will remain on the tree level. Some wording was added to clarify this point (lines 269-275 of the revised manuscript).

We realize that our manuscript focused too much on the technical aspects of the question and did not explain the more general implication of our results. We added a sentence in the introduction (line 32) to clarify that the development of new tree biomass allometric equations is still mobilizing a great deal of scientific efforts around the world. We also added a few sentences in the conclusion to clarify that our results may contribute to be more efficient in these efforts (lines 339-341 of the revised manuscript).

5. *“How can the results of this study influence future research on changes in carbon stocks in tropical forests? Are there gaps that still need to be addressed?”*

The question of research gaps on changes in carbon stocks in tropical forests is a very broad question. We here restrict it to the sub-question of the development of allometric equations. The determinants of tree biomass allometry are still not well understood. There is considerable effort in developing new allometric equations around the world (for more species, for more locations). However, with a few exceptions (like the metabolic scaling theory), there is no general theory underlying tree biomass allometry. As a consequence, the various efforts are difficult to aggregate under a common framework.

We added a few sentences in the discussion (lines 269-275 of the revised manuscript) to clarify that this is a research gap that undermines our understanding of forest biomass stocks.

6. *“What is the impact of this study on understanding the role of tropical forests in carbon sequestration, especially in the context of global climate change?”*

Tropical forests are an important carbon pool at the global level. There are still uncertainties

on the quantification of this pool. For instance, there are still major divergent estimates among large-scale biomass maps obtained through remote sensing and field data (Rodda et al., 2024). There are many factors contributing to these uncertainties. At the plot level, the uncertainty on the choice of the allometric equation used to convert inventory data into biomass estimates is one of the greatest sources of error (Picard et al., 2016). Our study contributes to making more informed choices among models.

We added two sentences in the introduction to clarify this point (lines 25-26 and 41-42 of the revised manuscript).

7. *“What are the main limitations of the methods used in the study, especially in terms of spatial scale? How might these limitations affect the interpretation of the results?”*

Additional sources of errors could be included in the MSS partition, such as measurement errors. However, previous studies have shown that measurement errors have a minor contribution to the overall biomass prediction error at the plot level (Picard et al., 2015a). Therefore, we also expect measurement errors to have a minor influence on our results.

Another limitation of our method is the use of a simulated forest to generate plot data instead of actual forest inventory data. We are not aware of any field data giving the measured biomass of every tree in a forest. Such a dataset probably does not exist given the tremendous cost it would incur, even if LiDAR may change the game in a near future. Therefore, some minimal assumptions are needed to generate large-scale plot biomass data (where biomass is measured, not estimated by a model). At least, a starting point to generate such data could be to use forest inventory data. We could imagine for instance that every tree in the forest inventory data would be assigned the observed biomass of the individual that is closest in size to this tree. Even if tree biomass would not be actual measurements, this process would preserve the shifts in forest structure and species composition that are observed in real forests.

In our study, the bias contribution to MSS is almost independent of plot size (see Figure 2c). We expect this result to change if forest inventory data was used in place of the simulated forest. We would then expect the bias to increase with plot size. Therefore, the relative importance of bias in model selection for large plots would be even greater than it is at present. We thus expect our results to be conservative with respect to the role of bias in model selection.

We added a paragraph in the discussion to clarify these limitations (lines 276-280 of the revised manuscript). So as not to make the discussion too long, two paragraphs of the previous version of the discussion were dropped (lines 258-261 and lines 271-275).

8. *“What were the main challenges in quantifying uncertainty associated with the methods associated with different plot sizes and individual trees, and how might this influence the results?”*

As already said, we are not aware of any dataset giving the measured biomass of every tree in a large plot, not to say a forest. Terrestrial LiDAR may change the game in a near future by providing non-destructive measurement of tree volume for all trees in a plot (this point was clarified in the introduction at the line 37 of the revised manuscript). We circumvented this issue by resampling measured trees. The bias contribution to MSS may thus have been underestimated in large plots.

9. *“Are there any limitations related to the representativeness of the field data about the diversity of tropical forests? How might the lack of representativeness have impacted the results?”*

The method we propose to assess the predictive performance of allometric equations is general and can be applied to any forest. As explained in lines 256-257, the specific ranking of allometric equations is then dependent on the specific forest under study. We could investigate the influence of the forest structure on the model ranking by varying the parameter μ of the simulated forest.

The calibration dataset \mathcal{X} has a greater proportion of large trees than the simulated forests \mathcal{F} . Therefore, by comparing the bias statistics $b_{\mathcal{X}}$ and the bias statistics $b_{\mathcal{F}}$ given in Table 2, we can already predict how the model ranking would change if the forest had many large trees. Because the model performance for large plots is driven by the bias component, we expect the model ranking to shift from the ranking of $b_{\mathcal{F}}$ to the ranking of $b_{\mathcal{X}}$ as the proportion of large trees in the forest increases.

Main Scientific Contributions:

1. *“The study offers significant contributions to the science of ecology and the understanding of tropical forests as carbon sinks. What are the main methodological innovations presented?”*

The main methodological innovation lies in the strategy to rank and select allometric equations. When the objective is to estimate plot-level biomass, allometric equations should be selected on their bias performance at the forest level rather than on their residual error at the tree level. We largely rewrote the introduction to clarify this point (see in particular lines 60-61 and 69-70 of the revised manuscript).

2. *“How does the study advance knowledge about spatial variation of biomass in tropical forests? What new insights does it offer for these forests’ conservation and sustainable management?”*

Our study could contribute to reduce the uncertainty on the model choice that represents an important part of the uncertainty of biomass estimates in tropical forests. The drivers of spatial variation of biomass in tropical forests could then be more easily identified and understood. Some sentences were added in the introduction to clarify this point (see lines 25-26 and 41-42 of the revised manuscript).

3. *“How can the results of this study be applied to other tropical regions in addition to the areas studied? Is there potential for replicating the methodologies in other areas or biomes?”*

There is no restriction to apply the method we propose to other tropical regions. On the contrary, we encourage this method to be replicated in other tropical areas and other biomes. We expect the relative importance of bias, plot variability and coefficient variability in model selection to change from one place to another. However, the decreasing importance of plot variability with plot size should be a constant feature.

Response to Reviewer #2’s comments

1. *“The authors repeatedly assert: “So far, model selection for allometric equations has been performed based on the tree-level predictive performance of the models.” This is not entirely true. It suggests that the authors’ understanding of the overall situation regarding the application and development of plot level models worldwide is incomplete. In other words, they seem*

to focus only on the application of the model in developed countries such as Europe and North America, which ignoring its application in the broader context of developing countries. Let me give you an example. In China, both plot level model and the tree level model are used. Plot level models have been used to estimate and predict forest biomass for decades. There is a substantial body of literature on this topic. I only list some papers as follows:

Fang J, Chen A, Peng C, Zhao S, Ci L (2001) Changes in forest biomass carbon storage in China between 1949 and 1998. *Science* 292:2320–2322

Pan Y, Luo T, Birdsey R, Hom J, Melillo J (2004) New estimates of carbon storage and sequestration in China's forests: effects of age-class and method on inventory-based carbon estimation. *Clim Chang* 67:211–236

Fang J, Guo Z, Piao S, Chen A, (2007) Terrestrial vegetation carbon sinks in China, 1981–2000. *Science in China Series D: Earth Sciences* 50(9):1341–1350

Guo Z, Fang J, Pan Y, Birdsey R (2010) Inventory-based estimates of forest biomass carbon stocks in China: a comparison of three methods. *Forest Ecol Manag* 259(7):1225–1231

Fang J, Guo Z, Hu H, Kato T, Muraoka H, Son Y, (2014) Forest biomass carbon sinks in East Asia, with special reference to the relative contributions of forest expansion and forest growth. *Global Change Biology* 20(6):2019–2030.

Fang J, Yu G, Liu L, Hu S, Chapin FS (2018) Climate change, human impacts, and carbon sequestration in China. *PNAS* 115:4015–4020

The model they used is $\text{biomass/volume} = \text{BEF} = a + b/\text{volume}$, which is (biomass per hectare) = $b + a * (\text{volume per hectare})$. This is a typical plot-level model. Beside this kind of linear model, there are also some models using power and polynomial functions, which contain variable DBH and tree height. The reason for using the plot-level model is straightforward. In China, only provincial forest inventory data (forest area and volume for each age group) are released to the public, excluding DBH and tree height data. Consequently, the researchers have to use various plot level models (volume-to-biomass model) to convert from volume to biomass per unit. This data issue is universal, as DBH and tree height data are not released in forest inventory reports in many developing countries. In this manuscript, the application and development of the plot level model do not align with what the authors describe. I therefore suggest that the authors enhance the review in their manuscript to be comprehensive and avoid the straw man fallacy.”

We acknowledge that we overlooked BEF methods and other plot-level models in the introduction. We acknowledge too that we overlooked biomass studies from Asia. BEF and other plot-level models necessarily rely on plot-level biomass data for their calibration. Not all studies on BEF and plot-level models clearly indicate how they obtained these biomasses at plot-level. In many cases, plot-level biomass was actually obtained from tree-level measurements and tree-level allometric equations to convert these measurements into biomass. Pan et al. (2004), cited by the Reviewer, proceeded in this way. So did Brown et al. (1989), which is also an often-cited reference on BEF methods. Using allometric equations to derive plot-level biomass is precisely the point we are addressing in our manuscript. If the tree-level allometric equation is biased, so will be the plot-level biomass data obtained from it, and so will be the BEF and plot-level model fitted to these data.

In other words, BEF and plot-level models are not really an alternative to tree-level allometric equation. They are rather an intermediary step to scale up biomass estimates from the tree level to higher levels (plot, forest, region, country, continent...).

We changed the introduction to clarify that in the chain of measurements that starts from the tree and end with remote sensing techniques, there is an additional intermediary step that consists

in BEF and plot-level methods. Lines 29 & sqq. were changed as follows: “Plot-level biomass can be used to fit plot-level models that predict plot biomass from plot volume and other plot characteristics, using biomass expansion factors or related approaches (Pan et al., 2004; Fang et al., 2007; Guo et al., 2010). These plot-level models can then be used to estimate forest biomass at the country (Fang et al., 2007) and continental (Fang et al., 2014) scales. Plot-level biomass can be used too to calibrate remote sensing indices to predict the biomass of pixels in satellite images [...]”.

2. *“Mathematical content takes up too much space. Since this journal is not highly technical, and the potential readers have a broad knowledge background, I recommend including only the most necessary mathematical derivations, expressions, and explanations in the text. The rest can be put into supplementary information. This will improve the readability of the article.”*

For smoother reading, we compiled the mathematical expressions of the predictive performance statistics in a table that was merged with Table 1. The new Table 1 has three columns: statistic; mathematical expression; level (tree, plot or forest). All the equations related to the decomposition of the sum of squared errors (viz. equations (5) to (19)) were collated and put into an appendix (following the author guidelines that state that theoretical developments should be included as appendices rather than as supplementary material). Because equations (20)-(24) were already given in Table 2, we removed them from the text.

3. *“Overall, the introduction is lengthy, and the discussion is inadequate. Some descriptions in the Introduction could be moved into the Methods section.”*

We largely rewrote the introduction to streamline it. We put more emphasis on the ideas that motivated our study and less emphasis on technical considerations. Accordingly, technical parts (e.g. lines 46-48, lines 54-57, and lines 68-72) were moved from the introduction to the methods section.

4. *“In the Discussion, I believe two points need to be mentioned and analyzed. The first is model structure. From Equation 20 to 24, despite these are certainly sound in their application, Sileshi (A critical review of forest biomass estimation models, common mistakes and corrective measures. For. Ecol. Manag. 329, 237–254. 2014) has pointed out that these equations are problematic in their expression of physiological characteristics of trees. I strongly suggest that the authors touch upon this problem. Although I note that the first author has analyzed this in a previous article, this should not be a reason to avoid the issue in this article.”*

The models we proposed are all rooted in the concept of allometry. We added the following text in the methods section (at line 190) to clarify their biological background: “All these models are rooted in the concept of allometry as defined by Huxley and Teissier (1936). It assumes that the relative growth rates of two parts of an individual correlate (Gould, 1966). Models (3) to (6) correspond to simple allometry, where the ratio between relative growth rates is fixed. As discussed by White and Gould (1965), the biologically meaningful parameters are the coefficients associated to covariates. Model (7) correspond to complex allometry, where the relative growth rate of biomass is a convex function of the relative growth rate of diameter. After back-transformation from the log-transform, model (7) also correspond to a log-normal model (Picard et al., 2015b). Its parameters correspond to maximal biomass, the diameter where biomass reaches its maximum, and a shape parameter. This model can account for senescence: as a tree grow, it accumulates biomass as its diameter increases, until it reaches senescence. When senescent, it may lose biomass (because of dead branches, holes in the trunk, etc.) while its

diameter still increases.”

Other model forms could indeed be included in the analysis. While we agree that biomass models should aim at providing a biological interpretation and relate to theories, we respectfully disagree that model fitting should be restricted to those models with a theoretical basis. Theories need to be tested against observations and data, not the other way around. Therefore, we also added the following text in the discussion (at line 285): “Using plot-level predictive performance is desirable to predict plot biomass. However, to disentangle the biological processes that contribute to biomass allometry, goodness-of-fit should still be assessed at the tree level. The models we compared were all rooted in the allometry concept. Another family of models that predict tree-level biomass consists of geometric models, which are rooted in the tree taper concept. They predict biomass as wood density times volume, where volume is integrated from a taper equation (Manso et al., 2024). Another family of models emerges from the carbon allocation strategy of trees (Wolf et al., 2011; Yang et al., 2024). These different model families must be compared against the observations to build a theory of allometry.”

5. *“The second point is about model performance. Judging by the performance of the models, their R^2 s are all greater than 0.97 (Table 2). This suggests that there is no significant difference in the application effect of these models. However, if the range of independent variables expands to a certain extent (which is certain in rainforests), the performance of the model may deteriorate, necessitating a different set of parameters. My question is, is the error of predicting small trees with the plot level model and tree level model greater than that of predicting large trees? I suggest that the author increase the discussion of this issue.”*

One way to assess the prediction error when covariates extend beyond the calibration range is to partition the dataset in two subsets depending on tree size, calibrate the allometric equation using one subset, and assess the prediction error using the other subset. This approach is very similar to what we did in Section 4.2 based on tree height. Hence, we added this analysis in Section 4.2. We complemented Fig. 4 with two panels showing the partition of MSS when the model is fitted to one subset and MSS computed using the other one. The error of predicting the biomass of large trees with an allometric equation fitted to small trees was much greater than the error of predicting the biomass of small trees with an allometric equation fitted to large trees. There is nothing really new in these results. Indeed, due to heteroscedasticity, there is much more variability in tree biomass in large trees than in small trees.

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