Referee #2 - A. FAYOLLE

General comments

The overall aim of the study is to examine interspecific variation in allometric scaling among coexisting species in BCI, Panama, in relation to life history traits. Allometric relationships between tree height and diameter, and between crown area and diameter, were modelled using a hierarchical Bayesian approach, allowing to identify the best functional form (saturating or not), and including trait information.

The authors identified strong interspecific variation in tree height-diameter and crown- diameter allometries, respectively related to sapling growth and wood density. They confirmed the saturating shape of the tree height-diameter relationships (best modelled with a generalized Michaelis Menten model) and showed the consequences for the estimation of biomass at the tree level, and across the 50 ha plot. Not using a saturating tree height-diameter relationship at community or species level, provided larger biomass estimates for large trees.

I really enjoyed reading the manuscript, specifically the relationships between the interspecific variation in allometric scaling and traits, though only few traits were examined. . . In a relatively recent work, we did find some nice relationships between crown allometry and dispersal mode among 45 coexisting species in central Africa though the inclusion of traits in the modelling was finally not included in the paper, we only kept relationships between functional traits and architectural traits derived from species-specific allometries (Loubota Panzou et al., 2018). The second aspect of the study examining consequences of height-diameter allometry on biomass estimates is more classical, and mostly confirmed previous work, though I believe it is nice to accumulate such evidence.

The way trees were sampled is not crystal clear, and additional information might be useful for the readers. In Figure 1, I would have preferred to see the raw data (not log-transformed, as in Figure 2d).

Below are some specific and sometimes really minor comments to help clarify the manuscript for the readers that might be less familiar with the study area and/or approach used.

> AR: We really appreciate the feedback including the detailed and useful suggestions. We took advantage of them and those by the other reviewers to improve the manuscript and amend all the weak points highlighted. We included the references suggested, framing and discussing our results in the context of previous work. We also emphasized the novel aspects of this study, with a sound methodological approach that allowed us simultaneously to examine species variation in tree allometry in relation to functional traits and to compare alternative models. We provided more details on the data collection following your recommendations and explained the rationale behind fitting the model in log scale.

Specific comments

P1 L11 Perhaps clarify 'finite size effects at the smallest and largest sizes' For the largest diameters, this refers to the saturation of the tree height-diameter relationships, but for the smallest diameters, it is not clear for me. Is that related to the inventory threshold?

AR: We revised the text and avoided the term ‘finite size effects’ (e.g. Enquist & Bentley 2012 *in* Sibly et al. *Metabolic Ecology*). Allometric exponents generally decrease with individual tree size, and these size-associated changes have been associated with changes in architecture and wood density during early development, and with the proportionally larger investment in reproduction of larger trees.

CHANGE: *In tropical forests, allometric relationships are often modeled by fitting scale-invariant power functions to pooled data from multiple species, an approach that fails to capture changes in scaling during ontogeny and physical limits to maximum tree size, and that ignores interspecific differences in allometry.*

P1 L13-14 List the trait data used since they are only 3 of them: wood density, growth and mortality. I was expected a larger set of traits at first reading.

CHANGE: […] *Here, we analyzed allometric relationships of tree height (9884 individuals) and crown area (2425) with trunk diameter for 162 species from Barro Colorado Island, Panamá using species-specific data on wood density and sapling growth and mortality.*

P2 L10 The limitations of the power model for predicting the height-diameter allometry are nicely discussed in Molto et al. (2014).

AR: Good point, we added an additional citation to Molto et al. (2014).

P2 L23-26 I have the impression that dissociating the two arguments here, (1) the recognition of interspecific variation in allometry, and (2) the way to model it appropriately (with a hierarchical approach), would help clarify the text.

AR: We restructured the text as suggested.

CHANGE: *Species differ systematically in allometric relationships, suggesting that these differences reflect underlying interspecific variation in life-history, physiology, morphology, and/or phylogeny (Westoby et al., 2002; Adler et al., 2014). Hierarchical approaches based on functional traits can provide a useful approach for capturing this interspecific variation in tree allometry (Dietze et al., 2008; Iida et al., 2011).*

P2 L28 ‘a large dataset for a single site’ might indicate that the 162 study species are coexisting? or do they cover multiple habitats?

AR: All the crown area data were collected in one 50 ha plot, and we only included species for which we had crown area data. So, all species co-occur within an area of 50 ha. Some species are widespread within this area, and some are associated with different habitats defined by topography or canopy height (Harms et al. 2001; Dalling et al. 2012). Whether they all stably coexist within this area rather than simply co-occur is debated. Approximately half the tree height data were collected on a 38.4 ha plot on Gigante, ~6 km away, on species also found on the 50 ha plot. We don't think this can be considered a multi-site study, so it seems appropriate to refer to it as a single site.

P3 L15 Please consider adding a map, with the information on the old-growth and secondary forests, if possible, and sampled trees.

CHANGE: We referred readers to Mascaro et al. 2011 who provide a detailed description of BCI, including a map with the distribution of old-growth and secondary forests in the island. For the Gigante peninsula, we referred readers to Wright et al. 2011, who provides a map, and to Denslow and Guzman 2000, who give forest age for selected plots.

P3 L12 'Allometric data' sounds bizarre for me, since allometry describes relationships between tree dimensions. I would suggest 'Tree measurements' instead.

CHANGE: Subsection title revised to: *2.2 Tree measurements.*

P3 L24 In the combined height-diameter and crown-diameter datasets, the number of trees differ, but the total number of species sampled remain the same (n=162 species). It would be nice to precise the average number of trees sampled per species, and the extreme values. . .

CHANGE: We included the requested information on each panel of Fig S1 and alerted readers of the availability of this information in the main text.

P3 L29-30 Missing space after and before '-'

AR: Corrected, thanks.

P4 L1 Growth and mortality at sapling stage were considered as proxy of shade tolerance. I wonder whether more classical information on crown exposure at small size would be available on the site for the study species. The crown exposure index (CEI) at 10 or 15 cm is a good indicator of species light requirement or shade tolerance (e.g. Sheil et al., 2006), since there are always paradoxical species that deviate in their trait-performance relationships.

AR: We agree that in principle this could be an even better proxy for shade-tolerance, but it is not available for our species. Fortunately, previous research shows that sapling growth and mortality rates are excellent proxies for shade-tolerance (Wright et al. 2010).

P5 L9-11 The generalized Michaelis Menten fitted here has 3 parameters while the 2 parameters model has shown to provide good fit as well to height-diameter allometries at plot (Molto et al., 2014) and species (Fayolle et al., 2016) levels. I did not get the advantage of including the b parameter.

AR: The third parameter essentially adds flexibility to the traditional Michaelis-Menten model, which becomes a special case corresponding to the exponent b =1. When the exponent b is less than one, the log-log slope of the height-diameter relationship at small sizes is shallower than in the traditional Michaelis-Menten model. The best generalized Michaelis-Menten model for height had a cross-species mean exponent b = 0.73, substantially and significantly different from 1 (90% CI 0.72, 0.75), and the vast majority of species-specific exponents were also significantly different from 1 (Table S2). Thus, it is clear that the generalized Michaelis-Menten is a much better fit than a traditional Michaelis-Menten with b=1. We note that this issue was addressed in the discussion, in section 3.1.

CHANGE: We added the suggested references.

P6 L3 The models were fitted after log-transformation, and this conditioned the way the results are presented (log-log scales in Figures 1 and S1). I did not get why? To be comparable with the power models?

AR: The residuals of height and crown area are heteroscedastic, with increasing variance at increasing diameters. Log-transformation makes the residuals essentially homoscedastic, simplifying model fitting. In general, allometric data tend to show this type of proportional variation, and are thus well-suited to analysis after log-transformation.

CHANGE: We included a citation to Mascaro et al 2014, a manuscript discussing log transformation in allometric studies.

P6 L6 The ‘no trait’ model includes interspecific differences, but considered random?

AR: Yes, as detailed in the description of the models in P5L27, ‘no trait’ models regard variation in allometric parameters among species as random. We revised the text to remind readers about that;

CHANGE: […] *four possibilities for functional traits (wood density, sapling growth, and sapling mortality, but also ‘no trait’ models featuring only random variability in allometric parameters across species)*.

P7 L3 Check the units ’g cm-3’

CHANGE: We corrected the typo.

P7 L7-8 I would have preferred to have this information on the sampling per species in the Material and Methods

CHANGE: We moved this sentence to the Materials and Methods (section 2.2).

P8 L18 In the whole paragraph, please insist on the tree level (in kg) and forest level (50 ha pooled, in kg ha-1).

CHANGE: We revised the text to detail the units of each biomass quantity and to prevent any confusion; thanks for the suggestion.

P8 L21 In the Figure 4, I do not understand the rationale behind the fit. . . AGB is predicted from Chave et al. (2014) using three predictors : wood density, diameter, and height. . . Here you have pairs of AGB estimates for each tree using height modelled with the power model and height modelled with the generalized Michaelis Menten model. . . I would suggest a simpler approach plotting the AGB_Hpow against AGB_HgMM, and the 1:1 line. . . and perhaps separately for the size classes examined in the Table 3.

AR: We have stressed in the text and in the caption of Figure 4 that there is no fit since there are no AGB measurements. We choose to graph the data in this way because we wanted to highlight the increasing divergence at larger diameters. A 1:1 graph would show the relative difference in AGB at larger AGB, but would provide no link to diameters.

CHANGES: Section 3.3 – *AGB estimates calculated using tree height predictions based on the power model ~~estimates~~ exceeded those based on the gMM model ~~estimates~~ by ever larger proportions at higher trunk diameters, with an overestimate of 10% at D = 66 cm [52, 80]90%, reaching 59% [51, 67]90% at D = 250 cm (Figs. 4 and 5).*

[Figure 4 caption] *Comparison of estimates of aboveground biomass (AGB, Kg dry matter) as a function of DBH based on observed tree heights (grey points) with those based on height predicted from community level power function (orange lines) or generalized Michaelis-Menten (blue lines) models. ~~for individual trees based either on measured heights (grey points) or on heights predicted from a power function fit (orange) or a generalized Michaelis-Menten fit (blue).~~ All AGB estimates were based on the biomass allometry of Chave et al. (2014) and used the average value of wood density across species (ρ = 0.5304 g cm^{-3}; data from Wright et al., 2010) to highlight variation related to the height allometry. Predictions from the allometric models are based on simulations of the posterior distribution (lines correspond to the median and 90% posterior central interval) of the community-level, across-species relationships.*

P9 L8 Why 'ecological traits' here ? Please homogeneize throughout the manuscript.

AR: Good point; we now use "functional traits" throughout the text.

P9 L19 Perhaps provide the average and range of the scaling coefficient across species for the power model, and mention the differences in estimated coefficients as well as the lack of fit of the power model.

AR: We revised the text at this location to reference the mismatch in exponents and the lack of fit of the power model. Given the poor fit of the power model in general, we do not think it is useful to discuss the fitted values in more detail.

CHANGE: *Metabolic theories based on hydraulic constraints predict a constant logarithmic scaling between tree height and trunk diameter with an exponent close to 2/3 (Niklas and Spatz, 2004; West et al., 2009), inconsistent with our results, which show that community-level power function exponents differ significantly from 2/3, and that the data diverge strongly from the power function.*

P9 L23-26 This might be different in other tropical forests. In moist semi-deciduous forests that are widely distributed across central Africa, the forest canopy is dominated by long-lived light demanding species. . . and there are only few shade tolerant species that can attain large stature. . . This might be different in wet forests. The analysis of the relationship between functional trait (including shade tolerance) and architectural traits describing species stature is provided in our recent paper mentioned earlier (Loubota Panzou et al., 2018).

AR: We agree that our original wording gave the misleading impression that there was a strong and consistent relationship between shade-tolerance and maximum stature among tree species within tropical forests. We have revised our wording to make clear that this is not the case, not even in our own focal site.

CHANGE: *Interspecific variation in tree height scaling parameters was associated with sapling growth rates, which suggests a tendency for shade-tolerance and allometric strategies to be aligned in this community (Wright et al. 2010). At one extreme are fast-growing, light-demanding tree species that have larger heights at small stem diameters; at the other extreme, slow-growing, shade-tolerant species have higher heights at larger diameters (Bohlman and O'Brien, 2006), and higher asymptotic heights (parameter a). This does not mean that shade-tolerant species tend to have larger maximum heights, because maximum heights depend on maximum diameters and are often much less than asymptotic heights for small-statured species (Figure S1). In general, shade-tolerance and maximum height are largely independent axis of variation among tropical tree species (Bohlman and Pacala 2012; Rüger et al., 2018), and may if anything tend to be negatively correlated across species (Poorter et al. 2006, Loubota-Panzou et al. 2018, Wright et al. 2010). The differences in allometric parameters should be interpreted in terms of differences in trajectories, especially at small diameters, where light-demanding species take greater risks.*

P10 L1-24 There is a kind of contradiction between the two paragraphs: community average and interspecific variation in crown allometry.

AR: Indeed, we tried to highlight the contrast between the consistency in community average allometries across sites, and the variation among species within sites, which we agree may at first seem contradictory. We now detail the range of exponents estimated across species (b = [1.09, 1.77]) to clarify the latter point. We also revised the wording of the first sentence (which previously began “Crown area presented a constant scaling with trunk diameter”) to avoid confusion regarding what is meant by “constant”.

CHANGE: *Crown area and trunk diameter presented a scale-invariant relationship, with no indication of saturation even for the largest trees in our dataset. […] This large-scale consistency in community-level relationships emerges despite local variation among species (e.g. the exponent b ranged between 1.09 and 1.77 among our species, Table S2). Modeling studies show that community-level crown area allometric parameters crucially determine the scaling of tree growth and mortality and the parameters of tree size distributions (Muller-Landau et al. 2006 a,b; Farrior et al., 2016).~~, and suggests the operation of a general mechanism in the emergence of community-level allometric scaling in crown geometry (Farrior et al., 2016).~~*

P10 L15-18 The trait influence on crown allometry was weak. In a relatively recent work, we did find some nice relationships between crown allometry and dispersal mode among 45 coexisting species in central Africa though the inclusion of traits in the modelling was finally not included in the paper (Loubota Panzou et al., 2018).

AR: We added a citation to Loubota Panzou et al. (2018) highlighting that maximum tree height and maximum crown area tend to be larger in wind dispersed species.

CHANGE: *However, other traits might explain these differences. For instance, Louboza Panzou et al. (2018) found that wind-dispersed species had taller heights and larger crown dimension.*

P10 L24 Please clarify 'resource partitioning within stands', do you mean crown plasticity in response to competition?

AR: We revised the wording as suggested:

CHANGE: [...] *other factors can be important in shaping crown geometry in large trees, including crown plasticity in response to competition (Thomas, 1996; Poorter et al. 2008)*.

P10 L31-32 In central Africa, using a massive destructive dataset (845 trees sampled for biomass in 6 sites), we found only little advantage of including height and crown dimensions for the prediction of AGB, possibly due to compensation between height and crown size across sites (Fayolle et al., 2018).

AR: Thank you for pointing us to this impressive study, which was published while this manuscript was under review. We added a citation to this publication following references to Goodman et al (2014) and Ploton et al (2016) to note the contrasting results.

CHANGE: [P10L30] [...] *crown dimensions have also been incorporated in some models (Goodman et al., 2014; Ploton et al., 2016; although Fayolle et al. 2018 found a minor role of either crown or height dimensions on biomass estimates)*

[P12L3] *Finally, we evaluated only crown area, even though crown depth and crown shape are also important for the estimation of tree biomass (Goodman et al., 2014; Ploton et al., 2016; but see also Fayolle et al. 2018) and for characterizing tree life history strategies (Canham et al., 1994; Poorter et al. 1996; Bohlman and O'Brien, 2006).*

P11 L1-2 This has been already evidenced and discussed elsewhere (e.g. Feldpausch et al., 2011; Molto et al., 2014; Fayolle et al., 2016).

AR: True, and we did not intend to suggest that our results were novel in this respect.

CHANGE: We have reworded, changing "*highlight*" to "*confirm*", and added the references at this point to make this clear.

P12 L10 This has been already done elsewhere (Poorter et al., 2003, 2006; Loubota Panzou et al., 2018).

AR: We have revised the text to include the above-mentioned references.

P12 L21-22 This a confirmation of previous work.

CHANGE: We changed "*show*" to "*confirm*" and added citations.

References

Mascaro, J., G. P. Asner, H. C. Muller-Landau, M. Van Breugel, J. Hall, and K. Dahlin. 2011. Controls over aboveground forest carbon density on Barro Colorado Island, Panama. Biogeosciences 8:1615-1629.

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