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Biogeosciences
Discussions

Interactive comment on “Do species traits determine patterns of wood production in Amazonian forests?” *by* T. R. Baker et al.

T. R. Baker et al.

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We thank all the reviewers for their comments and consideration of this manuscript. All three reviewers agree that the question addressed and dataset employed are valuable. However, the reviews raise concerns about the suitability of the methods employed, the structure of the manuscript and the need to discuss explicitly the limitations of the study. We have prepared a revised manuscript, and have addressed these concerns by (1) using a more flexible analytical approach based on resampling to explore how functional composition determines coarse wood (greater or equal to 10 cm diameter) productivity (CWP), (2) focussing the manuscript more strongly on the main question by reorganizing and rewriting both the introduction and discussion, and (3) explicitly discussing the potential limitations of our approach.

Detailed responses

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Line numbers refer to the revised manuscript.

Reviewer 1 (bgd-5-S1777)

1. (Reviewer comment: Lacks a clear hypothetical framework and inelegant model structure). Reviewer 1 suggests a range of alternative approaches for assessing the effects of biodiversity on ecosystem function. As discussed in our initial response (bgd-5-S1929), there are a range of approaches that can be applied which are relevant for different aspects of these questions. Indeed, as interest grows in testing ideas concerning biodiversity/ecosystem relationships at large scales, a range of new analytical approaches have been developed, based on resampling (e.g. Bunker et al., 2005), decomposing variation in ecosystem function into the variation in the abundance and performance of different functional groups (e.g. Lavorel and Garnier, 2002), or understanding how ecosystem function is distributed amongst individuals in a community (Balvanera et al., 2005). These different approaches aim to develop a more mechanistic understanding of biodiversity/ecosystem function relationships useful for predicting future trajectories, and avoid the limitations of regression-based methods for determining causation (Suding et al., 2008). The philosophy behind these more mechanistic approaches to understanding biodiversity/ecosystem function relationships lies behind the approach we take in this manuscript and this issue is now discussed in the manuscript (lines 91-104).

Our original framework aimed to test the hypothesis that variation in forest functional composition determines regional-scale variation in CWP. This framework is maintained in the revised manuscript and our hypotheses are more clearly stated (lines 102-114 and Table 2). However, the methodology has been changed: in the revised manuscript, we use a resampling approach rather than strictly defined functional groups for creating our estimates of CWP (lines 106-114). Related to other studies that have examined the effect of biodiversity change over time on ecosystem function (Bunker et al., 2005), this approach has two advantages: we can easily test the sensitivity of our results to different ways of defining functional composition (e.g. Table 2), and this method avoids

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any assumptions about the distribution of growth rates within groups: it is entirely based on the data. Overall, we think that this methodology is a simpler and more rigorous approach to address our question.

2. (Reviewer comment: Comparison between regions are not relevant for the question at hand). As noted in our reply to reviewer 1, there is no a priori reason why it is more relevant to assess the effect of functional composition at a regional- , landscape- or local-scale. In particular, the aim of our study is not to choose a scale of comparison where it is more or less likely to achieve a significant effect of biodiversity on ecosystem function, but rather to perform an analysis at a scale that is relevant to the application of biodiversity/ecosystem function relationships to understanding large-scale patterns of carbon cycling (Hooper et al., 2005). The importance of scale and considering these larger spatial and temporal scales has been emphasized in the literature (Naeem et al., 2007; Balvanera et al., 2005) and is discussed in the text (lines 52-67 and 377-389).

3. (Reviewer comment: Tables 1 & 2 unnecessary): Responding to the suggestions from both reviewers 1 and 3, that the manuscript should focus more on the relationship between functional composition and CWP and less on the description of the dataset of species maximum heights, the discussion has been reorganized and shortened, Table 1 removed, and much of the details of the new dataset on species maximum heights has been placed in the methods section (lines 170-176). However, although condensed, we consider that it is important to include much of the material presented previously concerning the maximum height dataset as this information is new and unpublished. In particular, Table 2 in the original manuscript shows that the differences in overall trait values between regions correspond with variation in taxonomic composition (lines 170-176). This result emphasises and supports the overall differences in trait values between regions (Fig. 2) and we think that this is useful to retain.

4. (Reviewer comment: The manuscript really falls down in comparing wood production between separate functional groups). We have now adopted a resampling approach that generates the estimates of CWP to test the effect of functional composition and

size class variation on CWP for different hypotheses (Table 2). This new approach allows a larger number (up to 36 different categories for hypotheses 3 and 6, compared to a maximum of nine groups originally) and more flexible definition of functional groups than the original approach. This approach therefore allows greater use of the trait data, whilst acknowledging the limitations of current literature-based compilations (lines 409-424). Although species-level analyses would be desirable, the extremely high diversity of these forests (line 148) means that some kind of grouping system remains unavoidable for analyzing community-level patterns, as species-level analyses can only be performed for a small number of taxa. Given that the aim of this manuscript is to analyse the impact of functional composition on community-level patterns of ecosystem function, and therefore inform the degree of definition of functional composition that is required in dynamic vegetation models (Prentice et al., 2007, lines 59-62), we argue that some kind of flexible approach for categorising continuous trait distributions, such as we suggest here, is a valid approach.

5. (Reviewer comment: Analysing trends in different diameter classes adds unnecessary complexity. Figure 4 is very unkind to the reader). Variation in tree size is a key parameter for understanding variation in tree growth rates and if it were not included in the analysis, leads to large overestimates in CWP (Fig. 4, hypothesis 4). However, we agree that the original Fig. 4 did not effectively demonstrate that biomass growth rates are lower across all types of tree in central and eastern Amazonia. We have redrawn this figure, without the classifying by different diameter classes (Fig. 5).

Reviewer 1 (bgd-5-S1931)

The second comment of reviewer 1, highlights their concern about using functional groups, discussed in response 4, above, and also a perceived lack of rigour in the analytical approach. As discussed in our original reply to comment S1777, and above, we think that the approach we employ, allows additional and different insights to regression-based approaches (lines 91-114). In addition, the value of developing alternative methodological approaches similar to ours for addressing biodiversity/ecosystem function questions at large-scales is supported by other recent studies (e.g. Balvanera et al., 2005; Suding et al., 2008). Finally, one aim of the resampling approach that we use in the revised manuscript, is to allow us to test the sensitivity of our results to different formulations of the functional composition of the stands, based on their underlying trait distributions. The similar results for the different formulations (Table 2) provide a more rigorous approach for testing if variation in functional composition causes variation in CWP.

Reviewer 2 (bgd-2008-0110)

Reviewer comment: Lack of key references: I thank the reviewer for highlighting the references concerning the mechanistic links between wood density, maximum height and growth-relevant parameters. These references are now included (lines 76-79, 363).

Reviewer comment: Start of discussion: The start of the discussion (lines 292-298), together with the paper in general has been focused away from describing the new data of species maximum heights, and towards the relationships between functional composition and CWP. The discussion of phenological patterns is relevant to understanding variation in the kinds of trees that occur in understorey communities, but in an attempt to focus the paper more clearly, has been deleted from the revised version.

Reviewer comment: Use of temperate examples: We consider it important not just to focus on the relevance of these results to the tropical literature but place the work in the context of similar studies in other ecosystems, but the additional reference has been added (line 363).

Reviewer 3 (bgd-2008-2173)

Reviewer comment: Consistent terminology needed: We agree that our original terminology was unclear: CWP has now been defined (lines 70-71) and used throughout the paper to refer to the coarse aboveground wood productivity of trees greater or equal than 10 cm diameter. This parameter is the main focus of the paper. However, the term

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productivity is also used in a more general sense (e.g. when referring to work including other components of NPP such as lines 95 & 357-375)

Reviewer comment: The study lacked precision: We agree that uncertainty in the biomass allometries and trait values are important limitations to this kind of study, similar to Keeling et al. (2008), and these are now discussed (lines 391-424). In particular, no significant differences in crown/stem allocation between groups differing in wood density (Keeling et al. 2008), no significant differences between sites or forest types in biomass allometric relationships (Chave et al. 2005), and no significant differences in asymptotic height (an estimate of canopy height) across 24 plots in Amazonia (T.R. Baker unpublished data) suggest this is not an unreasonable assumption. Also, although not strictly relevant to this study that focuses on wood production, foliar production is significantly correlated with wood production for the sites where it has been studied (Malhi et al. 2004), suggesting a similar proportional allocation across sites. Incorporating intraspecific variation in traits into this kind of analysis in the future is a major challenge. However, understanding the impact of environmental factors both directly on tree growth rates, and indirectly through effects on plant traits, is likely to reinforce our conclusion concerning the overriding importance of environmental factors, rather than composition, for driving CWP. All these points are now discussed (lines 391-424), but we agree that both are also matters for future research (lines 405-408 & 416-418).

Lines 74-75: The definition of terms has been clarified through the use of the CWP shorthand.

Equation 1: This has been removed, with the change in analytical technique.

Lines 134-135: The intention was to confirm that the same protocols had been employed within these study sites only and a reference has been included to clarify this (lines 134-137). Although some differences remain, efforts continue to standardise plot measurement protocols between different large-scale projects (e.g. CTFS, TEAM and

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RAINFOR).

Lines 148-159. Further information is available in the cited publication (Chave et al. 2006): for example, data from over 5400 individual measurements from cut segments of large trees, or cores of adult trees was used (added in line 180). We acknowledge in the discussion that this dataset includes variation caused by both environmental and genetic factors (lines 410-413).

Lines 182-183: This analysis has now been deleted as suggested by the reviewer, to focus the paper more clearly on the relationships between CWP and functional traits.

Lines 187-189: Yes: the new information on CWP in these plots is not included in Malhi et al. (2004). This is mentioned in lines 148-151.

Lines 193-196: Rather than define fixed functional groups, the revised version uses different ways of dividing species along the gradient of maximum size, so the nomenclature of species with differing maximum sizes is avoided. In addition, the flexible resampling approach allows us to test a variety of ways of splitting up the maximum size and wood density axes, reducing the dependence of the conclusions on any specific bin sizes and limits. The limits used in the different hypotheses (Table 2) were designed to evenly divide the trait values between bins. For the maximum size axis, 30 m is a reasonable first division for species that will tend to have a final position above surrounding trees for neotropical forests, compared to those below: the average asymptotic height across 24 plots in Amazonia was 31.5 (S.E. 1.5 m) (T.R. Baker, unpublished data; line 400).

Lines 207-209. In the original manuscript, the means were across individuals not species. The resampling approach in the revised manuscript also operates on an individual level.

Lines 209-210. Both palms and Strelitziaceae are more common in the plots in south-western Amazonia. Certainly, better information on the productivity of these plants, and particularly leaf production could uncover an important biodiversity effect on total forest productivity and this idea is now included (lines 365-369). However, for the current analysis, only diameter growth contributes to CWP, so the contribution of palms to CWP is low, as their stems are small and diameter growth rates low.

Lines 218-220. Resampling allows asymmetric confidence limits to be created around mean values that reflect the underlying non-normal distribution of the data. However, this was not clearly explained in the original manuscript, and this has been amended in the revised version (lines 221-228).

Lines 296-299. These results have been completely rewritten.

Lines 365-368. I am grateful for the reviewer for this interesting comment that suggests that the patterns and associations reported here are also relevant to Asian tropical forests. In the revision, the focus has been sharpened on the discussion of the relationship between functional composition and CWP, and as a result the discussion of patterns of understorey composition, compressed. As a result, the biogeographical explanation has been presented in a more cautious way, following the reviewers suggestion (line 313).

Forest fertilization experiments: This work, showing that tropical forests can respond to increased nutrients, is relevant and now briefly mentioned (lines 354-355).

Figure 4: Redrawn following this suggestion.

We thank the reviewers and editor for their comments on this manuscript and hope that it is now more suitable for consideration for publication in Biogeosciences.

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