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Interactive comment on "Responses of leaf traits to climatic gradients: adaptive variation vs. compositional shifts" *by* T.-T. Meng et al.

Anonymous Referee #2

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General Comments:

This manuscript addresses a scientifically interesting and important topic – the connection between biophysical, biochemical and physiological leaf traits and climate. It is asking the question how temperature and water availability influence selected leaf traits, and if observed variability in leaf traits is due to continuous adaptive trait shifts within plant functional types (PFTs), or due to PFT replacements along climatic gradients. Although many contemporary Dynamic (Global) Vegetation Models (DGVMs) still rely on the PFT concept, more recent developments in vegetation modeling focus on PFT-less trait-based approaches, arguing that the conventional PFT-based approaches may be too rigid, general, and over-simplifying. As PFTs are usually assigned a fixed set of parameter values in many DGVMs, continuous adaptive variation cannot be

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modeled directly, but needs to be mimicked by PFT replacement, disregarding that within-PFT variability of traits can equal or exceed between-PFT variability. Especially with respect to the more recent development of trait-based DGVMs that allow continuous trait variation within defined ranges of trait space this study provides valuable new data material for model parameterization, calibration and evaluation. Moreover, it contributes to an improved understanding of the linkages between different leaf traits and climate.

The abstract is clearly structured, presenting the motivation for the presented study, the methods used to address the problematic, a very short summary of the main results found in the study, and a brief outlook on the significance of the presented results.

The introduction provides background information on the PFT concept in vegetation modeling and its inherent drawbacks, and establishes a connection to related studies in the field. However, although the scientific questions acting as motivation for this study are inherently present hidden in the introduction text, I would like to see them listed and phrased directly as such (bullet points, listed by numbers, or in a similar way) at the end of the second paragraph (p. 7097, l. 21).

The scientific methods used to address the research questions are well-established and appropriate to address the presented research questions. Results and conclusions are generally presented in a transparent, structured and concise way and sufficiently illustrated with figures and tables.

The discussion part is well-structured, but section 4.3 (Comparison with previous studies of trait variation within and between PFTs) is rather short and basically only focuses on Kattge et al. (2011) and Zhang et al. (2012). If available, it would be desirable to (shortly) include a few more studies related to this topic here.

The only part where I do not fully agree with the authors is the last section (4.4 Implications for modelling). Their results nicely show that within-PFT trait variability is often continuous and can be as high or higher as between-PFT trait variability, and that PFT-

replacement only partially explains trait variation along climate gradients. Nonetheless, they strongly argue in favor of PFT-based vegetation models, when in fact their results justify and support the development and existence of PFT-less trait-based models that allow dynamic plant community assembly in dependence of prevailing environmental conditions. I would have liked to have seen a slightly more balanced discussion here with respect to the advantages/limitations of PFT-based vs. trait-based vegetation models, as in my opinion both model types have their right to exist, depending on the research questions under consideration.

In general, the manuscript is sufficiently referenced to allow making connections to related research. In a few places where more references would be desirable, it is highlighted in the "Detailed Comments" section of this review.

The provided supplementary material is of good quality and sufficient to transparently present the results in a more in-depth way than possible in the manuscript itself.

Overall, I consider this study to be a valuable contribution to the field, and suggest its publication in BG after minor revisions.

Detailed Comments:

p. 7096, l. 19-22: " Usually a fixed set of properties (parameter values) is assigned to each PFT. This expedient simplifies modelling, but it is a potential weakness because it disregards continuous adaptive variation within PFTs and the possibility that such variation is "universal" – that is, manifested similarly within and between species, PFTs and communities." Should phrase this even more clearly: the definition of a limited number of PFTs with fixed parameter values is an artificial generalization concept used by vegetation modelers to discretize continuous trait combinations into a manageable number of seemingly distinct categories. However, this oversimplification neglects that the range of trait variations within these artificial PFT-categories in reality may be as large or larger than between PFT categories, which leads to an underestimation of the plasticity and adaptive potential of vegetation to environmental change and vegetation

feedbacks to climate.

p. 7097, l. 10-21: this part reads a bit confusing, as the arguing in favor of trait-based approaches vs. PFT-based approaches goes back and forth and from the phrasing is not clear enough. Please first talk about the advantages of trait-based modeling, and then make it clear that afterwards you are talking about circumstances in which leaf-traits have been discovered to be distinctly different between PFTs, thus indicating that PFT-based modeling also can be justified based on focus and circumstances.

"An advantage of trait-based modelling is that it can take better advantage of the wealth of georeferenced data now available on plant functional traits (Kattge et al., 2011)." This may indeed be one advantage, but in my opinion the more relevant advantage of trait-based modeling is that it allows to simulate continuous trait variation, thereby allowing the development of plant community assemblies that are adapted to site-specific biotic and abiotic environmental conditions and can react more flexibly to environmental change, as well as allowing new approaches to simulate functional diversity and competition (see, e.g., the trait-based aDGVM2 model as described in Scheiter et al., 2013).

"On the other hand, some leaf traits can have different relationships to climate depending on the PFT": I'm not entirely sure I understand correctly what you mean to say with this sentence. Do you mean that certain leaf traits within one PFT behave one way along a climate gradient, while they behave the opposite way along the same climate gradient for plants that belong to another PFT, or do not vary with climate at all for a third PFT? If possible, rephrase this to make it more clear.

p. 7097, l. 25: "on all of the species present at 80 sites, with a wide geographic spread.": How many species did you sample overall? And what was the range of species numbers between sites (minimum and maximum number of species per site)?

p. 7098, l. 2-4: " Area-based nutrient contents provide no independent information, as they are simply derived from mass-based nutrient contents and SLA, but they provide

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Interactive Discussion

Discussion Paper

an alternative perspective on the regulation of leaf nutrient contents." In what way do they provide an alternative perspective? Please elaborate a bit more closely, or else it becomes hard to justify why you are presenting both if they are not independent.

p. 7098, l. 12: "The sites (Table 1) represent...": Please also point out Figure 1 here, as you show the location of your sampling sites on a map in Figure 1. I find it helpful to also see the location of the sites on a map, and would have asked for a map figure, but then realized that the sites are actually highlighted in Fig. 1 when looking at the figure later on.

p. 7099, l. 11/12: "except for a few species with very small leaves at the driest sites": What did you do for these? No sampling, or sample as much as was available?

p. 7099, l. 19: "Leaf C was measured by the potassium dichromate volumetry method and leaf N by the microkjeldahl method." Please add a reference if possible, as it is not instantaneously clear to everybody how these methods work.

p. 7103, l. 7/8: "Figure 1 also shows the frequency of different GDD 0 -α combinations among grid cells, and the site positions in this climate space." , and p. 7121, Fig. 1: frequency distribution and location of sampling sites in climate space: The chosen sampling sites cover a large range of the occurring GDD0-α combinations and are therefore well-suited for the pursued study purpose. However, no sites cover the very low end of GDD0 values, and in the area of GDD0-values between 6000 and 9000 and α between 0.4 and 0.9. Which areas of China would these combinations correspond to? Probably high-altitude grid cells for the low GDD0-values, and places in Southern China with high GDD0 and intermediate to high α values? Maybe point this out briefly either in the Figure caption or in the text.

p. 7103, l. 14-16: "Deciduous trees and deciduous shrubs favor cooler and drier climates, corresponding to the deciduous forests of central eastern China." I generally agree with your four PFT groups based on optimum and tolerance thresholds, except maybe for this group, as their tolerance range compared to the ones of the PFTs in the

other groups is very wide, and therefore makes these two PFTs overlap with group (1) and group (3).

p. 7104, l. 3-6: "Inclusion of PFTs as predictors (Fig. S1 in the Supplement) shows that there are some differences among PFTs in the typical trait values found at any given α. This is most obvious for biophysical traits – LA, SLA and LDMC – and area-based nutrients." Are the differences statistically significant? (Same question applies to Fig. S3)

p. 7104, l. 25/26: "Warmer climates also show somewhat reduced potential and actual quantum yield." So both dry conditions and warm climate show reduced QY. Can you make a judgment which of these two factors has the greater effect? I suppose that, since dry conditions and warm conditions are not statistically independent, the decrease in QY is a combination of both, but nonetheless it would be interesting to know more about the relative importance of each factor.

p. 7105, l. 24/25: "The observed continuous biophysical trait variations with moisture availability are consistent with previous studies..." Please add some references for these studies.

p. 7108, l. 24-28: "Our findings suggest that vegetation models should retain the PFT concept and a minimal set of PFTs, because the distinctions between woody and herbaceous, de- ciduous and evergreen, and angiosperm and gymnosperm plant types systematically influence the values of key biophysical traits in ways that would not be predictable from assumed universal relationships." I do not agree with this statement. Vegetation models using the PFT concept may be useful and sufficient to address many scientific questions with respect to vegetation dynamics, but it is not true that using the PFT concept is the only way to get clear distinctions between key biophysical traits. Trait-based vegetation models not necessarily need to assume universal relationships, but may define a potentially allowed maximum range of values for key biophysical traits. If plants are assigned values from within these ranges at birth, se-

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lection through environmental conditions such as temperature and water availability will lead to the emergence of successful trait value combinations, whereas unsuccessful combinations will be eliminated through competition and/or environmental pressure. Whether woody or herbaceous, deciduous or evergreen, plants with low or high SLA, etc. will prevail therefore is not predefined, but will be an emergent property of simulated trait selection through environmental filtering. No PFTs need to be predefined, but an a posteriori classification of simulated plants into PFT categories based on simulated successful trait combinations is possible and will also pick up PFT replacement over time and space where it occurs. Trait-based vegetation models such as, e.g., the aDGVM2 model (Scheiter et al., 2013) therefore offer completely new approaches to simulate changes in functional diversity, trait selection through environmental conditions, and competition for resources (water, light) that in such a way are not possible with classical PFT-based vegetation models.

p. 7122, Fig. 2: Change "boardleaf" to "broadleaf in figure caption. What are the grey background points? The GDD0 vs. α combinations of all the 10 km grid pixels in China?

p. 7123, Fig. 3: Change "boardleaf" to "broadleaf in figure caption

p. 7124, Fig. 4: Change "boardleaf" to "broadleaf in figure caption

Supplementary Material: Please also change "boardleaf" to "broadleaf" in figure captions where applicable.

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