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Interactive comment on "Structural, physiognomic and aboveground biomass variation in savanna-forest transition zones on three continents. How different are co-occurring savanna and forest formations?" *by* E. M. Veenendaal et al.

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We thank both reviewers for their careful and detailed examination of our paper. They both have made valuable comments on how to improve the paper. We note with pleasure that both have few issues with the actual data presented and methodology followed. Most of the reviewer's points deal with the scientific interpretation of the data and discussion points emanating.

The concerns that reviewers have raised also represent respectable widely held views concerning, in particular the role of fire, that determine the forest-savanna boundary dynamics. In recent years such views have been suggested as being supported by detailed remotely sensed data analysis (particularly the MODIS vegetation continuous fields VCF data set). Our interpretation based on extensive field observation does raise some questions concerning these widely held views. To stimulate debate and critical examination, in the end we chose to publish our results in a public access journal with a discussion phase such as this. As our paper cross-cuts many disciplines and is relevant for ecologists, remote sensing specialists and those working on earth system models and carbon stocks, there can be little doubt that the paper is well suited for Biogeosciences. Here we respond with particular reference to the questions that we believe our data raise to the present interpretation of the role of fire as a driver in the forest savanna boundary and other general points of criticism raised by the reviewers.

Points raised by Reviewer 1:

A main point raised concerns the representativeness of the sampled sites as to other forest/savanna boundary areas. The reviewer states for instance: "The sites of this study do not cover the complete environmental envelop in which savanna-forest is found, at least not the Australian sites". Indeed not all worldwide existing forest savanna transitions were sampled (e.g. Venezuela in South America, savannas in Asia; Thailand and Papua New Guinea , Northern Australia (as mentioned by the reviewer), Southern Africa). There is however no a priori reason to expect that the results as found by us in 60 sites in three continents would not hold elsewhere. In passing the reviewer specifically mentioned as example (North Australia) adding SPECIAL data (See Table 2; Hutley et al 2011) to Figure 1 would not alter this figure , but rather support it, despite inherent differences in data collection between projects.

The reviewer is in our view mistaken in his view that many of the plots are far apart . Plots in central Ghana, central Cameroon and Brazil and even Northern Queensland have all been chosen for representativeness of ZOT areas (see also fig. 8 and 9). To suggest that savanna sites are "inliers" which implies in some way "out of the ordinary" is in our view a misnomer. We have sampled representative formations that are often in close proximity and sometimes span a wider transect and climatic range. This can readily be seen by investigation of the map in Torrelo-Raventos et al. (2013) to which the reader is referred. And indeed, has it not already been argued (e.g. Murphy and Bowman) that vegetation formations growing where they are not expected to be (i.e. savanna inliers) actually provide evidence of alternative stable states (ASS). And there is certainly no case where it could be argued that any of any the sites we have sampled is outside the areas of 'bistability' as claimed to exist by some ASS proponents. As perhaps a minor point, Reviewer 1 observes the change in relationship between CAI and LAI above CAI of 2.5 in our data set We agree this is indeed interesting and represents a change in tree canopy architecture of trees in closed vegetation (wider crown for the same leaf area carried) in closed vegetation (fractional crown cover > 0.6; See e.g. Torello Raventos et al 2013).

The reviewer notes the importance of remote sensing for the interpretation of global vegetation and climate relationship studies. As such we wholly subscribe to this notion. Indeed aerial photographs and e.g. Landsat imagery present powerful tools as do MODIS products as the vegetation continuous fields products (VCF, MODIS44B). In our paper we show that there is a reasonable relationship between our data set and the MODIS 44B and e.g. CAI (Fig S7) despite the fact that the VCF pixels and our plots cannot be interpreted 1 to 1, as Plot resolution (100m x 100m and pixel resolution (500 x 500 m) do not allow for this. (for other problems of applying VCF in savanna-forest Mosaics Fritz and See (2008) and later in this response). Despite the variation figure S7 illustrates that the remotely sensed forest savanna transition of fractional cover of 0.6 in MODIS44b roughly equates with a CAI/LAI of 1.5 -2. An area where canopy can be considered closed, particularly if subordinate tree layers are included (see also figure 1 and further in main text of paper).

Subsequently problems have been noted with the VCF product that is being used in

the many global studies including publications in the highest impact journals that the reviewer refers to (indeed, if desired by the editor, we would be happy to include a more elaborate introduction and discussion of this particular literature as requested by the reviewer) necessitating a critical re-examination of the interpretation of VCF when applied to forest savanna boundary studies. We raise here three points: Firstly, the calibration/training of remote sensing products with field data is critical. Hanan et al (2014; cited in our paper) have recently demonstrated that the calibration procedure of MODIS44B leads to clustering of the distribution pixels among average vegetation cover leading to an artificially introduced bimodal distribution of vegetation covers, often cited as evidence for alternate states. This distribution is thus at least partly an artefact of the remote sensing product and leads to underestimating of in between cover classes. We were ourselves in the process of undertaking a similar analysis as done by Hanan et al. (2014) when it was published and would be happy to provide our independently obtained results (Hooftman, Gerard et al. unpublished) as supporting evidence as they appear in line with Hanan's et al (2014) conclusions. Secondly: The training data of remote sensing products like VCF determine also the results. This may sound trivial as this phenomenon is well known in the remote sensing community but is of importance here. It is for instance illustrated in a comparison of the use of different remote sensing products in assessing forest cover (Fritz and See 2008). Interestingly the MODIS land cover product with a different set of classes and different training sets "sees" a different tree cover than for instance the MODIS VCF product (illustrated in fig 6d-e in Fritz and See 2008). The notion that we put forward in our manuscript that we have to be cautious with the interpretation of remote sensing products if training data do not include detailed vegetation layers is justified, particularly in the interpretation of cover in the forest savanna boundary. This point should in no way detract from the significance of remote sensing for global studies, in which many of the authors of our paper participate, but merely begs caution when applied to forest-savanna boundary studies.

Thirdly the use of VCF has general limitations in forest savanna mosaics (see for instance as example Fritz and See 2008) as well as with seasonal variation in vegetation cover. This in our view, justifies the cautious view of analyses that solely depend on VCF. Reviewer 1 asserts that many papers have comprehensively described vegetation layers across the forest-savanna boundary and that our study is not new, but we beg to disagree. While indeed regional data sets exist (Some of the IGBP terrestrial Transects e.g. NATT and the Kalahari Transect), we know of no study that has done so as comprehensively as our study using comparable methods for the total dataset on different continents similar to protocols developed in RAINFOR for global studies. Although we note that Ref 1 is correct in that other workers have noted the importance of subcanopy layers in recruitment , this is a completely different issue to our presentation of the new observation/notion that as canopy closure occurs there is effectively a replacement of grasses by understory shrubs. We wholeheartedly subscribe to the reviewer's point of knowing the site history. In some of the sites used in this paper such studies were undertaken (e.g. Cameroon; Mitchard et al 2009). Presently we are undertaking a historical site study in Central Ghana, where we have obtained aerial photographs spanning more than 7 decades). However these analyses represent complete studies in themselves, that also need further information on past management, and climate for proper further interpretation. We principally disagree with the notion of the reviewer that our study represents a snapshot. While indeed each plot was visited at one time the total data set represents variation in past and present climatic, soil conditions and management across three continents. This variation is an inherent part of the variation presented in the data set and thus taken into account. Therefore referring to the data set as a whole as a snapshot is fundamentally incorrect.

Reviewer 1 notes the importance of fire history. The size of our plots (100 x 100m) and the way the plots have been laid out in boundary areas (vicinity of plots to other vegetation types in a heterogeneous landscape) has technically precluded the possibility of properly tying fire history and frequency to individual plots. For Africa, the generally cited paper by Hennenberg et al (2006), providing empirical evidence for the suppression of fire (percolation effect) by forest cover, suggests that a relative thresh-

old cover for suppression is around > 0.6. We find from our own as yet unpublished work (field studies) that this cover estimate is quite reasonable for fire suppression. We also find that fires occurring at values higher than this canopy cover tend to be of low intensity and so, although still common in dry forest, are often not observed with remote sensing (Schroeder et al 2008). Fire events detected using remote sensing are found by searching for thermal anomalies in time-series of thermal observations acquired at $\sim$ 1km resolution. An anomaly often represents a fire event of medium to high intensity which cannot be located exactly within this 1km grid. Thus we felt it would seem very difficult to provide a defensible fire history for plots in the dynamic forest-savanna boundary based on remote sensing alone. Reviewer 1 notes the co-existence of savanna's and forests in the climate-soil envelope in the Zone of Transition (Figure 9) as evidence for alternate states. We disagree. The fact that physiognomically, there are forests, "forest-like savannas" and savannas in the same climate soil envelope suggests to us that soils and climate have a greater influence on the location of the boundary and vegetation structure than fire. This is notwithstanding the fact that open vegetation in the ZOT will have a higher fire frequency than closed vegetation and that in open vegetation fire can interact with vegetation towards a vegetation structural balance quite different from when fire would not be present as demonstrated in fire exclusion plots. Indeed, even if we had been able to deduce an accurate and unambiguous fire history for each plot then what would that have actually told us ? We suggest no more than the already well known 'fact' that more open savannas tend to burn more frequently. That observation by itself, however, can shed no light on the existence of ASS (or not) as fire frequency (at least in our view) can be as much a function of vegetation structure as opposed to being the prime cause of observed differences per se.

Indeed there have been extensive studies of soil conditions within the project from which this paper emanates (see e.g. Saiz et al. 2012) but the isotope data are presently still forthcoming. The importance of differences in soil conditions has been previously highlighted for South America (Cerrado versus forest soils or Australia (basalt versus granite derived substrate). The reviewer mentioned soil transect work. In fact, we have from this study and several others subsequent data from such transects, but this is being reserved for a separate publication. (But suffice to say, we would not have written the current paper the way we had were not this currently unpublished data also to be in general support of the arguments presented here).

In conclusion we differ in principle on the notion of “snapshots” We predict that where fire history is known it would show that open vegetation formation with fuel cover would likely burn more often than closed formations, but this would not be evidence for fire feedback mediated alternate stable states. Finally, we are not sure why the reviewer takes issue with our treatment of the previous literature as we extensively cite the most recent reviews on this subject. In terms of those directly applicable to the forest savanna boundary (as opposed to differences in woodiness within the savanna biome itself) we have cited all the relevant recent reviews and we also note that single site studies looking at forest invasion of grasslands or effects of fire on vegetation structure do not, on their own, in any way constitute an actual testing of the ASS hypothesis.

Reviewer 2

Whilst we admit the content of the paper is multidimensional in content, its structure seems to us (at least) logical. We present the structural data, interpret relationships between the various canopy strata, and then evaluate allometric relationships. Finally, we show that ZOT occur under different precipitation regimes on the various continents and provide an explanation for this. We admit there is a lot there but do not agree with Ref 2 that it is the general shemozzle that he/she seems to be suggesting. In response to his/her comments, however, we will be seeking input from coauthors not directly involved in the actual manuscript writing for input regarding ways in which the structure and presentation can be improved (few actual specifics having been provided by Ref 2). Especially as, judging from his/her review, some of the more important points of the paper would appear to have not been adequately communicated. Response to the specific comments by reviewer 2.

1. The argument here is how the lower vegetation (not just shrubs but in fact mostly what by savanna ecologists refer to as trees) lift the cover estimates above the value of a relative canopy cover mostly above 0.6, a value above which fire percolation is generally assumed to occur. We have in our response to reviewer 1 already referred to the fact that – independent of our work here – other doubts exist as to the actual extent of a discontinuity at a relative cover of 0.6 in VCF and finally we demonstrate that fire tolerant formations exist in this zone of transition (as an aside, transitional “Forest” tree functional types exist too). These are all strong arguments for a critical re-examination of fire mediated feedbacks, where one views the world as consisting just of closed canopy fire sensitive PFT’s on one hand and open canopied fire tolerant PFT’s on the other (and with nothing in between). Already in the 1950’s and 60’s transitional woodland/forest types were observed and described (as “problematic”). Here, after a careful examination of the ZOT vegetation formations we quantitatively demonstrate their existence and potential role in savanna forest transition

2. We agree with reviewer 2 that the fact that the overall relationship saturating is trivial. But, in figure 2 (apart from reminding the casual reader that fractional crown cover is not a linear representation of the amount of crown area present) that is hardly the point. Equation 1 refers to the relationship between cover indexes (scale 1 - >4) and relative cover (scale 0 – 1) while in 2 the x axis is not relative cover but crown area index. That here the y axis reaches a maximum while the x axis is still increasing is relevant in the understanding of structural vegetation changes. In short, we presented the data the way we did so as to make the 0.6 gap in upper cover (Fig 2a) most apparent and with the main point being that the contribution of the various layers to the fractional cover (as would be seen from satellite or aerial photograph) is not constant, but that the lower layers (stated by the authors of the VCF as not being detected by their product) figure 2b and further contribute progressively more as total canopy cover increases.

We are not sure why Ref 2 finds the increase in shrub cover in the taller canopy covers around CAI = 1 less than convincing (also noting as an aside the Ref 1 argues that this is somewhat 'old hat'.

3 and 4. The term "axylale" (to be found in some text books: for example Ingrouille and Eddie's Plants: Evolution and Diversity - snapshot included here) comes from Raunkier's system which in our view is a reasonable pedigree. But we agree it is not widely used and that it is not all that surprising that the Referee is unfamiliar with it. It was introduced in Torello-Raventos et al (2013) as it provides a precise description of the lowest layer which can be either grass or herb (or a mixture) . "Herbaceous" may be regarded as a synonym, but phrases like 'an increasing abundance of herbs in the herbaceous layer' then assume what might be termed "nonsensicality".

Symbols are a bit of a carryover from previous papers and we are more than happy to make a table of symbols used to make up part of the supplementary information.

5. Reviewer 2 is correct in saying that forest species become more abundant under savanna cover in wetter areas. However the wetter savanna plots in figure 5 are indeed all in the zone of transition (ZOT) where under similar rainfall, most scientists are of the view that fire mediated feedbacks cause the alternate biome formation. In Figure 9 we show the importance of climate in the positioning of the ZOT also in relation to soil conditions. In Figure 5 we show that indeed in the ZOT if canopy is denser in savannas more forest species occur. The increasing existence of forest species in denser savannas in the ZOT in our view is illustrative of a possible alternative mechanism by which savannas can transition into forests => Denser savanna canopies can reduce fire effects, nurture forest species and given the right soil and climate conditions with forest species eventually dominating. For our revision we have made a note to clarify this idea in the main text further.

6. This part of the paper has been included for the benefit of the remote sensing community interested in relating LIDAR measurements to carbon stocks. We intended here to provide access to this finding without scattering data over too many separate papers. We agree with reviewer 2, however, that the integration of this section in the

main paper needs improvement. The significance of these figures will be discussed in a more erudite manner in the Discussion section of the revised version.

7. We agree that figure 8 is small and there were problems in pdf conversion. We will look into the possibilities of improvement.

8. It is a two dimensional graph where one axis is climate space and the other is soil chemistry (more akin with ordination techniques than the classical bivariate association approach) . What is important is where the points lie in relation to the two axes (joint climate/soils space).

On behalf of all authors:

Elmar Veenendaal, , France Gerard, Mireia Torello-Raventos and Jon Lloyd

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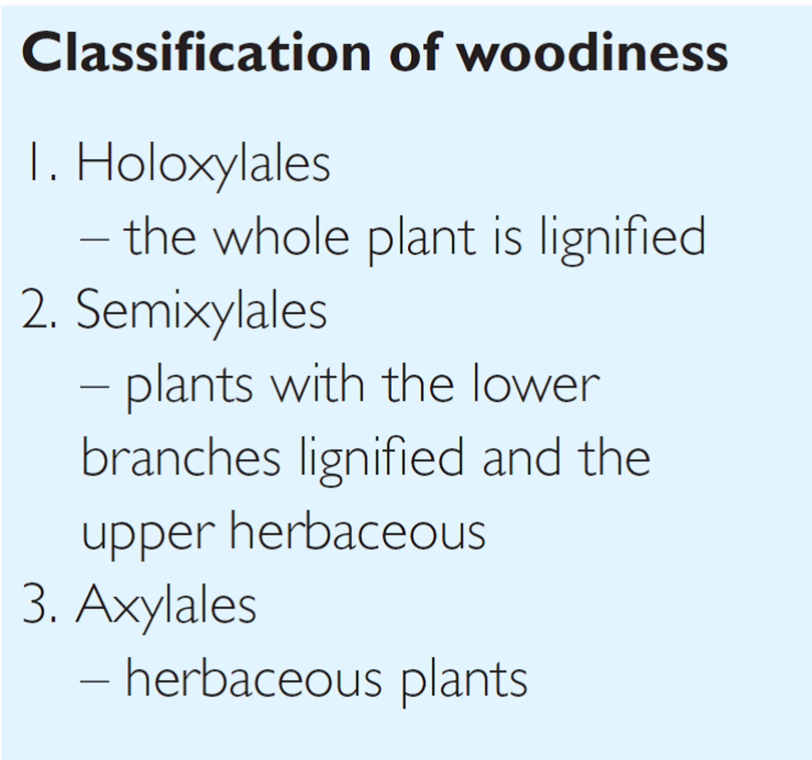

Fig. 1. textbook example