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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.

Anonymous Referee #1

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Factors that determine the distribution of tropical savanna and forest and their transition is a much researched topic, with the boundary determined by a range of factors. Climate, hydrology, herbivory, fire, typography and soil characteristics can all influence the distribution of savanna relative to forest as has been detailed in reviews and global analysis's by Lehmann et al 2011 and a review by Murphy and Bowman (2012). A common thesis suggests fire is a dominant driver that shapes the distribution of these two vegetation types, with other factors such as changes in soil type and climate also sig-

nificant but secondary. The resultant distribution is in effect a 'fire-mediated alternative stable state'.

This paper is a challenge to the notion that fire is the most significant factor as has been previously suggested. It is claimed that previous analyses are largely based on modelling, remote sensing and 'theoretical propositions', with little on-ground data to support the 'fire-school's' position that fire is the major determinant of savanna – not-savanna / forest dynamics. This study is a substantial field program, with sites across 3 continents that examined structural attributes of forest and savanna stands located within 'zones of transition' (ZoT) that focuses not on fire, but on soil, climate and structural attributes of savanna. The definition, size and spatial scale of the ZoT is thus critical to considerations of distribution.

61 sites were examined with floristics, LAI and canopy area index quantified. LAI-canopy area index relationships were found to overlap significantly between savanna and forest types, and a smooth continuum was observed (Fig 1) between the two vegetation types if all canopy layers were included. It was hypothesised that there would be a discontinuity in this relationship (Figs 1 and 2) between the two different vegetation types, savanna vs forest and the absence of an abrupt slope in this relationship was interpetted as suggesting there is not an 'alternate stable state' but a continuum of cover change driven by factors other than fire, perhaps soil and climate.

Not surprisingly, forests were found to have 3 times the biomass. Savanna/forest transition zones were found to typically occur at higher precipitation regimes for South America than for Africa. It was claimed coexistence was found to be confined to a well-defined edaphic/climate envelope consistent across all three continents with both soil and climate playing a role as the key determinants of the relative location of forest and savanna.

I had a number of issues with the paper.

Firstly, is it suitable for the journal, Biogeosciences – should it not have been submitted

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to any of the biogeography journals or New Phytologist for example, who have published a number of papers on savanna vegetation dynamics over the last 5 years. Why not continue with Plant Ecology & Diversity?

The paper references all sites, descriptions, methods, nomenclature and approach from Torello-Raventos et al. (2013) in Plant Ecology & Diversity and could have been considered as a series of papers. This appears to me to be an ecological / biogeographical study, there are limited aspects describing biogeochemical cycling or ecosystem function between the two vegetation types. Not my call but I found that odd.

It is refreshing to see concept or idea challenged and the paper has a rather ambitious aim given that previous studies on this topic over the last 2 to 3 decades have suggested that fire, fire frequency and severity, along with soil properties, herbivory, rainfall seasonality are all factors shaping the distribution. This is clearly a substantive piece of work which I am sure was a significant logistical exercise to obtain the data, but I didn't think the approach was well designed to test the notion that fire-derived alternative stable states does not capture the nature of the savanna-forest boundary.

Sixty sites were selected across the three continents, providing us with 20 sites per continent grouped within ZoTs. Sites were "selected with a view to maximising differences in climate and soils". Sites were either within a rainforest massif, within the ZoT or within a savanna inlier. None appeared to be closely co-located across a boundary. I examined Queensland sites used and they were mostly > 1200 mm. In the NT and WA, savanna can exist at 500-600 mm with boundaries between savanna and very sharp, only meters of ecotone where specialist species may exist. These savannas experience a stronger monsoonal influence with more sharply defined seasonal rainfall distribution than Qld. Savanna is the dominant vegetation, with a mosaic of small rainforest patches embedded. As such the sites of this study do not cover the complete environmental envelop in which savanna-forest is found, at least not the Australian sites. If lower rainfall, savanna dominated (vs forest dominated) zones of transition were sampled, I wonder if the smooth curves of Fig 1 and 2 would be observed? Do

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the authors consider the vegetation in the ZoT to be unstable-alternative states?

Is it so surprising this relationship is observed in high rainfall areas ? There is actually a change in slope at canopy are index of 2.5, with all bar one site above this threshold forest. In short, the sites are not truly representative of the entire domain – can we shift our paradigm and thinking based on 20 sites on each continent? I wasn't totally convinced.

It is precisely this reason, the broad climate / available moisture regime that savanna-forest occupies, that remote sensing tools have been previously used in such analyses. Thousands of points in space and time can be sampled if classification of cover is undertaken carefully. Remote sensing provides spatial and temporal data, especially powerful when air-photos are used and we can go back 4 or 5 decades in time. Such analyses reveal highly dynamic boundaries – this study is largely a 'snap shot' in time. This also was a concern for me - what was the fire and boundary 'history'.

Numerous papers have described the importance of sub-canopy layers e.g. in biomass, in recruitment and fire sensitivity studies. I didn't think this was as novel as was portrayed in the paper. Given the open nature of savanna woody canopies, I also didn't accept the suggestion remote sensing products are unable to 'see' these sub-layers and previous analysis's are thus less accurate. Correlation between remote sensing of LAI, cover in savanna is generally good, see campaigns by Scholes et al from the SAFARI program, or even the SPECIAL campaign in Australia.

If fire, soil and climate were the variables under investigation, why was fire history of these sites not included in the suite of analyses ? Fire history is now available from the remote sensing record for 20+ years. I would have thought fire history of each site / patch could have been included to examine what fire regime was associated with the zone and boundary. Fig 9 demonstrated the available water – soil nutrient envelope sites within the ZOT were located, this was an interesting figure and does support the notion that a combination of soil nutrient status and water holding capacity can support

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both vegetation types. Within this zone fire is likely to move the boundary I would think. A fire analysis would provide interesting data.

Why was soil type across boundaries not investigated in more detail i.e. soil sampling across transects through boundaries? C3/C4 ratios of soil carbon across savanna – ecotone – forest would have shed light on the notion that soil is a more critical driver than previously thought, as well as providing insights into boundary dynamics over time. Perhaps this is coming, Lloyd has been a pioneer using such approaches in the 1990's and 2000's - this site ensemble would lend itself to such analyses I would think.

The number and distribution of sites in this paper is not enough to elucidate and conclude what has been concluded – a snap shot in time with no fire analysis. It is a shame it wasn't integrated and informed by Lehmann's study of 2011 with a design to more comprehensive test boundary dynamics and history across the 3 continents. Lehmann et al. suggested a multi-dimensional space with different factors more important at high rainfall / low soil fertility combinations, factors also in common with this study.

I would view the mosaics of savanna and closed-canopy systems as evidence that across mesic environments these are distinct, alternative ecosystem states. This was an interesting study but I wasn't total convinced by the conclusions drawn and it didn't shift me from the notion that rainfall, rainfall seasonality, soil factors and fire all contribute to shaping the complex spatial and temporal boundary dynamics. Most previous studies arrive at this conclusion.

Specific comments

Odd terminology and units - axylale" for herbaceous, annual rainfall of 1000 mm expressed as 1.0 m a-1

Shading in Fig 8 did not reproduce well, I assume there should be shaded zones on each figure?

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discontinuities and the existence of alternative stable states does not seem to have been actively sought." I would have thought the large literature of Hoffman, Bowman, Bond, Staver, San Jose, Ratnam, Archer, Scholes, Archibald, Lehmann, Cook, Russell-Smith mainly observational studies focussed on drivers of savanna-forest boundaries suggests there is a wealth of such studies. Perhaps consensus has not been reached, that is a reasonable suggestion, but not that observations to examine this problem have 'not been sought'.

None of this literature is reviewed and the paper is poorly framed. Perhaps Hoffmann's review and synthesis paper in Ecological Letters (DOI: 10.1111/j.1461-0248.2012.01789.x) could be captured briefly to provide existing thoughts on the forest-savanna transition. This could establish a case for the current 'fire mediated bistability' model which can then be dissected using the evidence presented in this study. That to me would make for a more rounded paper.

So I would not recommend rejection but response to these issues are required, I don't a) think that previous research on this topic discounts the significance of climate and soil as much as the authors claim and b) I didn't think their measurement design justified their conclusions, a lack of fire data the major concern. This is not to say the data were not interesting and useful but I wasn't convinced this is evidence that disproves a fire mediated driver of alternate stable states.

Interactive comment on Biogeosciences Discuss., 11, 4591, 2014.