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Interactive comment on "Edaphic, structural and physiological contrasts across Amazon Basin forest-savanna ecotones suggest a role for potassium as a key modulator of tropical woody vegetation structure and function" *by* J. Lloyd et al.

Anonymous Referee #2

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This study on the effects of soil properties on vegetation structure in the Amazon Basin will, in my view, make a significant contribution to the literature. I applaud the authors for the amount of detail provided and their rigorous approach to finding patterns in their dataset. There are, however, several assumptions and concepts presented that I question. I suggest that the final paper discusses these potential flaws, and that the authors provide counterpoints.

1) I suggest that it is very questionable to work with the underlying assumption that the photosynthetic potential of a site (as influenced by e.g. water availability and fertility of soils) will directly influence the amount of biomass on that site (i.e. whether the site is a forest or a savanna). This assumption does appear to underpin the study. Such an assumption may be intuitive – probably because of a natural bias to assume that large organisms (such as trees) are more powerful than small organisms (such as shrubs or grasses) – but it needs deep scrutiny for the following reasons. a) Short vegetation can be extremely productive (and therefore arguably extremely powerful); indeed some of the most productive ecosystems on the planet have short vegetation. b) Grasslands often occur on extremely fertile soils, and intensive competition from grasses in some ecosystems is known to exclude trees. An increase in soil fertility could therefore potentially increase the competitiveness of grasses relative to trees. The greater soil fertility – and associated photosynthetic potential – of the forest sites compared with the savanna sites does not therefore explain why trees would prevail more on the forest sites. Forests often occur on extremely leached soils (e.g. Eucalyptus forests in Australia, Miombo woodlands in Africa), so fertility per se does not seem to be a prerequisite for forests.

2) I suggest that it is very questionable to assume that potassium is causal in terms of determining whether a savanna or forest establishes on a particular site. There are several other nutrients that I suggest are more likely to be causal factors. Notwithstanding the fact that K is an important osmoticum in plants, it's relevant to note that all nutrients play critical roles in plant growth and metabolism, and consequently all nutrients are potential candidates for promoting the competitive strength of one plant life form over another. The question to be tackled is 'why would one particular nutrient favour a woody plant over a herbaceous plant like a grass growing in a savanna?'. Is there any reason why K, more than any other nutrient, will give trees a competitive edge over grasses growing in a savanna? The paper does not discuss this in depth, yet it lies at the heart of the question being addressed by the paper.

3) There are many other nutrients, like Cu and Zn, that would potentially favour grasses over trees. This is because grasses catabolise more of the photosynthate that they produce compared with trees (which invest some of their photosynthate in wood). Catabolism requires relatively large amounts of Cu and Zn. The authors cannot of course be expected to reanalyse the soils for other nutrients. However, I suggest that it needs to be pointed out that there are several other potentially important nutrients such as Fe, Mn, Cu and Zn that were not analysed. Potassium could be showing a correlative relationship in the dataset, with other unmeasured soil nutrients being ultimate factors. The reasons why I suggest the availability of Cu and Zn (relative to Mg and Mn) are more likely to be causal (in terms of determining a particular vegetation structure) than other nutrients are explained in detail in the following papers:

âĂć Milewski, A. V. and Mills, A. J. 2015. Why was the Highveld treeless? Looking laterally to the Pampas for global edaphic principles beyond biogeographical accidents. – S. Afr. J. Bot.: 10.1016/j.sajb.2015.05.019. âĂć Mills, A. J. et al. 2013. Constraint on woody cover in relation to nutrient content of soils in western southern Africa. – Oikos 122: 136-148. âĂć Mills, A. J. et al. 2013. Boundary of treeless grassland in relation to nutrient content of soils on the Highveld of South Africa. – Geoderma 200: 165-171. âĂć Milewski, A. V. and Mills, A. J. 2010. Does life consistently maximise energy intensity? – Biol. Rev. 85: 859-879.

4) Potassium is likely to be strongly influenced by fire regimes. Fires, which presumably occur on occasion in the savannas in this study, are likely to result in depletion of K (see e.g. Mills, A. J. and Fey, M. V. 2004. Frequent fires intensify soil crusting: physicochemical feedback in the pedoderm of long-term burn experiments in South Africa. – Geoderma 141: 45-64). It is therefore unsurprising that a fire-free forest will have greater K in the soil than in adjacent fire-prone savannas. To see this pattern as causal is therefore questionable.

5) The fact that K is an important osmoticum does not explain why trees would become more competitive than grasses (or shorter trees) in relatively K-rich soils. Grasses

also use K, and an increase in K could also be invoked as a reason for why grasses are thriving. Potassium is used for wood cambial growth, but there are many other nutrients that are used in the manufacture of wood (e.g. Ca, Cu, B), so it is unclear why K would be the most important limiting factor preventing trees from dominating in savanna sites.

6) Although K is sometimes deficient in agricultural environments, there are numerous other nutrients that are frequently deficient in such environments. Potassium is therefore a very unlikely candidate for being a nutrient that is so scarce that vegetation structure is dictated by its availability. Other nutrients that are in general far more likely to be deficient than K in agricultural environments include Cu, Zn, and B. Potentially useful thought experiments are as follows: a) Would the savannas be converted to forests if fertilized with K? b) What nutrients would one apply to the savannas to make them more grassy and less wooded in time? I would hypothesise (for the reasons discussed throughout this report) that applying K would have negligible effect on the savannas and that applying nutrients such as Cu and Zn would make the savannas more grassy and less wooded.

7) I suggest that it would be useful to frame the savanna-forest question as follows: what makes the grasses relatively competitive in the savanna sites? One explanation would be that the relatively balanced nutrient profile of the savanna sites favours the growth of grasses, with a sufficient supply of various scarce nutrients for catabolising photosynthates produced.

Minor points:

Further proofreading of the manuscript to excise typographic and grammatical errors is required before publication. For example: page 7886: ‘continues to exceeds rainfall’, and a missing bracket on line 20 of page 7887.

Interactive comment on Biogeosciences Discuss., 12, 7879, 2015.