Wageningen, The Netherlands, 16 September 2015

Dear Editor,

Thank you for allowing us to submit a revision of our manuscript 'Sharp ecotones spark sharp ideas: comment on "Structural, physiognomic and above-ground biomass variation in savanna-forest transition zones on three continents – how different are co-occurring savanna and forest formations?" by Veenendaal et al. (2015)' to *Biogeosciences*. We have studied the referees' comments and improved our manuscript based on their helpful recommendations. Please find below the referees' comments (in italics) and our response to them (in plain text), followed by the revised manuscript. All changes are marked using "track changes" in MS Word.

We further made small changes throughout the text to improve clarity and flow, and added relevant references.

We believe that our revisions have increased the quality of the manuscript and its relevance to the broad readership of *Biogeosciences*. Thank you again for considering it for publication,

Kind regards,

Arie Staal and Bernardo M. Flores

Referee 1:

The opinion piece written by Staal and Flores touches on important processes controlling vegetation dynamics in forest-savanna transitions, which could indeed have been more explicitly addressed by Veenendaal et al. The manuscript merits publication. However, the authors should reconsider some of their assumptions to address two specific issues:

First, the influence of nutrient-disturbance interaction is misrepresented. Figure 2 is over-simplistic and the authors should revisit the citations used to support that conceptual representation (e.g. Hoffmann et al. 2012 Eco Letters) and include more comprehensive conceptual models such as that proposed by Franco et al. 2014 in Theor. Exp. Plant Physiol addressing "Cerrado: The role of functional types, resource availability and disturbance in regulating plant community responses to rising CO2 levels and climate warming".

Second, the multimodal distribution shown in Fig 1 could be explained by how different plant communities respond to soil resource availability and disturbance. This is a critical point that is surprisingly absent in the current version of the manuscript. Many of the studies cited by the authors have emphasized the existence of nutritional and disturbance thresholds for tree establishment and forest expansion into savannas. A recent meta-analysis by Silva, Hoffmann, et al. 2013 (Can savannas become forests? A coupled analysis of nutrient stocks and fire thresholds in central Brazil. Plant & Soil) demonstrate that the ability of trees to reach a fire-resistant size under nutrient limitation *depends on the functional group in question. Those authors concluded that "forest species require a lower nutrient supply to attain closed canopies and suppress fires; therefore, the ingression of forest trees into savannas facilitates the transition to forest". The authors also asserted that in central Brazil soils of many savannas have "sufficient N, K, and Mg, but require additional P and Ca to build high-biomass forests". In other words tradeoffs between nutrient requirements and adaptations to fire reinforce savanna and forest as alternate stable states, explaining the long-term persistence of vegetation mosaics in the seasonal tropics, and probably the multimodal distribution shown here in figure 1.*

First, we appreciate the insightful comments by referee 1. We agree that Fig. 2 was too simple and lacked some important components of the system dynamics, in particular the difference between functional types (savanna- and forest-tree species) in their responses to soil nutrient content and fire. Therefore, encouraged in particular by the above cited literature, we updated our conceptual model. Our new conceptual model includes the different interactions that savanna- and forest-tree species have with soil fertility and fire. Furthermore, in lines 77-102 (lines 104-128 of the text with track changes) we discuss these processes and how they could explain the multimodal tree-cover distributions that we show in Fig. 1.

Referee 2:

Staal and Flores provide a short but effective commentary on Veenendaal et al. (2015) "Structural, physiognomic and above-ground biomass variation in savanna-forest transition zones on three continents – how different are co-occurring savanna and forest formations?" (doi:10.5194/bg-12-2927-2015).

Current thinking suggests tropical forest and savanna occupy alternative stable states for a given climatic/soil combination, with fire a major factor controlling the relative distribution of the savanna-forest interface. Change in fire regime, either frequency and/or severity controls tree:grass balance with frequent fire maintaining low woody cover, and high woody cover suppressing grass production (fuel) and fire occurrence. There is a wide range of evidence supporting this notion from observations and experiments in fire ecology, physiology and remote sensing.

This evidence is efficiently described by the authors and they then challenge the conclusions of Veenendaal et al. (2015) who present field data suggesting a continuum of savanna-forest cover dynamics rather than an abrupt transition, with fire having far less influence than the current paradigm suggests. In effect, Veenendaal et al. provides a significant challenge to current thinking on savanna-forest dynamics and tipping points. Staal and Flores provide an elegant re-assessment of key cover data given in Veenendaal et al. Probability density functions off upper stratum and total cover data given in the original paper suggest a tri- and bi-modal distribution is evident in Veenendaal et al.'s data. This is similar to remote sensing evidence of woody cover in the tropics that points to three states of cover; forest, savanna, and a treeless state.

This analysis appears to support the author's contention that Veenendaal's data actually supports the current paradigm rather than disproving it. I found this a compelling and simple argument and this comment by Staal and Flores makes an interesting contribution to this debate. I didn't find Fig 2 particularly useful, the feedback with high nutrient sites and fire is well described in the text of the comment and it could be deleted.

We thank referee 2 for supporting the comment. The referee considered Fig. 2 redundant and suggested to delete it. Instead, we decided to improve the figure based on the suggestions by referee 1.

Sharp ecotones spark sharp ideas: comment on "Structural, physiognomic and above-ground biomass variation in savanna-forest transition zones on three continents – how different are co-occurring savanna and forest formations?" by Veenendaal et al. (2015)

A. Staal[1] and B. M. Flores[1,2,3]

[1] Aquatic Ecology and Water Quality Management Group, ~~P.O. Box 47, 6700 AA,~~ Wageningen University, P.O. Box 47, 6700 AA, Wageningen, The Netherlands

[2] Resource Ecology Group, Wageningen University, P.O. Box 47, 6700 AA, Wageningen, The Netherlands

[3] Department of Ecology, Center for Biosciences, Federal University of Rio Grande do Norte, 59072-970 Natal, RN, Brazil

Correspondence to: A. Staal (arie.staal@wur.nl)

Scientific progress occurs as ideas are developed, challenged and debated. ~~The history of ecology is full of such~~Such debates between different schools of thought ~~(Real and Brown, 1991)~~are plentiful in the history of ecology (Real and Brown, 1991). One emerging ecological paradigm is that tropical forest and savanna can be alternative stable states under the same environmental conditions. There is increasing consensus that savannas can be self-stabilizing through a positive feedback mechanism between fire and ~~landscape flammability. Fires may maintain an open landscape whereas they are suppressed by~~ low tree cover. Also, the closed ~~canopy~~canopies of forests~~.~~ can prevent fire to occur by outshading flammable herbaceous vegetation and creating a humid microclimate (Hoffmann et al., 2012). Thus, under ~~certain~~given climatic conditions, ~~either~~both forest ~~or~~and savanna can be present. Evidence for this forest-savanna bistability is derived from fire-exclusion experiments (Moreira, 2000; Higgins et al., 2007), vegetation mosaics observed in the field ~~surveys~~ (Warman and Moles, 2009; Favier et al., 2012; Hoffmann et al., 2012; Dantas et al., 2013; Gray and Bond, 2015), vegetation shifts in the paleo-ecological record (Fletcher et al., 2014), mathematical models (Staver and Levin, 2012; Van Nes et al., 2014; Baudena et al., 2015; Staal et al., 2015) and analyses of remotely sensed estimates of tree cover (Hirota et al., 2011; Staver et al., 2011a,b). The latter studies~~,~~ have fuelled this debate by showing that tree-cover frequency distributions across the global tropics are bimodal~~,~~ within a range of climatic conditions (with peaks ~~at about~~around 20% and >80% cover ~~under a range of conditions whereas~~and intermediate ~~values are~~cover being rare~~, have fuelled this debate.~~).

In a recent publication in this journal, Veenendaal et al. (2015) presented a global field study of tropical forest-savanna ecotones~~,~~ (or “zones of transition”), arguing that their data are inconsistent with the hypothesis that tropical forest and savanna can be alternative stable states through a ~~grass-fire~~ feedback~~. In this comment~~ between fire and low tree cover. Here we assert that the results presented do not refute, but rather support the emerging view of alternative stable states in the tropics and the role of fire therein. Nevertheless, we acknowledge that the picture is far from complete and believe that insights presented by the authors can contribute to ~~the integration between different approaches towards~~ a coherent understanding of forest-savanna dynamics. ~~Therefore, we also identify knowledge gaps that, if filled, could reconcile conflicting views in this debate.~~

Veenendaal et al. (2015) investigated the effect of climate and soil conditions on vegetation structure of 61 one-hectare plots near forest-savanna ecotones ~~(or “zones of transition”)~~ in South America, Africa and Australia. Based on their extensive data collection, they provide two main arguments supporting inconsistency with the alternative stable states hypothesis. Firstly, in contrast to what is expected from discontinuities in the remote sensing data~~,~~ (Hirota et al., 2011; Staver et al., 2011b), they ~~report~~argue that woody plant cover in ~~the~~their field plots shows no signs of discontinuity ~~due to the progressive replacement of the herbaceous stratum (referred to as “axylales”) by the subordinate woody vegetation particularly composed by shrubs~~. Secondly, they consider a soil-climatic envelope to be sufficient to explain the forest-savanna transition and thus discard the role of fire. The implication is that, by considering soil in addition to water availability, it would no longer be necessary to postulate a non-deterministic relation between environment and vegetation structure.

To support their first point of canopy~~-~~-cover continuity, Veenendaal et al. (2015) presented observations of the cover of different canopy layers (the upper, middle and lower strata), as opposed to the commonly used remote sensing product ~~(MODIS VCF; DiMiceli et al., 2011) that~~(MODIS VCF; DiMiceli et al., 2011), which can only detect coverage at heights above 5 m. The inclusion of all strata in canopy measurements is ~~a valuable contribution.~~an advance to previous work. However, it is unfortunate that their plot locations were not randomly selected, which limits their capacity to correctly test continuity in canopy cover. Nevertheless, here we show that the distribution of canopy cover from 41 field plots (Fig. 4 ~~from~~in Veenendaal et al. 2015), even including all canopy strata, is multimodal (Fig. 1). We tested the number of modes (1–3) of the distributions of upper stratum canopy cover (representing trees with a diameter at breast height of at least 10 cm) and total canopy cover. Upper stratum canopy cover was significantly trimodal and total canopy cover was significantly bimodal. Thus, including all strata in the analysis does not alter the multimodality in tree cover observed ~~in~~with remote sensing ~~images~~ (Hirota et al., 2011; Staver et al., 2011b~~; Murphy and Bowman, 2012~~)~~. The distribution of the upper stratum canopy cover is remarkably consistent with broad-scale remote sensing data (Hirota et al., 2011), having peaks at a tree cover of 0.03, 0.34 and 0.82 (Fig. 1A). The total cover has peaks at 0.42 and 0.91 (Fig. 1B), which seems to reproduce well the closed canopy of tropical forests. Thus, our re-~~. The distribution of the upper stratum canopy cover, having peaks at a tree cover of 0.03, 0.34 and 0.82 (Fig. 1A), is remarkably consistent with broad-scale remote sensing data reported by Hirota et al. (2011). The total cover has peaks at 0.42 and 0.91 (Fig. 1B), the latter of which seems to adequately reproduce the closed canopy of tropical forests. Thus, our analysis confirms that the MODIS tree-cover product does not detect all canopy cover, but nevertheless rightly captures its bimodality. It remains unclear whether this bimodality is caused by fire, as no data on fire history have been presented for the plots. The authors expect, however, that fire frequency is higher in the savanna plots and claim that this is merely an effect of lower canopy cover, but not its cause. This contradicts a number of studies that demonstrate the negative effects of fire on trees (e.g. Bond, 2008; Hoffmann et al., 2009; Lehmann et al., 2014) and a feedback between low tree cover and fire (e.g. Jackson, 1968; Cochrane et al., 1999; Grady and Hoffmann, 2012; Hoffmann et al., 2012; Murphy and Bowman, 2012).

The second main point of Veenendaal et al. (2015) defends a deterministic effect of soil and climatic conditions on vegetation structure. However, the field plots in Veenendaal et al. (2015) are not randomly selected from all possible tropical forest-savanna ecotones~~. Field studies~~ across climatic conditions. Nevertheless, the authors show that soil exchangeable cations are ~~essential~~positively correlated to ~~complement the understanding of the dynamics~~canopy cover, and conclude that cation concentration is a crucial factor shaping ~~the~~vegetation structure~~ of forest and savanna provided by~~

~~broader-scale studies~~. Indeed, nutrient availability affects vegetation structure in several ways. Firstly, it enhances the rate of tree recruitment after fires (~~Hirota~~Hoffmann et al., ~~2011; Staver et al., 2011b~~2012; Murphy and Bowman, 2012). ~~, but need to capture a realistic distribution of the vegetation and its predictors across the landscape. Still, Veenendaal et al. (2015) show that soil exchangeable cations were positively correlated to canopy cover and conclude from it that cations are a crucial factor shaping vegetation structure. It is well known that nutrient availability increases tree recruitment; yet this does not exclude the role of fire and the interaction between these two predictors. In addition to its effects on trees (Hoffmann et al., 2009), fire can also lead to negative changes in the soil by exporting nutrients from the organic matter and facilitating leaching and erosion (Certini, 2005). Locations with higher soil quality are able to recover faster after fires, increasing the chance of being found in the forest state (Bond, 2010; Grady and Hoffmann, 2012; Hoffmann et al., 2012). Therefore, fire frequency becomes a crucial factor for tree growth, as suggested by Dantas et al. (2013) showing simultaneous breakpoints in a range of soil variables, community structure and fire adaptation traits in trees at a savanna-forest transition in Brazil. Thus, the results of Veenendaal et al. (2015) do not justify discarding the effect of fire on vegetation structure and soil, but actually support the idea (Jackson, 1968; Bond, 2010) that a soil-plant-fire feedback may exacerbate bistability (Fig. 2). However, further research on this subject is needed to obtain a full understanding of these dynamics.~~

Secondly, it affects savanna and forest trees differently (Hoffmann and Franco, 2003). Savanna trees, on the one hand, allocate many resources to fire resistance, for instance by developing thick barks (Keeley et al., 2011). Communities of savanna trees are thus generally not able to attain closed canopies (Silva et al., 2013). This strategy allows coexistence with flammable herbaceous vegetation, stimulating the occurrence of frequent fires. Forest trees, on the other hand, allocate more resources to leaves, and therefore require about three times less nutrients to reach canopy closure than savanna trees (Silva et al., 2013). Although forest trees are less resistant to fire, their ability to close the canopy allows them to suppress fire. These different responses of savanna and forest trees to nutrient availability help explain the bimodal tree-cover pattern presented in Fig. 1. However, we argue that this picture is not yet complete (Fig. 2).

When a fire penetrates a tropical forest, high amounts of nutrients can be exported through volatilization (Kauffman et al., 1995; Certini, 2005), thus lowering soil fertility. The same process has also been shown in savannas (Kauffman et al., 1994). In the absence of fire, soil fertility in forests is maintained by efficient nutrient recycling (Vitousek and Sanford, 1986; Silva et al., 2013). Indeed, in many parts of the tropics, as confirmed by the results of Veenendaal et al. (2015), forest soils are more fertile than savanna soils (Bond, 2010; Veldman and Putz, 2011; Wood and Bowman, 2012; Dantas et al., 2013; Silva et al., 2013; Lehmann et al., 2014). When forests expand, their trees have a positive effect on the nutrient availability of the relatively poor soils of savannas (Silva et al., 2008; Silva and Anand, 2011; Paiva et al., 2015). This mechanism creates a positive feedback between forest trees and soil fertility, in which forest favours forest. The existence of this mechanism also suggests that the reverse mechanism of soil degradation occurs when savannas expand (dashed arrow in Fig. 2), but more research is needed to test this hypothesis. Nonetheless, the idea that soil fertility can shift along with tree cover seems reasonable. Our conceptual model (Fig. 2) demonstrates how the tree cover-soil feedback and the tree cover-fire feedback may interact synergistically to enhance forest-savanna bistability.

We appreciate both the exploration of global patterns that generate hypotheses on how tropical ecosystems function as well as efforts to confront them with field evidence. Veenendaal et al. (2015) attempted to test in the field the hypothesis that tropical forest and savanna can be alternative stable states. ~~However, we conclude~~They claimed that ~~the presented~~their results ~~are not inconsistent~~conflict with this hypothesis~~.~~, but we conclude that they in fact support it. We encourage future tests in the field~~ studies~~ that implement randomized sampling, include data on fire history ~~and~~as well as on fire traits of the vegetation~~ to~~. These would allow appropriate comparisons with remote sensing observations and advance in our understanding of tropical vegetation dynamics. Recognizing tropical forests and savannas as alternative stable states maintained by fire has major implications for conservation strategies~~ that aim to protect ecosystems and to mitigate possible effects of climate change.~~. The distribution of ~~both states~~forests and savannas across the world's tropics may shift together with climate-induced fire regimes (Lehmann et al., 2014). Therefore, ~~establishing~~understanding how fire affects ~~the vegetation~~tree-cover stability in different tropical regions will ~~contribute to enabling~~enable societies to ~~properly~~locally manage ecosystems and increase their resilience to climate change (Scheffer et al., 2015).

Acknowledgements

We thank Marina Hirota, Milena Holmgren, Egbert H. van Nes and Marten Scheffer for ~~providing helpful comments on this manuscript and giving advice along the way.~~discussing ideas for the manuscript. We also thank both anonymous reviewers for insightful comments that contributed to improve the manuscript. AS is supported by a PhD scholarship from SENSE Research School. BMF is supported by CAPES, Brazil, and the Sandwich Fellowship Program from Wageningen University.

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Figure captions

Figure 1: The probability density of upper stratum canopy cover (A) and total canopy cover (B) extracted from Figure 4 in Veenendaal et al. (2015). The data (n = 41) ~~were~~are significantly trimodal (A) and bimodal (B), as indicated by the lowest values of the Akaike Information Criterion as well as the Bayesian Information Criterion. We used latent class analysis on arcsine square-root transformed fractions of canopy cover (as in Hirota et al., 2011).

Figure 2: ~~The relations~~ Relations between forest-tree cover, savanna-tree cover, fire and soil ~~nutrients. Nutrients may reinforce the~~fertility. These relations create positive feedback loops that ~~creates~~explain alternative stable states in tree cover. The dashed arrow is hypothetical, but note that the positive feedback loop does not depend on it. The model is based on previous studies (Jackson, 1968; Bond, 2010; Wood and Bowman, 2012; Dantas et al., 2013; Silva et al., 2013; Franco et al., 2014; Bowman et al., 2015; Gray and Bond, 2015; Paiva et al., 2015).

Figure 1

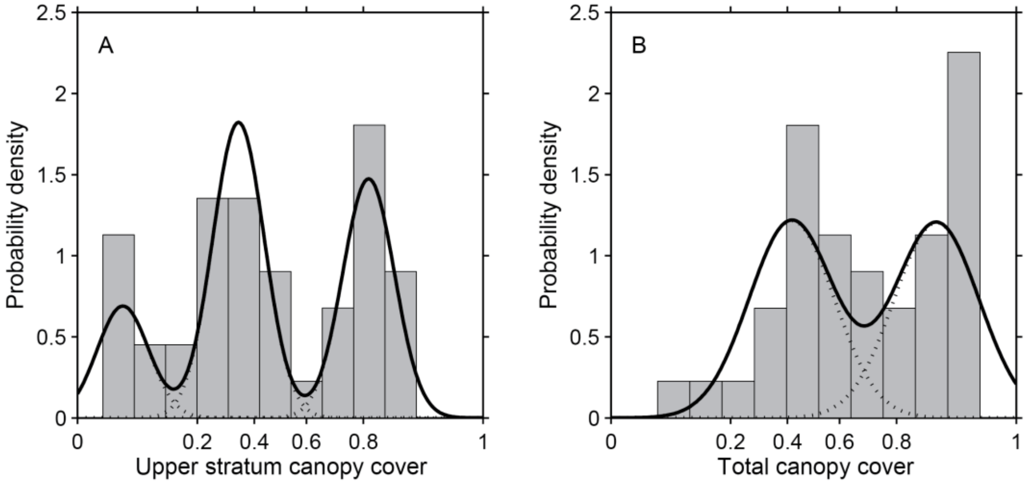
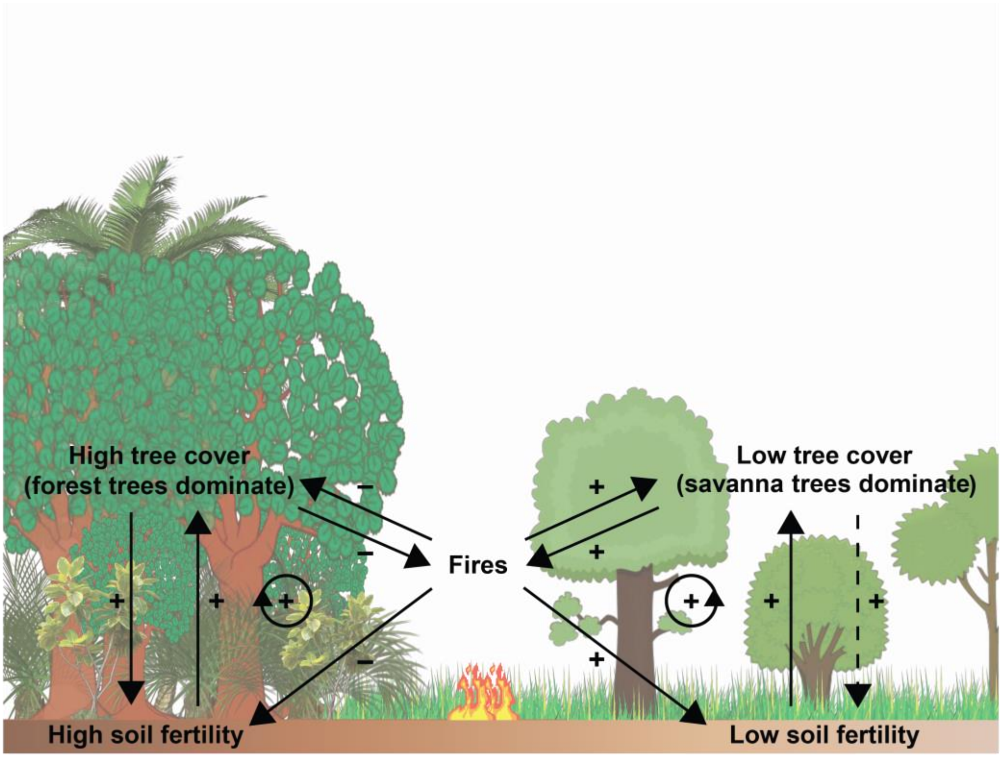

A
Probability density
2.5
2
1.5
1
0.5
0
0
0.2
0.4
0.6
0.8
1
Upper stratum canopy cover
B
Probability density
2.5
2
1.5
1
0.5
0
0
0.2
0.4
0.6
0.8
1
Total canopy cover

Figure 2


High tree cover
(forest trees dominate)
Low tree cover
(savanna trees dominate)
Fires
High soil fertility
Low soil fertility
−
−
−
+
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