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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)

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Scientific progress occurs as ideas are developed, challenged and debated. The history of ecology is full of such debates between different schools of thought (Real and Brown, 1991). One emerging 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 feedback mechanism between fire and landscape flammability. Fires may maintain an open landscape whereas they are suppressed by the closed canopy of forests. Thus, under certain climatic conditions, either forest or savanna can be present. Evidence for this forest-savanna bistability is derived from fire-exclusion experiments (Moreira, 2000; Higgins et al., 2007), field surveys (Favier et al., 2012; Hoffmann et al., 2012; Dantas et al., 2013), 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, showing that tree-cover frequency distributions across the global tropics are bimodal, with peaks at about 20 and > 80 % cover under a range of conditions whereas intermediate values are 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, 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 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

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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, they report that woody plant cover in the 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) which can only detect coverage at heights above 5 m. The inclusion of all strata in canopy measurements is a valuable contribution. 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 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 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-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

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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 (Bond, 2008; Hoffmann et al., 2009; Lehmann et al., 2014) and a feedback between low tree cover and fire (Jackson, 1968; Cochrane et al., 1999; Grady and Hoffmann, 2012; Hoffmann et al., 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 are essential to complement the understanding of the dynamics shaping the structure of forest and savanna provided by broader-scale studies (Hirota et al., 2011; Staver et al., 2011b), 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

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bistability (Fig. 2). However, further research on this subject is needed to obtain a full understanding of these dynamics.

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 that the presented results are not inconsistent with this hypothesis. We encourage future field studies that implement randomized sampling, include data on fire history and on fire traits of the vegetation to 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 across the world's tropics may shift together with climate-induced fire regimes (Lehmann et al., 2014). Therefore, establishing how fire affects the vegetation stability in different tropical regions will contribute to enabling societies to properly manage ecosystems and increase their resilience to climate change (Scheffer et al., 2015).

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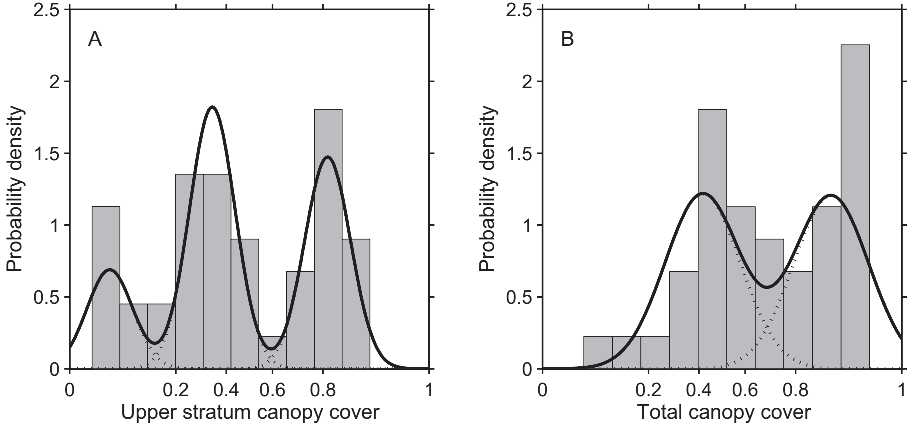

Figure 1. The probability density of upper stratum canopy cover **(a)** and total canopy cover **(b)** extracted from Fig. 4 in Veenendaal et al. (2015). The data ($n = 41$) were significantly trimodal **(a)** and bimodal **(b)**, as indicated by the lowest values of the Akaike Information Criterion 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).

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Comment on: "How different are co-occurring savanna and forest formations?"

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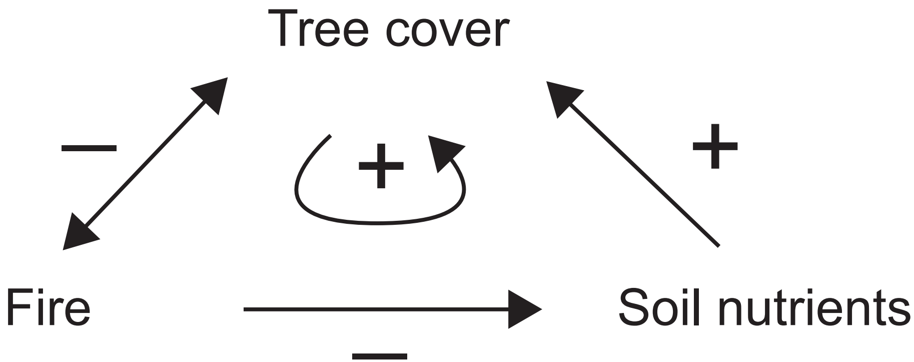

Figure 2. The relations between tree cover, fire and soil nutrients. Nutrients may reinforce the positive feedback that creates alternative stable states in tree cover.

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