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. Such debates between different schools of thought 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 low tree cover. Also, the closed canopies of forests can prevent fire to occur by outshading flammable herbaceous vegetation and creating a humid microclimate (Hoffmann et al., 2012). Thus, under given climatic conditions, both forest 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 (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 around 20% and >80% cover and intermediate cover being rare).

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 feedback 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 a coherent understanding of forest-savanna dynamics.

Veenendaal et al. (2015) investigated the effect of climate and soil conditions on vegetation structure of 61 one-hectare plots near forest-savanna ecotones 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 argue that woody plant cover in their field plots shows no signs of discontinuity. 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 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 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 with remote sensing (Hirota et al., 2011; Staver et al., 2011b). 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 across climatic conditions. Nevertheless, the authors show that soil exchangeable cations are positively correlated to canopy cover, and conclude that cation concentration is a crucial factor shaping vegetation structure. Indeed, nutrient availability affects vegetation structure in several ways. Firstly, it enhances the rate of tree recruitment after fires (Hoffmann et al., 2012; Murphy and Bowman, 2012). 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. They claimed that their results conflict with this hypothesis, but we conclude that they in fact support it. We encourage future tests in the field that implement randomized sampling, include data on fire history as well as on fire traits of the vegetation. 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. The distribution of forests and savannas across the world's tropics may shift together with climate-induced fire regimes (Lehmann et al., 2014). Therefore, understanding how fire affects tree-cover stability in different tropical regions will enable societies to locally manage ecosystems and increase their resilience to climate change (Scheffer et al., 2015).

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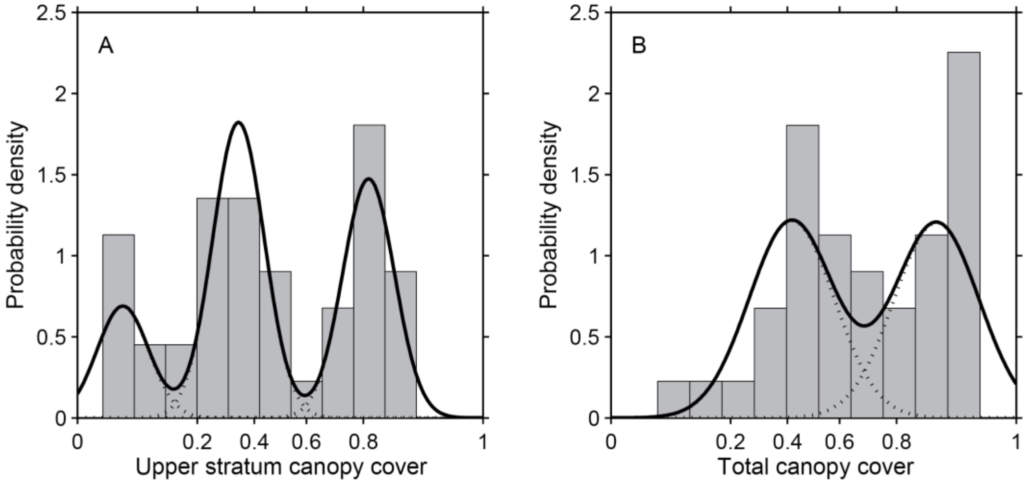
Figure captions

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) 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).

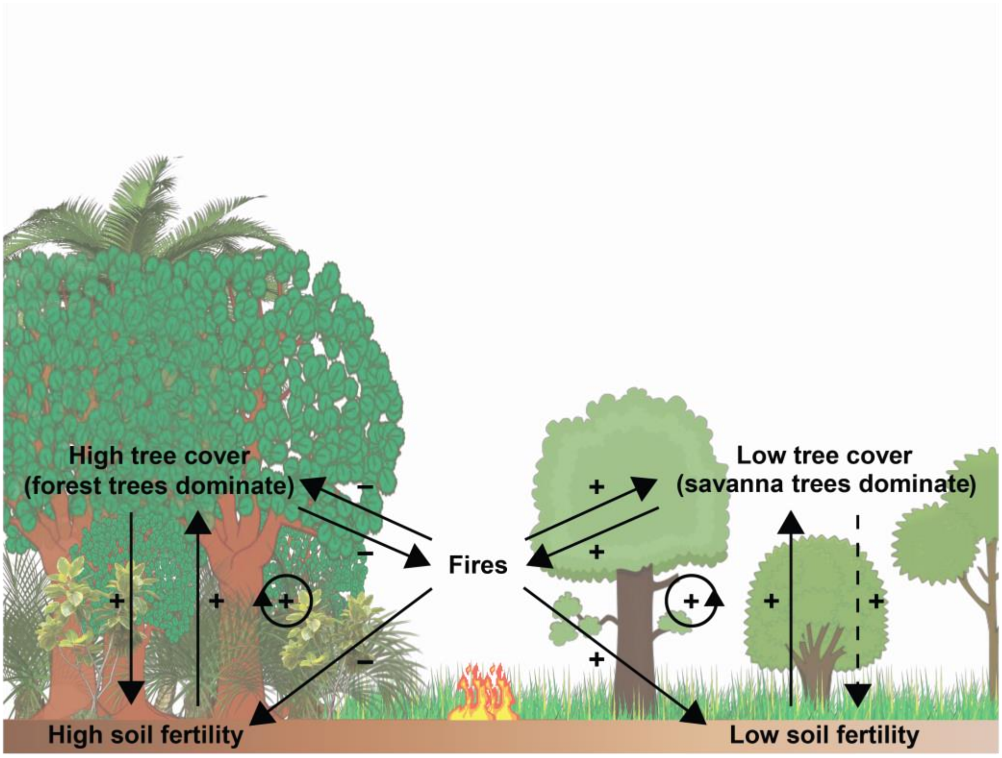
Figure 2: Relations between forest-tree cover, savanna-tree cover, fire and soil fertility. These relations create positive feedback loops that explain alternative stable states in tree cover. The dashed arrow is hypothetical, but note that the positive feedback loop does not depend on it. The model 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
B
Probability density
Probability density
Upper stratum canopy cover
Total canopy cover
0
0.5
1
1.5
2
2.5
0.2
0.4
0.6
0.8

Figure 2


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