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Remotely sensed canopy height reveals three pantropical ecosystem states: a comment

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Xu et al. (2016) recently demonstrated the existence of three ecosystem states in the tropics: forest, savanna and "treeless". Using remotely sensed tree cover and canopy height measurements, they conclude that (1) savannas and forest represent alternative states due to their climatic overlap in moist conditions (1,500–2,000 mm mean annual precipitation [MAP]), and (2) that "treeless" and savanna ecosystems do not occur in the same MAP range, and that an abrupt shift from one ecosystem state to the other occurs at 600 mm MAP. While the first conclusion accords with existing studies (Hirota et al. 2011, Staver et al. 2011, Ratajczak and Nippert 2012), the second one contradicts our own observations from Africa and Australia as well as empirical data from published studies (February et al. 2007, Ward et al. 2013, Dohn et al. 2017), all of which indicate that savanna ecosystems certainly do occur within this dry rainfall range (<600 mm) and thus constitute an alternative ecosystem state to the "treeless" one. Furthermore, treeless grasslands can also dominate in the rainfall range of 600–1,200 mm MAP (Sankaran et al. 2005). We, therefore, challenge the second conclusion especially because its acceptance could lead to inappropriate management approaches and policy decisions about these remarkable "uncertain ecosystems" (sensu Bond 2005).

The concept of alternative states has found many applications in ecological systems, improving our understanding of complex processes such as abrupt transitions and hysteresis (Beisner et al. 2003). In certain cases, alternative ecosystem states predicted by theory have been reproduced in experiments manipulating microcosms (e.g., Veraart et al. 2012) and whole ecosystems (e.g., Carpenter et al. 2011, Seekell et al. 2013). Studying alternative ecosystem states with respect to savannas, though, is challenging, primarily due to the lack of an unambiguous savanna definition (e.g., Ratnam et al. 2011). This is almost certainly because the savanna ecosystem itself exists in different manifestations or states (e.g., definitions in Lloyd et al. 2008, p. 458), complicating the comparison of a "savanna state" to alternative ecosystem states and fueling the long and ongoing debate surrounding savanna dynamics (Sarmiento 1984, Jeltsch et al. 1996, Scholes and Archer 1997, Higgins et al. 2000, 2010, Lehmann et al. 2011, Moncrieff et al. 2016).

The notion of alternative ecosystem states in the savanna literature was popularized when earlier theoretical studies (Higgins et al. 2000, Jeltsch et al. 2000, van Langevelde et al. 2003) demonstrated that savannas, regarded as ecosystems where trees and grasses coexist (Walter 1971), occurred under the same rainfall or environmental (e.g., grazing, fire) conditions as forest or grassland ecosystems. As more data became available, alternative ecosystem states were defined based on tree cover (Sankaran et al. 2005); sites with little or no tree cover (grassland), sites with a closed canopy (forest) and everything in between (savanna), further emphasizing the lack of a robust savanna definition (e.g., see different savanna/forest boundary with respect to tree cover in Higgins and Scheiter (2012) compared to Staver et al. (2011)) or of the alternative states of the savanna ecosystem itself.

Xu et al. (2016) expanded the focus to include canopy height in combination with tree cover in the classification of tropical sites. Applying advanced remote sensing techniques and utilizing newly available laser data, Xu et al. (2016) examined tree cover and canopy height across three continents, South America, Africa and Australia. They found that combining cover and height resulted in three distinct ecosystem states: forest, savanna and "treeless". The authors demonstrated the value of their approach by correctly categorizing forest relicts, which have sparse tree cover and which would have otherwise been categorized as savannas based on tree cover alone, an issue previously raised by Ratnam et al. (2011). Their results also accord with existing

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studies that forest and savanna ecosystems represent alternative ecosystem states (Staver et al. 2011, Murphy and Bowman 2012) under moist conditions (1,500–2,000 mm MAP).

While this finding is significant for the management and conservation of moist tropical ecosystems, we disagree with the authors' other result, namely, that "for the shift from savanna to the treeless state centered around 600 mm MAP, there is little evidence for the co-occurrence of alternative states over a range of rainfall conditions" and hence that the savanna state does not occur in this dry rainfall range. Below we present four critical lines of evidence which we believe led to their finding of a single, "treeless" ecosystem state.

First, Xu et al. (2016) define the "treeless" state as one that "may be dominated by shrubs and grasses". Though grasses and shrubs can be similar in height, they represent distinct (and essentially opposing) classes in terms of their function in savanna systems (Augustine and Mcnaughton 2004). Woody and herbaceous vegetation are the two competing plant types found in savannas, and this dichotomy has formed the basis of extensive studies of savanna systems globally (Walter 1939, Walker and Noy-Meir 1982, Belsky 1990, Scholes and Archer 1997, Ward et al. 2013). Given that shrubs are woody plants, if anything, they should be grouped functionally with trees rather than grasses. This is clear from the abundant literature on shrub encroachment from drylands (see reviews from Graz 2008, Eldridge et al. 2011, D'Odorico et al. 2012).

The phenomenon of shrub encroachment describes the processes whereby shrubs, generally <3 m tall, increase in density or cover, reducing grass cover. Encroachment is thought to occur in response to overgrazing, increases in atmospheric concentrations of carbon dioxide or reductions in fire frequency (Bond and Midgley 2012, Buitenwerf et al. 2012, Eldridge et al. 2013). While shrub encroached savannas have been found to be compositionally, structurally and functionally different to the grass dominated state from which they are derived under the same MAP (D'Odorico et al. 2012), Xu et al. (2016) define both states as "treeless". Critically, shrub encroachment has been shown to cause hysteresis (Gil-Romera et al. 2010), providing the strongest indication that the two ecosystems represent truly alternative states. We, therefore, do not find the current "treeless" definition ecologically relevant with respect to the functioning of actually treeless (grassland) and savanna ecosystem states. Moreover, according to the authors, the "treeless" state has a maximum (90th percentile) canopy height of 2 m. However, fig. 1a of Xu et al. (2016) shows that the first significant collection of points in terms of canopy height occurs between 2 and 5 m height, which further undermines their definition of the "treeless" state.

Second, the importance of variation in tree cover and canopy height is not equivalent across the full range of rainfalls (0–3,500 mm MAP) considered by Xu et al. (2016). While small variations in tree cover do not alter the ecosystem state at the higher end of the rainfall gradient, the same does not necessarily apply in dry environments. The wide tail at the lower end of the tree cover distribution in fig. 1a of Xu et al. (2016) attests to the extent of variation, and the resulting categorization of sites with tree cover ranging from what seems to be little more than 0% to approximately 40% as savannas will encompass ecosystems that are as distinct as grasslands and shrublands. Hence, the mean tree cover value applied along the MAP gradient (fig. 1b in Xu et al. 2016) will lack important information differentiating the dry sites with low cover.

A similar issue afflicts their canopy height analysis in Fig. 1c. Splitting canopy heights of 0–20 m in dry environments (<600 mm) into only six bins corresponds to a range of approximately 3.4 m height per bin. This will inevitably include most shrub species in the first bin. Thus the unimodal distribution of canopy height for the 0–300 mm and 300–600 mm MAP regions presented in Fig. 1c of Xu et al. (2016) does not in itself preclude the existence of alternative savanna and treeless states. Therefore, the lack of a finer resolution at the lower end of the tree cover and canopy height distributions fails to discriminate between markedly different communities at the dry end of the rainfall gradient (e.g., grasslands, grasslands with scattered small shrubs, shrublands, or open woodlands with scattered shrubs).

Third, the grid cell size used by Xu et al. (2016), i.e., 0.5°, 55 × 55 km^2, is large enough to encompass multiple, alternative ecosystem and savanna states. It is quite common for drylands in Africa and Australia to vary significantly at spatial scales of <0.5 km (Favier et al. 2012, Moustakas et al. 2013, Linstädter et al. 2015). Thus grassland, shrubland and woodland-shrubland mixtures will occur in close proximity (Eldridge et al. 2013), all with markedly different vegetation composition and structure. Therefore, aggregating data over extensive areas will likely lump together two or more quite different ecosystems. This could be the reason why the study presents a large collection of sites with canopy heights of 2–5 m with <5% tree cover (fig. 1a in Xu et al. (2016)), all classified as "treeless". Hence, while maximum canopy height may be appropriate for forests where the canopy is homogeneous, using maximum height across systems with significantly different woody heights will misrepresent these dryland systems. Furthermore, variations in mean annual rainfall amounts over scales of a few kilometers are common in tropical drylands (Gillson and Ekblom 2009, Veldhuis et al. 2016), potentially introducing substantial bias when aggregating data over such a large spatial resolution. Therefore, combining these potential errors resulting from poor resolution in tree cover, canopy height and annual precipitation is likely to produce an unreliable metric.

Finally, the data presented in the Xu et al. (2016) study came from sites in South America, Africa and Australia. The drivers of savanna tree dynamics differ between the three continents (Lehmann et al. 2014) and thus savannas in each continent are markedly different structurally and compositionally (Lloyd et al. 2008). Moreover, these ecosystems occur in different rainfall conditions across continents. African and Australian savannas have much smaller and drier rainfall ranges (Hirota et al. 2011, Staver et al. 2011) while the South American savannas have a wider range and account for most sites in Xu et al. (2016) with MAP >2,000 mm. Therefore, pooling the data from all three continents without accounting for the differences in rainfall conditions and underlying dynamics can produce misleading conclusions. Using a finer resolution for Africa and Australia would be a first step in dealing with this which could vastly improve the results at the drier end of the gradient.

We read the study of Xu et al. (2016) with great interest and agree it provides valuable insights into the categorization of savannas and forests in moist environments based on both tree cover and canopy height. However, we argue that their conclusion that there is a clear transition between savanna and treeless states centered around 600 mm MAP, and hence no climatic overlap between these two ecosystem states, is inconsistent with a vast body of literature (Sankaran et al. 2005, Bucini and Hanan 2007, Bond and Midgley 2012, Ratajczak and Nippert 2012). We showed that Xu et al. (2016) could not have identified alternative ecosystem states below 600 mm due to methodological limitations (in the analysis and spatial resolution of their data), a lack of an ecologically meaningful "treeless" definition and because data were not linked to mechanisms known to impact these ecosystems. The absence of a bifurcation pattern (i.e., the presence of alternative states) with respect to rainfall does not suffice to rule out the existence of alternative states. As Sankaran et al. (2008) demonstrated, tree dynamics in savannas and what Xu et al. (2016) would describe as "treeless" ecosystems result from complex interactions between different processes. Fire (Bond et al. 2003, Bond 2005) or herbivory (Hempson et al. 2015), for example, have been shown to be key drivers of the structure, functioning and distribution of alternative ecosystem states in the tropics across a broad rainfall range. Our comment aims to draw attention to the significance of carefully considering potential methodological biases when interpreting data (Hanan et al. 2014) and of linking observed data to ecological mechanisms accordingly (van Nes et al. 2014).

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