Changing the narrative: encroached savannas are not forest

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CLP, RDB, JMB and CEL devised the paper. CLP wrote the first draft. All authors contributed to subsequent drafts and approved the final version.

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Abstract

1. Savannas are globally important ecosystems but are often misclassified as forests because they can support high tree cover, leading to misguided management. This misunderstanding arises because the presence of grasses, a key defining component of savannas, critical for their structure and functioning, is overlooked.
2. Fundamental tree-based misunderstandings affect the interpretation of woody plant encroachment, a novel threat facing savannas, which now affects >5 million km² of savanna globally. High tree cover can degrade savannas by reducing grasses, altering fire regimes, and harming biodiversity and livelihoods.
3. We highlight that savannas can naturally vary in woody cover, and therefore high tree cover does not necessarily equate to an encroached state. We also clarify that even in an encroached state, high tree cover does not necessarily create forests. We identify three end-states, determined by rainfall and proximity to true forest, that may emerge as an outcome of encroachment: encroached, novel savanna, hybrid forest and true forest.
4. **Synthesis** Forests should not be viewed as superior to savannas. Savannas are biodiversity hotspots and vital for human survival. Effective management requires moving beyond structural definitions, understanding thresholds, and assessing ecosystem value based on biodiversity and function, not tree cover alone.

1. Savannas and Woody Plant Encroachment

Savannas cover more than 20% land area globally, support more than a billion people worldwide and are important reservoirs for unique biodiversity (Lehmann & Parr, 2016). These environments are characterized by a near-continuous C4 herbaceous ground-layer (Ratnam et al., 2011), and although they can support trees, tree cover varies greatly in both space and time (Sankaran et al., 2005; Ratnam et al., 2011). Fire and herbivores play major roles in savannas, generating important feedbacks that maintain an open and high light environment critical for the plants and animals these systems support (Bond & Keeley 2005; Ratnam et al., 2011). In contrast, tropical forests are low-light environments with a ground layer dominated by litter (not grass) (Ratnam et al., 2011). These two systems are compositionally, structurally and functionally distinct (Flake et al., 2022), but both are important and unique. Critically, what distinguishes these systems from each other is the presence or absence of a grassy understory, not trees (i.e. high tree cover/presence ≠ forest).

Relative to forests, from a scientific, policy and lay perspective, savannas have been misunderstood and overlooked (Bardgett et al., 2021; Hughes et al., 2021; Overbeck et al., 2015; Pillar & Overbeck, 2025; Silveira et al., 2022,). Although both forests and savannas are threatened, because for centuries trees and forested ecosystems have received disproportionate attention (Pilon et al., 2025; Silveira et al., 2022,), savannas, like other tropical grassy ecosystems, have been misclassified and marginalized (Parr et al., 2014). In regions where savannas support high tree number (e.g. miombo in Africa, savannas of India), they are often mistaken for forest with the important grassy understory overlooked (Bond et al., 2019; Gopalakrishna et al., 2024); this misclassification as forest can lead to the potential mismanagement of savannas, for instance through the suppression of fire (e.g. Kumar et al., 2020).

In contrast to well-documented deforestation and tree loss in forests (e.g., GlobalForestWatch.org; Hoang & Kanemoto, 2021; Li et al., 2022), savannas worldwide are undergoing large increases in tree cover. Tree cover is increasing via active planting, which is generally linked to afforestation schemes for restoration and climate mitigation (Parr et al., 2024), but also via a more passive process of woody thickening (i.e. an increase in tree cover and density) referred to as woody plant encroachment (WPE; IPCC, 2019). Woody plant encroachment is pervasive, currently estimated to be occurring over > 5 million km^2, ~ 7% of global land area (Garcia Criado et al., 2020; Stevens et al., 2016; Stevens et al., 2022; Venter et al., 2018,). The drivers of the encroachment process include both local land management practices (e.g. fire suppression, overgrazing) and global drivers (enhanced atmospheric CO_2) (Archer et al., 2017; Buitenwerf et al., 2012; Wigley et al., 2010), although direct attribution at a site level is often difficult. Nevertheless, evidence is mounting that the increase in trees associated with woody plant encroachment can have detrimental impacts on savanna biodiversity (White, et al. 2024; Wieczokowski & Lehmann, 2022), water availability (Honda & Durigan, 2016), fire occurrence (Abades et al., 2014; Archibald et al., 2009) and human livelihoods (Luvuno et al., 2022; White et al., 2022). Despite this, WPE has received relatively little attention among scientists and policy makers partly because the notion of trees as a threat runs counter to most societies' norms and values (e.g., Esperon-Rodriguez, 2025; Jones & Cloke, 2002; O'Brien, 2005; O'Brien et al., 2024; Schroeder, 1995).

While increasing tree cover has been widely documented across savannas, as have the drivers involved (see above), far less is known about the mechanisms underlying this process and its consequences for biodiversity and ecosystem function. Therefore, to provide a road map to better understanding of the mechanisms and consequences, here we: (1) unpick and clarify some of the misunderstandings about savannas and WPE; (2) identify outstanding questions concerning the distribution and consequences of WPE; and (3) offer testable hypotheses to help guide future research efforts on WPE. In doing so we critically examine the idea that high tree density creates forests and introduce the novel hypothesis that increasing tree cover in savannas does not lead to one outcome but can result in three different end states, namely encroached savanna, hybrid forest and true forest that differ structurally, functionally, and compositionally, and depend on whether there has been an increase in the density of savanna woody species or forest species invading savanna. Moreover, we argue that one of these states, 'encroached savanna", represents a novel and depauperate ecosystem state of reduced biodiversity and functioning.

2. Increasing trees doesn't necessarily equate to an encroached state

In its simplest form, wood thickening is the gain of trees via an increase in density and/or cover (Archer et al., 2017). The terms thickening and encroached are, however, often used interchangeably in studies on tree increases in savannas although some studies focus on documenting increases in tree cover (the process, e.g. Venter et al., 2018), while others focus on the altered (degraded) state that occurs at high tree cover (end-state, e.g. Sirami et al., 2009; Wieczorkowski & Lehmann, 2022). We argue that greater consideration and care is needed to avoid conflation. Distinguishing between the process (woody thickening via increases in tree cover) and the end-state (encroached) is necessary for interpreting findings.
Savannas can exhibit huge natural variation in tree cover both spatially and temporally (for example from 5 to 80% tree cover, Parr et al., 2014; Ratnam et al., 2011; Sankaran et al., 2005), as a function of processes that govern tree growth and death, such as fire, animals, drought and rainfall, along with global changes in climate and atmospheric CO_2 (Aleman et al., 2017; Gopalakrishna et al., 2024; Sankaran et al., 2005). Therefore, the gain of trees, or woody thickening, is not necessarily problematic - tree cover can fluctuate as part of natural system flux without any notable impact on biodiversity and functioning. However, of concern is that woody thickening can result in an encroached state where some upper threshold has been passed and there is a shift in system state and associated functioning (i.e. the system is operating outside normal bounds) (Fig 1). Critically, in savannas, if there are too many trees, C4 grasses decline, precipitating a system state shift with deleterious consequences for biodiversity and ecosystem function.

C4 grasses are highly efficient under high light conditions due to the structure of their photosynthetic machinery (Wasilewska-Debowska et al., 2022). However, C4 grasses are sensitive to thresholds in tree cover and associated shading (Abdallah et al., 2016; Charles-Dominique et al., 2018; Pilon et al., 2021) because photosynthetic efficiency of C4 grasses declines with shading (Tazoe et al. 2008; Pignon et al. 2017). Consequently, when tree cover increases and shade thresholds are exceeded, the ground layer qualitatively shifts from grass to litter dominance; C4 grasses lose resilience to disturbance due to reduced belowground allocation inhibiting resprouting capacity (Pilon et al., 2021) and decline in competitiveness leading to their loss from the ecosystem (e.g., Archer et al. 1995).

The transition from grass to a litter-based state is associated with the loss of key savanna consumers (fire and herbivory) (Abades et al., 2014; Hoffmann et al., 2011; Ratajczak et al., 2014; Sala & Maestre, 2014), and detrimental consequences for biodiversity and some ecosystem services (Bardgett et al., 2021); note that this is in contrast with the situation in litter-based systems (e.g., shrublands or forests) where gaining trees is less problematic because there is no change in the ground layer structure or function, and therefore no state shift. Currently, for savannas, the threshold in woody cover where an encroached (degraded) state is reached is unknown but likely varies with environmental and ecological context.

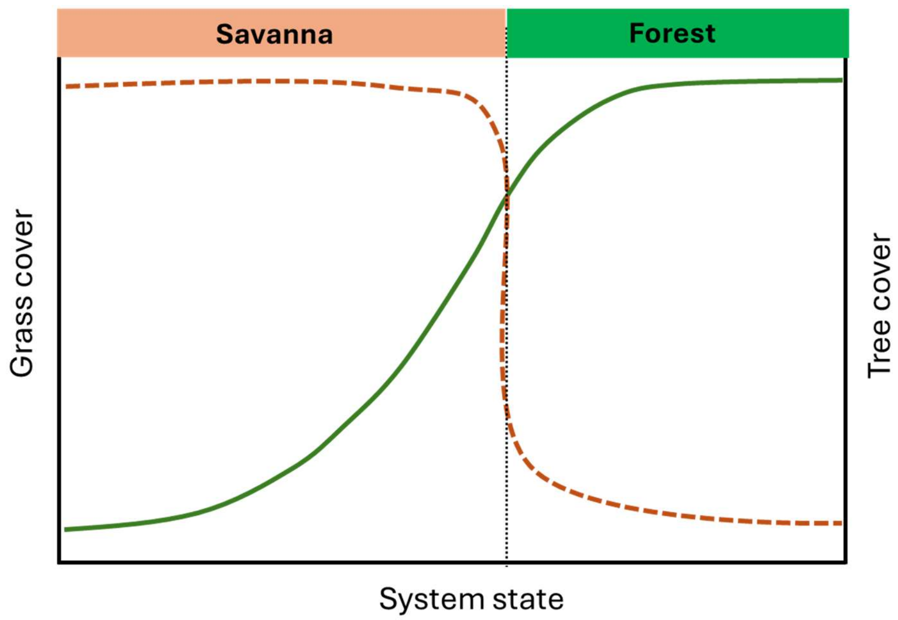


Figure 1. Savanna system state switch that results from increasing tree cover and decreasing C4 grass cover (here shown for transition to forest).

3. Gaining of trees frequently does not result in a forest.

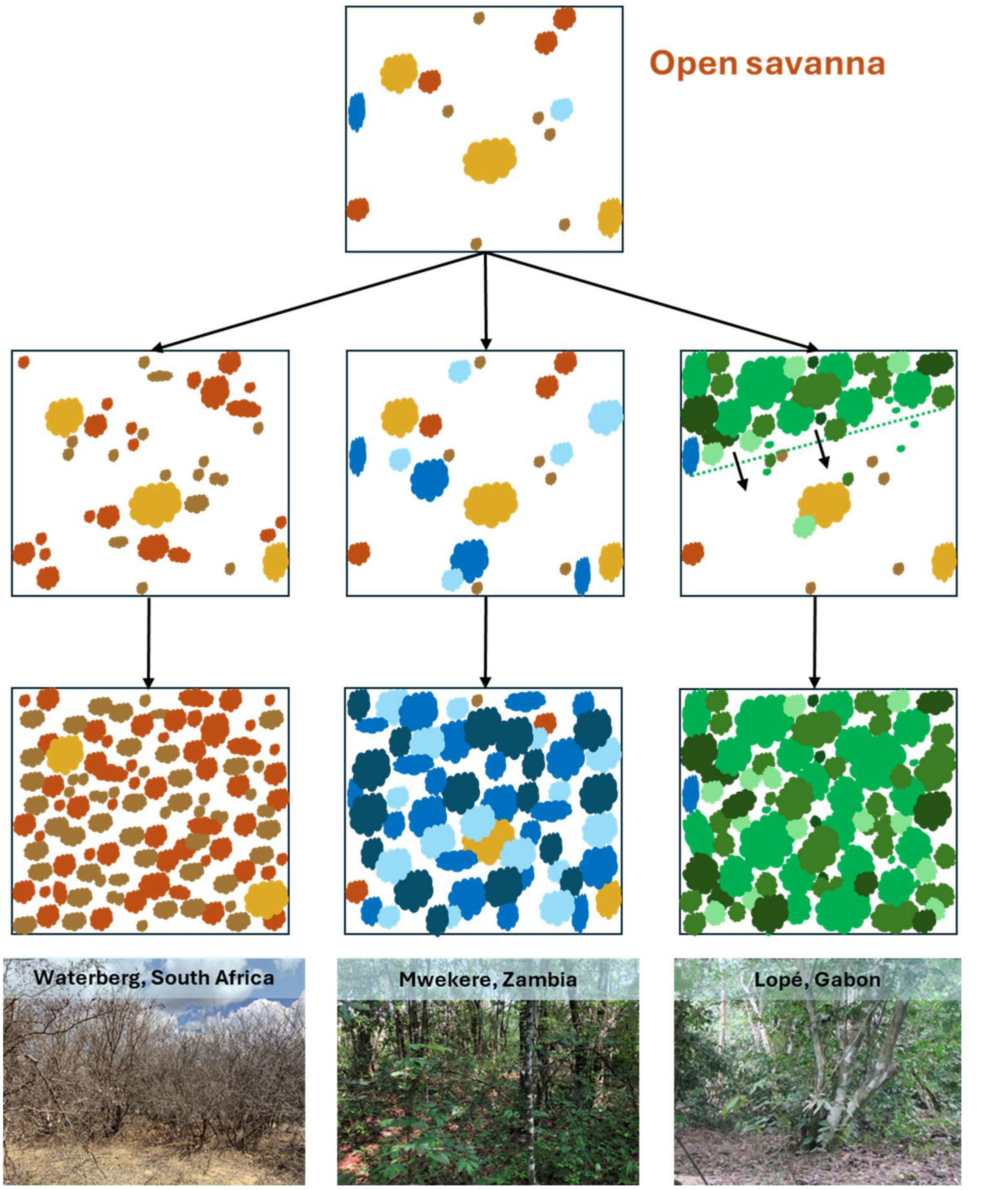
Many widely used definitions of forest are structural, focusing on trees and canopy cover (e.g., FAO and UNFCCC state forests have a min 10% tree cover). There is, therefore, the risk that the process of woody thickening in savannas will be misconstrued as resulting in forest; in other words that the encroached state is forest because systems with high tree cover are classified as forest.
The misconception that more trees equate to forest is reinforced by the conventional and prevailing view that across vast swathes of the Tropics, vegetation exists as either forest or savanna (as alternative stable states or alternative stable biomes) (e.g., Aleman et al., 2021; Pausas & Bond, 2020; Staver et al., 2011). The widespread use of structural measures (i.e. tree cover) combined with remote sensing to map trees further reinforces this view. However, evidence for the alternative stable states of forest and savanna is scarce, particularly once species floristics are considered (Higgins et al., 2025, although see Wieczorkowski et al., 2024). A structural perspective to classifying vegetation fails to recognize that the key defining parts of ecosystems are not always trees; characteristics of the ground layer (e.g. presence of a C4 grassy understory) and, therefore, key processes (e.g. fire) are arguably more important in determining savannas (e.g. IUCN global ecosystem typology, Keith et al., 2022).

The 'more trees = forest' misunderstanding may also arise because the term 'encroachment' suggests movement in, or advance of, trees from elsewhere and therefore forest expansion; for example, the Merriam-Webster dictionary defines encroachment as "*to advance beyond usual limits*". In some regions, forest expansion does occur (examples in: Mitchard & Flintrop, 2013), but for most areas an encroached state results from an increase in density of pre-occurring savanna tree species and therefore forest expansion is neither the process, nor is forest the end-state.

Here we argue that from a compositional and functional perspective, three system states are possible as a consequence of WPE (or increase in tree cover). Furthermore, with increasing tree cover there can be quite different end-states depending on whether there has been an increase in the density of savanna woody species, or forest species invading savanna (e.g. expansion of forest). We propose that with increasing tree cover, the system outcome depends principally on total rainfall (as a proxy for productivity in these tropical systems) and distance to forest (as a seed source of forest associated species) (Fig. 2). The drivers can differ with location – for example, grazing is a more important consumer at lower rainfalls, than at higher rainfalls where the herbaceous layer tends to be less palatable. We argue that there are three broad end-states, with all representing system state shifts that differ structurally, functionally and/or compositionally (Fig. 2):

State 1: In many regions, encroached savannas are characterized by hyper-dominance of one or two woody species. These are often shrubs relatively low in stature; for example, dominance of *Dichrostachys*, *Terminalia* or *Acacia* in many regions in sub-Saharan Africa (e.g., Sirami et al. 2009, Leitner et al. 2018, Bora et al. 2021). These woody species can grow at very high densities such that the vegetation can be almost impenetrable. Importantly, this state is not forest because, although the C4 grassy understory is lost, the tree species are floristically classified as savanna species (i.e., not forest-associated) (Fig. 2). Indeed, even at very high tree density and cover, forest tree species are not found because rainfall is too low, and true forest is too distant geographically (Fig. 2). Consequently, the biota represents a depauperate, nested subset of the intact savanna. These savannas are dysfunctional because the lack of a (C4) grass layer means they can no longer support key processes of fire and large mammalian herbivory (Keith et al., 2022). In sum, they are functionally, compositionally, and often structurally, distinct from true forest. From a compositional perspective, we term these novel ecosystems '**encroached savanna**' (Fig. 2). We hypothesize these regions are found in drier savanna regions (650-700 mm and less) where rainfall is too low to support forest species (Fig. 3). We predict their extent is likely to be considerable on some continents where large areas of more arid savanna occur (e.g. Africa).

State 2: We identify a depauperate forest-like state in wet savanna regions (>800mm) that are not near true forest (Fig. 3). This state is intermediate to high rainfall savanna and true forest. In these regions, the increase in tree cover (e.g. with suppression of fire) can result in nested community with an increase in forest-associated species that already exist in the wider savanna landscape (e.g. fire sensitive trees in riparian zones, savanna-forest edge species) and more shade-tolerant savanna tree species, and a loss of light-loving, fire-resistant savanna species (Fig. 2). Structurally these systems resemble a forest (e.g., high tree cover, tall trees, shady, absence of C4 grassy understory), but they lack true forest species because distance from forest is a major dispersal limitation (Fig. 3). We therefore call this state a '**hybrid forest**' (Fig. 2). This state can occur in wetter savanna regions such as the miombo savanna in southern Africa (Wieczokowski et al., 2024), or in the Cerrado in Brazil (Moreira, 2000) where fire is suppressed. Smaller areas of this state may occur naturally linked to topography and the occurrence of natural barriers (e.g. lower-lying wetter areas, or areas protected from fire) or as a transition state before succession to forest. This state is likely to cover a smaller area than States 1 or 3.



	State 1: Encroached savanna	State 2: Hybrid forest	State 3: Forest
C4 grass layer	Absent	Absent	Absent
Fire & vertebrate herbivory	Decline	Decline	Fire = absent
Trees: Savanna spp.	1-2 species hyperdominant	Few savanna species	No savanna species
Trees: Forest spp.	None	None?	Common
Similarity to open savanna state:			
Structure	Partly	No	No
Function	No	No	No
β Diversity	Nested	Nested	Turnover
Driver of change	Over/undergrazing, fire suppression, CO_2	Fire suppression, CO_2	Fire suppression, CO_2

Figure 2. Potential pathways and state outcomes with increasing tree cover in savannas: 1: Encroached savanna, 2: Hybrid forest, 3: True forest. Brown and yellow colours = savanna tree species, blue colours = forest-associated tree species, green colours = true forest tree species. Only tree species are shown. White = understory, principally either grass or litter. Example locations for different end-states shown in photos.

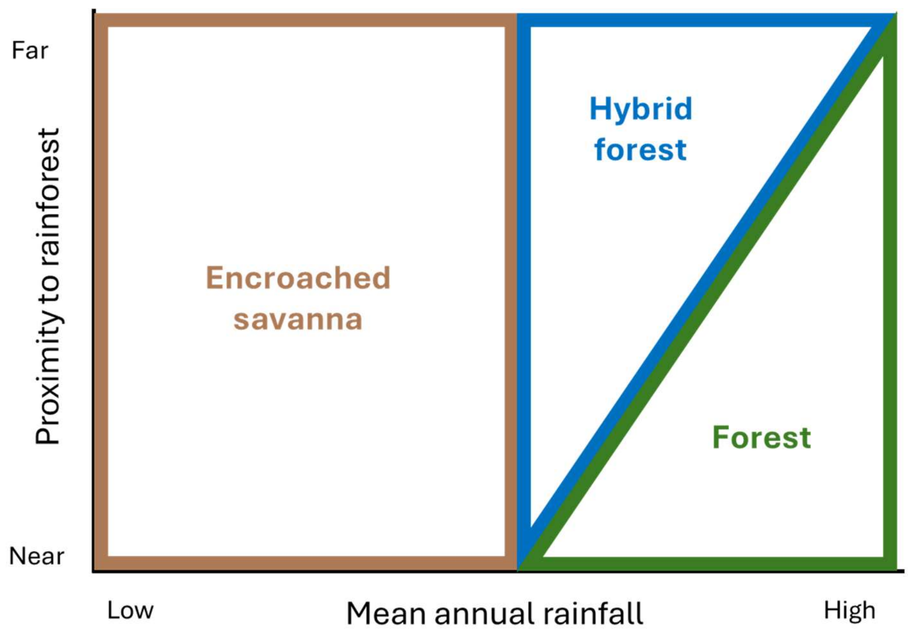


Figure 3. The occurrence of different encroached savanna states is determined by rainfall and proximity to tropical rainforest. The extent of encroached savanna is limited by rainfall, while hybrid forest is limited principally by distance to forest (i.e. reduced opportunity for rainforest propagules to disperse). The occurrence of forest requires high rainfall and close proximity to forest (movement of propagules possible where dispersal community is intact).

State 3: Finally, in regions where savanna-grasslands occur in mosaics or close proximity with tropical forest and rainfall is high, increasing tree cover in savannas can result in a system switch to **true [tropical rainforest] forest** (Figs. 2 & 3). This is because environmental conditions can support forests (e.g. sufficient rainfall) and there is a pool of forest species that can disperse into the open ecosystems. We predict turnover of tree species and loss of C4 grasses and forbs with the shift to true forest (i.e. with true forest species) (Fig. 2). We anticipate this situation is common where forests expand into savanna (Figs. 2 & 3), particularly along savanna-forest boundaries (e.g., in Brazil [Abreu et al., 2021] and in Gabon [Cardoso et al., 2021], Fig. 3). In these regions, forest is gained, but the important and unique biodiversity of high rainfall savannas is lost. Fire suppression and CO_2 are common drivers of this change in state.

4. Forest is not the ideal state

Finally, the lack of understanding about tree gain in savannas is impeded by the general belief that more trees are a good thing *per se*. Trees are particularly valued biota (Dove, 2004; Wall, 2022), with forest often seen as the preferred or ideal state (Duvall et al., 2018; Pillar & Oberbeck, 2025; Stott, 1999; Silveira et al., 2022). These ideas have centuries' long history and have been perpetuated by colonialists, politicians, philosophers, and artists (Davis, 2016 and references within, Ratnam et al., 2016). Indeed, forests were promoted by colonial powers as the desired state; the low tree cover they encountered in open, grassy ecosystems prompted colonialists to describe these savanna landscapes as 'wastelands', 'degraded' and even 'wretched' (Bardgett et al., 2021; Davies, 2016). Views from Western scientists in temperate, well-forested regions have also had a powerful influence on ecology. For example, in ecology, theory on vegetation dynamics has been driven by observations of change over time primarily derived from temperate ecosystems, or turnover of ecosystems along elevational gradients (Moret et al., 2019; Vera, 2000). Many of these ecological ideas were uncritically transferred to tropical regions: Frederick Clement's (1916) theory of succession promoted the view that the ideal climax community is forest, and savanna was seen as a non-climax deviation, the 'savanna problem' (Sarmiento, 1984; Sayre, 2017; Veldman, 2016) – despite the fact that the prevalence of disturbance is supported through the productivity and seasonality of climates. Collectively, this thinking has led to flawed notions that forested ecosystems are somehow superior intrinsically, for the services they deliver and the biodiversity they support (Murphy et al., 2016; Pillar & Overbeck, 2025).

Half of the world's biodiversity hotspots are in grassy systems; they support more people than forested regions, play key roles in earth-atmospheric process and global net primary productivity, and are the cradle of humankind (Lehmann & Parr, 2016). There is no basis for concluding forests are 'better' - they are simply one of multiple biomes on Earth, each of which contributes to the Earth System in all its facets. Encroachment should be assessed relative to the value more trees bring – for example, in terms of ecosystem services or biodiversity. Although encroached savannas with their high density of trees are commonly classified as 'forest', these depauperate and dysfunctional savannas (States 1 and 2 above) are often of less value than intact, functioning savannas when considered in terms of biodiversity (less biodiverse), carbon (likely less carbon), and ecosystem services (reduced or altered provision), and considerably less value than natural forest. We therefore urge that value is not simply a function of tree cover but instead is determined by the extent to which biodiversity, ecosystem services and other values are supported (Bardgett et al., 2021). It is critical we consider both what is lost, as well as what is gained.

5. Conclusion

Here we consider how increased tree cover can result in three structurally, functionally and compositionally different end-states as opposed to a single end-state of forest (Figs. 2 & 3). Yet, we do not know the potential distribution of these different end-states and under what specific conditions there is potential shift to these different states (e.g. rainfall thresholds). Such information is sorely needed to understand the consequences of WPE more fully and manage landscapes effectively, especially in regions where wholesale system change could have major consequences for the biodiversity and people living in these areas (Lehmann & Parr 2016). Space-for-time studies sampling along gradients of tree cover in different regions would be a major advance to understanding where there is the potential to switch to forest, but is arguably more important, where novel, depauperate savanna systems result. While all three 'encroachment' states exist in Africa, we expect only States 2 and 3 in South America (because savannas there are wetter) and State 3 in Australia (because narrower trees canopy architecture means less shading and therefore States 1 and 2 are less likely). We predict all three states will be possible in Asia due to similarities with Africa. To what extent similar states may exist, or be possible, in temperate regions requires further investigation.

The persistent assumption that high tree cover equates with forest is problematic for developing evidence-based conservation and restoration of savanna ecosystems. There is an urgent need to look beyond structural definitions of vegetation states, otherwise we risk misclassifying and managing ecosystems. The implications of switches in savanna state to novel, encroached savannas or hybrid forests are severe given that a large proportion of the global population depends directly on savannas for their existence/livelihood. Yet, many research challenges remain and will require future research to address them. Under global change, it is critical we work to understand the potential ecosystem trajectories better including the potential environmental niches of different states, the speed of change, the consequences for humans and the biosphere upon which we depend and the capacity for ecosystem-state reversal.

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