

# Comment on “Limited climatic space for alternative ecosystem states in Africa”

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Higgins et al. (1) use a species distribution model to estimate the climatic niches of 11 plant functional types across Africa. Two of these PFTs, evergreen trees and C<sub>4</sub> grasses, are then used as explanatory variables in a logistic regression model to predict savanna vs. forest occupancy in Africa. On this basis, the authors conclude that savanna-forest bistability (or Alternative Ecosystem States; AES) is highly restricted in extent and therefore irrelevant when modeling vegetation at continental scale. A corollary is that the effects of fire in regulating savanna extent are negligible. However, the logic in this study is flawed in several ways, calling into question these conclusions:

*The AfroTropTree data are not appropriate for this application.* The AfroTropTree were originally assembled to study floristics of African forests (2) and savannas (3). Later work used the dataset to classify species into savanna vs. forest types, but crucially, then mapped forest and savanna ecosystem extent using herbarium records of the same species and not the original dataset (4). The reason for this, as explicitly discussed in the original paper, is that the AfroTropTree sites are not randomly distributed across Africa but rather are selectively placed with a probable systematic bias toward forest representation (see, e.g., the absence of Dahomey gap savannas despite the inclusion of sites in the region) and spanning decades in sample dates. Different data sources with more complete spatial and coherent temporal extent would be far more appropriate for validating this work, e.g., White’s map of

vegetation (5), the historical forest extent for tropical Africa (6), and/or even a map of tree cover in major protected areas.

Regression approaches are weak evidence of climate determinism. Logistic regression was used by Higgins et al. to argue that savanna and forest are not bistable, yet qualitatively similar approaches have been used in the past to support the existence of AES (Figure 1B in (7)). Hirota et al. (7) use the same approach to argue that savanna and forest are bistable for a wide range of rainfall and that the increase in probability of forest with rainfall reflects an increase in forest *resilience*.

For the purposes of illustration, consider a logistic regression of biome identity as a function of mean annual rainfall (using data from Aleman et al. (4)). Such a model correctly classifies savannas vs. forests 83% of the time across the entire range of observations and thus performs nearly as well as the model in Higgins et al. (89% accuracy) with a single predictor and without the need for phytoclimatic transformations. This reflects the obvious importance of rainfall for biome distributions, especially at high and low rainfall. However, this classification accuracy drops precipitously over the intermediate rainfall range, where bistability is thought to influence biome distributions. Between annual rainfall of 700 and 1900mm (the bistability zone identified by Aleman et al. (4) and ~ 40% of the total African land area), classification accuracy falls to 75%. Between 1000 and 2000mm (the bistability zone identified by Staver et al. (8) and ~ 28% of the total African land area), classification accuracy falls to 72%. Finally, between 1000 and 1500mm (~ 18% of the total African land area), classification accuracy falls to 59%, which is barely better than random. The values of these thresholds are undoubtedly sensitive to the data used to estimate them (including ecosystem extent (9) and climate data (10)), so debate about the true extent of bistability is expected. However, it is nonetheless obvious that estimates of classification accuracy that reflect rainfall extremes are not strong evidence of ecosystem dynamics at intermediate rainfall.

Theoretical models predict that climate may appear to determine biome distributions even as fire changes them. In over a decade since Staver et al. (11), a body of literature has emerged putting potential savanna-forest bistability into a spatial context. Models based on reasonable assumptions can produce rich and varied behaviors, including slow cycles in ecosystem structure (12), stable vegetation mosaics (13, 14), shifting vegetation patterns (15), and more. These spatial models show that local spatial interactions (like dispersal and fire spread) can couple neighboring sites to each other, resulting in the aggregation of savanna with savanna and forest with forest.

Of particular relevance to Higgins et al. are a family of spatial models that predict that fire-vegetation feedbacks with spatial dynamics can lead to the formation of a stable biogeographic boundary between savanna and forest that is closely, although not perfectly, predicted by climate (16–19). These models show that fire can expand savanna distributions substantially, whilst stabilizing the boundary between savanna and forest at a deterministic value of rainfall that does not correspond to the maximum potential forest extent. This theoretical result suggests that, even supposing that climate were perfectly deterministic of biome distributions, it would nonetheless be incorrect to conclude (as Higgins et al. do) that forest extent is at its maximum potential.

Species distributions models can only model observed extent, not potential extent. Processes that restrict species distributions to a smaller area than their climate potential (including fire, herbivory, competition, and others) limit the utility of species distribution models for mapping potential species extent. In ecology, this is commonly referred to as the “realized” vs. “fundamental” niche (20). In this case, evergreen trees are climatically viable in a much broader range of environments than Higgins et al. predict (see, e.g., plantations (21) and evergreen “thickets” (22–24)). Similarly, C<sub>4</sub> grasses are also clearly viable in areas mapped as being unsuitable (see, e.g., pasture and C<sub>4</sub> croplands in central Africa (25), pockets of savanna in the Congo forest (26), floating grass mats in the Congo river that persist under annual burning).

Multiple other lines of evidence support extensive savanna-forest bistability. Higgins et al. also misrepresent the multiple lines of evidence in support of the extent of AES.

First, fire experiments have long provided evidence that fire is crucial for maintaining savannas where forest is present in the landscape (e.g., in patches or along rivers) and for decreasing tree cover and increasing grass cover within savannas. Higgins et al. neglect several large syntheses of fire experiments showing large and consistent fire impacts (27, 28). They do cite a few local-scale studies. For instance, a recent study of a 45-year time series of vegetation and fire in a forest-savanna mosaic of Cameroon showed that recent forest encroachment has been the result of decreasing fire frequencies (29); Higgins et al. curiously neglect clear evidence for changing fire management as a driver of landscape change and instead misuse the study as evidence that savannas in mosaic with forest are unstable. Higgins et al. also excluded sites from analyses due to “topographic effects” at sites where fire has a clear effect in shaping the locations of savanna vs. forest patches (see, e.g., photos in Figs. S4 and S5), in total discarding almost 70% of sites where their model misclassified the vegetation state, ascribing misclassifications to abiotic factors (including topography, soil types, microclimates).

Secondly, while we agree with Higgins et al. for the need to study AES dynamics over an extended temporal framework, they totally ignore the existing paleo-evidence that supports savanna-forest bistability. For instance, the African Humid Period (~14.5 to 5.5 kya) caused forest expansions in parts of eastern and western Africa that were not reversed when rainfall decreased again, indicating hysteresis, which is a hallmark of bistability (30). Some drier sites did convert to savanna during this re-aridification (~ 5 to 2 kya (31)), and interestingly these sites largely did not revert to forest during a later phase of increased rainfall in the late Holocene (32, 33), again indicative of hysteresis and the absence of simple climatically determined transitions between savanna and forest.

Finally, Higgins et al. understate the ability of global models to reproduce the effects of fire. Although dynamic global vegetation models are rarely used to explicitly examine potential savanna-forest bistability (but see (34)), models consistently demonstrate that fire has major and widespread effects on ecosystem structure (35).

Could underestimating forest extent and fire effects really save savannas? We agree with Higgins et al. that widespread tree planting and afforestation of savannas is a major threat to the biome, with limited carbon sequestration potential (36) and major biodiversity costs (37). However, their proposed interpretation has important conservation and policy downsides. First, tree planting could shift to non-native species if native species are perceived as inviable, which is not a gain; plantations of non-native

trees are already expanding, due in part to work that frames them as a natural climate solution (21, 38). More importantly, this work implies that fire management is not a crucial factor for maintaining savanna distributions. This view has resulted in well-documented and widespread degradation of native savannas via woody encroachment and forest invasion in Brazilian cerrado, Cameroonian savannas, and globally (39). To claim that fire is not vital for savanna conservation – despite overwhelming evidence to the contrary – advances neither science nor practice.

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