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We need mechanistic models to explain Alternative Ecosystem States in tropical vegetation

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In their paper "*Limited climatic space for alternative ecosystem states in Africa*" (8 June, p. 1038), Higgins *et al*. use a plant growth model applied to species distribution and climate variables, to argue that Alternative Ecosystem States (AES) have limited importance in Africa. However, their model does not account for key ecological factors in Africa such as large herbivores and fires (*1*, *2*). Their exclusion raises serious doubts about the model's validity. Higgins *et al*. emphasise how well their model predicts the distribution of forests and savannas. However there is a poor fit in the maps predicting optimal areas for several growth forms (*3*, *4*). The model failed to identify the major areas of shrub dominance in Africa, fynbos and karoo shrublands in the south-west and steppe shrublands in north-east Africa (their Figure 1). Succulents are predicted for the north African Mediterranean coast where there are none (and for large areas of southern Africa) presumably by erroneous extrapolation from succulent distribution in South Africa. Optimal 'relative climatic suitability' for C_4 grasses is predicted for the southern margins of the Sahara desert (their Figure S2) but not the vast savannas that cover most of the rest of the continent.

Higgins *et al*. argue that the maps they derived show limited potential for tree growth in areas they identified as climatically limited savannas contradicting other studies identifying large areas of mesic savannas as suitable for large-scale tree planting. However, their model fails to predict a forest-suitable environment in areas supporting large-scale commercial forestry plantations, e.g. in southern Africa (*5*). In fact, it is unknown how much of the areas they predict as savannas, and are actually savannas ("true savanna predictions"; in their Fig. 3), could sustain a forest, and would therefore be examples of AES. Higgins *et al*. gloss over additional evidence for AES including paleoecological studies of system shifts between savanna and forest, hysteresis, historical studies, remote sensing and multi-decadal fire suppression experiments, both natural and by design, in Africa and elsewhere showing major ecosystem shifts typically linked to fire suppression or addition (*6*–*10*).
We conclude that Higgins *et al*. cannot be used as a basis for interpreting alternative ecosystem states, the potential for tree planting in Africa, or whether climate and physical site factors determine forest

and savanna distribution. We suggest that the problem may lie in assuming that the distribution of species represents a fundamental niche and not a realised niche so that their apparently physiologically based model is really a rather complex correlative model following a long line of predecessors. The models lack seedling and sapling stages, widely considered to be key to whether trees can escape the flame zone and thereby exist in savannas or be restricted to forests (*11*). Fire is not included as a source of biomass loss. Nor is there any explicit consideration of shade, a major factor separating forest from savanna species (*12*). It lacks most of the fundamental mechanism to simulate a dynamic system such as African ecosystems. Exploration of the dynamic response of the model, for example to changing CO_2 from 400 ppm to 280, might help reveal its sensitivity to environmental drivers outside those used to derive physiological parameters from inverse models of contemporary plant species distributions. Process-based models based on measured physiological, and fire response traits, are more appropriate tools for exploring the potential for alternative stable states because they test what could be and are not restricted by what is (*13*–*15*)

Higgins *et al*. model contributes little to the understanding of the processes assembling African ecosystems, and cannot be taken as evidence against AES. In our changing world, we need more mechanistic and dynamic models before casting aside all evidence for fire and herbivores limiting distributions of forests (*2*).

References

1. N. Owen-Smith, *Only in Africa: The Ecology of Human Evolution* (Cambridge University Press, Cambridge, 2021).
2. W. J. Bond, *Open Ecosystems: Ecology and Evolution Beyond the Forest Edge* (Oxford University Press, 2019).
3. F. White, “The vegetation of Africa: a descriptive memoir to accompany the UNESCO/AETFAT/UNSO vegetation map of Africa by F White” (Natural Resources Research Report XX, UNESCO, Paris, France, 1983), pp. 1876–1895.
4. D. A. Keith, J. R. Ferrer-Paris, E. Nicholson, R. T. Kingsford, Eds., *IUCN Global Ecosystem Typology 2.0: descriptive profiles for biomes and ecosystem functional groups* (IUCN, International Union for Conservation of Nature, 2020).
5. Z. Du, L. Yu, J. Yang, Y. Xu, B. Chen, S. Peng, T. Zhang, H. Fu, N. Harris, P. Gong, A global map of planting years of plantations. *Sci Data*. **9**, 141 (2022).
6. L. Gillson, Evidence of a tipping point in a southern African savanna? *Ecol. Complex.* **21**, 78–86 (2015).
7. Z. S. Venter, M. D. Cramer, H. J. Hawkins, Drivers of woody plant encroachment over Africa. *Nat. Commun.* **9**, 2272 (2018).
8. J. C. Aleman, O. Blarquez, H. Elenga, J. Paillard, V. Kimpuni, G. Itoua, G. Issele, Staver A. Carla, Palaeo-trajectories of forest savannization in the southern Congo. *Biol. Lett.* **15**, 20190284 (2019).

9. J. G. Pausas, W. J. Bond, Alternative biome states in terrestrial ecosystems. *Trends Plant Sci.* **25**, 250–263 (2020).

10. H. Beckett, A. C. Staver, T. Charles-Dominique, W. J. Bond, Pathways of savannization in a mesic African savanna-forest mosaic following an extreme fire. *J. Ecol.* **110**, 902–915 (2022).

11. C. P. Osborne, T. Charles-Dominique, N. Stevens, W. J. Bond, G. Midgley, C. E. R. Lehmann, Human impacts in African savannas are mediated by plant functional traits. *New Phytol.* **220**, 10–24 (2018).

12. T. Charles-Dominique, G. F. Midgley, K. W. Tomlinson, W. J. Bond, Steal the light: shade vs fire adapted vegetation in forest–savanna mosaics. *New Phytol.* **218**, 1419–1429 (2018).

13. W. J. Bond, F. I. Woodward, G. F. Midgley, The global distribution of ecosystems in a world without fire. *New Phytol.* **165**, 525–538 (2005).

14. S. I. Higgins, S. Scheiter, Atmospheric CO2 forces abrupt vegetation shifts locally, but not globally. *Nature*. **488**, 209–212 (2012).

15. G. Lasslop, S. Hantson, S. P. Harrison, D. Bachelet, C. Burton, M. Forkel, M. Forrest, F. Li, J. R. Melton, C. Yue, S. Archibald, S. Scheiter, A. Arneth, T. Hickler, S. Sitch, Global ecosystems and fire: multi-model assessment of fire-induced tree cover and carbon storage reduction. *Global Change Biol.* **26**, 5027–5041 (2020).