

Research review

Reassessing the alternative ecosystem states proposition in the African savanna-forest domain










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Summary

Ecologists are being challenged to predict how ecosystems will respond to climate changes. According to the Multi-Colored World (MCW) hypothesis, climate impacts may not manifest because consumers such as fire and herbivory can override the influence of climate on ecosystem state. One MCW interpretation is that climate determinism fails because alternative ecosystem states (AES) are possible at some locations in climate space. We evaluated theoretical and empirical evidence for the proposition that forest and savanna are AES in Africa. We found that maps which infer where AES zones are located were contradictory. Moreover, data from longitudinal and experimental studies provide inconclusive evidence for AES. That is, although the forest-savanna AES proposition is theoretically sound, the existing evidence is not yet convincing. We conclude by making the case that the AES proposition has such fundamental consequences for designing management actions to mitigate and adapt to climate change in the savanna-forest domain that it needs a more robust evidence base before it is used to prescribe management actions.

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Introduction

In an age where the climate is changing at an unprecedented rate, it is not an exaggeration to say that the issue of whether ecosystem states can be predicted from knowledge of the climate system is of existential importance. Standard works in ecology and vegetation geography (Schimper, 1903; Walter, 1973; Whittaker, 1975; Woodward, 1987) are built on the foundation that climate is the fundamental determinant of the distribution of terrestrial ecosystems. This would suggest that the ecological forecasting research agenda involves understanding how climate and the abiotic environment determines ecosystems. A crack in this research agenda was revealed when Bond (2005) pointed out that

Whittaker's (1975) mean annual temperature, mean annual rainfall biplot suggested that climate fails to predict vegetation over vast portions of the world (see Fig. 1a). This apparent failure of climate determinism led Bond (2005) to articulate the multi-colored world (MCW) hypothesis, which proposed that factors such as predation, herbivory and fire often overwhelm the influence of climate system factors.

Many studies exploring the MCW hypothesis have interpreted it through the lens of the alternative ecosystem states (AES) hypothesis (e.g. Moncrieff *et al.*, 2014, 2016; Midgley & Bond, 2015; Pausas & Dantas, 2017; Charles-Dominique *et al.*, 2018; Pausas & Bond, 2019, 2020; Stevens *et al.*, 2022; Adie & Lawes, 2023). The AES hypothesis maintains that for a

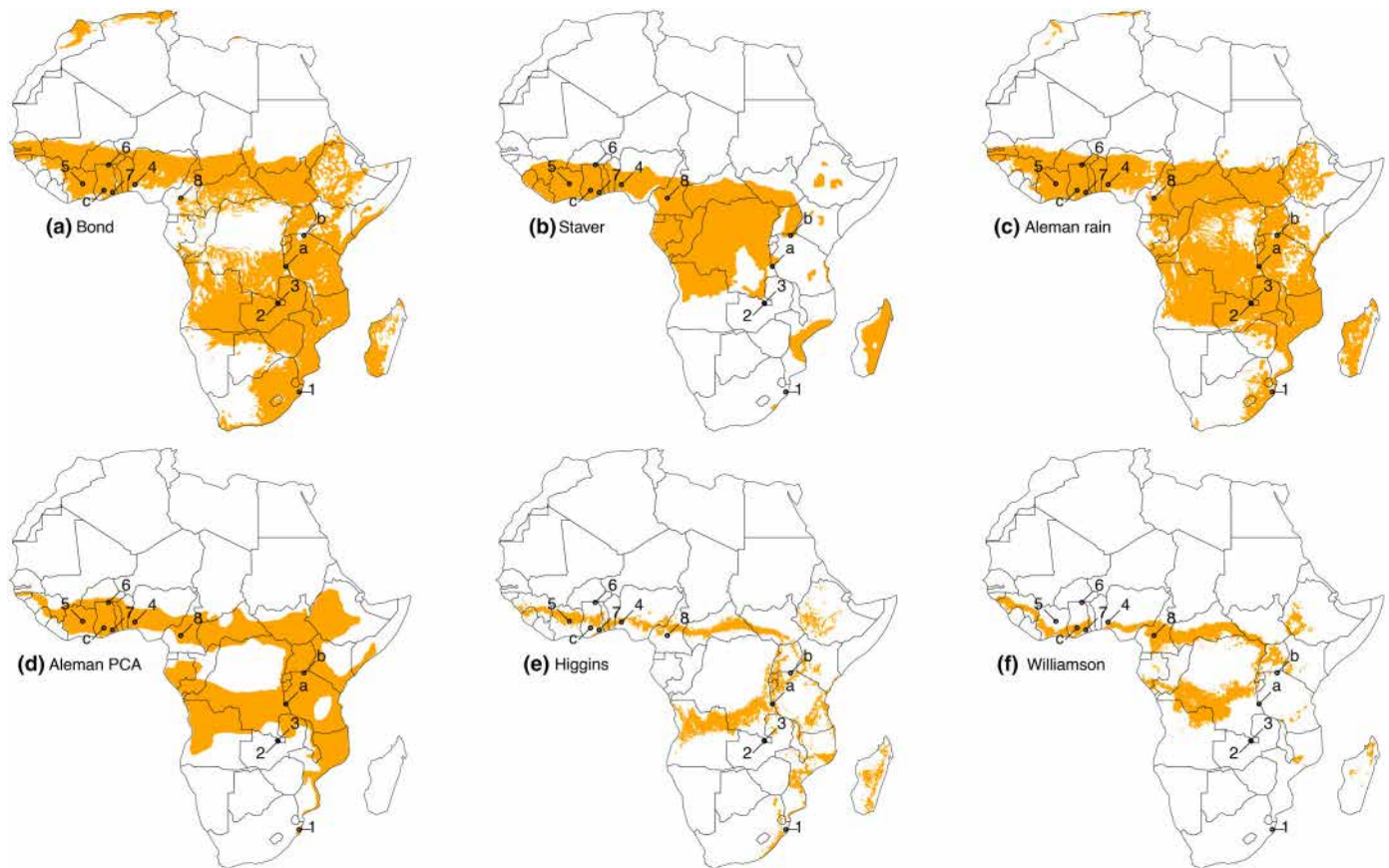


Fig. 1 Projections of uncertainty in ecosystem state. Several authors have projected into geographical space uncertainty in predictions of the ecosystem states savanna and forest in Africa. Bond's (2005) projection highlights uncertainty in the Whittaker (1975) model of biome distribution, which used mean annual rainfall and mean annual temperature to predict ecosystem state (a), Staver *et al.*'s (2011b) projection is based on bimodality in MODIS tree cover and is defined by mean annual rainfall and dry season length (for elevations below 1200 m) (b), Aleman *et al.*'s (2020) rainfall model used floristic survey data and is purely based on overlap in the mean annual rainfall range of forest and savanna (c), Aleman *et al.*'s (2020) PCA model uses the approach described in (c) but replaces the rainfall axis with a principle component axis which is defined by multiple environmental variables (d), Higgins *et al.*'s (2023) model uses the same floristic survey data as Aleman *et al.* (2020), but constructed a model based on the climatic suitability for evergreen tree growth and C4 grass growth (e), Williamson *et al.* (2024) used data from 25 000 manually classified assessments of ecosystem state to construct a model based on climatic, topographic and human-influence factors (f). Notably, (a)–(d) were interpreted by the study authors as alternative ecosystem states (AES) regions, whereas (e, f) were interpreted as zones of model prediction uncertainty within which AES may hide. The maps in (a) and (c) were reconstructed based on descriptions in the original publications and may differ from the original publications due to our usage of different climatic data products. For (b) and (d) the maps were manually digitised from the maps in the original publications and therefore may smooth over some features. The map in (d) did not consider Madagascar. For (e) and (f) the uncertainty band was assumed to cover the range where the probability of forest was greater than 0.33 and less than 0.66. Sites discussed in the text are numbered 1–8 in the order Hluhluwe–Imfolozi, Ndola, Mwekera, Olokemeji, Kokondekro, Red Volta West Forest Reserve, Kpong, Mpem-Djim National Park and three pollen core sites are labelled a to c in the order Tanganika, Victoria, Bosumtwe.

single set of external forcing factors, multiple alternative ecosystem states can arise. This definition derives from the mathematical concept of multiple alternative stable states. Mathematically, multistability is defined as a system that, for a single set of model parameters, can have more than one possible stable state; which state is realised depends entirely on the initial state of the system (Petraitis, 2013). In dynamical systems theory and ecology a variety of related terms are used to refer to this syndrome including bistability and alternative biome states. We use the term AES in this manuscript to emphasise our focus on ecosystems. Importantly, in AES systems it is positive feedback processes in the internal system dynamics, acting on some historical ecosystem state, that determine the system's equilibrium state rather than the parameters which

describe the influence of forcing variables such as climate, soils and management on the system's dynamics (see Box 1 for definitions).

The AES interpretation of the MCW hypothesis was fuelled by an influential study which used MODIS tree cover data to conclude that forest and savanna were AES throughout large portions of tropical and sub-tropical regions (Staver *et al.*, 2011b). The areas proposed to be AES zones were large (see Fig. 1b). Moreover, the projections for Africa provocatively suggested that the majority of the continent's rainforests were in AES zones (Staver *et al.*, 2011b). In parallel to this macroecological perspective, field studies were identifying the feedback mechanisms (see Box 1 for definitions of positive and negative feedbacks) that could make the ecosystem state (savanna or forest) dependent on initial conditions. Although there

Box 1 Definitions of concepts relevant to AES.

Ecosystem state, system state: The values of the (eco)system's state variables at a particular point in time.

Initial condition: The values of the system's state variables at the starting point or some reference point of the analysis or simulation.

Time zero: The specific point in time chosen as the starting or reference point for the analysis or simulation.

Initial condition dependency: The sensitivity of a dynamical system's behaviour to its initial conditions. A system is initial condition dependent when differences in the initial conditions can, over time, lead to significantly different system states.

External forcing: Factors external to the system that impact the behaviour of the system's state variables. In ecosystem models, external forcing are typically the parameters that describe the role of environmental factors such as temperature, soil moisture, soil nutrients, solar radiation, or human factors such as fire management, deforestation or other land use interventions.

Internal dynamics: The dynamical processes within the system itself. Internal dynamics are driven by the system's state variables and the positive and negative feedback relationships between them. In ecosystem models, internal dynamics typically include processes such as biomass growth, nutrient cycling, competitive and trophic interactions including fire.

Positive feedback: A combination of mechanisms in the internal dynamics of a dynamical system where a change in a state variable of the system leads to further changes that reinforce the initial change, amplifying its effects.

Negative feedback: A combination of mechanisms in the internal dynamics of a dynamical system where a change in a state variable of the system leads to further changes that oppose or counteract the initial change, dampening its effects.

Stable state: A condition where the system's state variables return to a specific value or trajectory after being perturbed, indicating that the system tends to resist external disturbances and return to its original state. In system's exhibiting multiple alternative stable states, the state variables will, after a perturbation, converge to the stable state with the strongest basin of attraction; which basin is most attractive is contingent on the position of the system state in the phase space after the perturbation.

Succession: A trajectory of ordered temporal change in the state variables that describe an ecosystem's composition and structure towards a stable ecosystem state. Internal dynamics can enhance or retard succession.

Space for time substitution: A method that uses spatial variation in ecosystem states to infer temporal trajectories of ecosystem change. Assumes that significant components of observed spatial variation are conditional on the initial ecosystem state and can thereby be attributed to the passage of time.

Alternative ecosystem states (AES): A syndrome where the existence of multiple fixed points in a dynamical system's phase space allow for qualitatively different ecosystem states to emerge due to initial condition differences.

Hysteresis: A syndrome where a dynamical system's state is dependent on its history and not on the values of the external forcing parameters, that is hysteresis is equivalent to AES. The hysteresis effect may vary depending on the direction and rate of change of the forcing factor.

Apparent AES: When differences in observed ecosystem states are erroneously attributed to differences in initial conditions, when in fact they are caused by unmeasured differences in external forcing parameters.

are variations on this theme, how these feedbacks operate was well summarised by Hoffmann *et al.* (2012): The savanna state can be maintained by a positive feedback between grass fuel and fire which prevents tree dominance even though the climate and soils can support tree growth. Analogously, the forest state can be maintained by a positive feedback between tree leaf area and fire-suppression, here high tree leaf area reduces light availability to grasses and thereby suppresses the accumulation of grass fuel. Negative feedbacks also play a role, for instance there is a negative feedback setting an upper limit to the tree leaf area. Together the field and macro-ecological perspectives have supported a master narrative that savannas and forests may be alternative ecosystem states (Bowman *et al.*, 2015).

Studies that have sought to identify the geographical distribution of AES zones have not reached a consensus on how large AES zones are, or where they are located (Fig. 1). Fig. 1 shows geolocations where different models of ecosystem state are uncertain; some authors have interpreted these zones of prediction uncertainty as AES zones. But although these zones are where AES are permitted by the model, there may also be other reasons for the prediction uncertainty (Fig. 2). Using Africa as an example, an analysis that used floristic data (Aleman *et al.*, 2020) to avoid potential bias associated with the MODIS tree cover data used by Staver *et al.* (2011b) (see Hanan *et al.*, 2014; Gerard *et al.*, 2017 for a discussion of biases associated with MODIS tree cover data) projected that the AES zones were smaller and in different locations to those reported by Staver *et al.* (2011b) (Fig. 1d). A simplified model reported in Aleman *et al.* (2020) suggested that AES zones are considerably larger than those projected by Staver *et al.* (2011b) (Fig. 1c). An analysis that used the same floristic data as in Aleman *et al.* (2020) but different environmental drivers and statistical methods suggested that AES zones are considerably smaller (Higgins *et al.*, 2023) (Fig. 1e). More recently a study that used manual classification of high resolution satellite imagery has also suggested that AES regions are geographically more restricted than previously proposed (Williamson *et al.*, 2024) (Fig. 1f).

The persistent uncertainty regarding how large savanna-forest AES zones are and where they might be located suggests that it is time to review the proposition that savanna and forest are often AES. We focus on Africa simply because it is relatively well studied in this regard and because the details of how AES works in Australian, Indian and South American savannas and forests may differ (Lehmann *et al.*, 2014; Hubau *et al.*, 2020).

Theoretical evidence for savanna-forest AES

In AES models, the state of the ecosystem can be represented by the position of a ball on a surface consisting of multiple basins, where each basin represents an ecosystem state (Fig. 3a–f, see also Beisner *et al.*, 2003). In Fig. 3 the ball's horizontal position represents the value of the model's state variable whereas the surface is determined by the parameterised model. In panels a and b only one basin exists and the system has one stable state (forest in a, savanna in b). If the surface has two basins then the initial state (position 1, panel c) of the ball determines its stable state (position 2, panel c). The ball can move to another stable state if it is perturbed sufficiently to move

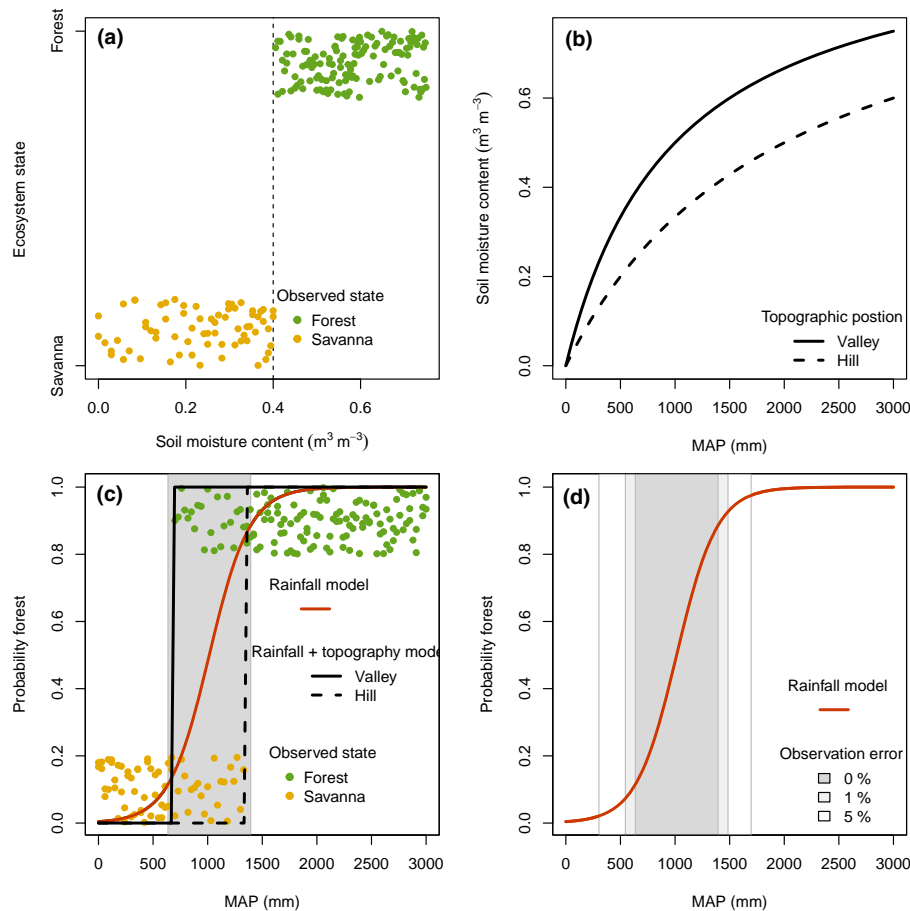


Fig. 2 Model error and observation error can lead to apparent alternative ecosystem states (AES). Various categories of uncertainty contribute to prediction uncertainty. To demonstrate this Higgins *et al.* (2023) used a simulation to show how two of these categories, model and observation uncertainty, could lead to a confounding of apparent and true AES. In this context, apparent AES is when alternative states are erroneously attributed to initial conditions when in fact they are caused by the influence of environmental forcing being incorrectly specified in the model. The simulation considers a world in which the boundary between forest and savanna can be perfectly predicted by soil moisture, at soil moisture < 0.4 the simulation prescribes savanna and at soil moisture ≥ 0.4 forest is prescribed (a). It then adds to the simulation that soil moisture increases with mean annual rainfall (MAP, mm) and that more moisture accumulates in valleys than on hilltops (b). Fitting an incomplete model that proposes that ecosystem state can be predicted from MAP, provides strong support for the notion that rainfall can predict ecosystem state (red line, c). At very low rainfall and very high rainfall the model has high predictive accuracy. However, at intermediate rainfall the predictions are uncertain (shaded area, c). In such situations one might be tempted to conclude that over a broad range of conditions that climate cannot reliably predict ecosystem state. However, the truth of this simulated example is that in addition to rainfall, topographic position (hill or valley) also influences soil moisture and thereby ecosystem state. Fitting a model that considers both rainfall and topography as factors leads to perfect prediction accuracy (black lines, c). Adding observation error to the rainfall model shown in (c), by misclassifying savanna as forest and vice versa further increases the size of the rainfall band where prediction uncertainty is high (shaded areas, d). Note that the green and orange points in (a) and (c) are plotted at randomly displaced y-axis coordinates to enhance visibility.

into the domain of attraction of the alternative state (position 3, panel d). Because the basin bottoms can have different depths, moving in one direction may require larger perturbations than moving in the other direction. Alternatively, if the parameters describing the model are modified the surface can change form, potentially allowing the system to move to an alternative state (panel e). This externally induced parameter change may be transient and the surface may revert to its previous form (panel f). It is important to note that the parameter changes illustrated in panels e and f, if they were permanent, would effectively change the system from a system capable of supporting alternative ecosystem states, to one where only a single ecosystem state is supported (i.e. the situations shown in panels a and b). Examples of changes in external

forcing parameters are changes in parameters describing rainfall, fire frequency, herbivory levels, a growth rate or how a growth rate responds to rainfall. State changes induced by changing the parameters of a model (e.g. moving from Fig. 3a to Fig. 3b) change the system and are therefore not evidence that a system supports AES. However, if such parameter changes are transient they can temporarily reshape the surface, thereby providing a mechanism for shifting the system from one state to the other, while preserving the systems capacity to support AES (Fig. 3e,f).

Fig. 3 panel g illustrates a spatial projection of the situations shown in panels a to d. Along the x-axis is an environmental forcing gradient (e.g. soil moisture availability). When the level of this environmental forcing factor (u) is below u_1 the system is always in

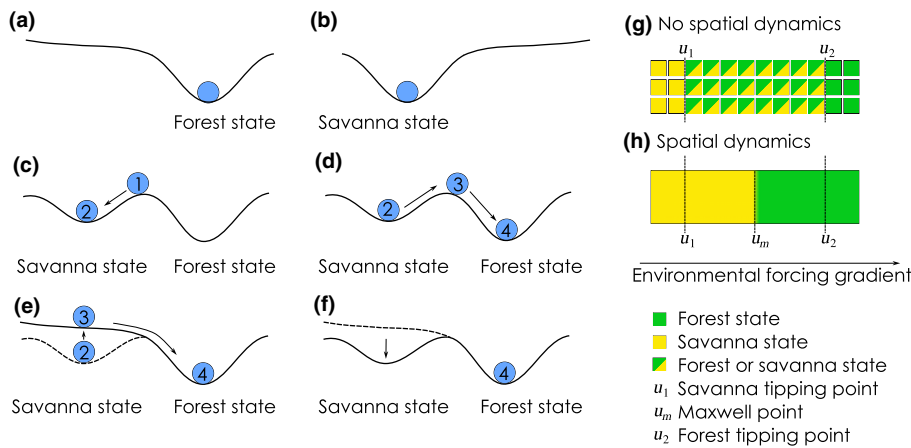


Fig. 3 Models of alternative ecosystem states (AES). In models of AES, the state of the ecosystem can be represented by the position of a ball on a surface with one or more basin, where each basin represents an ecosystem state (a–f). The main text describes how the landscape configurations shown in (a–f) can influence the system stability and transitions between ecosystem states. Panel (g) shows the model situations represented in (a–d) projected in space and panel (h) illustrates that adding spatial dynamics, such as diffusion, to an AES model can qualitatively change the model predictions such that the AES disappear.

the savanna state (as in panel b), when above u_2 it is always in the forest state (as in panel a). Between u_1 and u_2 in Fig. 3(g) alternative ecosystem states occur and which one occurs at each spatial location depends on the previous history and the past perturbation of states (e.g. Fig. 3c,d) or transient shifts in parameters (e.g. Fig. 3e,f).

A variety of non-spatial theoretical models that make reasonable ecological assumptions have demonstrated that savanna and forest can be AES (e.g. van Langevelde *et al.*, 2003; Scheiter & Higgins, 2007; Accatino *et al.*, 2010; Baudena *et al.*, 2010; Staver *et al.*, 2011a; Staver & Levin, 2012; Goel *et al.*, 2020; Djeumen *et al.*, 2021; Magnani *et al.*, 2023). Such models demonstrate that for a single set of parameters that the ecosystem states forest or savanna can emerge as stable states and which emerges depends on the initial conditions (Fig. 3). In such models that do not consider spatial processes, the geographic size of the AES zones can, when projected into geographic space, be large.

Spatial extensions of AES models add a number of important caveats, which collectively make generalization more difficult (Bastiaansen *et al.*, 2020; Rietkerk *et al.*, 2021; Banerjee *et al.*, 2023). In a simple spatial extension of a system where two alternative states are possible, diffusion can drive traveling fronts of the state variables. These traveling fronts ensure that the entire landscape can be invaded by the savanna state when $u < u_m$ and by the forest state when $u > u_m$ (Fig. 3h). Here u_m is the Maxwell point: the point on the gradient u where neither state can invade the other (van de Leemput *et al.*, 2015; Goel *et al.*, 2020; Banerjee *et al.*, 2023). That is, in such cases the AES zone shrinks down to a point in parameter space. Although it is beyond the scope of this study, it is worth emphasizing that adding spatial processes to a model can both expand and contract the size of the AES zone (see Bastiaansen *et al.*, 2022; Banerjee *et al.*, 2023).

Of course the fact that analytical and simulation models can accommodate the possibility of savanna-forest AES does not mean that we will observe them in the field. Indeed, most models of this kind have been heuristic in nature, and while they are based on reasonable ecological assumptions and the authors do attempt to relate the parameters to field observations, they have not been explicitly parameterised from field data. Djeumen *et al.* (2021) addressed this problem by restricting their model definition to measurable parameters and using available field information

to parameterise it. Using this parameterisation approach they found that savanna and forest were AES in a small area of parameter space. It remains to be seen whether other non-spatial and spatial heuristic models capable of simulating savanna and forest as AES when parameterised from field data would predict more extended or more restricted parameter domains where AES are possible. Moreover, it is important to know how the AES parameter domains project into geographic space. Parameterising models also requires specifying the initial model state, that is the values of the state variables at the model's time zero (Box 1). In practice, identifying an appropriate time zero is often difficult. For example, an observed savanna state might be the legacy of initial conditions set by drier glacial times or by more recent drought or forest harvesting events (Stott, 1988; Vamborg *et al.*, 2011). In a field experiment designed to test AES, the experiment starts at time zero and the initial state is defined by the grass and tree biomass at the start of the experiment. For example, in some experiments described in Table 1, the initial state was created by clear-cutting the trees, that is the state variable tree biomass is shifted close to zero. For these reasons, it can also be difficult to resolve whether the current state is a transient or equilibrium state and it can therefore be difficult to resolve whether the current state depends fundamentally or trivially on the previous ecosystem state (Fukami & Nakajima, 2011). Even though defining a system's state at time zero is difficult, without an agreement on the appropriate way to identify time zero, it is difficult to develop standardised tests of AES theory (see Box 1 for definitions of concepts related to time zero).

Empirical evidence for savanna-forest AES

Snap-shot observational studies are often used as evidence for AES. This type of study can be traced back to Bond's interpretation of the Whittaker (1975) biplot (Bond, 2005); Fig. 1 summarizes studies of this kind. The premise of such studies is that failure of a statistical model to reliably predict ecosystem state is evidence for AES. This premise is not necessarily correct because prediction uncertainty stems not only from initial condition uncertainty but also from model uncertainty, parameter uncertainty, process uncertainty and observation uncertainty (Dietze, 2017; Simmonds *et al.*, 2022). Demonstrating AES from such analyses would require

Table 1 A summary of fire exclusion experiments and other experiments that are cited as experimental examples of alternative ecosystem states (AES).

Attribute	Study number											
	1a	1b	2a	2b	3	4a	4b	5a	5b	6a	6b	7
Direction of transition	F-S	F-S	S-F	S-F	S-F	S-F	S-S	S-F	S-S	S-F	S-S	S-F
Initial state stable or old-growth	?	?	Y	?	?	?	?	?	?	?	?	?
Transition to alternative state induced	Y	N	Y	N	N	Y	Y	Y	Y	N	Y	Y
Alternative state verified	Y	N	N	N	–	Y	Y	Y	Y	–	Y	Y
Alternative state stable	?	–	–	–	–	?	?	?	?	–	?	?
Summary	C	I	I	I	I	C	C	C	C	I	C	C

F, forest; S, savanna; C, consistent with AES; I, inconsistent with AES. Citations: (1a) Hluhluwe–Imfolozi; Beckett *et al.* (2022). (1b) Hluhluwe–Imfolozi; Beckett *et al.* (2022). (2a) Ndola – old growth miombo; Trapnell (1959) and Chidumayo (1997). (2b) Ndola – clear cut miombo; Trapnell (1959) and Chidumayo (1997). 3. Mwekera – clear cut miombo; Chidumayo (1997). (4a) Olokemeji – secondary savanna, fire protection; Rose-Innes (1972). (4b) Olokemeji – secondary savanna, regular fire; Rose-Innes (1972). (5a) Kokondekro – secondary savanna, fire protection; Louppe *et al.* (1995). (5b) Kokondekro – secondary savanna, regular fire; Louppe *et al.* (1995). (6a) Red Volta – clear cut savanna, fire protection; Brookman-Amissah *et al.* (1980). (6b) Red Volta – clear cut savanna, regular fire; Brookman-Amissah *et al.* (1980). (7) Kpong – savanna, fire protection; Swaine *et al.* (1992).

demonstrating that prediction uncertainty stems entirely from initial condition uncertainty. We are unaware of any study that has done this. It is rather trivial to show that model uncertainty or moderate levels of observation uncertainty can sufficiently inflate prediction uncertainty to accommodate the possibility of AES (Fig. 2). It could therefore be argued that such statistical analyses of snapshots of patterns in the spatial distribution of ecosystem states are inappropriate for testing the AES proposition. However, if such a statistical model could predict ecosystem state perfectly, it would exclude the possibility of AES, which means that pursuing better models is a worthwhile endeavor (Fig. 2). Indeed, recent studies of this type have shown it is possible to develop models that greatly constrain the spatial extent of the locations where AES might be found (Fig. 1, Higgins *et al.*, 2023; Williamson *et al.*, 2024).

Box 2 provides a summary of the criteria that studies need to fulfill to be considered as evidence for AES. Essentially, it should be experimentally demonstrated that a system is in a stable state and that a pulse perturbation that mimics a natural event in extent, duration and intensity can induce a switch into an alternative state and that this alternative state can persist without additional intervention (Petraitis, 2013). This is clearly not trivial in the case of savannas and forests, simply because a functioning savanna or forest requires space and time to develop. It is therefore not surprising that Bond (2019) in his review reports that no study in the savanna-forest domain seems to fully meet these criteria. This does however not mean that there is no empirical evidence for the AES hypothesis from other ecosystems; Schröder *et al.* (2005) in their review of experimental studies from a broad range of ecosystems do provide examples of experimental evidence for AES. In the African savanna-forest domain, several studies have been cited as evidence for AES (Table 1). In Supporting Information Notes S1 we describe and evaluate whether these studies support AES using the Petraitis (2013) criteria summarized in Box 2. The locations of the study sites are shown in Fig. 1.

Our review of the evidence from these studies (Notes S1) reveals that they do not clearly support the AES proposition (Table 1), that is, we concur with previous reviews (Veenendaal *et al.*, 2018; Bond, 2019; Pausas & Bond, 2020) that no study convincingly

fulfils the Petraitis (2013) criteria. The studies were mostly not designed to test the AES hypothesis, so it is unfair to be critical of their design. Nonetheless, in the context of AES theory an important weakness relates to uncertainty regarding the ecological history of the sites, which makes it difficult to know if we are observing succession (Box 1) or a switch in ecosystem state. In the context of the criteria discussed in Box 2, this means that it is not demonstrated that alternative ecosystem states can persist at the site and it has not been demonstrated that the putative alternative ecosystem states can persist without external intervention.

Another line of empirical evidence for evaluating AES theory comes from time series reconstructed from the paleo-record. AES posits that when external forcing changes, a system in the AES domain would remain in its initial state (Fig. 3). However, AES theory also allows for state transitions in the absence of changes in external forcing so long as a perturbation of sufficient magnitude occurs (Fig. 3). That is, both state stasis and state change can be consistent with AES. An alternative external forcing hypothesis would predict that ecosystem state should only change when external forcing changes. In a study of 25 pollen core sites in a putative AES zone, Aleman *et al.* (2020) found that 16 of 25 sites showed evidence of state transitions. If these sites were in an AES zone and the spatial extent of the AES zone remained constant over the time window of the study, we would have expected to observe no transitions unless perturbations capable of inducing switches were common (Box 2). Unfortunately, without knowing the prevalence of relevant perturbations and the extent to which the relevant forcing variables changed over the observation time windows it is not possible to distinguish between the different possibilities. That is, we must conclude that patterns of change or stasis observed in vegetation proxy time series alone cannot be taken as evidence for or against AES.

Karp *et al.* (2023) address this problem by combining vegetation proxy time series with time series of external forcing proxies. Specifically, they combine vegetation, fire and rainfall proxies for 7 sites over a time window that spans the African Humid Period (AHP). Three of these sites (Tanganyika, Victoria and Bosumtwe, Fig. 1) are within the AES zone identified by Aleman *et al.* (2020).

Box 2 Evaluating evidence for AES.

At least three different types of evidence can be used to test AES: manipulative experiments, invasion tests and hysteresis diagnosis (Box 1 provides a definition of hysteresis). Of these, manipulative experiments provide the only means to produce unequivocal evidence for AES. Petraitis (2013) has summarized the criteria that such manipulative experiments need to meet:

- (1) There should be no environmental differences between the sites used in the experiment.
- (2) It should be demonstrated that alternative ecosystem states are possible at the experimental sites.
- (3) It should be demonstrated that an experimentally induced pulse disturbance that mimics a natural disturbance event in intensity, extent and duration can shift the system into an alternative ecosystem state.
- (4) The ecosystems should be self-replicating. That is, the ecosystem state induced by the pulse disturbance should persist without external intervention.

Invasion tests involve demonstrating that an ecosystem can not be invaded by the alternative ecosystem type. For example, a forest-savanna system that meets criteria 1 and 2 above should show that the forest state cannot invade the savanna ecosystem state and vice versa. In this context invasion is defined as an increase in abundance of the alternative state from low abundance.

Longitudinal observational studies construct time series through direct observation or space for time substitution (Box 1). Such studies can use the hysteresis concept (Box 1) to make inferences about AES. Under hysteresis, the system state should not respond to changes in the forcing variable. Large changes in the forcing variable that move the system out of the AES domain are needed to induce a state shift. Furthermore, when the forcing variable returns to its original level, a recovery to the initial state will not follow. A complication is that some systems may respond to a shift in the forcing variable with a temporal lag, making it difficult when analysing time series data to distinguish between hysteresis and lags. Additionally, the behaviour of other covariates can induce apparent hysteresis. A further complication is that under hysteresis a system would be expected to remain in its current state unless perturbed by a pulse disturbance event (cf. criteria 3 above). Observing a predominance of shifts from one state to the other could be explained by a predominance of a particular type of pulse disturbances inducing shifts from one state to the other (an AES explanation), but they could also be explained by directional and persistent changes in the forcing regime (a non-AES explanation).

The *a priori* prediction of AES theory is therefore that they should remain in their pre-AHP state through the AHP (Karp *et al.*, 2023). Using the criteria in Box 2 it is apparent that the evidence is mixed. Sometimes the vegetation proxies change with the climate proxies, suggesting the system is following climate forcing. In other cases the vegetation proxies remain constant in the face of changes in the climate proxies. While AES theory may be an explanation for the cases when ecosystem state does not track the rainfall proxies, it may be that the system is simply not sensitive to the rainfall proxy and more sensitive to other forcing factors such as rainfall seasonality, evaporative demand, soil fertility, atmospheric CO₂ concentrations, soil water balance and human activities. Furthermore, if the AES region is defined to lie in the rainfall band 700–1900 mm mean annual precipitation (Karp *et al.*, 2023, Fig. 1c)

and the AHP was on average 280 mm per annum wetter (Karp *et al.*, 2023), then individual sites may have moved in and out of the AES domain over the record. That is, another complication with interpreting the paleo-record is that we are unsure how the AES regions shifted in space with changes in the climate regime. Clearly, better paleo-climatic reconstructions (cf. He & Clark, 2022) are needed to interpret the paleo-evidence for AES.

External forcing and internal dynamics

A source of cross-talk in the debate on AES relates to discriminating between external forcing and internal dynamics. In Fig. 3 the surface represents the parameterized model, and the ball the system state; that is, the surface is defined by the parameters that define the external forcing and the position of the ball is defined by the internal dynamics and depends on initial conditions in the case when the model represents AES (Fig. 3c,d). That is, the shift in ecosystem state shown when moving from Fig. 3(c) to Fig. 3(d) is caused by manipulating the ecosystem state, whereas the shift in ecosystem states shown in Fig. 3(a,b) are caused by manipulating the external forcing (the model parameters, cf. Beisner *et al.*, 2003). Moreover, in Fig. 3(c,d) changes in the external forcing parameters do not induce a change in system state, that is the influence of external forcing is overwhelmed by the influence of the internal dynamics. In Fig. 3(e,f) the external forcing parameters are changed in a transient or permanent way and this induces shifts in ecosystem states.

When observing real ecosystems it is difficult to know which of the cases (3a–f) is operating, meaning it is difficult to know if external forcing or internal dynamics are driving the system. Moreover, we need to decide when designing a study whether it is appropriate to consider the effect of a factor as part of the internal dynamics, as external forcing or as a combination. Fire provides an illustrative example. Fire responds to both external forcing by the climate system and to the state variables that define the internal system dynamics. That is, we need to answer, is fire acting in response to internal state variables to keep the system state in one of the basins on the surfaces shown in Fig. 3(c,d), despite changes in external forcing? Or is fire being manipulated by factors external to the model such that the form of the surface is changing permanently or transiently (Fig. 3e,f)?

It is for this reason that we are sceptical of the value of fire manipulation experiments for testing the AES proposition: although these experiments reveal how fire impacts ecosystem properties (Pellegrini *et al.*, 2021), they do not reveal if an ecological event can reset the ecosystem such that it develops into an alternative state that persists over ecologically relevant time scales (Box 2). The same logic applies when interpreting the results of herbivore addition or removal experiments; such studies reveal that herbivores have undeniable impacts on ecosystem metrics (Staver *et al.*, 2021; Xu *et al.*, 2023), but additional information or a different experimental design (Box 2) is needed to demonstrate that herbivory is responsible for AES in the savanna-forest domain. In this context, we would recommend that authors when discussing AES seek to clarify whether an ecological factor is acting to manipulate an external forcing parameter or to

manipulate a state variable defined by the ecological processes internal to the system.

A recent longitudinal study conducted in the Mpem-Djim National Park, Cameroon (Sagang *et al.*, 2022, site 8 in Fig. 1), provides a useful example for interpreting the interplay between external forcing and internal dynamics involving fire, herbivory and human actions. This study examined four decades of savanna-forest dynamics in a forest-savanna transition area. Sagang *et al.* (2022) detected a consistent trend of savanna transitioning to forest and essentially no evidence for forest transitioning to savanna. That is, the study area appears to be in a parameter domain where ecosystem state is sensitive to the external forcing parameters (non-AES explanation) or to perturbations of the system state (AES explanation). The predominance of savanna-forest and the absence of forest-savanna transitions could be explained in different ways. An AES explanation is that a particular type of perturbation is occurring and this is causing the exclusive savanna-forest transition (the state variable perturbation shown in Fig. 3d). Another AES explanation is that a particular external forcing that is transient (the external forcing variable change shown in Fig. 3e,f) is driving the change. A non-AES explanation is that the external forcing is changing so that the system is moving from the one defined in Fig. 3(b) to that in Fig. 3(a). Sagang *et al.* (2022) provide a nuanced discussion hypothesizing that changes in how humans use the land may have shifted fire season and reduced fire frequencies. That is, it is proposed that permanent or transient changes in model parameters (Fig. 3e,f) and not changes in the state variables (Fig. 3d) that explain the observed transitions from savanna to forest.

Conclusion: why it matters

The previous sections suggest that although the theory behind the AES hypothesis is sound, empirical support for the hypothesis is equivocal. This leads us to suggest that AES may not be widespread in the African savanna-forest domain, inviting consideration of alternative interpretations of the MCW hypothesis. The MCW hypothesis essentially postulated that in extensive climatic regions knowledge about the influence of herbivory and fire are necessary to predict ecosystem state. We suggest reducing the focus on ecosystem state and using the valuable ideas in the MCW hypothesis to better understand how climate, fire, herbivory and edaphic factors interact to influence ecosystem properties (Holdo & Nippert, 2023). This changes our predictor variable from multinomial ecosystem states, to multivariate continuous ecosystem metrics. It goes without saying that the predictions of ecosystem state will be a byproduct of this focus on ecosystem metrics. When following this research agenda, focus shifts to understanding how external forcing factors (e.g. climatic variables and management actions) and internal system dynamics (e.g. trophic interactions) combine to influence the properties of ecosystems. As a consequence the driving research question becomes, how do trophic processes interact to influence ecosystem properties in different external forcing domains? Here trophic processes are broadly defined and include fire (Bowman *et al.*, 2016). This encourages us to ask how can managers

manipulate the external forcing and internal dynamics sufficiently to induce desired changes in ecosystem dynamics?

Previous influential studies (Bond, 2005, 2019; Bond *et al.*, 2005; Aleman *et al.*, 2020; Pausas & Bond, 2020) have suggested that large swathes of tropical regions are climatically suitable for forests (Fig. 1a), which implies that the forest potential of such regions represents a globally relevant nature based opportunity for climate change mitigation (Bastin *et al.*, 2019). However, recent studies have shown that savannas and forest have clearer environmental profiles (Higgins *et al.*, 2023; Williamson *et al.*, 2024). These findings should discourage attempts to establish forests (native or non-native) at sites that are climatically and edaphically unsuitable for forest. This reduced incentive to transform savannas into forest will have the upside of protecting savanna ecosystems. Moreover, it will prevent economically costly attempts to establish forests at sites where trees are doomed to succumb to one of the things (frost, inundation, drought, herbivory or fire) that many trees do not tolerate.

Whether AES regions are widespread or not in the savanna-forest domain is also highly relevant for how we manage ecosystems using fire. In an AES world, all we as managers need to do is shift the state variable, e.g. clear a forest, and then we can stand back and let feedbacks between savanna vegetation and fire maintain the savanna ecosystem state. Analogously we could suppress fire in a savanna for a defined period of time and then step back and let the resulting forest suppress fire and thereby maintain the forest ecosystem state. Conversely, in a world without AES, the manager is an agent that needs to sustain ecosystem manipulations to maintain the processes necessary for the desired ecosystem state. This view acknowledges that a more interventionist fire management may be needed to maintain a desired ecological state. This view also forces us to confront the fact that as climate change progresses, severe fire conditions will become more common, which will in turn lead to the overstepping of a boundary beyond which fire management alone becomes ineffective.

More generally, if we make errors in defining the domain in which AES are possible, we as ecologists will make incorrect global change mitigation and adaptation recommendations. In the domain of AES, forecasts of future ecosystem states are completely dependent on previous ecosystem states, which suggests that our forecasting problem is largely an initial condition problem. Outside the AES domain we shift our focus to asking what are the external forcing factors that control the boundaries between forest and savanna, how will these factors change as climate change progresses and how can managers manipulate the interplay between climate system and trophic processes to attain desired outcomes and to influence the rate at which these desired outcomes can be attained. This view not only rephrases the problem it also provides a trophic framework for analyzing the positive feedbacks and the strong non-linearities characteristic of the savanna-forest interface (Bowman *et al.*, 2016). Achieving a capacity for forecasting the future of the savanna-forest domain will also require a coherent framework for defining models and estimating their parameters in a statistical framework that facilitates the partitioning of model, parameter, initial condition and observation uncertainty (Dietze, 2017).

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






Competing interests

None declared.

Author contributions

SIH wrote the first draft of the manuscript. SB, MB, DMJSB, TC, PC, LMK, RBO'H, GJW contributed to improving the manuscript.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Notes S1 Review of seven field studies that have been interpreted as evidence for AES in the Africa savanna-forest domain.

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