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The Global Extent and Determinants of Savanna and Forest as Alternative Biome States

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Theoretically, fire–tree cover feedbacks can maintain savanna and forest as alternative stable states. However, the global extent of fire-driven discontinuities in tree cover is unknown, especially accounting for seasonality and soils. We use tree cover, climate, fire, and soils data sets to show that tree cover is globally discontinuous. Climate influences tree cover globally but, at intermediate rainfall (1000 to 2500 millimeters) with mild seasonality (less than 7 months), tree cover is bimodal, and only fire differentiates between savanna and forest. These may be alternative states over large areas, including parts of Amazonia and the Congo. Changes in biome distributions, whether at the cost of savanna (due to fragmentation) or forest (due to climate), will be neither smooth nor easily reversible.

Fire is a strong predictor of the global distribution of the savanna biome (1, 2) and of tree cover within savannas (3–5). Experimental work shows that fire can impact tree cover and can maintain savanna where climate can support forest (6–8). Meanwhile, fire spread depends on a continuous grass layer, to which tree cover acts as a barrier; **tree cover has little effect on fire spread, frequency, or size until it reaches a threshold (45 to 50%) at which fire can no longer spread (1, 9, 10).** Thus, fire can theoretically act as a **positive feedback within savannas that maintains open canopies,** which, in turn, promote fire spread. These effects depend on climatic context. In Africa, low rainfall deterministically results in savanna and high rainfall in forest (1, 2). At intermediate rainfall, forests and savannas both persist and tree cover is bimodal, indicating that savanna is a distinct and possibly alternative stable state to forest (1).

Fire feedbacks provide a plausible mechanism to explain observed bimodalities in tree cover, but questions remain as to how globally widespread they are and about potential alternative drivers. The prevailing wisdom is that, whereas Africa is characterized by variable, bimodal tree cover at intermediate rainfall, tree cover in Australia is more tightly constrained by rainfall (8, 11). Australian savannas may have a unique ecology, driven by, for example, the distinct physiology of eucalypts (8). Alternatively, determinants of savanna distributions may be poorly understood. Little is known about tree-cover distributions in South America, although constraints appear to be less deterministic than in Australia (2).

The universality of fire feedbacks as primary drivers of the distribution of savanna in areas of intermediate rainfall is also uncertain. Two major additional factors—soils and rainfall seasonality—may also have strong impacts, either directly on

tree cover or on the potential distribution of fire effects. Locally, big differences in soil texture can have substantial effects on tree cover (11, 12), whereas at the continental scale, soil texture and fertility have limited effects on tree cover (2, 3, 5). Marked rainfall seasonality is also associated with savannas and tends to decrease tree cover in the tropics/subtropics [(2, 13), but see (4)], although continental analyses have not yet identified seasonality as driving bimodalities in tree

cover. Seasonality, although globally constrained by total rainfall, varies substantially, as exemplified in the extreme by the monsoon in Australia. If seasonality does affect tree cover, it may profoundly affect savanna and forest distributions. Mechanisms are largely unknown, but the effects of seasonality have been attributed to effects on tree physiology and/or fire spread (2). Direct physiological limitations to tree growth (2, 14) might prevent forest establishment in seasonal environments, whereas indirect positive effects of long dry seasons on the likelihood of fire spread (15) could limit either savannas to seasonal environments (if seasonality is necessary for fire spread) or forests to aseasonal ones (if seasonality makes fire so likely that forest cannot persist).

A comprehensive understanding of tree-cover distributions and of the potential for fire feedbacks to maintain savanna and forest as distinct states requires more extensive, global evaluation. Incorporating not only tree cover, mean annual rainfall, and fire frequency, but also rainfall seasonality and soils into this analysis would provide additional insights into whether fire is a primary driver of biome distributions worldwide. We analyzed spatial patterns of tree cover [from the Moderate Resolution Imaging Spectroradiometer Satellite (MODIS)] with respect to rainfall [from the Tropical Rainfall Measuring

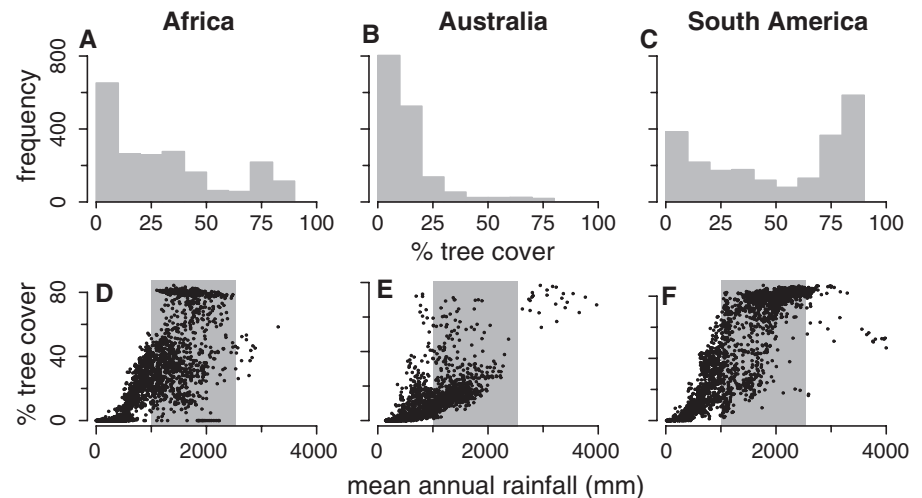


Fig. 1. Frequency distribution of tree cover (A to C) and relation of tree cover to mean annual rainfall (D to F). Gray zones denote intermediate rainfall [1000- to 2500-mm mean annual rainfall (MAR)].

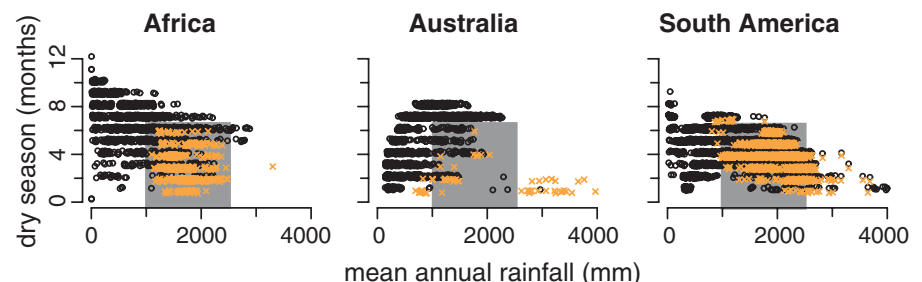


Fig. 2. Dry season length versus mean annual rainfall for areas with forest (>55% tree cover, yellow crosses) and savanna (<=55% tree cover, black circles). Gray zones denote intermediate rainfall (1000- to 2500-mm MAR) with mild seasonality (<7 months).

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Mission (TRMM)], rainfall seasonality (from TRMM), soil texture (from the Food and Agriculture Organization's Harmonized World Soils Database), and fire frequency (from MODIS), using satellite-derived data sets with complete spatial coverage of tropical and subtropical Africa, Australia and Southeast Asian islands, and South America (16). These data permit evaluations of not only the global prevalence of bimodalities in tree cover but also the extent to which fire, versus climatic and edaphic factors, is globally responsible for differentiating savanna from forest.

Herbivory, both grazing and browsing, may also play a role in shaping tree cover at the continental scale. We have largely excluded systems where the impacts of modern humans and domesticated grazers are intensive by excluding cropland and converted pasture (16). However, experimental and observational work has demonstrated that wild herbivores can be direct primary drivers of local tree cover (17, 18) and can even influence characteristic fire regimes (19). An appropriate global herbivory data set would provide a critical tool for evaluating the global relevance of those impacts.

Tree cover across sub-Saharan Africa and South America was distinctly bimodal, with an abundance of low (<50%) and high tree cover (>60% in Africa and >55% in South America).

Intermediate tree cover between 50% and 55 to 60% was scarce (Fig. 1, A and C). Mean annual rainfall was strongly related to tree cover on all continents (table S1). In Africa and South America, tree cover increased predictably with increasing rainfall until 1000 mm, when a closed canopy became possible (1). At this point, bimodalities in tree cover appeared (Fig. 1, D and F, and fig. S1). The maximum rainfall at which savanna persisted was difficult to define in Africa because areas with high rainfall were uncommon, but South American data suggest that savannas persisted up to rainfall of 2500 mm (fig. S1). High rainfall (>2500 mm) deterministically resulted in closed canopies. Meanwhile, in Australia, tree-cover patterns were not bimodal, not because intermediate tree cover was abundant but because high tree cover was scarce, and tree cover increased more predictably with rainfall (Fig. 1, B and E). At intermediate rainfall, where both savanna and forest occurred on other continents, Australia was dominated by savanna (8, 11). Either the Australian flora has different environmental constraints, or some other factor prevented forest occurrence.

Adding estimates of seasonality improved predictions of tree cover (table S1). Globally, forest (>55% tree cover) only occurred where dry seasons were shorter than ~7 months (and rainfall >1000 mm) (Fig. 2 and fig. S1). This suggests

that long dry seasons prevent the establishment of forests and act as a rigid limitation on global tree cover, although this large-scale correlative approach can offer no insights into mechanism. It also severely limits the extent of forest in Australia; aseasonal to mildly seasonal environments were common in the 1000- to 2500-mm rainfall range on other continents, but these climatic conditions did not occur in Australia. Geographical patterns of rainfall and seasonality are largely driven by the prevalence of the monsoon in northern Australia. Monsoonal rainfall is characterized by heavy precipitation during only a few months of the year, resulting in intermediate rainfall systems with severe rainfall seasonality. Thus, differences in tree-cover patterns and their relation to rainfall in Australia were largely explained by differences in geography, rather than by intrinsic continental differences in the Australian ecology (table S1). The Australian example highlights the pivotal role that extreme seasonality plays in determining the global extent of savanna and forest, but the climatic processes that shape tree cover appear to be global.

Although strong seasonality constrained forest distributions, the data showed little indication that mild seasonality constrained savanna occurrence. Savannas occurred in areas with rainfall of up to 2500 mm, regardless of dry season length, although savannas occurred only rarely in African areas with dry seasons shorter than 2 months (Fig. 2 and fig. S1) (2). This suggests that long dry seasons are unnecessary for savanna persistence. The result is a climate envelope, with intermediate rainfall and mild seasonality, in which both savanna and forest are common.

As in Africa (1), fire was a powerful predictor of tree cover (table S1) and strongly differentiated between savanna and forest within the climate envelope in which either could persist (Fig. 3 and table S1). On all three continents, fire was ubiquitously present in savanna, and forest occurred more commonly where fires were absent. However, patterns were weaker in South America, where fire occurred in forests more frequently. Soil texture (like seasonality) did not distinguish between areas with high versus low tree cover at

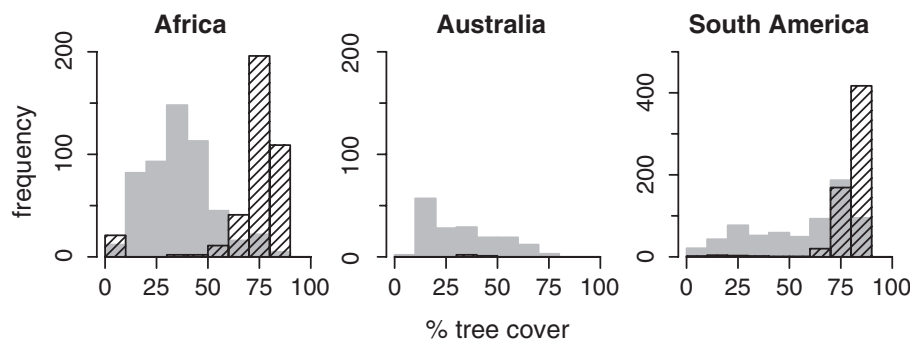
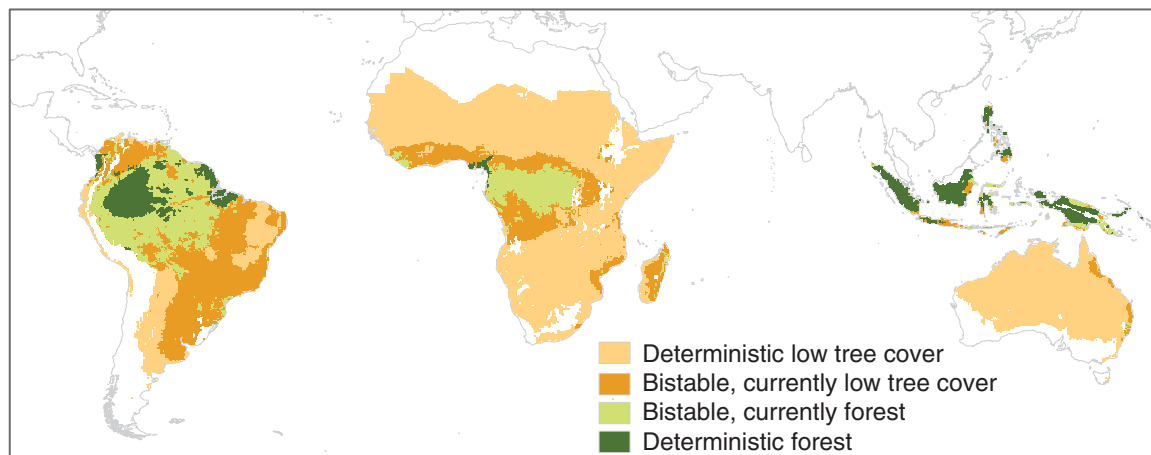


Fig. 3. Frequency distributions of tree cover in areas of intermediate rainfall (1000- to 2500-mm MAR) and mild seasonality (dry season <7 months), with fire present (gray bars) and with fire absent (hashed black bars).

Fig. 4. Distributions of biome types across sub-Saharan Africa, South America, and Southeast Asia/Australia. Biome types are defined as areas where climate (i) deterministically supports low tree cover (low rainfall, high seasonality); (ii) supports biome bistability (intermediate rainfall, mild seasonality), currently savanna; (iii) supports biome bistability, currently forest; and (iv) deterministically supports forest (high rainfall).



intermediate rainfall (fig. S2), although it was weakly predictive of tree cover (table S1). It is possible that global soils data sets are insufficiently accurate or fine-scaled, but this analysis suggests that soils do not provide an alternative mechanism for explaining global bimodalities in tree cover.

Patterns of fire, tree cover, and climate are consistent with the idea that fire can function in savanna systems as a positive feedback, wherein fire suppresses tree cover (6–8) and low tree cover promotes fire spread (1, 9, 10). This feedback affects observed tree cover patterns by expanding the range of savanna beyond areas with climates that directly limit tree cover and by maintaining the bimodalities that define savanna and forest as distinct states. However, the not-infrequent incidence of fires in high-tree-cover areas of South America suggests that some dynamic change between states may be possible. Under hot, dry conditions, forest litter can carry fires; forests have only a limited capacity to recuperate from such events (20, 21). These South American forests may be more subject to an ongoing process of encroachment of fire and savanna than are African forests.

The global impacts of these fire feedbacks on savanna and forest distributions are extensive (Fig. 4). If savanna and forest are alternative stable states over large parts of their range, as we argue, explicit considerations of transitions between the two are fundamental to understanding historical and future changes in biome distributions globally. C₄ grass evolution and the global expansion of savanna occurred during the Miocene, a period marked not only by aridity but also by increased rainfall seasonality (22). Paleoeological work suggests that contemporary savannas occurring in areas now wet enough to support forest were probably established during drier periods in Earth's history (23), in line with the idea that fire feedbacks promote the persistence of historical biome distributions.

Ongoing human-driven global change is likely to have major impacts on those distributions for a variety of reasons. Historical biome distributions were certainly affected by humans in some areas (24, 25), but modern human activities are much more extensive and intensive. Fire exclusion experiments (6–8) and documentation of forest encroachment from around the world (26, 27) provide evidence that changing burning practices and patterns through landscape fragmentation and management policy have resulted in widespread encroachment of forest into savanna. The weakening of the monsoon could compound these effects (28). Meanwhile, recent work has suggested that global climate change could put Amazonia at risk of severe drying (29) and that increased fire risk could compound these effects (30, 31), potentially resulting in widespread transitions from forest to savanna. Depending on climatic context, massive areas of South America and possibly of Africa that are currently characterized by savanna and forest are potentially at risk for changes in biome state (Fig. 4). Those changes, whether at the cost of savanna or forest, are unlikely to be smooth or easily reversible.

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Supporting Online Material

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Materials and Methods
Figs. S1 and S2
Table S1
References (32–37)

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Global Resilience of Tropical Forest and Savanna to Critical Transitions

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It has been suggested that tropical forest and savanna could represent alternative stable states, implying critical transitions at tipping points in response to altered climate or other drivers. So far, evidence for this idea has remained elusive, and integrated climate models assume smooth vegetation responses. We analyzed data on the distribution of tree cover in Africa, Australia, and South America to reveal strong evidence for the existence of three distinct attractors: forest, savanna, and a treeless state. Empirical reconstruction of the basins of attraction indicates that the resilience of the states varies in a universal way with precipitation. These results allow the identification of regions where forest or savanna may most easily tip into an alternative state, and they pave the way to a new generation of coupled climate models.

Tree cover is one of the defining variables of landscapes, their ecological functioning, and their impact on climate. Despite insights into the effects of resource availability

and disturbances on tree growth and survival (1–4), our understanding of the mechanisms determining global patterns of tree cover remains fragmented. A major question is whether tree

cover will respond smoothly to climatic change and other stressors (5) or exhibit sharp transitions between contrasting stable states at tipping points (6). In some regions, forest, savanna, and treeless (barren or grassy) states have been suggested to represent alternative attractors (7–9). However, the case for multiple stable states of tree cover is largely based on models and on local observations of sharp transitions (6–9). Systematic studies of tree-cover distributions could help distinguish between hypotheses (1) but have been largely restricted to particular continents or biome types (4–6, 10, 11). To explore whether global patterns of tree abundance suggest gradual responses or, rather, alternative stable states, we

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