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Comment on “Global Resilience of Tropical Forest and Savanna to Critical Transitions”

Zak Ratajczak* and Jesse B. Nippert

Hirota *et al.* (Reports, 14 October 2011, p. 232) used spatial data to show that grasslands, savannas, and forests represent opposing stable states. Reanalyzing their data and drawing from temporal studies, we argue that spatial analyses underestimate the bistability of grasslands and savannas due to limitations of substituting space for time. We propose that temporal and spatial data are needed to predict critical transitions between grasslands and savannas.

Determining the bistability of tree cover is critical to forecasting how terrestrial ecosystems will respond to global change. Using spatial satellite data, Hirota *et al.* (1) found that tree cover in the tropics and subtropics is distinctly trimodal: Areas with a tree cover of 0 to 5% (grassland), 10 to 50% (savanna), or 60 to 80% (forest) predominate, whereas ecosystems with a tree cover of ~5 to 10% (grassland/savanna intermediate) and ~50 to 60% (savanna/forest intermediate) are comparatively rare. The authors propose that the frequency of these tree-cover ranges is proportional to stability and, thus, low-frequency ranges of tree cover constitute unstable intermediates situated between high-frequency stable states. These spatial analyses can reach unparalleled levels of replication but are limited by an inability to distinguish between environmental variability and error due to substituting space for time. In this comment, we test assumptions of spatial analyses by reanalyzing data from Hirota *et al.* (1) to determine the frequency of unstable states. Our results suggest that spatial techniques accurately capture savanna-forest bistability but underestimate the bistability of grasslands and savannas.

Spatial analyses of bistability ultimately seek to quantify temporal processes. Even if all patches of vegetation are strictly bistable, patches with an “unstable” level of tree cover occur as patches transition from one stable state to another. In a given area, the frequency of “unstable intermediates” will be greater when (i) state changes occur slowly; (ii) state changes occur frequently; and (iii) patches do not conform to stable-state dynamics and exist as otherwise unstable levels of tree cover. The first two factors are confounding and will make unstable intermediates appear stable across space, even if they are unstable across time. Differentiating these transitional patches from non-bistable patches is impossible with temporally limited satellite data.

Division of Biology, Kansas State University, 116 Ackert Hall, Manhattan, KS 66506, USA.

*To whom correspondence should be addressed. E-mail: zarata@ksu.edu

To test the potential influence of confounding factors, we reanalyzed frequency diagrams of tree cover from Hirota *et al.* (1), reporting the frequency of unstable intermediates as discrete states, instead of including them as part of the savanna state. We used the same tree-cover classes as (1) because a limited number of sites were used to calibrate low tree cover of satellite data (2), making narrower tree-cover classes inappropriate. However, we note that using narrower tree-cover classes results in similar, if not more dramatic, results than those reported below [figure S1 in (1)].

Along a precipitation gradient, the frequency of both unstable intermediate types reaches their

peak magnitude when the proportion of two opposing stable states is equal (Fig. 1). Peaks probably occur at these junctures because the attraction to any one stable state is not particularly strong, making the system more response to internal and external variation, and the unstable intermediates slightly more stable than usual.

More surprisingly, we found that the grassland-savanna intermediate is actually common at some levels of precipitation (Fig. 1). The grassland-savanna intermediate reaches a ~13.5% frequency for both 600 and 900 mm precipitation per year, which is 30% of either stable state and equivalent to 2000 km² (1). This frequency is impressive considering that the grassland/savanna intermediate only encompasses a 5% tree cover range, compared with an average range of 25% for stable states and a 10% range for the savanna/forest intermediate. In contrast, the savanna/forest intermediate peaks for just one value of mean annual precipitation (MAP) and reaches a 7% frequency (i.e., 15% as common as the opposing savanna/forest states).

The low frequency of the savanna-forest intermediate suggests that savannas and forests are highly bistable and that state shifts could occur rapidly in low-resilience areas identified by Hirota *et al.* (1). The high frequency of the grassland/savanna intermediate could indicate that grasslands and savannas are less bistable but several lines of evidence suggest that this over-representation is due to slow transition rates in semiarid ecosystems (600 mm

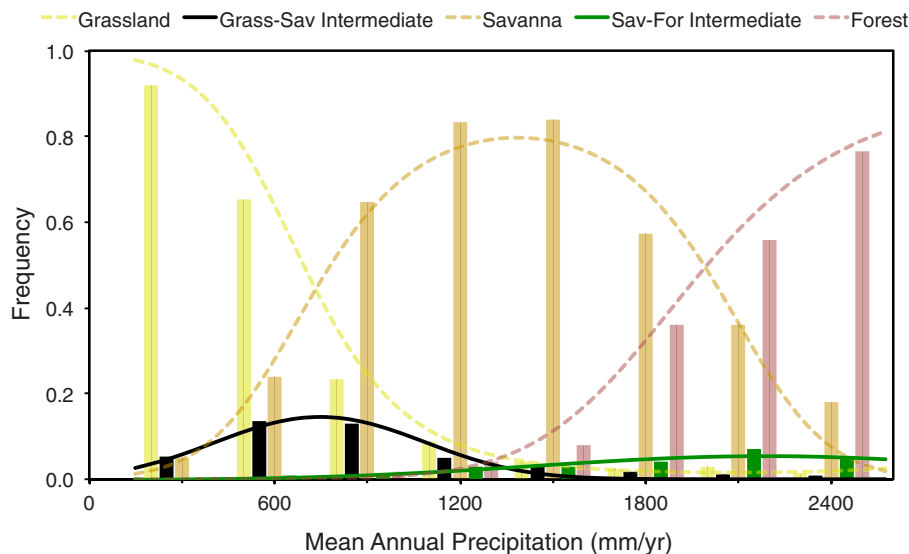


Fig. 1. The frequency of unstable states: grassland/savanna intermediate (black) and savanna/forest intermediate (green), compared with the frequency of stable states: treeless (yellow), savanna (orange), and forest (red). Following Hirota *et al.* (1), the grassland/savanna intermediate is all areas with a tree cover of 5 to 10%, the savanna/forest intermediate is 50 to 60%, the grassland state is 0 to 5%, the savanna state is 10 to 50%, and the forest state is 60 to 80%. Even though the unstable range for savanna/forest is smaller for some continents (e.g., 55 to 60%), we used this wider range of 50 to 60% because the results presented by (1) consider all continents together. Thus, the frequency of the savanna/forest intermediate should be considered to be an overestimate. Curves are fit to frequency diagrams using the same logistic regression model as Hirota and colleagues (1). Data encompass the tropics and subtropics of Africa, Australia, and South America, excluding mountainous and developed areas.

Table 1. A summary of existing fine-scale studies on grassland/savanna transitions over time.

Country	MAP (mm)	Transition type	Min. transition time (years)	Max. transition time (years)	Min. time-step (years)*	Transition mechanism	Woody plant type	Ref.†
North America	300	Grassland→Savanna	5	37	5	Soil feedbacks	Shrubs	(12)
North America	600	Savanna→Grassland	2	>2	2	Acute drought	Trees	(14)
North America	635	Savanna→Grassland	5	>5	5	Fire/soil feedbacks	Trees	(11)
Swaziland	675	Grassland→Savanna	8	50	8	Grazing/fire manipulation	Shrubs	(10)
Botswana	680	Grassland→Savanna	3	—	3	—	Trees	(15)
North America	850	Grassland→Savanna	2	—	1	Fire feedbacks	Tall shrubs	(9)

*Minimum time-step refers to the minimum number of years between temporal samplings. This variable is included so that minimum transition rates can be compared to the minimum transition rates detectable by each study. †We identified studies using the Thomson Reuters Web of Knowledge (wokinfo.com) and searching for “tree cover” time. We included only studies with reasonably small time-steps between sampling and excluded areas where the grassland state was dominated by C₄ grasses (the dominant type of grasses in most tropical and subtropical grasslands).

precipitation per year) and frequent state transitions in mesic ecosystems (900 mm precipitation per year).

In semiarid regions, population growth rates, especially for trees and shrubs, should be limited by water availability (1, 3–5). Likewise, the primary feedback mechanism responsible for semiarid state shifts (changes in soil properties) can take decades to act but creates highly stable states in the process (6). Together, these factors should make semiarid state shifts less frequent, but slow when they occur.

In mesic areas, grassland/savanna transitions should occur quickly because population growth is less water-limited (1, 3–5) and, along with savanna/forest transitions, these transitions are almost exclusively facilitated by fire (3, 5, 7). Fire feedbacks have an almost immediate effect and are more easily reversed (3, 8, 9), which should theoretically lead to quicker, but more frequent, state shifts. Indeed, dramatic tree-cover changes have occurred in Africa and North America after just 10 to 20 years of fire manipulation (3, 9, 10). This re-

silience is qualitatively lower than that of semiarid ecosystems, which can withstand several decades of exogenous forcing before undergoing a state change [e.g., (11, 12)].

The limited number of temporal tree-cover records supports our hypothesis that grassland/savanna transitions occur slowly in drier ecosystems (Table 1). For example, it takes ~35 years for desert grassland to increase from 5 to 10% shrub cover (12), whereas the fire-driven transition of wetter tallgrass prairie to savanna can occur in 2 years (9). Temporal studies also support the ideas that grasslands and savannas are opposing stable states and that 5 to 10% tree cover is also an unstable ecosystem state across space (1) and time (Table 1). In both tallgrass prairie of North America and savanna of southern Africa, the cover of tall shrubs increases slowly when the system is within 0 to 5% cover, but increases rapidly and consistently when the system is between 5 and 10% cover (9, 10).

Spatial data and novel techniques [e.g., (1, 7, 13)] can greatly expand the understanding of tree-cover stable states and identify areas that are

highly susceptible to critical transitions. We argue that these techniques are appropriate for savanna-forest transitions but that temporal studies are needed to properly quantify grassland-savanna bistability and predict how these ecosystems will respond to global change (Fig. 1, Table 1). It will be 10 to 20 years before Moderate-Resolution Imaging Spectroradiometer (MODIS) data can provide such temporal records; therefore, identifying existing records is crucial to understanding and predicting often-catastrophic tree-cover state shifts in grasslands and savannas.

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