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

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Ratajczak and Nippert note that transient states between treeless and savanna states are more common than between savanna and forest, and suggest that this can be explained by a slower rate of change in the intermediate conditions at drier sites. We show that probability distributions of tree cover rather reflect the interplay between intrinsic rates of change and perturbation regimes.

Although the concept of a stable state is a useful abstraction, fluctuations in the environment and perturbations prevent ecosystems from being in a stationary stable state. Our approach to reconstruct the alternative states and their basins of attraction (1) is based on the idea that the probability distribution of states reflects the balance of such stochasticity with the tendency to return to underlying attractors.

To illustrate this, we simulate dynamics of a simple model with alternative stable states, subject to stochastic forcing (Fig. 1). The system tends to be farther away from the equilibrium if its dynamics are slower (Fig. 1B) but also if the level of stochastic forcing is higher (Fig. 1D). Although it seems plausible that the transition from a treeless state to savanna is slow, one cannot directly deduce that from the stability landscapes. Also, the results from six (mostly nontropical) studies on treeless-savanna transitions summarized in table 1 of Ratajczak and Nippert (2) are too variable to infer the suggested relationship between rainfall and rates of change. This is not surprising in view of the likely role of factors such as initial tree cover, grazing, soils, and other factors that will differ between the cases.

We do not agree that our substitution of space for time would be problematic for reconstructing stability landscapes. As sampled points from satellite images can be considered snapshots from different time series, the theory, albeit originally developed for time series (3), still holds. Although we fully agree that there is an urgent need for long-term research, time series are certainly no panacea when it comes to inferring the existence of multiple attractors (4). Controlled field

experiments are better in this sense but are not easy to realize at relevant scales of time and space. Unraveling the stability properties and their gov-

erning mechanisms in such large complex systems will inevitably require a multifaceted approach (5), and the potential analysis is a modest but useful addition to the toolbox we have.

Importantly, the frequency of intermediate states does not imply that bistability would be underestimated, as suggested by Ratajczak and Nippert. As the results in Fig. 1 illustrate, rather than a problem, slowness of transients and stochasticity are actually a prerequisite for detecting basins of attraction. Obviously, there is a limit to that, in the sense that attraction basins are no longer found if stochasticity overwhelms the rates of return to underlying attractors. However, in such situations, the relevance of alternative attractors is questionable. The elegance of the potential analysis is that the results directly reflect the interplay between stochasticity and determinism that shapes the dynamics of ecosystems in nature. The fact that we find three distinct modes in the frequency distributions of tropical tree cover indicates that alternative attractors are

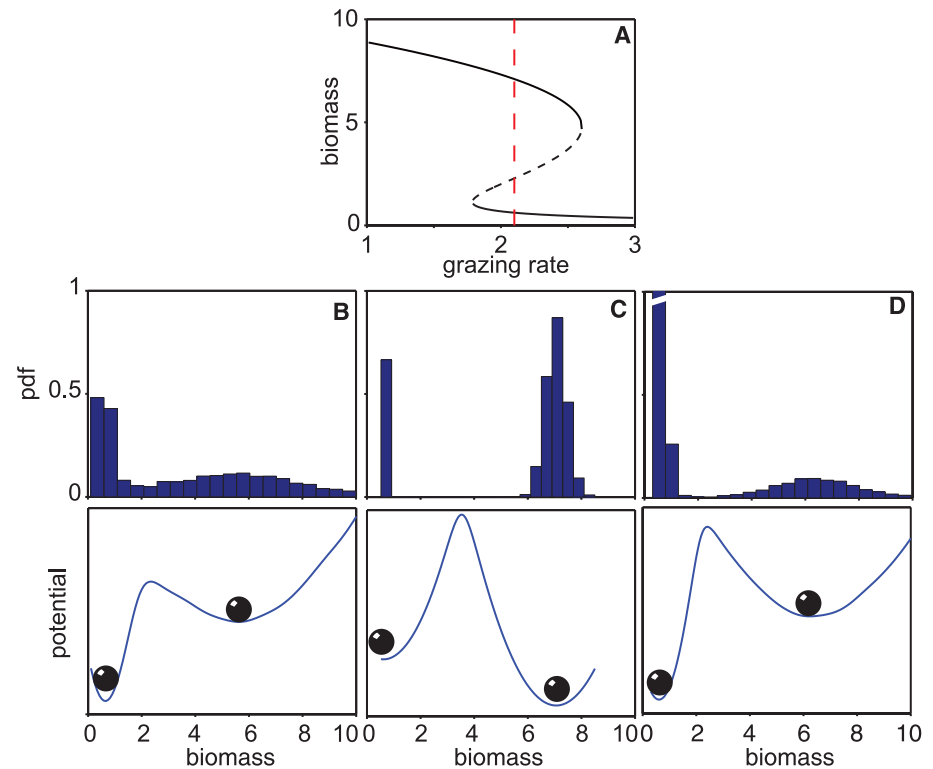


Fig. 1. The effect of the speed of change and the noise level to the occurrence of transient states in a simple bistable model. We use a stochastic version of a classical model of an exploited population (6)

(N): $dN = \gamma \left(rN \left(1 - \frac{N}{K} \right) - c \frac{N^2}{H^2 + N^2} \right) dt + \epsilon N dW$, where r is the growth rate, K the carrying capacity, c the maximum grazing rate, H the half-saturation of the Holling type II functional response, W a normally distributed Wiener process, and the scaling factor γ is used to tune the slowness of the system. To obtain snapshots of this model in time, we drew 1000 random initial conditions (between 0 and 10) and ran the model for 1100 steps. The first 100 steps were discarded, and after that, for each 100 steps one value was saved. We analyzed these values using potential analysis (1, 3). The nonstochastic version of the model can have two alternative stable states over a range of conditions (A). The red dashed line indicates the used grazing rate. The probability density function (pdf) and the estimated potentials (3) are calculated for (B) a slow system ($\gamma = 0.03$); (C) the default conditions ($\gamma = 1$; $c = 2.1$; $H = 1$; $K = 10$; $r = 1$; and $\epsilon = 0.05$) [the bandwidth of the kernel distribution was twice the default value (3) to get a continuous potential]; and (D) a highly stochastic system $\epsilon = 0.2$.

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sufficiently pronounced to dominate dynamics despite stochasticity and slow transients.

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