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TECHNICAL ADVANCE

Tipping points in tropical tree cover: linking theory to data

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Abstract

It has recently been found that the frequency distribution of remotely sensed tree cover in the tropics has three distinct modes, which seem to correspond to forest, savanna, and treeless states. This pattern has been suggested to imply that these states represent alternative attractors, and that the response of these systems to climate change would be characterized by critical transitions and hysteresis. Here, we show how this inference is contingent upon mechanisms at play. We present a simple dynamical model that can generate three alternative tree cover states (forest, savanna, and a treeless state), based on known mechanisms, and use this model to simulate patterns of tree cover under different scenarios. We use these synthetic data to show that the hysteresis inferred from remotely sensed tree cover patterns will be inflated by spatial heterogeneity of environmental conditions. On the other hand, we show that the hysteresis inferred from satellite data may actually underestimate real hysteresis in response to climate change if there exists a positive feedback between regional tree cover and precipitation. Our results also indicate that such positive feedback between vegetation and climate should cause direct shifts between forest and a treeless state (rather than through an intermediate savanna state) to become more likely. Finally, we show how directionality of historical change in conditions may bias the observed relationship between tree cover and environmental conditions.

Keywords: alternative stable states, climate vegetation feedback, remote sensing, savanna, simple model, tropical forests

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Introduction

Remotely sensed tree cover distributions in the tropics show three distinct modes: forest, savanna, and a treeless state, which have been suggested to represent alternative stable states (Hirota *et al.*, 2011; Staver *et al.*, 2011). Although there is no coherent theory to explain the complex relation among three alternative tree cover states and precipitation, much work has been done on the transitions between savanna and forest, and between savanna and treeless states. Bistability between savanna and forest is thought to be mainly driven by fire (Cochrane *et al.*, 1999; Bond, 2008; Staver *et al.*, 2011; Hoffmann *et al.*, 2012; Staver & Levin, 2012). Wildfires can keep the savannas open but once a critical tree cover has been reached, the suppression of grass fuels reduces fire occurrence and the extent of burnt areas (Liedloff & Cook, 2007; Archibald *et al.*, 2009; Warman & Moles, 2009). In addition to tree density, also precipitation plays a role in the occurrence of fires. Under very wet conditions, fires are rare and even when triggered they are not sufficiently intense to damage trees; on the other hand, under arid to semiarid conditions, tree cover is mostly limited by water supplies and less affected by fires (Bond *et al.*, 2005; Higgins *et al.*, 2007; Archibald *et al.*, 2009). Transitions to entirely treeless conditions have been described mostly in dry climates where a treeless state can be difficult to be (re)colonized by trees either because seedlings require the protection by adult nurse plants to survive the first life stages (Holmgren *et al.*, 1997; Rietkerk & Van De Koppel, 1997) or because seedlings recruit only during rainy periods when they grow sufficiently fast and in large numbers to successfully escape from herbivores, fire, and drought (Holmgren *et al.*, 2006; Scheffer *et al.*, 2008). This may create an elevated mortality at low densities (which is called inverse density dependence or the Allee effect, see e.g., Courchamp *et al.*, 1999). If this effect is strong enough it could cause the system to remain trapped in a stable treeless state (Rietkerk & Van De Koppel, 1997).

The availability of detailed satellite data of worldwide tree cover may offer unique possibilities to quantify the stability of these alternative stables states (Hirota *et al.*, 2011). However, interpretation of such

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field patterns is not straightforward (Scheffer & Carpenter, 2003; Hirota *et al.*, 2011; Van Nes *et al.*, 2012). Here, we construct a simple dynamical model that captures the tristability to explore how such underlying dynamics may interact with spatial heterogeneity of conditions and historical change in conditions to shape actual field patterns of tree cover. We also show how regional scale feedbacks between climate and vegetation (Brovkin *et al.*, 1998; Janssen *et al.*, 2008; Malhi *et al.*, 2008) could affect the hysteresis locally.

Model

The aim of our model is not to capture all suggested mechanisms that may be involved in shaping the alternative stable states. Other studies have already gone into more detail for mechanisms such as the fire feedback (see: Staver & Levin, 2012). Instead we want our equations to capture mechanisms in the simplest way that can still reproduce the observed patterns. The model describes the dynamics of tree cover (T in %) as a function of precipitation (P in mm yr^{-1}). All parameters and default values are explained in Table 1. The basis of the model is the logistic growth equation, describing the expansion of tree cover. We assume the expansion rate r (yr^{-1}) to be a function of the mean annual precipitation P. We added two nonlinear loss terms to this model. First, at a very low tree cover there is an elevated loss term, representing a lack of protective covering from 'nurse plants' to seedlings (Holmgren *et al.*, 1997; Rietkerk & Van De Koppel, 1997):

$$\frac{\mathrm{d}T}{\mathrm{d}t} = r(P)\ T\left(1 - \frac{T}{k}\right) - m_{\mathrm{A}} T \frac{h_{\mathrm{A}}}{T + h_{\mathrm{A}}} \tag{1}$$

Such lower net growth rate at low population densities is known in ecology as an 'Allee effect'. Although it is implemented by adding a loss term (with a maximum rate of m_{A}), it simply causes a net reduction of per capita growth at low densities. It is restricted to low tree cover by multiplying it with a Monod equation with a half-saturation constant of h_{A} (5% by default, defining the tree cover where this loss term is halved).

The second loss term we add [Eqn. (2)] represents fire mortality. For simplicity we do not model the effects of fire on differently sized trees explicitly. Instead we assume that fires cause on average a higher mortality. We assume that this fire mortality is much lower in a fully covered forest. Therefore, we define mortality due to fire to decline steeply after a certain critical tree density (h_{f}, which is round 60% tree cover). We use a sigmoidal Hill function, in which the exponent p determines the steepness of the sigmoid. The full model thus becomes:

Table 1 Description of parameters and state variables

Symbol	Description	Default value	Unit
T	Tree cover	–	%
h_A	Tree cover below which there is an increased mortality due to an Allee effect	10	%
h_f	Tree cover below which the fire mortality increases steeply	64	%
h_P	The precipitation where the expansion rate is reduced by a half of its maximum	0.5	mm day^{-1}
K	Maximum tree cover	90	%
m_A	Maximum loss rate for increased mortality at low tree cover densities	0.15	yr^{-1}
m_f	Maximum loss rate due to fire	0.11	yr^{-1}
p	Exponent in Hill function for fire effect	7	
P	Mean annual precipitation	[0.5–5]	mm day^{-1}
P_d	Mean annual precipitation over desert, so if there is no vegetation	[0.1–10]	mm day^{-1}
b	The effect of vegetation cover on precipitation which is defining the vegetation-precipitation feedback	0	mm day^{-1}
r_m	Maximum expansion rate of tree cover	0.3	yr^{-1}
r_P	Maximum rate toward equilibrium for precipitation	1	yr^{-1}

$$\frac{\mathrm{d}T}{\mathrm{d}t} = r(P)\ T\left(1 - \frac{T}{k}\right) - m_{\mathrm{A}} T \frac{h_{\mathrm{A}}}{T + h_{\mathrm{A}}} - m_f T \frac{h_f^p}{h_f^p + T^p} \tag{2}$$

We further assume that the relation between expansion rate and precipitation is a saturating function (a Monod equation) with a maximum expansion rate of r_{m} and a half-saturation constant of h_{P}:

$$r(P) = \frac{p}{h_{\mathrm{p}} + p} r_{\mathrm{m}} \tag{3}$$

Besides this basic model that we used for most simulations, we incorporated a feedback effect of vegetation on regional climate in the model. In some areas vegetation can cause a local change in the climate due to changes in local evapotranspiration (Nobre *et al.*, 1991; Dekker *et al.*, 2007; Malhi *et al.*, 2008), or in the patterns of monsoon circulations (Claussen *et al.*, 1998). We use the very simple approach of Brovkin *et al.* (1998) to illustrate the potential effect of such vegetation feedbacks on climate. In this approach we make the actual precipitation P a state variable. The equilibrium of precipitation (P_d+b T/K) is linearly dependent on the vegetation cover (T). The actual precipitation (P) approaches this equilibrium with a rate r_P (yr^{-1}):

$$\frac{\mathrm{d}P}{\mathrm{d}t} = r_P\left(\left(P_d + b\frac{T}{K}\right) - P\right) \tag{4}$$

Where P_d is the precipitation over a nonvegetated surface or bare soil, i.e., without accounting for the vegetation contribution, b is the strength of the effect of vegetation on precipitation, and T/K is the fractional vegetation.

Model analysis

First, we tuned the parameters of the model to roughly fit the effect of precipitation on the equilibrium states (Hirota *et al.*, 2011). We constructed the stability landscape ('potential function') of this model based on the physical idea of potential energy (Strogatz, 1994).

With this calibrated model we performed uncertainty analyses by evaluating the equilibria repeatedly with parameters drawn from normal distributions. As a first step, we explore the effect of spatial variation in conditions (e.g., soil fertility) other than precipitation that affect tree expansion. We used the parameters maximum expansion rate (r_m) and the sensitivity of vegetation to precipitation (h_P) to mimic this effect. As a next step, we explore how empirical relationships between vegetation distributions and precipitation will be contingent upon the climate history. To do this, we ran 5000 simulations with precipitation gradually increasing from 0 to 10 mm day^{-1} while drawing the parameters (r_m and h_P) from Normal distributions.

All simulations were performed in MATLAB using a Runga-Kutta solver. To detect hysteresis we performed a numerical bifurcation analysis by gradually increasing or decreasing precipitation in 40 steps. To find the approximate equilibrium, after each increment in precipitation we simulated for 600 time steps, which was enough for the dynamics to stabilize.

After running the model with randomly drawn parameters, we performed potential analysis as described in Livina *et al.* (2010) and Hirota *et al.* (2011) on the generated data. We only show the maxima and minima of the potential landscapes (Hirota *et al.*, 2011).

Results and discussion

With sufficiently strong mortality at low tree cover (Allee effect) and fire effects, the model presents three alternative stable states (Fig. 1). The critical values of precipitation where one of the three states becomes unstable (points F1-F3 and T1) are strongly dependent on the parameters. For some parameter settings all three stable states occur for the same precipitation levels.

Despite its simplicity this model can capture the hysteresis suggested by the data quite well for appropriate parameter settings (Fig. 2). However, as we will show, inferring the underlying dynamical properties from the relationship between spatial data on tree cover and

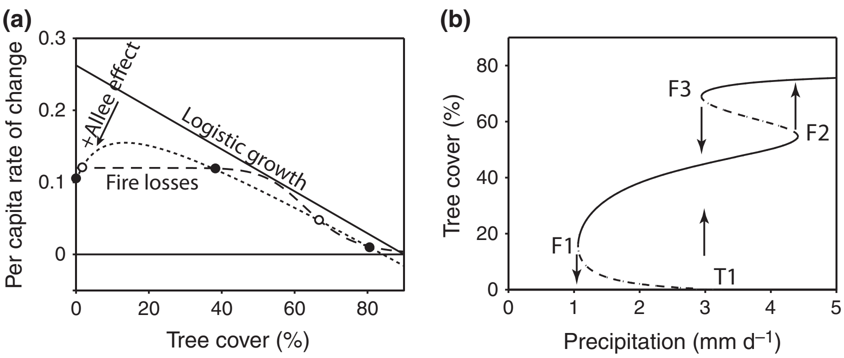

Fig. 1 The tristable minimal model of tropical tree cover. (a) Adding a mortality at low densities (Allee effect) depresses the per capita growth rate of the logistic growth model (straight solid line) at low tree densities (dotted line). Fire losses imply a constant mortality rate for tree covers lower than ca. 60% (dashed line). When these losses equal the net growth (dotted line) there is an equilibrium. This way we can obtain four intersection points representing two stable states (forest and savanna) and two unstable states. In addition, there is a stable treeless state at the intersection of the growth curve with the vertcal axis. (b) Plotting the intersection points against precipitation reveals the double hysteresis in the predicted response of tree cover. The stable equilibria are represented by solid curves, whereas the unstable equilibria are dashed. F1, F2, and F3 are fold bifurcations representing classical tipping points for transitions between forest, savanna, and the treeless state. The bifurcation at which the treeless state becomes unstable (T1) is a transcritical bifurcation.

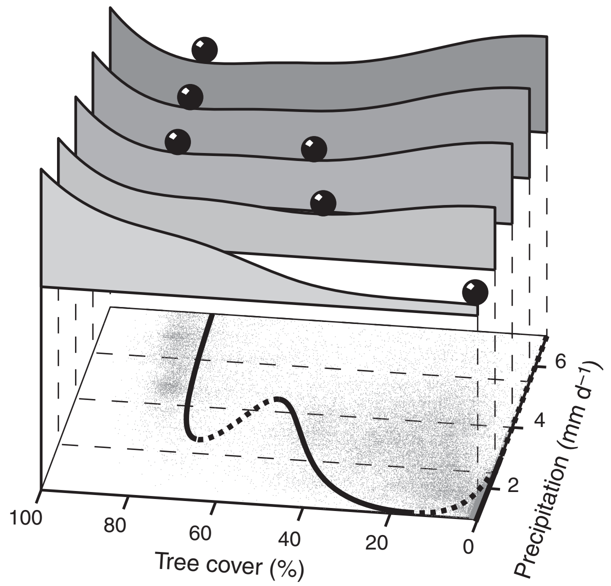

Fig. 2 Simulated 'potential landscapes' representing the stability properties of the system at different levels of precipitation. The balls mark the minima of the potential landscapes, corresponding to stable equilibria represented by the solid parts of the equilibrium curve (from Fig. 1b) projected in the bottom panel. Dots on the bottom panel represent empirical data on precipitation and remotely sensed tree cover in tropical regions globally used in the study of Hirota *et al.* (2011).

precipitation is not straightforward. We summarize the essence of our findings in a schematic graph (Fig. 3) and present the underlying technical results in supplementary figures (Figs S1–S3).

As a first step, we explore the effect of spatial variation in environmental conditions (e.g., soil or topography features) other than precipitation that affect tree expansion (Fig. 3c and Fig. S1). We used the parameters maximum expansion rate (r_m) and the sensitivity of vegetation to precipitation (h_P) to mimic spatial variation. The result confirms a point we made earlier (Hirota *et al.*, 2011; Van Nes *et al.*, 2012), namely, that large spatial variation in such background environmental conditions will cause the inferred hysteresis to be larger than the real hysteresis of local sites. The reason is intuitively straightforward. In a climate that becomes drier, some sites with particularly favorable conditions will keep trees for longer periods. Similarly in a wetting climate some sites with particularly unfavorable local conditions may only shift to a forested state at very high precipitation levels. As a result, the total range of precipitation levels over which the alternative states are found is larger if local site conditions differ more. This is not to say that the reconstructed stability landscapes (Livina *et al.*, 2010) do not capture the overall large-scale response well, but rather that this response consists of an aggregation of underlying smaller hysteresis responses at local scales.

As a next step, we explore how empirical relationships between vegetation distributions and the precipitation will be contingent upon the climate history (Fig. 3a and b). To do this, we perform 5000 simulations with precipitation gradually increasing from 0 to 10 mm day^{-1} (Fig. 3b and Fig. S2a). As the results illustrate, in a climate that has become gradually wetter, tree cover will remain in the lower equilibrium for a long time, before there is a shift to the forest or savanna state. By contrast, if the history of climate has undergone gradually drier conditions, the shift back to the savanna or vegetation less state will be at lower precipitation rates, due to hysteresis (Fig. 3a and Fig. S2b). The distributional data will either be biased toward the higher or lower tree cover states, depending on the climatic history. Hysteresis thus implies that actual tree cover distributions should be used with care for predicting future responses if there are gradual changes in rainfall.

Finally, we explore the effects of a feedback between vegetation cover and rainfall (Fig. S3 and Fig. 3d). While we know that tree cover responds to rainfall, the reverse is also true in some regions. For instance, in the western Sahara tree cover enhances Monsoon circulation allowing moist air from the ocean to feed clouds and rainfall over land (Brovkin *et al.*, 1998; Claussen *et al.*, 1998). Similarly in some parts of the Amazon, more than half of the rainfall consists of 'recycled water' that originates from evapotranspiration in the region (Eltahir & Bras, 1994; Malhi *et al.*, 2008), and trees contribute to this recycling as their deep roots bring otherwise unreachable deeper ground water into circulation. If strong enough, such positive effects of tree cover on precipitation may lead to regional alternative stable states: a high tree cover, wet state vs. a low tree cover dry state (Brovkin *et al.*, 1998; Claussen *et al.*, 1998; Malhi *et al.*, 2008; Nepstad *et al.*, 2008). It is important not to confuse this bistability with the hysteresis inferred from satellite data, as these analyses (Hirota *et al.*, 2011; Staver *et al.*, 2011) are based on the relationship between tree cover and the actual local rainfall (including possible effects of tree cover).

To analyze properly how local tristability might interact dynamically with climate, explicit simulations with Earth System Models would be needed. However, as a first step to explore how local hysteresis and regional feedback may interact to create dynamic equilibria of rainfall and tree cover, we expand our tristable model with the simple assumption that rainfall increases linearly with tree cover (Fig. S3). While the precise results depend on the strength of the tree-rain feedback, two qualitative results are immediately

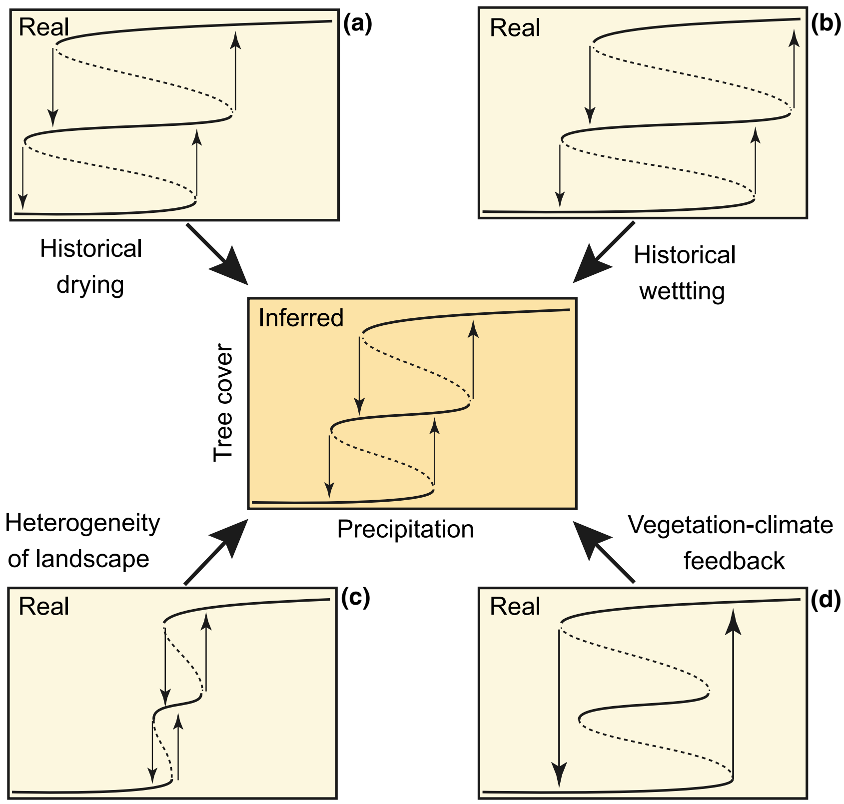

Fig. 3 Schematic representation of the way in which hysteresis in the response in tree cover inferred from remote sensing (central panel) may be biased in situations where the field patterns are affected by historical drying (a) or wetting (b); or by spatial heterogeneity of conditions (c) or a positive feedback between tree cover and rainfall (d). A full explanation is given in the main text. The qualitative patterns we represent in this figure are supported by quantitative analyses presented in Figs S1–S3.

obvious. First, the range of climatic conditions (defined as rainfall in the absence of trees) over which all three alternative states coexist is enlarged by the tree-rain feedback (Fig. 3d and Fig. S3). Second, at low rainfall it may be possible to have a direct transition from a full forest to a treeless condition without passing through a stable savanna state (Fig. 3d and Fig. S3). Similarly, at high rainfall we can have a direct transition from a treeless state to forest. Although the savanna state is still stable over a range of conditions, it may be more easily skipped as an intermediate state in transitions that occur close to the bifurcation points at which either the forest or the treeless states become unstable. The mechanisms are intuitively straightforward. For instance, in the case of the shift from forest to the treeless state: as trees start to disappear in a forest at marginally low precipitation regimes, rainfall drops as a result of this tree loss, making the climate even drier and increasing the likelihood of the system to turn into a treeless state rather than into a savanna state.

Clearly, our model is a rather oversimplified caricature of the complex interaction between tree dynamics and the environment. We intentionally kept the model 'minimal'; that is representing the simplest set of assumptions that can still produce the observed phenomenon of interest. This serves the modest goal of highlighting some points of attention when it comes to the interpretation of the stability properties that could explain observed multimodality of tree cover. However, in follow-up studies it would be useful to look deeper into aspects such as the effect of seasonal and interannual variation in precipitation on tree growth and fire dynamics (Archibald *et al.*, 2009; Staver *et al.*, 2011; Holmgren *et al.*, 2013). Also, fire mortality may drop not only at high tree cover, but also at low tree cover. Such sophistications may not change the qualitative result. For instance, defining fire mortality as a unimodal function of tree cover can give a similar tristable equilibrium curve (results not shown). However, if we wish to move toward a more realistic predictive version of the model it will be important to flesh-out the complex vegetation–fire–climate interaction in more detail.

Nonetheless, the simple model we present may serve as a starting point to include the apparent multiplicity of stable states and hysteresis of tropical tree cover in a new generation of coupled climate vegetation models.

As our preliminary analysis shows this could have profound implications for predicted effects of climatic change. Current global models do not take intrinsic hysteresis in vegetation states into account. The prediction of alternative stable states in some regions so far (Brovkin *et al.*, 1998; Claussen *et al.*, 1998; Nepstad *et al.*, 2008) is merely the result of a feedback between climate and vegetation. By contrast, the alternative stable states over ranges of rainfall inferred from satellite images (Hirota *et al.*, 2011; Staver *et al.*, 2011) reflect intrinsic hysteresis to rainfall resulting from other mechanisms (such as a feedback between fire and tree cover). Our findings illustrate that inclusion of this intrinsic hysteresis will greatly increase the area over which coupled climate vegetation models would predict alternative stable states and tipping points.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Density of equilibrium tree cover as a grayscale for 50 000 simulations with random initial conditions, uniformly distributed precipitation (between 0 and 15) and with two parameters (h_P, r_m) drawn from normal distributions: (a) Low stochastic: standard deviations h_P 0.005, r_m 0.003. (b) High stochastic: SD h_P 0.1, r_m 0.006.
Figure S2. Density of equilibrium tree cover as a grayscale for 5000 simulations with increasing or decreasing precipitation (see methods) and with two parameters (h_P, r_m) drawn from normal distributions (SD h_P 0.05, r_m 0.03). (a) Increasing precipitation and (b) decreasing precipitation.
Figure S3. The effect of a regional feedback of vegetation on precipitation on the size of the hysteresis.