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## Dynamical phase coexistence: a simple solution to the “savanna problem”

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We introduce the concept of *dynamical phase coexistence* to provide a simple solution for a long-standing problem in theoretical ecology, the so-called “savanna problem”. The challenge is to understand why in savanna ecosystems trees and grasses coexist in a robust way with large spatio-temporal variability. We propose a simple model, a variant of the Contact Process (CP), which includes two key extra features: varying external (environmental/rainfall) conditions and tree age. The system fluctuates locally between a woodland and a grassland phase, corresponding to the active and absorbing phases of the underlying pure contact process. This leads to a highly variable stable phase characterized by patches of the woodland and grassland phases coexisting dynamically. We show that the mean time to tree extinction under this model increases as a power-law of system size and can be of the order of 10,000,000 years in even moderately sized savannas. Finally, we demonstrate that while local interactions among trees may influence tree spatial distribution and the order of the transition between woodland and grassland phases, they do not affect dynamical coexistence. We expect dynamical coexistence to be relevant in other contexts in physics, biology or the social sciences.

Keywords: savannas, dynamical coexistence, contact process, statistical physics, stochastic processes

### I. INTRODUCTION

Savannas are open systems that feature a continuous grass layer and a discontinuous tree layer. They appear across a wide range of climatic and ecological conditions, and are characterized by the stable, though variable, coexistence of two distinct types of vegetation, trees and grasses [Sarmiento 1984]. This coexistence is dynamic in the sense that the density of trees varies widely both in space and time, as recently confirmed by observations of cyclic transitions between empty and dense tree distributions [Moustakas et al. 2008, Wiegand et al. 2006]. Savannas have been studied from both experimental and theoretical points of view, and have become an important subject of study in ecology. However, the origin, nature, and dynamics of savannas are not yet well understood. How is long-term coexistence of trees and grasses possible without the superior competitor taking over, as happens in other ecosystems (grasslands or woodlands)? This is one of the long

standing puzzles in theoretical ecology, commonly referred as the *savanna problem*. A tentative answer to this question is provided by niche models in which, assuming (soil, rain, etc) heterogeneities, each life form occupies the regions for which it is a superior competitor [Walter 1971, Walker et al. 1981, Walker and Noy-Meir 1982]. This type of solution is conceptually unsatisfactory and is, anyhow, not supported by recent empirical observations [Jeltsch et al. 2000, Higgins et al. 2000, Bond 2008, Scholes and Archer 1997].

Demographic (*stochastic*) bottleneck models [Sankaran et al. 2004] invoke stochastic explanations that rely on demographic and environmental fluctuations to generate dynamical heterogeneities [Chesson 2000, D’Odorico et al. 2007, Jeltsch et al. 2000, Jeltsch et al. 1996, Higgins et al. 2000, van Wijk and Rodriguez-Iturbe 2002, Meyer et al. 2007]. For example, the *storage effect* hypothesizes that long-lived organisms promote species coexistence in communities with birth rate variability, so that in an environment which is frequently adverse, a long life span buffers trees against extinction [Chesson 2000]. Other, similar in spirit, *buffering mechanisms* have also been proposed [Jeltsch et al. 2000]. Alternative *deterministic*

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descriptions, which do not rely on the assumption of rooting niche separation, have also been considered in [Scheiter 2007].

Our goal is to build a minimalistic savanna model that allows us to assess the contributions of the following features to long-term tree-grass coexistence: **i)** Variable weather conditions [Jeltsch et al. 1996, Higgins et al. 2000, van Wijk and Rodriguez-Iturbe 2002], **ii)** Mean annual precipitation, which has been reported to enhance and limit the maximum tree-cover [Sankaran et al. 2005, Sankaran et al. 2008, Bucini and Hanan 2007], **iii)** Adult tree longevity [Higgins et al. 2000], and **iv)** Positive and negative local density-dependent tree interactions [Jeltsch et al. 1996, Meyer et al. 2007, see Calabrese et al. In press]. Other ingredients to be studied are fire and dispersal limitation. Some existing demographic savanna models, which include these elements along with many others, can reproduce the main traits of real savannas [Jeltsch et al. 2000, Jeltsch et al. 1996, Higgins et al. 2000, Sankaran et al. 2004, van Wijk and Rodriguez-Iturbe 2002, Meyer et al. 2007]. However, these models do not clarify which ingredients are necessary to produce long-term coexistence and which are superfluous.

The gist of our minimal modeling is as follows. We start from a cellular automata defined on a square grid, in which each site can be occupied either by one tree or grass, and that follows the dynamical rules of the standard contact process (occupied sites are trees and empty ones are grasses; see next section). As in the standard contact process, depending on parameter values, two phases characterize the system: grassland (grass only) and woodland (tree dominated). “Dynamical phase coexistence” appears when the system is driven by a *random external driver* (fluctuations in rainfall or other environmental effects) which forces the system to visit the two phases randomly in time, alternating between grassland prone conditions and woodland prone condition. We shall show that the range of dynamical coexistence is much enhanced if the *age of the trees* is included, so that trees can typically endure harsh conditions. In any case, coexistence appears in a broad region of parameter space without fine-tuning of parameters.

This dynamical coexistence is not indefinite as the environmental fluctuations will eventually lead the system to the grassland or *absorbing state*, which is characterized by the complete absence of trees. Unlike previous work on environmental fluctuations and tree-grass coexistence [van Wijk and Rodriguez-Iturbe 2002, Jeltsch et al. 1996, Higgins et al. 2000], we focus here on characterizing the timescales over which dynamical coexistence is robust. Our approach consists of studying stability by means of the *mean*

*life-time*, that is, the mean time that takes the savanna to reach the final absorbing state. We show that this time diverges with system size  $N$  as  $N^\alpha$ , and can be enormous for even moderately sized systems [Leigh 1981].

Finally, let us remark that the generic phase coexistence observed in our model, i.e. coexistence occurring in a broad region of parameter space, is rarely found in other non-equilibrium model/systems and, in most cases, the domain of coexistence is typically small (see [Muñoz et al. 2005] and references therein). Additionally, given that the phenomenon of coexistence also happens in biological, physical and social sciences, the mechanism proposed in this paper is expected to be useful in many other contexts.

## II. MODEL

Consider the simple *contact process* (CP) [Harris 1974, Hinrichsen 2000]. Each node  $(i, j)$  of a two-dimensional square lattice can be either occupied  $z_{i,j} = 1$  (tree) or vacant  $z_{i,j} = 0$  (grass). The dynamics is as follows: a tree is randomly selected, and it is removed from the system with probability  $d$ , otherwise, with probability  $b$ , it generates an offspring, which is placed at a randomly chosen nearest neighbor (n.n) provided it was empty (i.e. short-range seed-dispersal).

Similar base assumptions underpin a number of CA savanna models including those of Menaut et al. (1990), Hochberg et al. (1994), [van Wijk and Rodriguez-Iturbe 2002], Kefi et al. 2007, and [see Calabrese et al. In press]. Even much more elaborate models such as those by [Jeltsch et al. 1996] and [Higgins et al. 2000] have a similar core. Thus the contact process (together with its extensions) is a widely used, though rarely explicitly acknowledged (but see [see Calabrese et al. In press]), basis for a savanna model. Here, we take full advantage of the body of results that has developed around the contact process, and in doing so we place our savanna model on firm theoretical ground. We then to build on this base in a systematic way and assess the contributions of the additional model components detailed below to tree-grass coexistence. Our goal is to identify a minimal set of processes that promote robust, long-term tree-grass coexistence, and we make no attempt to build a model that is a quantitatively accurate representation of any particular savanna. We therefore intentionally leave out many details considered in site-specific savanna models (e.g. [Jeltsch et al. 1996, Higgins et al. 2000, Meyer et al. 2007]).

As is usually done in sequentially updated Monte-Carlo simulations, every time a tree is selected, time  $t$  is increased by  $1/N(t)$ , where  $N(t)$  is the total number of trees in the system, so that when all trees have

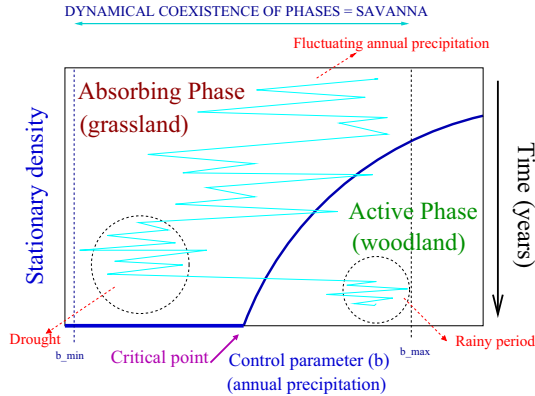


FIG. 1: Schematic representation of the system dynamics. The underlying pure model has two homogeneous phases: active (woodland) and absorbing (grassland), separated by a critical point (the transition could also be discontinuous as in Fig. 4). The control parameter fluctuates in time and shifts from one phase to another (droughts and rainy periods). This, combined with long-living trees, prevents the system from reaching a homogeneous steady state.

been selected once on average,  $t$  is increased in one unit, corresponding to one Monte Carlo (MC) step or one year. The dependence of the timestep on  $N(t)$  simply means that the more trees in the system the more individual updatings need to be done per each MC step.

Fixing  $d$ , a phase transition appears at some critical value  $b_c$ . For  $b > b_c$  the system is in the active (the system has a non-vanishing density of trees and can dynamically evolve) phase – woodland –, while for  $b < b_c$  it is in the absorbing – grassland – phase with zero tree-density (as schematically illustrated in Fig. 1). The reason for this last name is that if the system reaches this absorbing (i.e. only-grass) state, the situation is irreversible, it remains indefinitely trapped in it. Since there is no spontaneous generation of trees, the dynamics ceases if there are only grasses. This type of transition is commonly termed an absorbing phase transition [Hinrichsen 2000].

Now, we introduce the following two extra ingredients to model savannas:

**i) Fluctuating external conditions:** We assume that the birth probability depends on external conditions (mostly annual precipitation, but also fires, etc [Sankaran et al. 2005]), so  $b$  becomes a time-dependent random variable (see the zigzagging line in Figure 1). To account for possible temporal correlations in weather conditions we take a time-correlated (colored) noise as follows. With probability  $q$  a new value of  $b$  is extracted from a uniform random distribution in  $[b_{min}, b_{max}]$  at each MC step, otherwise (with probability  $1 - q$ )  $b$  is kept fixed. Here, we take  $b_{min} = 0$ , while  $b_{max}$  is the control parameter. This models weather cycles of typical length  $1/q$ . In a similar way, one could include more periodic weather

oscillations, as those induced by “El Niño”, which lead to similar results.

**ii) Age:** Field studies reveal that the mortality distribution of some savanna trees is consistent across years and climatic regimes [Moustakas et al. 2006], and that they have long lifespans. To model this we define trees with an intrinsic age-variable,  $a(i, j)$  measured in years. The death probability is taken to be age-dependent:  $d \rightarrow d(a(i, j))$ . In particular, a random number,  $\eta$ , is extracted from a Gaussian distribution of mean  $a_m$  and variance  $\sigma$  (typically,  $a_m = 100$  and  $\sigma = 20$ ). If  $a(i, j) \geq \eta$  then the selected old tree is removed; otherwise nothing happens.

Some other effects, such as density-dependent demographic rates, can also be easily implemented in the model.

**Density-dependence:** Negative and positive local density-dependent death probabilities account for tree-tree *competition* and *facilitation*, respectively. Both of these effects have been reported to act in savannas [see Calabrese et al. In press]. To model competition between a *young* tree at site  $(i, j)$  (tree with age  $a(i, j) \leq a_{est}$ , where  $a_{est}$  is the *establishment age*) and its neighbors, we increase its death rate as a function of the number of its nearest neighbors trees  $NN(i, j) = \sum_{(k,l)} z_{k,l}$ , where the sum is restricted to nearest neighbors sites of  $(i, j)$ . Thus, we take  $d(i, j) = 1 - \exp[-NN(i, j)]$ . Contrarily, to model strong facilitation we consider  $d(i, j) = 1$  for  $NN(i, j) = 0$  and  $1$ , and  $d(i, j) = 0$  for  $NN(i, j) \geq 2$ , that is, trees born in sites with only a few occupied neighbors die with certainty, otherwise they survive.

**Fire:** while fire is widely recognized as an important aspect of the ecology of many mesic to wet savannas, is clearly of secondary importance relative to the role played by moisture availability [Sankaran et al. 2005, Sankaran et al. 2008, Bucini and Hanan 2007, Bond 2008]. Over the long time scales which are our focus here, the dynamics of tree cover and the coexistence of trees and grasses will be dominated by fluctuations in climatic conditions. Over shorter time scales and when the details of tree spatial pattern are the main focus, fire should certainly be considered in more detail than we have here. However, given our long-term focus and our goal of identifying the primary driver of tree-grass coexistence on these time scales, its main effect can just be accounted for by the fluctuating parameter  $b$ ; years with (without) big fires will have smaller (larger)  $b$ .

**Dispersal limitation** The role of dispersal limitation in savannas is not completely resolved yet. However, it seems that there is some tendency for high seed densities near trees [Barot et al 1999, Witkowski and Garner 2000] and, consequently, in our model we have considered nearest-neighbor dispersal. Considering a slightly larger dispersion range (e.g., a first and second nearest-neighbor dispersal) gives rise to essentially the same type of clusters, even

if somewhat less compact. On the other hand, in the global dispersal limit clustering disappears. A larger discussion on this topic can be found, for a different but related model, in [see Calabrese et al. In press].

### III. MODEL ANALYSIS AND RESULTS

We first analyze the role of each ingredient we have added to the basic contact process separately. Taking a fluctuating  $b$  and a fixed death rate, i.e. **switching off the age effect**, the system shifts randomly between the tendencies to be in the active (tree density larger than zero) and in the absorbing (zero tree density) phase of the underlying pure model (notice the zigzagging trajectory in Fig. 1). For  $b_{max} > b_c$ , the system hovers around its critical point, while, if  $b_{max} < b_c$  (resp.  $b_{min} > b_c$ ) the fluctuating system is in the absorbing (active) phase, i.e. it is a grassland (woodland). In principle, if the time series of  $b$  happens to be adverse (i.e.  $b < b_c$ ) for a sufficiently long time interval, any finite system falls into the absorbing state; i.e. *the system has variability but little resilience to long adverse periods*.

The effect of weather correlations is as follows: for  $0 < q \ll 1$  the birth rate is constant for long periods and the system typically jumps, every  $1/q$  years, from a pure CP homogeneous state to another one and, therefore, when  $b$  takes a value smaller than  $b_c$  it falls ineluctably into the absorbing state. For  $q \approx 1$ , the rate of variation of  $b$  is very fast and the system does not have the time required to relax to any pure CP steady state, and reaches instead an averaged density value (see solid curve in Fig. 2). For realistic intermediate values (e.g.  $q = 0.03$ ), the system exhibits much larger oscillations (see the dashed and the dotted line in Fig. 2) which resemble those in real savannas [Moustakas et al. 2008].

On the other hand, taking a fixed birth rate,  $q = 0$ , i.e. **switching off the weather variability** the model becomes a CP with age. For this, if trees die at a fixed given maximum age,  $a_m$  (i.e. with  $\sigma = 0$ ), the density is known to exhibit damped oscillations in time of period  $2a_m$ , and to converge asymptotically to a homogeneous stationary value [Gerami 2002] (see dashed-dotted line of Fig. 2). Our model (with  $\sigma > 0$ ) exhibits analogous, though more variable, damped oscillations, and converges either to the absorbing state or to an active homogeneous state. Separating these two regimes there is a phase transition. In this case *the system is resilient but has little variability*. Obviously resilience grows with the maximum age.

As we demonstrate below, the full model, which includes both age and correlated variable rainfall, exhibits variability and resilience (see the dashed and dotted curves in Fig. 2); the larger the maximum age, the larger the resilience. The system fluctuates locally between the absorbing and the active phases,

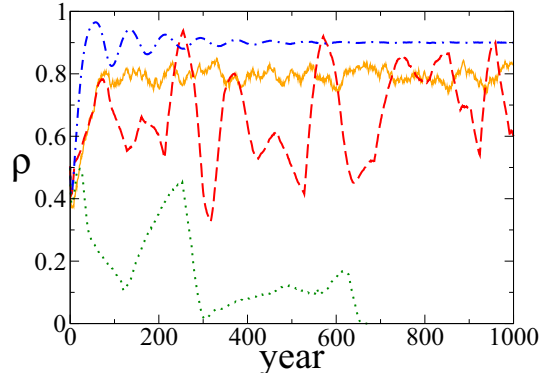


FIG. 2: Time evolution of the tree-density in different cases. All curves except the dotted one ( $a_m = 30$ ,  $\sigma = 6$ ) are for  $a_m = 100$ ,  $\sigma = 20$ . The dashed-dotted curve ( $q = 0$ , i.e. model without variability) exhibits damped oscillations. The solid line ( $q = 1$ ) shows small variability, while the dashed and dotted curves are for  $q = 0.03$  (intermediate variability). Notice that the one with smaller maximum age ( $a_m = 30$ ; dotted curve) does not survive to an adverse period, while its analogous for large age ( $a_m = 100$ ; dashed curve) does.

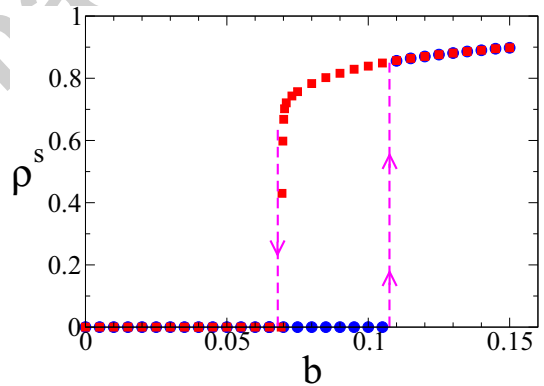


FIG. 3: Phase diagram for the underlying pure model ( $q = 0$ ) in the case of strong facilitation; observe the discontinuous transition and the hysteresis loop.

but it is able to preserve “islands” of the unfavored phase in a “sea” of the dominant phase, as is required for generic phase coexistence. This is the basic mechanism of *dynamical phase coexistence*.

The effect of **density-dependence** is as follows. Computer simulations show that, the underlying pure model ( $q = 0$  and no age), either in the absence of density dependence and in the case of competition or weak facilitation, exhibits a continuous absorbing phase transition (as schematized in Fig. 1). Instead, for strong facilitation the underlying transition can be discontinuous with a broad hysteresis loop (see Fig. 3), implying that around the transition the two dynamically coexisting phases are very different. Note that the appearance of a discontinuous transition in the underlying pure model is interpreted in biological terms as the ex-



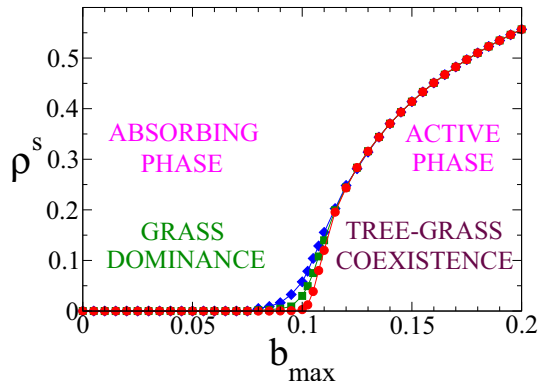


FIG. 4: Stationary tree-density  $\rho^s$  vs maximum birth probability  $b_{max}$ , averaged over surviving realizations for the model with competition,  $q = 0.1$ ,  $a_m = 100$ ,  $a_{est} = 1$ , and system sizes  $N = 40^2$  (diamonds),  $N = 80^2$  (squares) and  $N = 320^2$  (circles).

istence of catastrophic shifts that may result in sudden dramatic changes of the savanna properties [Scheffer et al 2009, Scheffer et al 2003]

Fig. 4 shows the stationary tree density as a function  $b_{max}$  ( $q = 0.1$ ,  $a_m = 100$ ,  $a_{est} = 1$ ) illustrating the existence of an active phase and a continuous phase transition in the full model with competition. The active phase of the full model is the phase of coexistence: the two phases of the pure model (grass and wood) coexist. A very similar continuous transition is obtained in the case of strong facilitation; even if the underlying pure-model transition is discontinuous, once varying conditions are switched on, the transition between the absorbing and the tree-grass coexistence phases becomes continuous.

For illustration purposes, Fig. 5 shows snapshots of such a phase for different parameters at different times. Panels (a) and (b) correspond to the case of competition, and both have the same parameter values but look quite different, illustrating the large spatio-temporal variability. Panel (c) shows that, in the case of facilitation more compact clusters are observed (as justified by the underlying discontinuous transition). These snapshots are visually very similar to pictures of real savannas [Moustakas et al. 2008]; notice the presence of irregularly distributed tree clusters of different sizes and shapes. Panel (d) corresponds to competition, but with slightly different parameters. We can conclude that density-dependence controls the shape of emerging clusters, but it is not an essential ingredient for dynamical coexistence.

Let us now scrutinize the stability of the active phase, where there is dynamical coexistence: how long does it persist through periods of adverse rainfall conditions?

In a single realization, independent of the value of  $b_{max}$  and provided that  $b_{min}$  is smaller than the critical values of the pure model, the density of trees reaches the absorbing state  $\rho = 0$ , that consists of a

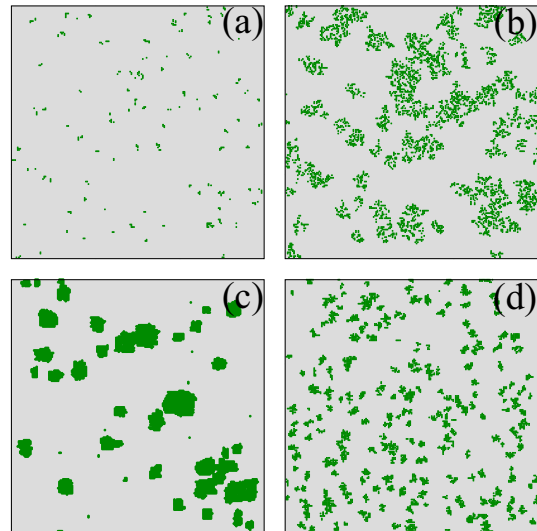


FIG. 5: Snapshots of the system for different versions of the model with  $q = 0.01$  and  $b_{max} = 1$ . (a) and (b) correspond to the same realization with  $a_{est} = 4$ , competition, and two different times. The system fluctuates locally and globally between small and large densities, as in real savannas. (c) Facilitation,  $a_{est} = 4$ . (d) Competition,  $a_{est} = 1$ .

totally empty lattice where no more trees are born, and therefore the evolution stops. In other words, trees go extinct in a time that depends on the specific realization, due to stochastic fluctuations, and the size of the system. We have computed the *mean lifetime*,  $\tau$ , that is, the average over many realizations of the time required to reach tree extinction, for several values of  $b_{max}$  and different system sizes  $N$  (see Fig. 6). The value  $b_{max}^c \simeq 0.1045$  at which  $\tau$  grows as  $\tau \sim (\ln N)^{3.68}$  [straight dashed line in Fig. 6(a)], agrees within error-bars with the point where the stationary density  $\rho^s$  goes to zero in Fig. 4, thus we take it as the active-absorbing phase transition point. In Fig. 6(b) we observe that, remarkably, in the active phase (circles)  $\tau$  diverges with  $N$  as a power law  $N^\alpha$  (with possible log corrections), where the exponent  $\alpha$  increases with  $b_{max}$  (see inset). That is, the mean life-time increases very rapidly with system size, and therefore one expects that real (large) savannas survive for very long periods. A similar behavior for the extinction time was found in a discrete-time population model (the lottery model) in the presence of a stochastic environment in [Chesson 1982]; waiting times for extinction increase at very different rates: power law, logarithmic and square-logarithmic. The author discusses the mathematical and biological properties of the system that give rise to each of these behaviors.

We now provide a simple analytical explanation for the power-law behavior of the extinction time with  $N$ . The relaxation time  $T_{relax}$  that the system takes to reach the absorbing state, when  $b$  takes

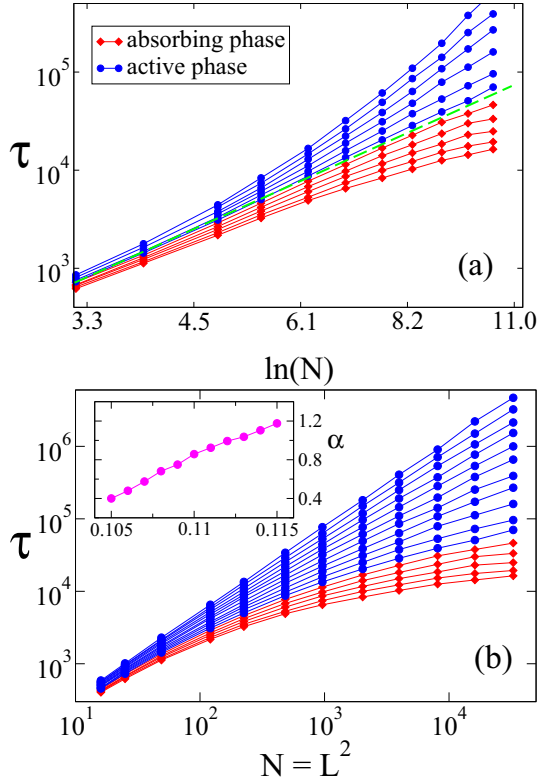


FIG. 6: (a) Savanna mean life-time  $\tau$  vs the logarithm of its size  $N$  on a log-log scale, for different values of  $b_{max}$  below (diamonds,  $b_{max} = 0.100 - 0.104$ ) and above (circles,  $b_{max} = 0.105 - 0.115$ ) the transition point  $b_{max}^c \approx 0.1045$ . At  $b_{max}^c$   $\tau$  grows as  $(\ln N)^{3.68}$  (straight dashed line). (b)  $\tau$  vs  $N$  on a log-log scale.  $\tau$  diverges as  $N^\alpha$  for  $b_{max} > b_{max}^c$  (circles), with the exponent  $\alpha$  proportional to  $b_{max}^c$  (inset), indicating that the active phase is stable when  $N \rightarrow \infty$ .

values below  $b_c$ , scales as  $T_{relx} \sim \ln(N)$ , because the density of trees decays exponentially fast to zero in the absorbing phase. The system dies when there is an “extreme event” consisting of a dry weather period larger than  $T_{relx}$ , that is, when  $b$  takes a value below  $b_c$  a number  $n = qT_{relx}$  of consecutive times, given that  $b$  takes a new value every average time interval  $1/q$ . Then the probability of having an extreme event is  $P \sim (b_c/b_{max})^n$ , so that the mean time  $\tau$  to observe this event by the first time is  $\tau \sim 1/P \sim (b_c/b_{max})^{-q \ln(N)} \sim N^\alpha$ , with  $\alpha \equiv -q \ln(b_c/b_{max})$ , showing the algebraically long surviving times. Note that the exponent  $\alpha$  is proportional to  $b_{max}^c$ , as it is observed in the inset of Fig. 6(b).

As an illustration of the mean-life time, consider a 1000 hectare savanna, which corresponds to a  $632 \times 632$  square lattice (assuming, say, neighboring lattice sites are separated by 5 meter distance), taking  $b_{max} \approx 0.111$ , which is not very deep into the active phase, then our model predicts that its expected time to extinction is of the order of 10 million years.

This leads to the conclusion that the coexistence of grassland and woodland phases is stable for extremely long time periods. Furthermore, we find that the exponent  $\alpha$  increases with the maximum tree age  $a_m$  (not shown), so that age strongly stabilizes the active phase and increases the savanna mean life-time time.

Our main conclusion is that, in the infinite size limit, the dynamical coexistence of savannas is truly stable, even if, for any finite size, surviving times are necessarily finite. The corresponding extinction times increase as power-laws of system-size; this is, systems with dynamical phase coexistence are less stable than homogeneous steady states (for which there is an exponential increase of surviving times upon enlarging system size), but still they are stable.

#### IV. EMPIRICAL EXAMPLE

To demonstrate that this simple model is a reasonable descriptor of savanna dynamics, we fit it to a paleoecological time series of tree-grass pollen ratios,  $R_{data}(t)$ , and lake depth levels,  $\delta(t)$ , from the Crescent Island Crater site in central Kenya [Lamb et al. 2003, Vershuren et al. 2000]. The long-term nature of this time series ( $> 1000$  years) allows us to examine a much wider range of density fluctuations than is possible with short-term, directly observed tree density data. The cost is that these paleoecological data sets rely on proxy measures (e.g. fossil pollen for vegetation, fossil midge and diatom assemblages for lake depth) and are thus necessarily much less precise than direct measures of tree density and rainfall. We digitized figures 3B and 3C in [Lamb et al. 2003] to obtain the pollen ratio and lake depth time series, respectively, using the program Engauge V 4.1 [http://digitizer.sourceforge.net/]. As these time series were both reconstructed at the same site, over the same time interval, they give us rough proxy measures for both precipitation patterns and tree density at this site going back over 1000 years (see Fig. 7).

We ran simulations of the model with a birth probability given by the expression  $b(t) = \gamma \delta(t)$  (where  $\gamma$  is a constant), that is, assuming that the amount of rainfall, and therefore  $b(t)$ , is proportional to the lake’s depth. We included neither age nor density effects. We also considered that the amounts of pollen from trees and grasses are proportional to the number of trees  $\rho L^2$  (with  $L = 100$ ) and the area covered by grass  $(1 - \rho)L^2$ , respectively, thus we took  $R_{num}(t) = \beta \rho / (1 - \rho)$  as the tree-grass pollen ratio in the simulations, where  $\beta$  is a constant. Then, for given values of  $\gamma$  and  $\beta$ , we averaged over 10 independent realizations of the dynamics, starting from the same initial density of trees, and calculated the sum of squared deviations between the model and the tree-grass ratio data over the 1000 years period



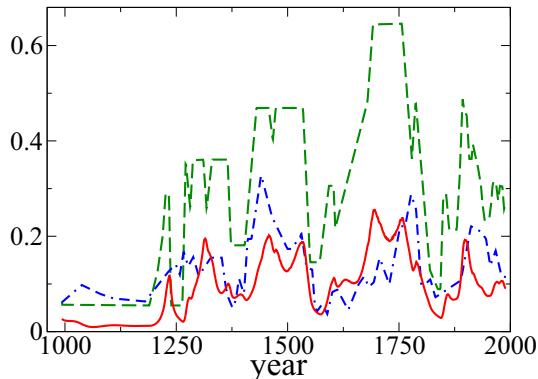


FIG. 7: Ratio of tree to grass pollen in the Crescent Island Crater core NC93 in Kenya (dashed-dotted line) and from numerical simulations of the model (solid line), on a  $100 \times 100$  square lattice, with age = 100. The time series of the birth probability in the simulations (dashed line) was taken to be proportional to the depth of the lake Naivasha, located next to the Island Crater, in Kenya.

as  $\sum_{i=1}^{1000} [R_{data}^i(t) - R_{num}^i(t)]^2$ .

Comparing the model to the paleoecological data from the Crescent Island Crater site, we found by numerical direct search that  $\gamma_{min} = 0.018$  and  $\beta_{min} = 0.005$  are the values that minimized the sum of squared errors. As can be seen in Fig. 7, the average time evolution of the tree-grass pollen ratio (solid line) is strongly biased by the temporal function  $b(t)$  (dashed line), and it has only a qualitative agreement with the evolution of the real ratio (dashed-dotted line). We have checked that the age of trees in the model does not affect the evolution of the ratio very much, and that single realizations are typically very similar, given that fluctuations coming from the system size are much smaller than fluctuations induced by the variation of  $b(t)$ . We also note in Fig. 7 that the real-data pollen ratio also roughly follows the variation of the lake's depth. These results demonstrate that this correlation between rainfall and pollen ratio, already noted in [Lamb et al. 2003, Verschuren et al. 2000], is correctly described by our very simple model. This correspondence is especially encouraging given that we have manipulated only two parameters here to fit the model.

## V. SUMMARY

Here we have shown that a simple extension of the contact process is capable of providing a robust and general explanation for tree-grass coexistence in savannas. Specifically, fluctuating rainfall levels force the system to oscillate between a tree-dominated woodland (active) phase and a grass-only (absorbing) phase; a behavior we call dynamical phase coexistence. Dynamical coexistence is not permanent,

but, as we have shown, it is expected to last for geologically significant periods of time. In other words, the mechanism discussed here facilitates coexistence over periods of time easily long enough to span the gaps between major disturbance events, such as ice ages, that can create and destroy savannas.

Strictly speaking, the only essential ingredient for dynamical phase coexistence is the presence of externally varying conditions. Said another way, dynamical coexistence is independent of the lifespans of trees, the degree of correlations in weather conditions, and the presence and nature of density-dependent local interactions among trees. Adding age-dependent tree death to the model greatly enhances the stability and robustness of coexistence. Adding weather correlations of intermediate magnitude increases the variability in tree cover and can help the model mimic the wide variability in tree cover that has been observed among sites with similar rainfall [Sankaran et al. 2005, Bucini and Hanan 2007, Sankaran et al. 2008]. Finally, adding local tree-tree interactions can allow the model to reproduce a range of tree spatial patterns that have been observed in real savannas, including dense thickets of trees and more widely spaced and open configurations [see Calabrese et al. In press, Moustakas et al. 2008]. Thus these additional features affect the nature of several observable features of savannas but are not the primary drivers of tree-grass coexistence.

This last point merits further discussion. While several stochastic savanna models have included varying weather conditions and many other factors [Jeltsch et al. 1996, Jeltsch et al. 1998, Higgins et al. 2000, Meyer et al. 2007, van Wijk and Rodriguez-Iturbe 2002], none has, to our knowledge, clearly identified the minimal conditions that facilitate tree-grass coexistence. Our strategy of starting from the well-studied contact process and extending the model in a stepwise fashion has allowed us to identify the contribution of each model component to tree-grass coexistence and to other features observed in real savannas. We can therefore unambiguously state that fluctuating external conditions alone are sufficient to facilitate long-term (though not indefinite) tree-grass coexistence. A further advantage of our minimalistic approach is that it does not require parameter fine tuning to achieve coexistence, as has been the case in other stochastic savanna models [Jeltsch et al. 1996, Higgins et al. 2000]. Finally, unlike previous studies, we have been able to clearly demonstrate the time scales over which dynamical phase coexistence persists.

Despite the simplicity of our model, we have shown that it is capable of describing qualitatively a 1000 year paleoecological dataset when it is given a quantity proportional to rainfall as a driving input. The

key result here is that the model is able to reproduce the correlation between weather patterns and tree-grass ratios. The rough quantitative agreement between the model and data is not surprising given that these data, which are based on proxy measures instead of direct observation, are relatively crude and that only two parameters of our dynamic, *non-linear* model, were tuned to achieve the fit. We note that though empirical data are frequently used in savanna modeling studies, such studies typically only consider single snapshots in time, or very short time series [Jeltsch et al. 1999, Higgins et al. 2000, van Wijk and Rodriguez-Iturbe 2002].

While we have focused here on savannas, the concept of dynamical phase coexistence is much more general than that. Variants of the Contact Process are used in many different fields including: Physics, Ecology, Epidemiology, Sociology, etc. Furthermore,

it seems likely that many of the systems to which these models are applied may feature some degree of forcing by externally varying conditions. Thus, we expect that the concept of dynamical phase coexistence will find broad applicability in a range of scientific disciplines.

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