

Multistability with a Metastable Mixed State

Kim Sneppen* and Namiko Mitarai

Niels Bohr Institute/CMOL, University of Copenhagen, Blegdamsvej 17, DK-2100 Copenhagen, Denmark

(Received 18 May 2012; published 5 September 2012)

Complex dynamical systems often show multiple metastable states. In macroevolution, such behavior is suggested by punctuated equilibrium and discrete geological epochs. In molecular biology, bistability is found in epigenetics and in the many mutually exclusive states that a human cell can take. Sociopolitical systems can be single-party regimes or a pluralism of balancing political fractions. To introduce multistability, we suggest a model system of D mutually exclusive microstates that battle for dominance in a large system. Assuming one common intermediate state, we obtain $D + 1$ metastable macrostates for the system, one of which is a self-reinforced mixture of all $D + 1$ microstates. Robustness of this metastable mixed state increases with diversity D .

DOI: 10.1103/PhysRevLett.109.100602

PACS numbers: 05.50.+q, 87.23.-n, 87.16.A-

Introduction.—Positive feedback among mutually opposing states may lead to bistable systems, provided that the competition involves cooperative interactions. A classical system is the genetic switch of phage λ where two proteins inhibit the production of each other [1,2]. Bistability, along with its associated epigenetics, is also found in systems of nucleosomes and “read-write” enzymes [3–10]. A central lesson from the analysis of epigenetics in Ref. [7] is that bistability can be obtained from two linear recruitment processes, provided they act across an intermediate inactive state.

Competing states are also part of society, where opinions spread through social contacts [11–23]. Especially studied are the “voter models” [14,15] where agents take one of two opinions, $+1$ or -1 , and update them by repeatedly setting the agents’ states of pairs to be equal. Other interesting approaches include the Axelrod model [11], in which opinions are multidimensional. These types of models do not predict bistability, although absence of noise [12,13,24] allows the systems to settle into a frozen state. Bistability has however been obtained in the naming game [25] where two words compete across an intermediate state and the agents accept both words [26]. Multistability has been introduced through the network model of Ref. [27].

Here we analyze multistability inspired by a model of epigenetics [7], which considers three states or species -1 , 0 , and $+1$. In terms of a political battle, the model translates into a force toward the left that involves a “left”-wing person in state “ -1 ” “recruiting” other persons from the “right” wing in state $+1$ to the neutral state 0 , or from state 0 to state -1 . In its symmetric variant, the model assumes that a right-wing person in state “ $+1$ ” imposes a similar opposing force. When these “recruitments” are supplemented with a low rate β for random spontaneous changes, the model predicts bistability.

We extend the model to D -active states or species ($D \geq 3$). We show that the $D \geq 3$ state allows multistability between dominating states (DS) where one of the active

species dominates and a metastable mixed state (MMS) where all the D -active species are almost equally present.

Model and the mixed metastable state.—Here we explore a system of D -active species that compete across a common intermediate species (IS). The model with $D = 3$ is defined in Fig. 1.

Figure 2 shows the trajectories for the $D = 3$ model. Note the transition from the mixed state (MS) at $\beta > 0.31$ to a tristable case with an alternating dominance state (DS) of one of the three active species at $\beta < 0.28$. Remarkably, however, for $\beta \sim 0.295$, the system can be trapped in the metastable mixed state (MMS).

Deterministic perspective.—The deterministic version of the $D + 1$ model is

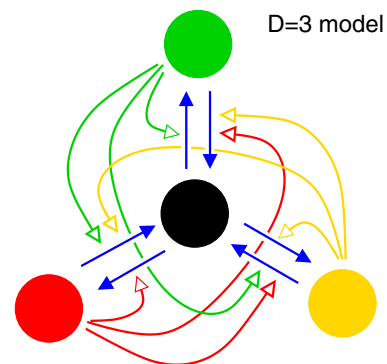


FIG. 1 (color online). Model with $D = 3$ active states or species that attack each other across an intermediate inactive state. At each time step, the system is updated by a recruitment step r and a noise step n : r) At each time step, a random site j is selected. If it is in one of the active species, it attempts a conversion of another randomly selected site k : If k is one of j ’s antagonistic species, it is reset to the IS. If k is IS, then it is converted to the same state as j . If the state of k is equal the state of j , then no change is made. n) Select a random site l with probability β and change its state: If l is active, it becomes IS, and if l is IS, it becomes one of the randomly chosen active species.

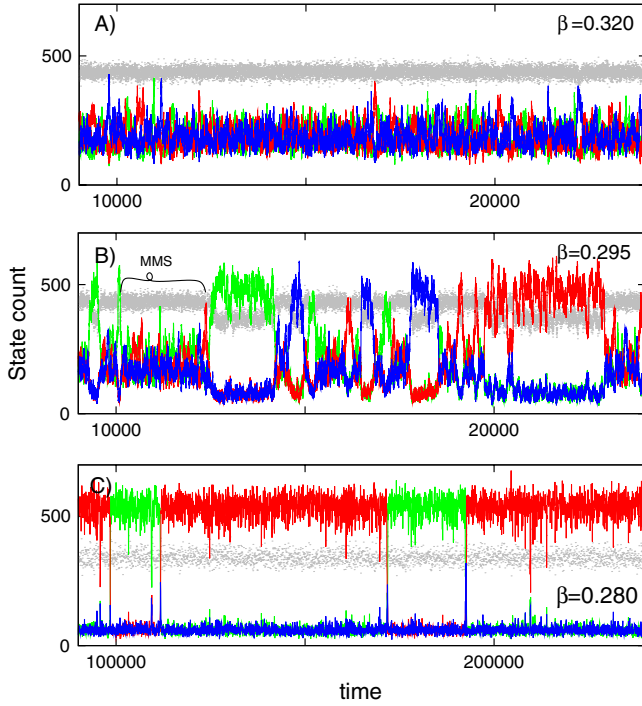


FIG. 2 (color online). Dynamical simulation of the $D = 3$ model in a system of size $N = 1000$. The grey dots refer to the IS. Time is counted in number of attempted pair interactions per site. Panel (C) examines a 10 times longer time interval than (A) and (B), showing that stability of states depends strongly on β . Panel (B) shows occasional appearance of the MMS.

$$\begin{aligned} \frac{dn_j}{dt} &= n_j n_0 - n_j \sum_{k>0, k \neq j} n_k - \beta n_j + \beta \frac{n_0}{D} \\ &= n_j(2n_0 - 1) + n_j^2 - \beta n_j + \beta \frac{n_0}{D}, \end{aligned} \quad (1)$$

$$\frac{dn_0}{dt} = (1 - n_0 + \beta)(1 - 2n_0) - \sum_{j>0} n_j^2, \quad (2)$$

with $\sum_{j>0} n_j = 1 - n_0$, where n_j ($j = 1, 2, \dots, D$) denotes the fractional occupation of the active species. The coupling between the active species occurs through depletion of n_0 . Note that Eq. (2) is redundant if we express n_0 in terms of n_j with $j > 0$ using $\sum_{j=0}^D n_j = 1$.

$$x = x_{\pm}(\beta) = \frac{1}{2D}[-2\beta + D \pm \sqrt{4\beta^2 + 4\beta D + 4\beta^2 D + D^2 - 4\beta D^2 - 4\beta^2 D^2}].$$

Here x_+ is a stable fixed point with n_1 domination, while x_- is an unstable fixed point. As β decreases, x_- will collide with the MS solution x_m at $\beta = \beta_M$, as shown for $D = 10$ in Fig. 3(c) [28].

The above solution does not include the case where one of the other active species is dominating. For each DS, the

Figures 3(a) and 3(b) show the trajectories and fixed points for the $D = 10$ model. We see that the model opens for a DS state at a low β , whereas it gives monostability of a mixed state at high β .

Fixed point analysis.—For $D \geq 3$, the metastable states are always either a MS or a state where one species dominates (DS). In such a case, Eqs. (1) and (2) can be solved analytically for the fixed points as well as for their linear stability. Consider a situation where one state $x = n_1$ competes against an equal partitioning of the other active species, each occupying a fraction $(1 - x - y)/(D - 1)$ where $y = n_0$ occupies the IS. Within this constrained “one against all” battle, Eqs. (1) and (2) reduce respectively to

$$\frac{dx}{dt} = x(2y - 1) + x^2 - \beta x + \beta \frac{y}{D}, \quad (3)$$

$$\frac{dy}{dt} = (1 - y + \beta)(1 - 2y) - x^2 - \frac{(1 - x - y)^2}{D - 1}. \quad (4)$$

The fixed points will be found on the nullcline of Eq. (3), $y = f(x) = -\frac{Dx(x-1-\beta)}{\beta+2Dx}$. Equations (3) and (4) always have a fixed point

$$x = x_m(\beta) = \frac{D - 2\beta D + \sqrt{D(-4\beta + D + 4\beta D + 4\beta^2 D)}}{2D(2D - 1)},$$

which is a MS, as it satisfies $f(x_m) + Dx_m = 1$, corresponding to equal participation of all active species. This fixed point has only negative eigenvalues for

$$\beta > \beta_M = \frac{-2 + 2D - D^2 + \sqrt{4 - 8D + 5D^2 - 2D^3 + D^4}}{-3D + 2D^2}.$$

However, this MS is metastable and thus an MMS only if there exists a stable competition. This is the case for

$$\beta < \beta_{DS} = \frac{D - D^2 + \sqrt{-3D^3 + 2D^4}}{2(D^2 - D - 1)},$$

where the system exhibits a saddle-node bifurcation “far” from the MS. As β is decreased below this point, there appears a pair of fixed points

population of any other active species, x_{minority} , will be small and given by $(D - 1)x_{\text{minority}} + x_+ + f(x_+) = 1$.

Figure 3(d) examines β_{DS} and β_M as a function of D . The MMS is sustained in a interval of $\beta \in [\beta_M, \beta_{DS}]$, which becomes wider for a larger D , because $\lim_{D \rightarrow \infty} \beta_{DS} = \frac{1}{2}(\sqrt{2} - 1)$, while $\beta_M \sim 1/(2D)$ for a large

D. When $\beta > \beta_M$, the MS is the only stable state. Note that the MMS cannot be observed at $D = 2$, where $\beta_{DS} = \beta_M$.

Locality and robustness.—The model can be interpreted in terms of an ecosystem of bacteria that kill each other by excreting bacteriocins [29]. The IS then corresponds to the dead situation. The change that an individual of species j causes on another active species $k \neq j$ represents a predator “killing” an individual. The recruitment from IS to the species j can be interpreted as growth of species j by consumption. In our well-mixed model, the predator kills without getting the immediate benefit from the kill; in other word, the “corpse” is left to be consumed by “whoever passes by.”

We now add a spatial component to the model. We first consider the case where the “consumption” of the resource and the associated growth happen always locally. In contrast, the “killing” interaction is assumed to happen nonlocally, for example, with diffusive toxins. Figure 4 defines and examines such a global-local model in one dimension. Even for the $D = 3$ species and small systems, we easily find β , where the dynamics exhibit an alternating pattern of a DS and a MMS.

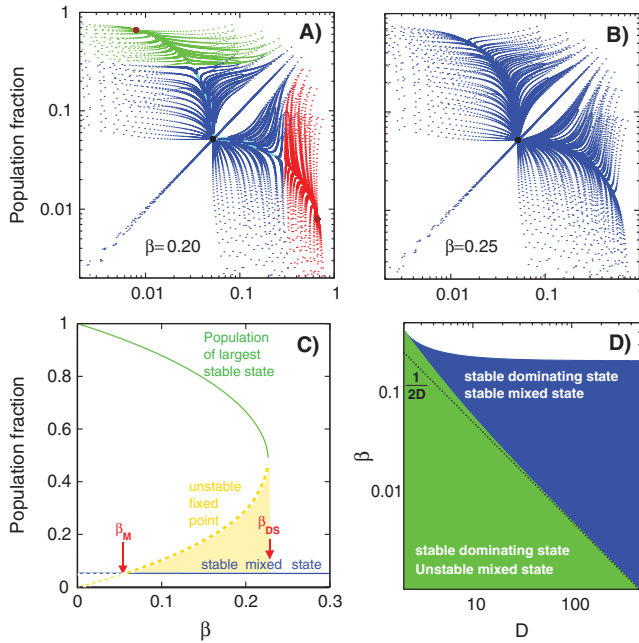


FIG. 3 (color). Deterministic dynamics for the $D = 10$ model. (A, B) Trajectories starting from uniformly distributed n_0, n_1, n_2 , with all other n_i equal, shown for $\beta = 0.20$ in (A) and $\beta = 0.25$ in (B). Trajectories are colored after their final fixed point. Fixed points are shown as solid red and black dots. Initial conditions fix n_i , $i \geq 3$ to be equal and thus exclude trajectories ending in DS with $i \geq 3$. (C) Population size of two of the stable states as a function of β for $D = 10$. The dashed “gold”-colored curve is the unstable fixed point that separates the MMS and the DS. (D) The parameter region with MMS (blue region) and DS (green + blue region), with varying D and β .

Figure 4(d) demonstrates that the MMS can be maintained even if the interaction strength is assigned randomly. Figure 4(e) further shows MMS robustness to the introduction of new species with new interactions [30] each time the population of one species collapses.

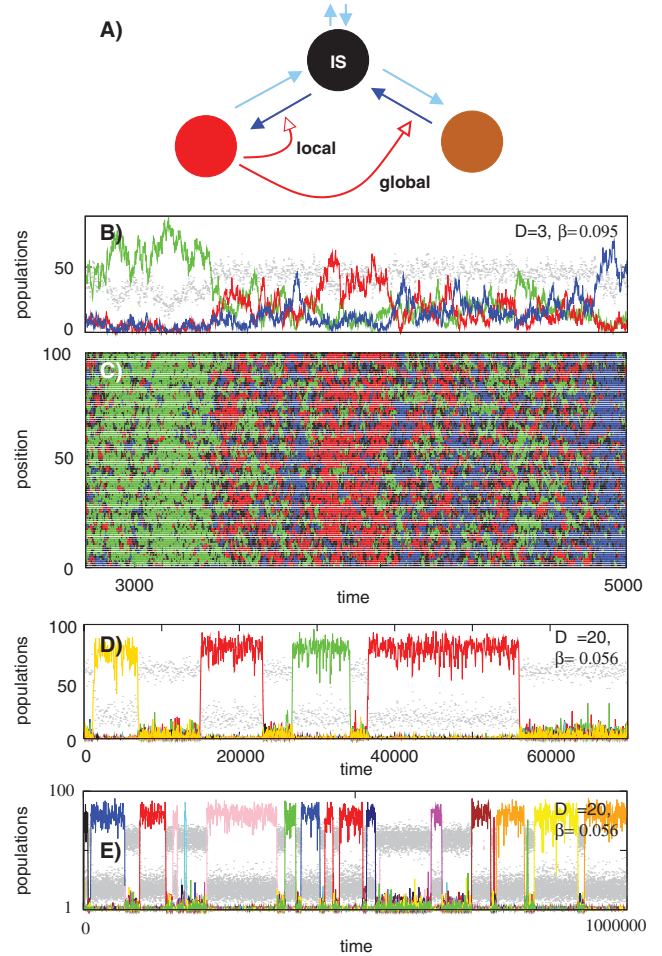


FIG. 4 (color). Dynamics of a variant model where conversion from IS is local and the general “kill” global [8], as illustrated in (A): Although noise (n) is unchanged, the recruitment (r) reads as follows: (r) At each time step, a random site j is selected, and if it is in one of the active species, then one of two moves is attempted: (i) With probability $\frac{1}{2}$, a neighbor k to j is selected, and if k is in IS, it is converted to a species of j ; (ii) else, a random site k is selected, and if k is one of j ’s antagonistic species, it is changed to the IS. If the selected j is not active or k is not fulfilling the corresponding requirements, then no change is made. (B, C) show the dynamics for $D = 3$, $\beta = 0.098$, and $N = 100$. Note the MMS for time $t \in [4000, 4800]$. (D) Dynamics of a corresponding $D = 20$ model where the interactions are randomly assigned a strength $r(i, j) \in [0, 1]$ at the start of the simulations. The recruitment of a species j by an active species i , tried in step (r-ii), is then accepted with probability $r(i, j)$. (E) As in (D), but with evolutionary reshuffling of its interactions $r_{i,j}$ each time a population of a species vanishes. Different colors represent different species, with grey dots referring to the IS.

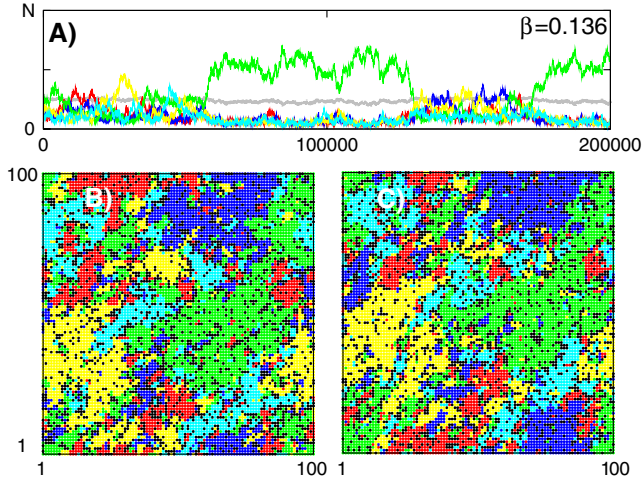


FIG. 5 (color online). Local $D = 5$ model, where species at positions x, y can only convert or recruit at positions $\in [x - 1, x + 1] \times [y - 1, y + 1]$. Simulations are for $N = 100 \times 100$ and $\beta = 0.136$. (A) Population dynamics, with IS shown as grey dots. (B, C) Snapshots of the system separated by $\Delta t = 20$. At a slightly smaller β , the DS dominates and the dynamics show punctuated switching between the dominating species.

Noticeably, the model where one combines a local kill with a global invasion gives a MMS (data not shown). This case may have some relevance for pollinating plants, which in principle could ‘kill’ neighbors, but spread their seed far with the wind.

In case all interactions are local, then even the DS cannot exist in one dimension (data not shown). However, in two dimension, the local version of the model shows punctuated switching between DS of the various active species for a small β . Moreover, Fig. 5 shows that the MMS is marginally sustained in a two-dimensional geometry, as it coexists with a DS for $\beta \in [0.135, 0.136]$. For a higher $D = 100$, the MMS remains fragile. Accordingly, the absence of global interactions in two dimension allows for a multiple competing DS, but weakens the MMS.

Cooperativity.—The MMS can also be obtained in a variant of the model where there is no IS, but where the active modifications instead consist of selecting two sites i and j , and if they are the same species $S_i = S_j = S$, one can recruit a random site k and set $S_k = S$ [8,9]. Its deterministic counterpart

$$\begin{aligned} \frac{dn_i}{dt} &= n_i^2(1 - n_i) - n_i \sum_{j \neq i} n_j^2 + \beta \left(\frac{1}{D} - n_i \right) \\ &= \sum_{j > 0} \left(n_i n_j - \frac{\beta}{D} \right) (n_i - n_j) \end{aligned} \quad (5)$$

supports a DS for $\beta < \frac{D}{4(D-1)}$ and a MMS for $\beta \in [\frac{1}{D}, \frac{D}{4(D-1)}]$.

Interestingly, for $\beta = 0$, $D = 2$, and reduced cooperativity ($n^2 \rightarrow n^{1.3}$), Eq. (5) simplifies to the language competition model of Ref. [31] that was used to describe global decay of language diversity during the last century. Our analysis shows that an appropriate noise or spontaneous fluctuation also allows Eq. (5) to describe metastable coexistence of multiple languages.

Furthermore, a network model proposed in Ref. [27] shows the same multistability features as found here. In that model, agents in the form of vertices on a network are allowed to have one of D opinions each. These opinions are updated by voter dynamics on the network. In addition, agents accept connections with other agents provided they have equal opinions. When links were removed and agents with no connections were assigned new opinions randomly, the model obtained a multistable system with a MMS of disconnected agents. The MMS then correspond to a dissolved society.

Outlook.—We introduced a model where states or species compete and exhibit multistability through combinations of antagonistic conversions. Thereby, we mimic features of bistability, multistability, and transitions between order and mixing in some complex systems.

The model is inspired by recent analysis of nucleosome-mediated epigenetics [7], but can also be considered in the context of a society with antagonistic political factions. In this interpretation, the MMS could correspond to a representative democracy with many balanced interest groups, whereas the extreme states correspond to a one-party system.

The model may also be interpreted in terms of an ecosystem, where the MMS would then represent metastable coexistence of many competing species. The coexistence is sustained even in the absence of spatial constraints. Although the modeled coexistence is primarily maintained by external noise or on-going reintroduction of extinct species, the coexistence also gains stability from a mutual balance. In particular, when the mixed state collapses, the repressed minority species become more vulnerable to extinction. The punctuated collapse of the high-diversity states in Fig. 4(e) may in this sense be seen as aspects of punctuated coevolution [32–34].

Our main finding is the persistence of the MMS for a wide range of parameters and model variants. This robustness is associated to the gap between the population of each species in the MMS and the population it need in order to defeat the sum of ‘‘everybody’’ else. The MMS crucially depends on either a two-step conversion over an intermediate state or on a direct cooperativity in conversion between active species. The robustness of the MMS also requires nonlocality in some of the interactions.

Thanks goes to Ian Dodd, Lin Lu Li, Martin Rosvall, and Steven Rønild for discussions. The study was supported by the Danish National Research Foundation.

*sneppen@nbi.dk

- [1] M. Ptashne and A. Gann, *Genes & Signals* (Cold Spring Harbor Laboratory, New York, 2001), ISBN 0879696338.
- [2] E. Aurell, S. Brown, J. Johanson, and K. Sneppen, *Phys. Rev. E* **65**, 051914 (2002).
- [3] M. Braunstein, R. E. Sobel, C. D. Allis, B. M. Turner, and J. R. Broach, *Mol. Cell. Biol.* **16**, 4349 (1996).
- [4] P. D. Kaufman and O. J. Rando, *Curr. Opin. Cell Biol.* **22**, 284 (2010).
- [5] D. Moazed, *Cell* **146**, 510 (2011).
- [6] A. Angel, J. Song, C. Dean, and M. Howard, *Nature (London)* **476**, 105 (2011).
- [7] I. B. Dodd, M. A. Micheelsen, K. Sneppen, and G. Thon, *Cell* **129**, 813 (2007).
- [8] I. B. Dodd and K. Sneppen, *J. Mol. Biol.* **414**, 624 (2011).
- [9] M. A. Micheelsen, N. Mitarai, K. Sneppen, and I. B. Dodd, *Phys. Biol.* **7**, 026010 (2010).
- [10] M. Sedighi and A. M. Sengupta, *Phys. Biol.* **4**, 246 (2007).
- [11] R. Axelrod, *J. Conflict Resolut.* **41**, 203 (1997).
- [12] K. Klemm, V. M. Eguiluz, R. Toral, and M. San Miguel, *Phys. Rev. E* **67**, 045101(R) (2003).
- [13] C. Castellano, S. Fortunato, and V. Loreto, *Rev. Mod. Phys.* **81**, 591 (2009).
- [14] P. Clifford and A. Sudbury, *Biometrika* **60**, 581 (1973).
- [15] R. A. Holley and T. M. Liggett, *Ann. Probab.* **3**, 643 (1975).
- [16] S. Galam, *Eur. Phys. J. B* **25**, 403 (2002).
- [17] K. Sznajd-Weron and J. Sznajd, *Int. J. Mod. Phys. C* **11**, 1157 (2000).
- [18] P. Chen and S. Redner, *Phys. Rev. E* **71**, 036101 (2005).
- [19] G. Deffuant, D. Neau, F. Amblard, and G. Weisbuch, *Adv. Compl. Syst.* **03**, 87 (2000).
- [20] S. Huet, G. Deffuant, and W. Jager, *Adv. Compl. Syst.* **11**, 529 (2008).
- [21] M. Rosvall and K. Sneppen, *Phys. Rev. E* **79**, 026111 (2009).
- [22] L. Lizana, N. Mitarai, K. Sneppen, and H. Nakanishi, *Phys. Rev. E* **83**, 066116 (2011).
- [23] F. Vazquez, P. L. Krapivsky, and S. Redner, *J. Phys. A* **36**, L61 (2003).
- [24] M. Scheucher and H. Spohn, *J. Stat. Phys.* **53**, 279 (1988).
- [25] J. Xie, S. Sreenivasan, G. Korniss, W. Zhang, C. Lim, and B. K. Szymanski, *Phys. Rev. E* **84**, 011130 (2011).
- [26] X. Castello, A. Baronchelli, and V. Loreto, *Eur. Phys. J. B* **71**, 557 (2009).
- [27] G. C. M. A. Ehrhardt, M. Marsili, and F. Vega-Redondo, *Phys. Rev. E* **74**, 036106 (2006).
- [28] Under the assumption of Eqs. (3) and (4), the fixed point x_- becomes stable for $\beta \leq \beta_M$. However, without constraint of $n_2 = n_3 = \dots = n_D$ this solution is unstable.
- [29] M. A. Riley and E. Wertz, *Annu. Rev. Microbiol.* **56**, 117 (2002).
- [30] J. Mathiesen, N. Mitarai, K. Sneppen, and A. Trusina, *Phys. Rev. Lett.* **107**, 188101 (2011).
- [31] D. Abrams and S. Strogatz, *Nature (London)* **424**, 900 (2003).
- [32] G. G. Simpson, *The Major Features of Evolution* (Oxford University Press, Oxford, 1953).
- [33] S. J. Gould and N. Eldredge, *Paleobiology* **3**, 115 (1977).
- [34] K. Sneppen, P. Bak, H. Flyvbjerg, and M. H. Jensen, *Proc. Natl. Acad. Sci. U.S.A.* **92**, 5209 (1995).