

# Global asymptotic coherence in discrete dynamical systems

David J. D. Earn\*<sup>†</sup> and Simon A. Levin\*<sup>‡</sup>

\*Department of Mathematics and Statistics, McMaster University, Hamilton, ON, Canada L8S 4K1; and <sup>‡</sup>Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544-1003

Contributed by Simon A. Levin, December 20, 2005

**Spatial synchrony (coherence) in dynamical systems is of both theoretical and applied importance. We address this problem for a generalization of coupled map lattices (CMLs). In the systems we study, which we term “meta-CMLs,” the map at each lattice point may be multidimensional (corresponding, for example, to multi-species ecological systems in which all species have the same dispersal pattern). Most previous work on coherence of CMLs has focused on local stability. Here, we prove a global theorem that provides a useful sufficient condition guaranteeing decay of incoherence in meta-CMLs regardless of initial conditions and regardless of the nature of the attractors of the system. This result facilitates useful analyses of a variety of applied problems, including conservation of endangered species and eradication of pests or infectious diseases.**

synchrony | synchronization | global stability | metapopulation dynamics

The simplest possible solutions of dynamical systems with spatial degrees of freedom are coherent (spatially homogeneous), so investigation of coherent solutions is usually the starting point of any mathematically rigorous study. Real-world applications of such analyses abound. For example, in ecological settings, if a species has low population density everywhere simultaneously then it is at risk of global extinction; spatially coherent population dynamics may therefore be associated with extinction risk (1). In epidemiology, coherence may facilitate eradication of pathogens (2). In neurobiology, coherence is associated with neuropathologies such as epilepsy (3–5). In economics, coherence may be stimulated by globalization of markets. The list goes on, including diverse areas of science, engineering, and social science.

Coupled map lattices (CMLs) provide a simple framework for investigation of spatial dynamical processes (6). CMLs are built from iterated discrete maps (7–10),

$$x^{t+1} = F(x^t), \quad t = 0, 1, 2, \dots, \quad [1]$$

such as the (normalized) logistic map,

$$F(x) = rx(1 - x), \quad x \in [0, 1]. \quad [2]$$

In general, given a fundamental state space  $X$  and a fundamental map  $F : X \rightarrow X$ , a CML is defined via

$$x_i^{t+1} = \sum_{j=1}^n m_{ij} F(x_j^t), \quad i = 1, \dots, n, \quad t = 0, 1, 2, \dots, \quad [3]$$

where  $x_i^t \in X$  is the state at lattice point  $i$  at time  $t$ ,  $M = (m_{ij})$  is the “connectivity matrix” and  $n$  is the number of lattice points. Letting  $\vec{x} = (x_1, \dots, x_n)^\top \in X^n$ , we define the “full map”  $\vec{F} : X^n \rightarrow X^n$  via

$$\vec{F}(\vec{x}) = \begin{pmatrix} \sum_{j=1}^n m_{1j} F(x_j) \\ \vdots \\ \sum_{j=1}^n m_{nj} F(x_j) \end{pmatrix} = M \cdot \begin{pmatrix} F(x_1) \\ \vdots \\ F(x_n) \end{pmatrix}. \quad [4]$$

For convenience, we define the abbreviated notation  $F(\vec{x})$  for the vector  $(F(x_1), \dots, F(x_n))^\top \in X^n$ , so the full map can be written

$$\vec{F}(\vec{x}) = M \cdot F(\vec{x}). \quad [5]$$

Thus, the trajectories of the CML (Eq. 3) are the sequences of points  $\vec{x}^t = \vec{F}^t(\vec{x}^0)$ , where  $\vec{F}^t(\vec{x}) = \vec{F}(\vec{F}^{t-1}(\vec{x}))$  for  $t \geq 1$  and  $\vec{F}^0(\vec{x}) = \vec{x}$ .

A CML is in a “coherent state” at time  $t$  if  $x_i^t = x_j^t$  for all  $i$  and  $j$ . A coherent solution is a sequence of coherent states that satisfies Eq. 3 or, equivalently, Eq. 5. We are thinking of a CML as a spatial generalization of the fundamental map, so we want to retain the trajectories of the fundamental map as coherent solutions of the corresponding CML. This occurs if and only if

$$\sum_{j=1}^n m_{ij} = 1, \quad i = 1, \dots, n, \quad [6]$$

i.e., each row of  $M$  sums to 1; equivalently, if we define the  $n$ -dimensional vector  $e = (1, 1, \dots, 1)^\top$  then

$$M \cdot e = e, \quad [7]$$

i.e.,  $e$  is an eigenvector of  $M$  with eigenvalue 1. Eqs. 6 and 7 are equivalent to the statement that if  $x^t$  is a solution of Eq. 1 then  $\vec{x}^t = x^t e$  is a coherent trajectory of the full map (Eq. 5).

In an ecological setting, a CML is known as a “metapopulation model” (11), because it represents a system of isolated patches, within which individuals reproduce and between which they disperse:  $x_i^t$  is the population density in patch  $i$  at time  $t$  and  $M$  is the “dispersal matrix.” In this case, the fundamental map  $F$  is called the “reproduction function.”

Dispersal matrices must be nonnegative, so we restrict attention to nonnegative connectivity matrices  $M$  that satisfy Eq. 6; such matrices are said to be “stochastic” because each row of  $M$  can be considered to be a discrete probability distribution on a sample space with  $n$  points (12). Eq. 6 may seem to preclude the possibility of death during migration in the ecological context, but this effect can always be included implicitly by absorbing an overall factor into the reproduction function  $F$ .

Research on coherence in CMLs has traditionally begun with the assumption that the state variables  $x_i$  and the fundamental map  $F$  are one-dimensional. A single dimension is certainly sufficient to generate rich dynamical structure, but is too restrictive to cover many important application areas. In the ecological setting, if the population is classified according to species, age, or other factors, then  $x_i$  becomes a vector of densities in the various classes, and  $F$  becomes a multidimensional map. Similarly, in epidemiology,  $x_i$  is a vector of densities

Conflict of interest statement: No conflicts declared.

Abbreviations: CML, coupled map lattice; GAC, global asymptotic coherence.

<sup>†</sup>To whom correspondence may be addressed. E-mail: earn@math.mcmaster.ca or slevin@princeton.edu.

© 2006 by The National Academy of Sciences of the USA

of individuals in each of a set of epidemiologic compartments (e.g., susceptible, infectious, recovered). With such models in mind, we define a “meta-CML” via Eq. 3 or 5 but with  $X$  a multidimensional state space.

When describing computations with meta-CMLs, it is often convenient to use notation that would be appropriate if  $X$  were one-dimensional, with the understanding that each component of a vector  $\vec{x} \in X^n$  is itself a vector  $x_i \in X$ . For example, writing the  $n$ -dimensional coherent unit vector  $\hat{e} = e/\|e\| \in \mathbb{R}^n$ , we use the notation  $\vec{x} \cdot \hat{e}$  to denote the “coherent component” of the state vector  $\vec{x} \in X^n$ , i.e.,

$$\vec{x} \cdot \hat{e} = \sum_{i=1}^n x_i \hat{e}_i = \frac{1}{\sqrt{n}} \sum_{i=1}^n x_i. \quad [8]$$

Since each  $x_i$  is a vector in  $X$ , the result of the dot product is also a vector. The “mean field” of  $\vec{x}$  is

$$\langle \vec{x} \rangle = \frac{1}{n} \sum_{i=1}^n x_i. \quad [9]$$

Again, like each  $x_i$ ,  $\langle \vec{x} \rangle \in X$  so it is a vector if  $\dim X > 1$ . Note also that

$$(\vec{x} \cdot \hat{e})\hat{e} = \frac{\vec{x} \cdot e}{\|e\|^2} e = \left( \frac{1}{n} \sum_{i=1}^n x_i \right) e = \langle \vec{x} \rangle e. \quad [10]$$

Thus, at any time  $t$ , the coherent component of  $\vec{x}^t$  corresponds to the state with the mean field in each patch. We shall say that a trajectory  $\{\vec{x}^t\}$  “relaxes to coherence” or that it is “asymptotically coherent” if  $\|\vec{x}^t - \langle \vec{x}^t \rangle e\| \rightarrow 0$  as  $t \rightarrow \infty$  (and “asymptotically incoherent” otherwise). We refer to  $\vec{x}^t - \langle \vec{x}^t \rangle e$  as the “incoherent component” of  $\vec{x}^t$ . Note that relaxation to coherence does not imply approach to an equilibrium; a coherent attractor can be periodic, quasiperiodic, or chaotic.

In the next section we briefly comment on local analyses of coherent trajectories in CMLs, which relate to the question of possibility or impossibility of coherence in practice. In ecological applications it is particularly important if a metapopulation relaxes to coherence regardless of initial conditions, because substantial extinction risk may then be unavoidable (1). It is this situation of inevitable synchrony or “global asymptotic coherence” that is our primary concern here. A slightly restricted version of the main result we present here was stated informally without proof in ref. 1, in which applications to conservation biology were emphasized.

### Local Stability of Coherence

In recent years, numerous studies have given local stability conditions for coherence in CMLs with specific classes of connectivity matrices (13–17). All of these results are subsumed by a proposition that we stated informally in ref. 1. A rigorous statement and proof of this proposition requires careful consideration of all ergodic invariant measures associated with the dynamical system (18, 19) and we defer a rigorous presentation of the local theory to another work (D.J.D.E., S.A.L., and D. A. Rand, unpublished results). Here, we briefly outline some key elements of the local results in order to provide context to the global analysis that we present below.

Consider an attractor  $\mathcal{A}$  of the fundamental map  $F$  and define the coherent set  $\mathcal{A}e = \{xe : x \in \mathcal{A}\}$ . The set  $\mathcal{A}e$  is invariant under the full map  $\vec{F}$  and, restricted to the coherent manifold,  $\mathcal{A}e$  is an attractor. The local theory establishes conditions under which  $\mathcal{A}e$  is also an attractor of  $\vec{F}$  in a neighborhood of  $\mathcal{A}e$  in  $X^n$ . The details of this theory are complicated (19), but the key points can be

expressed in rough terms through the local stability condition that we described in ref. 1.

The local stability condition depends primarily on two quantities. The first is the magnitude of (any) subdominant eigenvalue of the connectivity matrix  $M$  (an eigenvalue is subdominant if its magnitude is second largest among all eigenvalues). The second is the maximum Lyapunov characteristic exponent of the fundamental map  $F$  at a point  $x \in X$ , which can be defined as

$$\chi_x = \limsup_{T \rightarrow \infty} \frac{1}{T} \sum_{i=0}^T \log \|D_{F^i(x)} F\|. \quad [11]$$

The exponent  $\chi_x$  characterizes the dynamical nature of the trajectory of  $F$  that starts at  $x$ . If we restrict attention to “typical” points on an attractor  $\mathcal{A}$  of  $F$ , then, if we ignore subtleties, we can drop the dependence of  $\chi_x$  on  $x$  and characterize typical trajectories on  $\mathcal{A}$  by a single number  $\chi$  (this is an oversimplification, but it will allow us to get across the essence of the local stability condition without getting bogged down in details).

In addition to requiring that the connectivity matrix  $M$  be stochastic (and hence that 1 is an eigenvalue of  $M$ ), we require that the eigenvalue 1 be simple (i.e., has multiplicity 1) and strictly dominant (all other eigenvalues have magnitude strictly less than 1). Suppose that  $\lambda$  is a subdominant eigenvalue of  $M$  and that  $\chi$  is the maximum Lyapunov characteristic exponent for typical trajectories on an attractor  $\mathcal{A}$  of the fundamental map  $F$ . If

$$\log |\lambda| + \chi > 0, \quad [12]$$

then coherence is (in practice) impossible: almost all nearly coherent points  $\vec{x}$  near  $\mathcal{A}e$  lie on asymptotically incoherent trajectories. If instead

$$\log |\lambda| + \chi < 0, \quad [13]$$

then coherence is possible: most nearly coherent points that are sufficiently close to  $\mathcal{A}e$  lie on asymptotically coherent trajectories (making “most” precise here is complicated).

The stability condition (Eq. 13) is local not only in requiring that an initial point  $\vec{x}$  be nearly coherent ( $\|\vec{x} - \langle \vec{x} \rangle e\|$  must be small) but also in requiring that the coherent component of  $\vec{x}$  be close to an attractor  $\mathcal{A}$  of  $F$  ( $\langle \vec{x} \rangle$  must be close to  $\mathcal{A}$ ). The theorem we present in the next section is extreme in the opposite sense: it applies to all initial states and makes no reference to particular attractors of the system. Intermediate to these two extremes is the theory of normally hyperbolic invariant manifolds (20, 21), which could be used to develop stability conditions that apply to all coherent states (i.e., this would address the local stability of the entire coherent manifold as opposed to local stability of a coherent invariant set that is an attractor for the system restricted to the coherent manifold).

### Global Asymptotic Coherence (GAC)

Consider first the simplest possible case: a one-dimensional fundamental state space  $X$  (an interval) and only two lattice points (“patches”). The most general  $2 \times 2$  stochastic matrix has the form

$$M = \begin{pmatrix} 1-m_1 & m_1 \\ m_2 & 1-m_2 \end{pmatrix}, \quad [14]$$

where  $m_1, m_2 \in [0, 1]$ . Using a prime to denote the next iteration of the map, we have

$$x'_1 = m_1 F(x_1) + (1 - m_1) F(x_2), \quad [15a]$$

$$= F(x_2) + m_1 [F(x_1) - F(x_2)], \quad [15b]$$

$$x'_2 = m_2 F(x_2) + (1 - m_2) F(x_1), \quad [15c]$$

$$= F(x_1) - m_2 [F(x_1) - F(x_2)], \quad [15d]$$

and hence

$$x'_2 - x'_1 = -[1 - (m_1 + m_2)][F(x_2) - F(x_1)]. \quad [16]$$

We shall assume that the fundamental map  $F$  is differentiable, so the mean value theorem implies that there exists  $\xi$  between  $x_1$  and  $x_2$  such that  $F(x_2) - F(x_1) = F'(\xi)(x_2 - x_1)$ . If, moreover,  $F'$  is bounded (say  $r = \sup_{x \in X} |F'(x)|$ ) then for any  $x_1, x_2 \in X$ , we have

$$|x'_2 - x'_1| \leq |1 - (m_1 + m_2)| r |x_2 - x_1|. \quad [17]$$

If  $|1 - (m_1 + m_2)| r < 1$  then the difference between the states at each of the lattice points will decrease to zero asymptotically, regardless of the initial conditions. Thus,  $|1 - (m_1 + m_2)| r < 1$  is a sufficient condition for GAC in this simple model.

Now note that the eigenvalues of  $\mathbf{M}$  are 1 and  $\lambda = 1 - (m_1 + m_2)$ , and  $|\lambda| \leq 1$ . In fact, unless  $m_1 = m_2 = 0$  (in which case  $\mathbf{M}$  is the identity matrix) or  $m_1 = m_2 = 1$  (in which case the state at each of the two lattice points is simply swapped at each iteration),  $|\lambda| < 1$ . In these two special cases in which  $|\lambda| = 1$  (so  $\lambda$  is not subdominant) there is actually no connectivity between the two lattice points. If we exclude these cases, we can express the GAC condition as  $|\lambda| r < 1$ , where  $\lambda$  is the subdominant eigenvalue of  $\mathbf{M}$ . This observation motivates our formulation of *Theorem 1* below.

Before stating the theorem, we recall a few definitions. The segment joining two points  $x$  and  $y$  in a vector space is the set  $S_{x,y} = \{\alpha x + (1 - \alpha)y : 0 \leq \alpha \leq 1\}$ . A subset  $X$  of a vector space is convex if for any two points  $x, y \in X$  the segment  $S_{x,y}$  is contained in  $X$ . A Banach space is a complete, normed vector space. Given the norm  $\|\cdot\|$  on a Banach space  $\mathcal{B}$ , the norm of a function  $F : \mathcal{B} \rightarrow \mathcal{B}$  is

$$\|F\| = \sup\{\|F(x)\| : x \in \mathcal{B}, \|x\| = 1\}. \quad [18]$$

Where it exists, the derivative of  $F$  at  $x \in \mathcal{B}$  is the unique continuous linear transformation  $D_x F : \mathcal{B} \rightarrow \mathcal{B}$  with the property that

$$\lim_{h \rightarrow 0} \frac{F(x+h) - F(x) - D_x F h}{\|h\|} = 0, \quad [19]$$

where the limit is taken over all nonzero sequences that converge to zero.

**Theorem 1.** *Let  $X$  be a convex subset of a Banach space  $\mathcal{B}$  and suppose the fundamental map  $F : X \rightarrow X$  is differentiable at each  $x \in X$ , that  $\|D_x F\|$  is bounded in  $X$ , and that  $r = \sup_{x \in X} \|D_x F\|$ . Suppose  $\mathbf{M}$  is a stochastic  $n \times n$  matrix, the eigenvalue 1 is simple and strictly dominant, and  $\lambda$  is a subdominant eigenvalue of  $\mathbf{M}$ . If  $r|\lambda| < 1$  then the full map  $\tilde{F} : X^n \rightarrow X^n$ , defined by  $\tilde{F}(\tilde{x}) = \mathbf{M} \cdot F(\tilde{x})$ , is globally asymptotically coherent, i.e., every initial state  $\tilde{x}_0 \in X^n$  asymptotically approaches a coherent trajectory. If  $r < 1$  then  $\tilde{F}$  has a globally asymptotically stable fixed point.*

Usually the fundamental state space  $X$  is a subset of  $\mathbb{R}^k$ , but the theorem is valid for any  $X$  that is a convex subset of any Banach space. This extension to arbitrary dimensionality is a potentially useful generalization of the result as stated in ref. 1, because  $X$  can now represent, for example, a continuum of ages or continuous space, or both.

Note that from the definition of the maximum Lyapunov exponent (Eq. 11), we must have  $\chi_x \leq \log r$  for all  $x \in X$  (where  $r$  is defined in the statement of *Theorem 1*). Given the local coherence condition (Eq. 13) discussed in the previous section,

this observation increases the plausibility of *Theorem 1*. Our proof, however, does not rely in any way on the local theory.

### Proof of Theorem 1

Our proof of *Theorem 1* depends on two propositions that we state as lemmas. The first is a special case of a standard result of analysis, while the second expresses a useful algebraic property of stochastic matrices.

**Lemma 1 (The Mean Value Inequality).** *Suppose  $\mathcal{B}$  is a Banach space and  $S_{x,y}$  is the segment joining  $x, y \in \mathcal{B}$ . If  $F$  is a continuous mapping of a neighborhood of  $S_{x,y}$  into  $\mathcal{B}$ , and  $F$  is differentiable at every point of  $S_{x,y}$ , then*

$$\|F(x) - F(y)\| \leq r_{x,y} \|x - y\|, \quad [20]$$

where  $r_{x,y} = \sup_{z \in S_{x,y}} \|D_z F\|$ .

*Proof:* See Dieudonné (22), proposition 8.5.4, p. 160.

**Lemma 2.** *Let  $\mathbf{M} = (m_{ij})$  be an  $n \times n$  stochastic matrix and suppose the eigenvalues of  $\mathbf{M}$ , including multiplicities, are  $(\lambda_1, \lambda_2, \dots, \lambda_{n-1}, 1)$ . Let  $\tilde{\mathbf{M}} = (\tilde{m}_{ij})$  be the  $(n-1) \times (n-1)$  matrix defined via  $\tilde{m}_{ij} = m_{ij} - m_{nj}$  for  $i, j = 1, \dots, n-1$ . Then the eigenvalues of  $\tilde{\mathbf{M}}$  are  $(\lambda_1, \lambda_2, \dots, \lambda_{n-1})$ .*

*Proof:* Let  $\mathbf{A}$  be the  $n \times n$  matrix with 1s on the diagonal and along the last column, and zeros elsewhere. It is easily verified that  $\mathbf{A}^{-1}$  is the matrix with ones on the diagonal,  $-1$ s above the diagonal in the last column, and zeros elsewhere. If we define  $\mathbf{B} = \mathbf{A}^{-1} \mathbf{M} \mathbf{A}$  then  $\mathbf{B}$  and  $\mathbf{M}$  are similar matrices so they have exactly the same spectrum (12). But the submatrix consisting of the first  $n-1$  rows and columns of  $\mathbf{B}$  is  $\tilde{\mathbf{M}}$ , and (using stochasticity of  $\mathbf{M}$ ) the last column of  $\mathbf{B}$  is zero except in its last entry, which is 1. Consequently, the eigenvalues of  $\mathbf{B}$  (and hence of  $\mathbf{M}$ ) are the eigenvalues of  $\tilde{\mathbf{M}}$  together with 1.

*Proof of Theorem 1:* It is convenient to express the map (Eq. 3) as follows (where prime denotes one iteration of the map):

$$x'_i - x'_n = \sum_{j=1}^n (m_{ij} - m_{nj}) F(x_j), \quad i = 1, \dots, n-1, \quad [21a]$$

$$x'_n = \sum_{j=1}^n m_{nj} F(x_j). \quad [21b]$$

Now, since  $\sum_{j=1}^n m_{ij} = \sum_{j=1}^n m_{nj} = 1$ , we have  $\sum_{j=1}^n (m_{ij} - m_{nj}) = 0$ , so we can rewrite Eq. 21a above as

$$x'_i - x'_n = \sum_{j=1}^n (m_{ij} - m_{nj}) [F(x_j) - F(x_n)], \quad i = 1, \dots, n-1. \quad [22]$$

With  $\tilde{\mathbf{M}}$  defined as in Lemma 2, we can write Eq. 22

$$\begin{pmatrix} x'_1 - x'_n \\ x'_2 - x'_n \\ \vdots \\ x'_{n-1} - x'_n \end{pmatrix} = \tilde{\mathbf{M}} \cdot \begin{pmatrix} F(x_1) - F(x_n) \\ F(x_2) - F(x_n) \\ \vdots \\ F(x_{n-1}) - F(x_n) \end{pmatrix}. \quad [23]$$

Given the norm on  $\mathcal{B}$ , we can define a norm on  $\mathcal{B}^n$  in many ways, for example via  $\|\tilde{x}\| = \max_{i=1}^n \|x_i\|$  (we use  $\|\cdot\|$  to denote norms on both  $\mathcal{B}$  and  $\mathcal{B}^n$  with meaning hopefully clear from context). Adopting this particular norm on  $\mathcal{B}^n$  for convenience, Lemma 1 implies (since  $r_{x,y} \leq r$  for all  $x, y \in X$ ) that



# Corrections and Retraction

## CORRECTIONS

**APPLIED MATHEMATICS, POPULATION BIOLOGY.** For the article “Global asymptotic coherence in discrete dynamical systems,” by David J. D. Earn and Simon A. Levin, which appeared in issue 11, March 14, 2006, of *Proc Natl Acad Sci USA* (103:3968–3971; first published March 7, 2006; 10.1073/pnas.0511000103), the authors note that on page 3971, inequality 25 holds only for particular classes of matrices  $\mathbf{M}$ , and strict inequality never holds (Theorem 5.6.9, page 297 of ref. 12). The authors are grateful to Jinhu Lü for recognizing this error. The argument given in the paper proves the following revised version of *Theorem 1* (page 3970).

**Theorem 1.** Let  $X$  be a convex subset of a Banach space  $\mathcal{B}$ , and suppose the fundamental map  $F : X \rightarrow X$  is differentiable at each  $x \in X$ . Suppose that  $\|D_x F\|$  is bounded in  $X$ , and let  $r = \sup_{x \in X} \|D_x F\|$ . Suppose  $\mathbf{M}$  is a stochastic  $n \times n$  matrix, and define  $\tilde{\mathbf{M}}$  as in Lemma 2. Let  $\|\cdot\|$  be any matrix norm for which there exists a compatible monotone vector norm, and let  $\mu = \|\tilde{\mathbf{M}}\|$ . If  $r\mu < 1$ , then the full map  $\tilde{F} : X^n \rightarrow X^n$ , defined by  $\tilde{F}(\tilde{x}) = \mathbf{M} \cdot F(\tilde{x})$ , is globally asymptotically coherent, i.e., every initial state  $\tilde{x}_0 \in X^n$  asymptotically approaches a coherent trajectory. If  $r < 1$ , then  $\tilde{F}$  has a globally asymptotically stable fixed point.

The authors note that all  $l_p$  norms are monotone, so the matrix norm  $\|\cdot\|$  in the theorem can, for example, be taken to be any matrix norm induced by an  $l_p$  vector norm. The simplest examples are the maximum column sum and maximum row sum matrix norms, which are induced by the  $l_1$  and  $l_\infty$  vector norms, respectively. The original statement of *Theorem 1* is valid for some classes of matrices (for example, if  $\tilde{\mathbf{M}}$  is normal or triangular) but may not be true in the generality stated. In applications, the matrix  $\mathbf{M}$  will almost always be primitive; if  $\mathbf{M}$  is not primitive, then  $\mu \geq 1$ , in which case the theorem has nontrivial content only in the situation where  $r < 1$ .

The authors also note the following typographical errors, which do not affect the conclusions of the article. On page 3968, Eq. 7 should read: “ $\mathbf{M} \cdot \mathbf{e} = \mathbf{e}$ .” On page 3969, Eq. 14 should read:

$$\mathbf{M} = \begin{pmatrix} m_1 & 1 - m_1 \\ 1 - m_2 & m_2 \end{pmatrix}, \quad [14]$$

and on page 3970, left column, first full paragraph, “unless  $m_1 = m_2 = 0 \dots$  or  $m_1 = m_2 = 1$ ” should read: “unless  $m_1 = m_2 = 1 \dots$  or  $m_1 = m_2 = 0$ .” On page 3971, in Eq. 24d, there should be no primes (e.g., “ $x'_1 - x'_n$ ” should read: “ $x_1 - x_n$ ”).

www.pnas.org/cgi/doi/10.1073/pnas.0609526103

**CHEMISTRY.** For the article “Dewetting-induced collapse of hydrophobic particles,” by X. Huang, C. J. Margulis, and B. J. Berne, which appeared in issue 21, October 14, 2003, of *Proc Natl Acad Sci USA* (100:11953–11958; first published September 24, 2003; 10.1073/pnas.1934837100), the authors note that on page 11953, right column, eighth line from the bottom, “ $\varepsilon = 592.5$  cal/mol” should read: “ $4\varepsilon = 592.5$  cal/mol.” This error does not affect the conclusions of the article.

www.pnas.org/cgi/doi/10.1073/pnas.0609680103

**MICROBIOLOGY.** For the article “Evolution of sensory complexity recorded in a myxobacterial genome,” by B. S. Goldman, W. C. Nierman, D. Kaiser, S. C. Slater, A. S. Durkin, J. Eisen, C. M. Ronning, W. B. Barbazuk, M. Blanchard, C. Field, C. Halling, G. Hinkle, O. Iartchuk, H. S. Kim, C. Mackenzie, R. Madupu, N. Miller, A. Shvartsbeyn, S. A. Sullivan, M. Vaudin, R. Wiegand, and H. B. Kaplan, which appeared in issue 41, October 10, 2006, of *Proc Natl Acad Sci USA* (103:15200–15205; first published October 2, 2006; 10.1073/pnas.0607335103), the author name J. Eisen should have appeared as J. A. Eisen. The online version has been corrected. The corrected author line appears below.

**B. S. Goldman, W. C. Nierman, D. Kaiser, S. C. Slater, A. S. Durkin, J. A. Eisen, C. M. Ronning, W. B. Barbazuk, M. Blanchard, C. Field, C. Halling, G. Hinkle, O. Iartchuk, H. S. Kim, C. Mackenzie, R. Madupu, N. Miller, A. Shvartsbeyn, S. A. Sullivan, M. Vaudin, R. Wiegand, and H. B. Kaplan**

www.pnas.org/cgi/doi/10.1073/pnas.0609567103

**BIOCHEMISTRY.** For the article “Enzyme–microbe synergy during cellulose hydrolysis by *Clostridium thermocellum*,” by Yanpin Lu, Yi-Heng Percival Zhang, and Lee R. Lynd, which appeared in issue 44, October 31, 2006, of *Proc Natl Acad Sci USA* (103:16165–16169; first published October 23, 2006; 10.1073/pnas.0605381103), the authors note that on page 16167, at the top of the right column, the references to steady states 1 and 2 are switched, as may be seen from inspection of Table 1. The corrected text should read: “In continuous culture, a  $DS_{EM}^{ET}$  value of 2.72 is obtained based on microbial and SSF steady states 2, for which  $\approx 75\%$  of the feed cellulose was hydrolyzed. For microbial and SSF steady states 1, for which  $\approx 66\%$  hydrolysis was achieved,  $DS_{EM}^{ET} = 4.70$ . Values for enzyme–microbe synergy on a pellet cellulase basis,  $DS_{EM}^{EP}$ , are quite similar to values observed in continuous culture: 3.05 for microbial and SSF steady states 2 and 4.61 for microbial and SSF steady states 1.” This error does not affect the conclusions of the article.

www.pnas.org/cgi/doi/10.1073/pnas.0609576103

**MEDICAL SCIENCES.** For the article “Human cancers express a mutator phenotype,” by Jason H. Bielas, Keith R. Loeb, Brian P. Rubin, Lawrence D. True, and Lawrence A. Loeb, which appeared in issue 48, November 28, 2006, of *Proc Natl Acad Sci USA* (103:18238–18242; first published November 15, 2006; 10.1073/pnas.0607057103), several references to nucleotide instability (NIN) should have appeared as point mutation instability (PIN). On page 18238, in the key terms, “nucleotide instability (NIN)” should be replaced with “point mutation instability (PIN).” On page 18239, in the last sentence of the first paragraph of the *Discussion*, “nucleotide instability or NIN” should read: “point mutation instability or PIN.” Last, on page 18239, in the last sentence of the second paragraph of the *Discussion*, “an increase in NIN” should read: “an increase in PIN.” The online version has been corrected. These errors do not affect the conclusions of the article.

www.pnas.org/cgi/doi/10.1073/pnas.0610370103