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Stochastic Processes and Mean Field Systems Defined by Nonlinear Markov Chains: An Illustration for a Model of Evolutionary Population Dynamics

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Abstract In physics, there is a growing interest in studying stochastic processes described by evolution equations such as nonlinear master equations and nonlinear Fokker–Planck equations that define the so-called nonlinear Markov processes and are nonlinear with respect to probability densities. In this context, however, relatively little is known about nonlinear Markov processes defined by nonlinear Markov chains. In the present work, we demonstrate explicitly how the nonlinear Markov chain approach can be carried out by addressing a model for evolutionary population dynamics. In line with the nonlinear Markov chain approach, we derive a measure that tells us how attractive it is for a biological entity to evolve towards a particular biological type. Likewise, a measure for the noise level of the evolutionary process is obtained. Both measures are found to be implicitly time dependent. Finally, a simulation scheme for the many-body system corresponding to the Markov chain model is discussed.

Keywords Population dynamics · Markov process · Attractor strength · Noise level

1 Introduction

The key characteristics of nonlinear Markov processes is that they exhibit conditional transition probabilities that depend on occupation probabilities. In contrast, conditional probabilities of linear (ordinary) Markov processes do not exhibit such dependencies. Nonlinear Markov processes have been introduced in the mathematical literature by McKean Jr. [1, 2]. In physics, nonlinear Markov processes have primarily been studied in the context of nonlinear master equations and nonlinear Fokker–Planck equations [3–28] (for reviews, see e.g., [29, 30])—in particular with applications to nonextensive thermostatics [31, 32] and q -Gaussian distributions (for a review, see [33]). Although recently, some research has been conducted in the field of nonlinear Markov chains [34–36], our understanding of nonlinear Markov chain modeling is still limited.

The objective of the present study is to address evolutionary population dynamics from the perspective of nonlinear Markov processes in general and nonlinear Markov chains in particular. By studying evolutionary population dynamic from a nonlinear Markov perspective, we increase the scope of nonlinear Markov chain modeling and obtain new insights into the interpretation of nonlinear models of this kind (Section 2.1). In addition, we will obtain a model for evolutionary population dynamic that is closely related to the so-called meta-model proposed earlier [37, 38] (rooted in

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the theory of computational mechanics [39]) but also has its own peculiarities (Sections 2.2 and 2.3).

2 Nonlinear Markov Chain Modeling of Evolutionary Population Dynamic

2.1 From the Meta-Model to the Nonlinear Markov Chain Model

The meta-model considers a biological system composed of units (entities) that differ in type $k = 1, \dots, M$ [37, 38]. Due to interactions between the units, changes in type occur. As illustrated in Fig. 1, a unit of type j may affect a unit of type i such that the unit of type i becomes a unit of type k . In short, we are interested in modeling transitions from types i to k involving the impact of units of type j . The interaction matrix is denoted by $g(k|ij)$ and is semi-positive definite. The matrix is not necessarily symmetric with respect to the indices i and j meaning that the interactions under consideration do not necessarily exhibit a symmetry property. In what follows, we will assume that the interaction matrix satisfies $\sum_{k=1}^M g(k|ij) = 1$. In this case, the meta-model for evolutionary population dynamic [37, 38] can be studied from the perspective of nonlinear Markov processes—as will be shown next.

Let $\lambda_i(n)$ with $i = 1, \dots, M$ denote the probabilities to find units of type i in a biological system of interest at time step n ($n = 1, 2, 3, \dots$). According to the meta-model, the probabilities evolve like [37, 38]

$$\lambda_k(n+1) = \sum_{i,j=1}^M g(k|ij) \lambda_i(n) \lambda_j(n). \quad (1)$$

Fig. 1 Evolutionary transition from type i to k involving the impact of a unit of type j

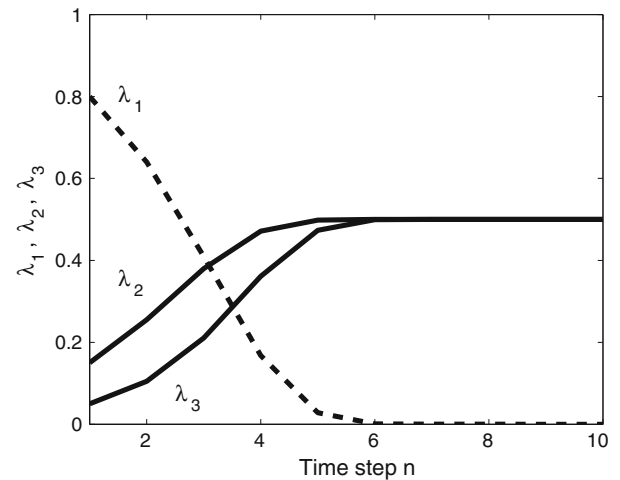
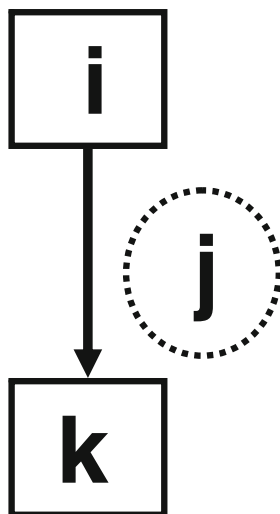


Fig. 2 From top to bottom: probabilities λ_1 (dashed line), λ_2 and λ_3 (solid lines) as functions of time n computed from Eqs. 1 and 4

On the other hand, the evolution of the distribution $\{\lambda_1, \dots, \lambda_M\}$ according to a nonlinear Markov chain is defined by [34–36]

$$\lambda_k(n+1) = \sum_i T_{ki}(\lambda_1(n), \dots, \lambda_M(n)) \lambda_i(n), \quad (2)$$

where T_{ki} are the coefficients of the conditional probability matrix of the process at hand. The coefficients T_{ki} satisfy $T_{ki} \geq 0$ and $\sum_{k=1}^M T_{ki} = 1$ and depend on the distribution $\{\lambda_1, \dots, \lambda_M\}$. Comparing Eqs. 1 and 2, we put

$$T_{ki} = \sum_{j=1}^M g(k|ij) \lambda_j(n). \quad (3)$$

In this case, the Markov chain model (2) corresponds to the meta-model (Eq. 1). Moreover, from $\sum_{k=1}^M g(k|ij) = 1$ it follows that the assumption $\sum_{k=1}^M T_{ki} = 1$ holds.

Let us illustrate the evolutionary dynamic described in Eq. 1 for a biological system with $M = 3$ different types of units and an interaction matrix [38]

$$g(1|\cdot) = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}, \quad g(2|\cdot) = \begin{pmatrix} 0 & 1 & 0 \\ 1 & 0 & 1 \\ 0 & 1 & 0 \end{pmatrix}, \quad (4)$$

$$g(3|\cdot) = \begin{pmatrix} 0 & 0 & 1 \\ 0 & 1 & 0 \\ 1 & 0 & 1 \end{pmatrix}.$$

Figure 2 depicts a simulation of Eq. 1 for initial distribution $\{\lambda_1, \lambda_2, \lambda_3\} = (0.80, 0.15, 0.05)$. The stationary distribution is $\{\pi_1, \pi_2, \pi_3\} = (0, 0.5, 0.5)$ (see also, [38]; note that by substituting $\{\pi_1, \pi_2, \pi_3\} = (0, 0.5, 0.5)$ together with Eq. 4 into Eq. 1, we see analytically that

$\{\pi_1, \pi_2, \pi_3\}$ is indeed a stationary distribution). The nonlinear Markov chain model (Eq. 2) involves its own peculiarities. First, attractor strength of the biological types and the noise level of the evolutionary process can be defined. Second, trajectories of the evolutionary process can be computed that in turn can be used to calculate expectation values and joint probabilities.

2.2 Attractor Strength and Noise Level

The “evolutionary pressure” to evolve towards a particular type or in other words the strength of attraction of evolving towards a particular type can be defined in terms of the matrix elements T_{ki} by [35]

$$\gamma_k = \frac{1}{M} \sum_{i=1}^M T_{ki}. \quad (5)$$

The variables γ_k for attractor strength are semi-positive definite and add up to unity: $\sum_{k=1}^M \gamma_k = 1$. Since T_{ki} depends on the probabilities λ_k , we see that the variables γ_k depend on these probabilities as well. In the stationary case, we obtain

$$\gamma_{k,st} = \frac{1}{M} \sum_{i=1}^M T_{ki}(\pi_1, \dots, \pi_M). \quad (6)$$

For the example mentioned above involving the matrices (Eq. 4), we obtain

$$T(\lambda_1, \lambda_2, \lambda_3) = \begin{pmatrix} \lambda_1 & 0 & 0 \\ \lambda_2 & \lambda_1 + \lambda_3 & \lambda_2 \\ \lambda_3 & \lambda_2 & \lambda_1 + \lambda_3 \end{pmatrix}. \quad (7)$$

The transitions described by the matrix (Eq. 7) are schematically illustrated in Fig. 4. For the stationary distribution $\{\pi_1, \pi_2, \pi_3\} = (0, 0.5, 0.5)$, we obtain

$$T(\pi_1, \pi_2, \pi_3) = \begin{pmatrix} 0 & 0 & 0 \\ 0.5 & 0.5 & 0.5 \\ 0.5 & 0.5 & 0.5 \end{pmatrix} \quad (8)$$

and $\gamma_{1,st} = 0$, $\gamma_{2,st} = \gamma_{3,st} = 0.5$. That is, type 1 is not at all attractive, whereas types 2 and 3 are equally attractive. Figure 3a illustrates the approach of the attractor levels γ_k towards their stationary values $\gamma_{k,st}$. The functions $\gamma_k(n)$ were computed from Eqs. 6 and 7 and the $\lambda_k(n)$ values shown in Fig. 2.

The noise level Q given a distribution $\{\lambda_1, \dots, \lambda_N\}$ has been defined by [35]

$$Q = \frac{S}{M \ln M}, \quad (9)$$

where S is the Shannon entropy of the conditional matrix:

$$S = - \sum_{k,i} T_{ki} \ln T_{ki}. \quad (10)$$

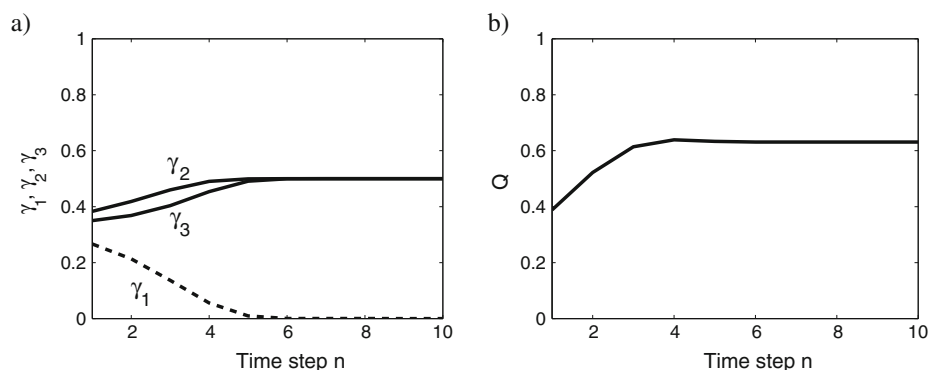
By definition, we have $Q \in [0, 1]$, where $Q = 0$ indicates a deterministic process (i.e., the coefficients T_{ki} are either zero or 1). The definition in terms of (9) and (10) holds for the non-stationary and stationary case. In the aforementioned example, we can compute the stationary noise level Q_{st} from the matrix (Eq. 8) and obtain $Q_{st} = \ln 2 / \ln 3 \approx 0.63$. The transient behavior of Q is shown in Fig. 3b.

2.3 Trajectories and Numerics

2.3.1 Transition Rule

A trajectory x_u of a unit u describes the type of the unit at time step n : $x_u(n) \in \{1, \dots, M\}$. The nonlinear Markov chain model defines trajectories for biological systems in the thermodynamic limit, i.e., when the number N of units goes to infinity [34]. The nonlinear Markov chain approach can also be used to construct models for system composed of a finite number N of units. In both cases, we can determine iterative for every unit $x_u(n) = i$ its value at the next time step $n + 1$. To this end, we draw a random number ϵ from

Fig. 3 **a** Attractivity $\gamma_k(n)$ of biological types as a function of time n . **b** Variations of the noise level $Q(n)$ of the evolutionary process



a uniform distribution in $[0, 1]$. If $\epsilon \in [z_{k-1}, z_k]$ then the unit has type k at $n+1$: $x_u(n) = i \rightarrow x_u(n+1) = k$. The z values are defined in terms of the coefficients T_{ki} like $z_k = \sum_{w=1}^k T_{wi}$ for $k \geq 1$ with $z_0 = 0$ and $z_N = 1$. Note that the z values depend implicitly on time—as we will discuss next (the mapping of a nonlinear Markov process to a non-homogeneous, time-dependent linear Markov process is in line with the notion of “strongly nonlinear Fokker–Planck equations,” for details, see Section 3 in Ref. [29]).

2.3.2 Model and Simulation for Infinitely Large Systems

In order to compute trajectories in the limiting case of an infinity large system, we can use a so-called two-layered approach (see Section 3.4 in Ref. [29]) and compute the evolution of the probabilities $\lambda_k(n)$ from the evolution Eq. 1 or 2. The coefficients T_{ki} can then be computed using Eq. 3 and the probabilities $\lambda_k(n)$. Moreover, the z values can be computed from the coefficients T_{ki} . It is clear that the z values depend explicitly on the probabilities $\lambda_1, \dots, \lambda_M$ which implies that they depend implicitly on time n .

Let us consider a set of N trajectories $\{x_1, \dots, x_N\}$. Let $\{x_u | x_u(n) = k\}$ denote the set of units that are of type k at time n and let $r_k(n) = |\{x_u | x_u(n) = k\}|$ denote the number of such units (where $|\{\cdot\}|$ is the size of a set). Then, in the limiting case $N \rightarrow \infty$ the probabilities λ_k obtained by solving Eq. 1 or 2 correspond to the probabilities $r_k(n)/N$ computed from the trajectories.

2.3.3 Model and Simulation for Finite Size Systems

The considerations in Section 2.3.2 can be used to define evolution equations for biological systems composed of a finite number N of units—consistent with the models 1 and 2. While in Section 2.3.2 the coefficients T_{ki} were computed from probabilities, in the case of a finite system size we compute the coefficients T_{ki} from the trajectories x_1, \dots, x_N . Since the trajectories depend on time, the coefficients T_{ki} become implicitly time dependent. In this context, we define the relative frequencies

$$f_k(n) = \frac{1}{N} |\{x_u | x_u(n) = k\}|. \quad (11)$$

By means of these frequencies, we define the coefficients

$$T_{ki} = \sum_{j=1}^M g(k|ij) f_j(n), \quad (12)$$

see also Eq. 3. Equations 11 and 12 in combination with the transition rule described in Section 2.3.1 constitute a closed dynamic description that can be used to compute the trajectories $x_u(n)$. In the limiting case $N \rightarrow \infty$, the finite size model corresponds to the model involving infinitely many units. Note that strictly speaking, the coefficients T_{ki} can be regarded as estimators of the “true” coefficients T_{ki} obtained by solving Eq. 1 or 2 together with Eq. 3 (which implies, e.g., that the coefficients T_{ki} as defined by Eq. 3 are *not* random variables whereas the variables T_{ki} as defined by Eq. 12 are random variables and exhibit fluctuations). For the sake of simplicity, our notation, however, will not reflect this difference.

Let us illustrate a finite size model for the example discussed in Section 2.1. From Eqs. 4 and 12, it follows that the matrix T of conditional probabilities reads

$$T(f_1, f_2, f_3) = \begin{pmatrix} f_1 & 0 & 0 \\ f_2 & f_1 + f_3 & f_2 \\ f_3 & f_2 & f_1 + f_3 \end{pmatrix}. \quad (13)$$

The transitions described by the matrix (Eq. 13) are the same as those illustrated in Fig. 4. The λ values in Fig. 4, however, need to be replaced by the corresponding f values.

In our computer experiment we considered a set of $N = 10,000$ units and used the same parameters as in Section 2.1. That is, as far as the initial condition is concerned, we randomly assigned 80% of all units to type 1, 15% to type 2, and 5% to type 3. Subsequently, we solved Eqs. 11 and 12 using the transition rule of Section 2.3.1. Figure 5 depicts a trajectory thus obtain. Figure 6 plots the relative frequencies f_1, f_2, f_3 (circles) computed from the trajectories in the same diagram as the probabilities shown in Fig. 2 (solid lines). The frequencies and probabilities show qualitatively the same behavior and even exhibit quantitatively a good correspondence. Figure 7 shows joint frequencies

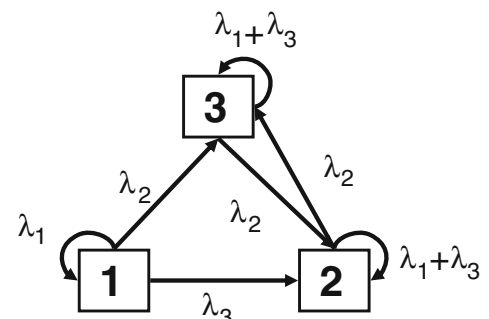


Fig. 4 Evolutionary transition from type i to k involving the impact of a unit of type j

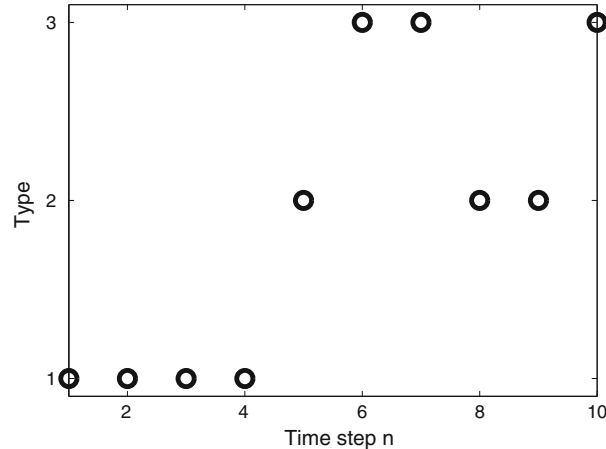


Fig. 5 Example of a trajectory computed from Eqs. 4, 11, and 12 and the transition rule described in Section 2.3.1

computed from the trajectories x_u . We computed the lag-1 joint frequency $f_{11}(n, n+1)$ of observing a unit in type 1 at time n and observing the same unit in type 1 at time $n+1$. In addition, we computed $f_{12}(n, n+1)$ (rel. frequency of the event: $x_u(n) = 1 \wedge x_u(n+1) = 2$) and $f_{13}(n, n+1)$ (rel. frequency of the event: $x_u(n) = 1 \wedge x_u(n+1) = 3$). Note that we did not average across time steps n . For example, we computed $f_{11}(1, 2)$, $f_{11}(2, 3)$, etc. Consequently, the joint frequencies are plotted as functions of n in Fig. 7. Figure 7 reveals that “the persistence” of type 1 units decayed in the computer experiment. Moreover, in the initial period between $n = 1$ and $n = 5$, there were a considerable

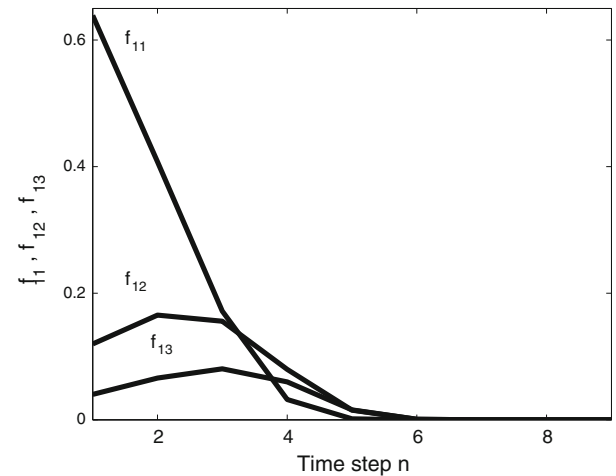


Fig. 7 Joint frequencies f_{11} , f_{12} , f_{13} (top to bottom) computed from the finite system size model (see Eqs. 4, 11, and 12 and Section 2.3.1) with $N = 10,000$ units. Initial conditions as in Fig. 2

amount of transitions from types 1 to 2 and from types 1 to 3.

3 Conclusions

We studied evolutionary population dynamics from the perspective of nonlinear Markov processes. To this end, we showed that a previously proposed model [37, 38] for evolutionary population dynamics can be cast into the form of a nonlinear Markov chain. The nonlinear Markov chain approach comes with a number of peculiarities. (1) The evolutionary process can be regarded as a nonlinear Markov process as introduced by McKean Jr. [1, 2]. Consequently, our re-interpretation makes a number of mathematical tools and concepts available that have not been related to evolutionary processes so far. (2) Attractor strength and noise level can be defined, where attractor strength describes the attractivity of evolving towards a particular biological type. (3) Trajectories can be computed numerically and used to determine joint frequencies and estimates for expectation values and joint probabilities.

We have shown in Section 2.3.2 that the attractivity of becoming (or evolving to) a biological entity of a certain type depends implicitly on time. The attractivity depends in general on the law according to which the different types are distributed. Likewise, we showed that the noise level (as defined in line with the nonlinear Markov chain approach) depends on the distribution which in other words means that the noise level—in general—is sensitive to the distribution of biological types.

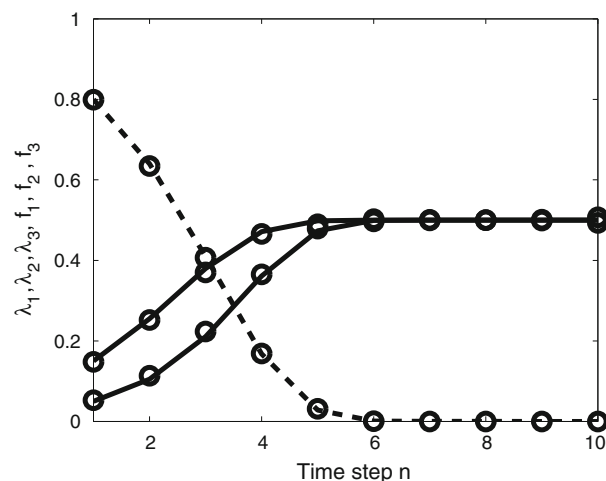


Fig. 6 Relative frequencies f_1 , f_2 , f_3 (circles; from top to bottom) depicted as functions of time n as obtained from a finite system size model with $N = 10,000$ units. Solid lines: as in Fig. 2. See text for details

We illustrated the impact of interactions in evolutionary population dynamic by calculating joint frequencies. In particular, we computed lag-1 joint frequencies from trajectories. Alternatively, joint probabilities (rather than frequencies) might be computed semi-analytically by exploiting the Chapman–Kolmogorov equation of nonlinear Markov chains [34] and by computing numerically the occupation probabilities λ_k as functions of time n . These two different numerical approaches should converge in the limit of $N \rightarrow \infty$. In a similar vein, in Section 2.3, we computed the evolution of the simple probabilities λ_k directly from the relevant nonlinear evolution equation for λ_k and indirectly via trajectories of an associated (finite system size) nonlinear Markov process (see also, Fig. 7) of size $N = 10,000$. When comparing the results (crudely, i.e. just by visual inspection), we found a good correspondence. This correspondence would improve when scaling up the system size N and would become worse when making N smaller.

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References

1. H.P. McKean Jr., Proc. Natl. Acad. Sci. **56**, 1907 (1966)
2. H.P. McKean Jr., in *Lectures in Differential Equations*, vol. II, ed. by A.K. Aziz (Van Nostrand Reinhold Company, New York, 1969), pp. 177–193
3. R.C. Desai, R. Zwanzig, J. Stat. Phys. **19**, 1 (1978)
4. M. Shiino, Phys. Rev. A **36**, 2393 (1987)
5. Y. Kuramoto, *Chemical Oscillations, Waves, and Turbulence* (Springer, Berlin, 1984)
6. H. Daido, Prog. Theor. Phys. **75**, 1460 (1986)
7. M. Doi, S.F. Edwards, *The Theory of Polymer Dynamics* (Clarendon Press, Oxford, 1988)
8. B.U. Felderhof, Physica A **323**, 88 (2003)
9. T.D. Frank, Phys. Rev. E **72**, 041703 (2005)
10. T.D. Frank, Phys. Rev. ST-AB **9**, 084401 (2006)
11. T.D. Frank, J. Phys. A: Math. Gen. **42**, 155001 (2009)
12. C. van den Broeck, J.M.R. Parrondo, R. Toral, Phys. Rev. Lett. **73**, 3395 (1994)
13. J. Garcia-Ojalvo, J.M. Sancho, *Noise in Spatially Extended Systems* (Springer, New York, 1999)
14. A.R. Plastino, A. Plastino, Physica A **222**, 347 (1995)
15. A. Compte, D. Jou, J. Phys. A: Math. Gen. **29**, 4321 (1996)
16. L. Borland, Phys. Rev. E **57**, 6634 (1998)
17. G. Kaniadakis, Physica A **296**, 405 (2001)
18. P.H. Chavanis, Phys. Rev. E **68**, 036108 (2003)
19. T.D. Frank, Eur. Phys. J. B **37**, 139 (2004)
20. E.K. Lenzi, C. Anteneodo, L. Borland, Phys. Rev. E **63**, 051109 (2001)
21. I.T. Pedron, R.S. Mendes, T.J. Buratta, L.C. Malacarne, E.K. Lenzi, Phys. Rev. E **72**, 031105 (2005)
22. V. Schwämmle, F.D. Nobre, C. Tsallis, Eur. Phys. J. B **66**, 537 (2008)
23. R. Kawai, X. Sailer, L. Schimansky-Geier, Phys. Rev. E **69**, 051104 (2004)
24. M. Shiino, K. Yoshida, Phys. Rev. E **63**, 026210 (2001)
25. M.A. Zaks, L. Schimansky-Geier, A.B. Neiman, Chaos **15**, 026117 (2005)
26. A. Ichiki, H. Ito, M. Shiino, Physica E **40**, 402 (2007)
27. C.F. Lo, Phys. Lett. A **336**, 141 (2005)
28. J.A. Acebron, L.L. Bonilla, C.J.P. Vicente, F. Ritort, R. Spigler, Rev. Mod. Phys. **77**, 137 (2005)
29. T.D. Frank, *Nonlinear Fokker–Planck Equations: Fundamentals and Applications* (Springer, Berlin, 2005)
30. T.D. Frank, in *Encyclopedia of Complexity and Systems Science*, vol. 5, ed. by R.A. Meyers (Springer, Berlin, 2009), pp. 5239–5265
31. C. Tsallis, J. Stat. Phys. **52**, 479 (1988)
32. C. Tsallis, Braz. J. Phys. **39**, 337 (2009)
33. S. Picoli, R.S. Mendes, L.M. Malacarne, R.P.B. Santos, Braz. J. Phys. **39**, 468 (2009)
34. T.D. Frank, J. Phys. A: Math. Gen. **41**, 282001 (2008)
35. T.D. Frank, Eur. Phys. J. B **70**, 249 (2009)
36. T.D. Frank, Physica A **388**, 4241 (2009)
37. J.P. Crutchfield, O. Görnerup, J. R. Soc. Interface **3**, 345 (2006)
38. O. Görnerup, J.P. Crutchfield, Artif. Life **14**, 245 (2008)
39. J.P. Crutchfield, K. Young, Phys. Rev. Lett. **63**, 105 (1989)