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Ako Sauga

THE INFLUENCE OF ENVIRONMENTAL FLUCTUATIONS ON THE DYNAMICS OF NON-LINEAR SYSTEMS

TLÜ KIRJASTUS
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Chair of Geoecology, Faculty of Mathematics and Natural Sciences, Tallinn University, Estonia.

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CONTENTS

LIST OF PUBLICATIONS

This thesis is based on the following papers, which will be referred in the text by their Roman numerals.

I. Laas, T., **Sauga, A**., Mankin, R., Ainsaar, A., Ugaste, Ü. & Rekker, A. 2006. Colored-noise-induced anomalous transport in periodic structures. *Nukleonika*, **51**, 63–69.
II. **Sauga, A**.& Mankin, R. 2005. Addendum to "Colored-noise-induced discontinuous transitions in symbiotic ecosystems". *Physical Review E*, **71**, 062103.
III. Haljas, A., Mankin, R., **Sauga, A**., & Reiter, E. 2004. Anomalous mobility of Brownian particles in a tilted symmetric sawtooth potential. *Physical Review E*, **70**, 041107.
IV. Mankin, R., **Sauga, A**., Ainsaar, A., Haljas, A., & Paunel, K. 2004. Colored-noise-induced discontinuous transitions in symbiotic ecosystems. *Physical Review E,* **69**, 061106.

Other publications in the relevant area:

V. Sauga, A. & Mankin, R. 2005. Colored-noise-induced discontinuous transitions in ecosystems with Gompertz self-regulation. In: *25th European Meeting of Statisticians.* 24–28 July 2005. Oslo, Norway. O-155.
VI. Sauga, A. & Mankin, R. 2005. Anomalous mobility of Brownian particles in a tilted symmetric sawtooth potential. In: *30th Conference on Stochastic Processes and their Applications*, Santa Barbara, California, USA, June 26–July 1, 2005. 89.
VII. Sauga, A., Mankin, R. & Haljas, A. 2004. Colored-noise-induced discontinuous transitions in symbiotic ecosystems. In: *Joint Conference MPD 7 – DeStoBio 3, Computational and Mathematical Population Dynamics,* Trento, Italy, June 21–25, 2004. 130.

Author's contribution

Publication I: The author is responsible for the analysis of absolute negative mobility. He also made some of the figures.

Publication II: The author is responsible for the analysis of self-consistency equation. He also made all of the figures and participated in the preparation of the manuscript.

Publication III: The author is responsible for the analysis of absolute negative mobility. He also made some of the figures and participated in the preparation of the manuscript.

Publication IV: The author is responsible for the analysis of self-consistency equation and for numerical analysis. He also made all of the figures and participated in the preparation of the manuscript.

LIST OF ABBREVIATIONS

ANM – absolute negative mobility
DUT – doubly unidirectional transitions
GVLB – generalized Verhulst model with a large beta, $\beta > 1$
GVSB – generalized Verhulst model with a small beta, $0<\beta<1$
HDR – hypersensitive differential response
SUT – single unidirectional transitions

PREFACE

Within the past twenty years noise-induced phenomena in nonlinear systems have received considerable attention. Development of resources management, new techniques in pollution/waste control, a better understanding biophysical processes in living organisms are some results of these studies in ecological context.

We have considered *N*-species Lotka-Volterra stochastic models of symbiotic ecological systems with the generalized Verhulst (IV) and Gompertz (II) self-regulation mechanism. The effect of a fluctuating environment on the carrying capacity of a population was taken into account as dichotomous noise. The main result is that environmental noise can cause discontinuous transitions in population densities even if the system is monostable in the absence of noise. (II, IV).

Another model we have studied concerns an overdamped Brownian particle in a periodic symmetric one-dimensional sawtooth potential subjected to both thermal noise and spatially nonhomogeneous trichotomous noise. It was established that the mobility depends nonmonotonically on the parameters of nonequilibrium and thermal noises. For this reason, anomalous negative mobility and other anomalous transport properties appear, which can be used in particle separation techniques. (I, III).

The present dissertation consists of two parts. The first is a summary of the studies and the second consists of published papers.

1. INTRODUCTION

1.1. ECOSYSTEMS WITH FLUCTUATING ENVIRONMENTAL PARAMETERS

The dynamical stability of populations and ecosystems governs their responsiveness to fluctuating environmental conditions and determines with what reliability these natural resources provide life-sustaining services to society. Thus, it is important that designers of environmental management plans should not overlook any impacts to the stability of ecosystems. Population and ecosystem dynamics is thus a major structuring theme in ecology.

Ecological systems are open systems in which the interaction between the component parts is nonlinear and the interaction with the environment is noisy. This intrinsic nonlinearity can give rise to a complex behaviour of the system, which becomes very sensitive to initial conditions, various deterministic external perturbations, and to fluctuations always present in nature. Mathematical approaches provide powerful tools in the analysing of such problems and many different models have been used to study the dynamics of interacting species in a variety of different contexts (May, 1973a; Murray, 1989; Renshaw, 1993; Turchin, 2003).

Work on theoretical models has implied that ecosystems may switch abruptly from one stable state to a contrasting alternative one. To test such ideas, ecological time-series analysis is necessary. The key characteristic of such a regime shift is that remarkably sudden switches to contrasting community states may occasionally occur, while the time-scale for the change between states is much shorter than the time within alternate states. Nowadays regime shifts have been documented for a wide range of ecosystems, including the open ocean (Hare & Mantua, 2000; deYoung et al., 2004), lakes and ponds (Scheffer, 1998; Ruggiero et al., 2005), rivers and wetlands (Strehlow et al., 2005), and coral reefs (McCook, 1999; Nystrom et al., 2000). A regime shift has taken place in the Baltic Sea as well (Munkes, 2005). The forcing for the change is generally external to the biological ecosystem, that is, those changes are not simply biological oscillation patterns within the ecosystem, but arise from changes in the physical environment. This is why the obvious intuitive explanation for a sudden dramatic change in nature is the occurrence of a sudden large external impact. However, theoreticians have long stressed that this need not be the case. Even a tiny incremental change in conditions can trigger a large shift in some systems if a critical threshold known as ‘catastrophic bifurcation’ is passed.

Observations of catastrophic shifts in different ecosystems are interpreted in the light of stability theory (Ludwig et al., 1997; Scheffer et al., 2003; Scheffer & Carpenter, 2003). Such catastrophic transitions have also been noted in various theoretical models, assuming that the deterministic counterpart of the model is multistable (Scheffer et al., 2001; Vandermeer & Yodzis, 1999; Rozenfeld et al., 2001). Regime shifts are formally associated with the ideas of nonlinear amplification (Dixon et al., 1999), an alternative basis of attraction (Sutherland, 1974), multiple stable states (Steele & Henderson, 1984), hysteresis and fold catastrophe (May, 1974; Scheffer et al., 2001), all of which require the underlying dynamics to be nonlinear.

Researchers have mainly been interested in the dynamical consequences of population interactions, often ignoring environmental variability altogether. However, the essential role of environmental fluctuations has recently been recognized in theoretical ecology. Future advances in community dynamics will require the use and analysis of nonlinear stochastic models, as illustrated by the studies reviewed by Bjørnstad and Grenfell (Bjørnstad & Grenfell, 2001). The environmental fluctuations or noise, via its interaction with the nonlinearity of the system, has given rise to new counterintuitive phenomena: stochastic resonance (Gammaitoni et al., 1998; Blarer & Doebeli, 1999; Valenti et al., 2004), noise-enhanced stability (Agudov & Spagnolo, 2001), resonant activation (Doering & Gadoua, 1992), noise-induced nonequilibrium transitions (Horsthemke & Lefever, 1984; Van den Broeck et al., 1997; García-Ojalvo & Sancho, 1999), noise-induced multistability and nonequilibrium phase transitions (Jülicher & Prost, 1995; Mangioni et al., 1997; Reimann et al., 1999; Li & Hänggi, 2001; Berry, 2003), and amplification or suppression of diffusion (Lindnder et al., 2001; Örd et al., 2005). Notably, noise-induced effects on population dynamics have been a subject of intense theoretical investigations (Vilar & Solé, 1998; Rogers, 2003; Houchmandzadeh, 2002; McKane et al., 2000; Spagnolo et al., 2002; Chesson, 2003; Kinezaki et al., 2003).

Environmental noise can be generated by a range of factors, such as climatic effects, natural enemies, interspecific competition, or anthropogenic change. The most productive abstraction of noise-like influence from the environment is the case of Gaussian white noise. There the problem is considerably simplified as the corresponding transition probability densities satisfy the Fokker-Planck equation, which in certain specific cases can be solved exactly. However, time-series of real environmental variables contain positive temporal autocorrelation (Steele & Henderson, 1994; Cuddington & Yodzis, 1999), which is often referred to by its effect on the colour (the relation between the frequency and amplitude) of the time-series. Large-scale climatic fluctuations are characteristically autocorrelated, showing a dominance of multiannual or decadal variability (e.g. the El Niño-Southern Oscillation and the North Atlantic Oscillation) (Bjørnstad & Grenfell, 2001). Positive temporal autocorrelation results in low-frequency fluctuations with a high amplitude, which by analogy to red light is often referred to as reddened noise. For example, Steele suggested that terrestrial noise should be white, while marine noise should be brown, based upon a few empirical records and simple forcing models (Steele & Henderson, 1994). This statement was corroborated by the authors of (Vasseur & Yodzis, 2004). However, as researchers continue to use white-noise models, even in the face of contradictory environmental data, research that focuses on providing a solid theoretical framework for the analysis of reddened environmental variation is sorely needed (Green et al., 2005).

A number of investigations suggest that population dynamics is sensitive to noise colour (Ripa & Lundberg, 1996; De Blasio, 1998; Caswell & Cohen, 1995; Petchey, 2000; Xu & Li, 2003; Laakso et al., 2006; Hiltunen et al., 2006). Clearly important aspects to tackle are the question of how the frequency of environmental noise affects the probability that the ecosystem will shift to another attractor (Steele & Henderson, 1994; Steele, 1998) and how extinction risk depends on environmental stochasticity (Halley & Kunin, 1999; Wichmann et al., 2003; Heino & Sabadell, 2003).

Different studies show that external multiplicative noise can induce multistability as well as first-order phase transitions in some complex systems (Kim et al., 1997; Kim et al., 1998; Gudyma, 2004). Analysing the dynamics of salinity in an ocean model Timmermann found that red noise generates new nondeterministic equilibria (Timmermann & Lohmann, 2000). Inspired by these studies the authors of (Mankin et al., 2002) have investigated whether some catastrophic shifts occurring in ecosystems could be regarded as induced by multiplicative coloured noise. The answer is again positive, as in a symbiotic ecosystem, described by an N-species generalized Lotka-Volterra model with logistic self-regulation, coloured fluctuations of the carrying capacities of populations have been shown to produce discontinuous changes from a stable state to an unstable one. Note that symbiotic Lotka-Volterra models with the true Verhulst (logistic) self-regulation have some special properties, such as transitions from stability to instability, even in the absence of noise (Rieger, 1989; Mankin et al., 2002; Ciuchi et al., 1996). If there are no transitions from stability to instability, as is true for most natural ecosystems, the features of the system can be different. A more fundamental question is, both from theoretical and practical viewpoints, whether coloured fluctuations of the carrying capacities can also induce bistability of such systems and produce abrupt switching between their stable states.

Thus motivated, in the current thesis we consider *N*-species Lotka-Volterra models of symbiotic ecological systems with Richard self-regulation, focusing on coloured-noise-induced discontinuous transitions. The effect of fluctuating environment on the growth of populations is modelled as a dichotomous (two-level) noise of the carrying capacity.

1.2. TRANSPORTATION OF NANOOBJECTS

There are two environmental implications of nanotechnology: one is positive and the other is potentially negative. Some of the positive features from the ecological viewpoint are as follows (Theodore & Kunz, 2005):

- novel sensing technologies or devices for pollutant and microbial detection;
- removal of environmental contaminants from various media;
- posttreatment of contaminated soils, sediments, and solid wastes;
- oil-water separation;
- destruction of bacteria.

The other implication of nanotechnology has been dubbed by many as “potentially negative”: the ability of nanoparticles and nanodevices to bypass natural defences of living systems. For example, a research team at the University of Rochester reported that inhaled carbon nanoparticles can travel directly into the olfactory area of the brain – not by crossing the blood-brain barrier as pharmaceuticals do, but by traversing neural pathways (Oberdörster et al., 2004). Air, water, and land (solid waste) concerns with emissions from nanotechnology operations in the future, as well companion health and hazard risks, receive extensive treatment. Transport phenomena play a crucial role in the above-mentioned processes.

Moreover, biological organisms on their primary cellular level function in a nanofluidic environment, and the solutions that have been found after billions of years of evolution deserve a thorough inspection. For example, nature has found a way to harness Brownian motion, which creates a very noisy environment at the molecular scale for active transport (Magnasco, 1993). In this context, Brownian motor theory leads us into the realm of intracellular transport research, specifically the biochemistry of molecular motors and molecular pumps (Reimann, 2002).

Starting from Magnasco’s theoretical work (Magnasco, 1993), there has been increasing interest in transport properties of nonlinear systems, which can extract usable work from unbiased nonequilibrium fluctuations (Mateos, 2000; Luczka et al., 1995; Ai et al., 2005a). The idea that noise, via its interaction with the nonlinearity of the system, can give counterintuitive results, has led to many important discoveries (for a review see (Hänggi & Marchesoni, 2005)). Among them, we can mention stochastic ratchets (Reimann, 2002; Magnasco, 1993; Astumian & Bier, 1994; Rousselet et al., 1994; Faucheux et al., 1995; Matthias & Müller, 2003; Ghosh & Khare, 2003), and absolute negative mobility (Eichhorn et al., 2002a).

A ratchet is a device that can induce directional motion of particles or molecules without a net external force or gradient. The operating principle of ratchets relies on the rectification of the effects of either thermal motion or a zero-average external field (Magnasco, 1993; Ajdari et al., 1994). Different types of ratchets (correlation, flashing, etc.) have been classified (Reimann, 2002). This is, indeed, a fascinating concept permeating many fields, from quantum mechanics to biophysics. Perhaps the current level of enthusiasm for ratchets is best illustrated by the special issue on the subject published in Applied Physics A (Linke, 2002). The technique has been used, for example, to transport micronsize colloidal particles through a silicon wafer with asymmetric pores by applying an oscillating pressure difference (Kettner et al., 2000) or an oscillating electrical field (Marquet et al., 2002). To date, the feasibility of particle transport by man-made devices has been experimentally demonstrated for several ratchet types.

It should be noted that dynamics in ratchet structures with its inherent spatial asymmetry generally exhibits a rich complexity, such as the occurrence of multiple current reversals and multipeaked current characteristics. The current reversal in ratchet systems can be engendered by varying system parameters (Bier & Astumian, 1996; Tammelo et al.2002; Ai et al., 2005a).

The models with current reversals are very important in new particle separation devices such as electrophoretic separation of microparticles (Kettner et al., 2000). Also, such models are of interest in biology (Henningsen & Schliwa, 1997). Motions of macromolecules are probably responsible for vesicle transport inside eukaryotic cells. A typical example is the motion of proteins along a microtubule, usually modelled by a ratchet (Oster & Wang, 2002). The two typical proteins – kinesins and dyneins – move along tubulin filaments in opposite directions and this can be explained by current reversal (Ai et al., 2005b).

A characteristic feature of models with absolute negative mobility (ANM) is that upon the application of an external static force, these models respond with a current that always runs in the direction opposite to that of the force. Notably, for zero external force no current appears due to the spatial symmetry of the system.

There are several categories of theoretical models for classical ANM. In (Eichhorn et al., 2002b; Eichhorn et al., 2002a; Eichhorn et al., 2003) various 2D spatial geometries have been proposed in which a single Brownian particle displays ANM. Two interesting basic 1D models for a single Brownian particle exhibiting ANM were presented in (Cleuren & Broeck, 2003; Jiménez de Cisneros et al., 2003). Although the mechanism of ANM in these 1D models is different, there is similarity in some aspects, notably, noise-induced switching between different potential configurations (states) can take place only when the particle passes certain specific positions. For example, for the spatially continuous model in (Cleuren & Broeck, 2003) the corresponding positions are the minima of the periodic potential with two minima per period. Note that as a result of the localized transitions between the different states, the dependence of the stationary current on the switching rate of noise disappears (Cleuren & Broeck, 2003).

As the "three-layer" basic diffusion mechanism for ANM described in (Cleuren & Broeck, 2003) is robust enough and can be easily realized experimentally, we applied a similar approach to 1D models where the transitions between different potential configurations are not localized at discrete points, i.e. the transitions appear rather in finite intervals. It is of interest, both from theoretical and practical viewpoints, to know whether such a modification of the basic model can cause novel unexpected effects.

1.3. OBJECTIVES

The general aim of this study was to analyse nonlinear modelsystems in the presence of coloured environmental noise.

The main objectives of the study were as follows:

1) to provide exact analytical results for coloured-noise-induced first-order-like phase transitions in model of symbiotic ecosystems over extended dichotomous noise parameters and interaction strengths by
    a) analysing how different self-regulation mechanisms, such as Richard and Gompertz laws can influence the behaviour of stochastic complex systems;
    b) establishing the exact conditions under which abrupt transitions occur, and analysing the role of the parameters of the Richard's growth model in such transitions.
2) Considering one-dimensional overdamped dynamical systems, where Brownian particles move in a spatially periodic piecewise linear symmetric potential,
    a) to report some interesting novel phenomena, which take place in systems described above, arising as a consequence of interplay between a nonequilibrium noise, a thermal noise, and a deterministic force;
    b) to apply the developed modelsystem of Brownian particles to the exploration of the phenomenon of absolute negative mobility at intermediate intensity values of environmental fluctuations.

2. MODELS AND METHODS

In studies where a dynamical system is perturbed by noise it is appropriate to model the dynamics of the system by stochastic differential equations. The use of such equations for modelling purposes has a long history in the physical sciences, the use of the Langevin equation to study Brownian motion being but one (Risken, 1989; Coffey et al., 1996), but is much less common in the biological sciences. In context of population dynamics these equations were first formulated about thirty years ago (May, 1973a; May, 1973b).

2.1. POPULATION GROWTH MODELS WITH A FLUCTUATING CARRYING CAPACITY

Many different types of mathematical and computer model of multispecies ecosystems have been developed (May, 1973a; Pastorok et al., 2002; Turchin, 2003). Time evolution of a two- species system is well-known as the Lotka-Volterra system. Our community models are based on the *N*-species generalized Lotka-Volterra equation

$$\frac{d}{dt}X_i(t)=X_i(t)\left[f_i(X_i(t))+\sum_{j\neq i}J_{ij}X_j(t)\right], \tag{1}$$

where $X_i(t)$ ($i=1,\ldots,N$) is the population density of the *i*-th species at time *t* (clearly, $X_i(t)\geq 0$). The function $f_i(X)$ is the density-dependent growth rate of the population and describes the development of the *i*-th species in the absence of others. In general, the growth rate may also have a different form (Takeuchi, 1996; Renshaw, 1993; Zwietering et al., 1990)

The matrix (J_{ij}) ($i, j=1,\ldots,N$) is an interaction (or coupling) matrix and represents the effect of the *j*-th species upon the *i*-th one. The elements of matrix J_{ij} may be positive (+), negative (-) or zero (0). Ecologists distinguish among five general classes of pairwise species interactions: competition (-,-), symbiotic (or mutualistic) interaction (+,+), commensalism (+,0), amensalism (-,0), and trophic interaction (+,-) (Turchin, 2003). Note that the well-known prey-predator relationship is one of the trophic interactions.

Only models with symbiotic relationship have been analysed in this study. Accordingly, $J_{ij}>0$ and $J_{ji}>0$, which means that the growth rate of each species depends positively on the population densities of the others. In nature there are a number of different types of mutualistic relationships (Begon et al., 2006; Bronstein, 1994), but from the viewpoint of Equation (1) they all are identical.

We analysed models with generalized Verhulst (or Richard) self-regulation, in which case the growth function can be written as

$$f_i(x)=\delta_i\left[1-\left(\frac{x}{K_i}\right)^{\beta}\right], \tag{2}$$

where δ_i is a density-independent growth rate and K_i is the carrying capacity of the *i*-th species (Levin et al., 1997; McGlade, 1999; Lindsey, 2004). Carrying capacity is a limiting factor on the population growth which is imposed by environmental factors, basically food and space limitations.

In the case of single species (J_{ij}=0) the differential equation (1) with Eq. (2) gives us the solution

$$X_i(t)=K_i\left\{1-\left[1-\left(\frac{K_i}{X_{i0}}\right)^{\beta}\right]\exp(-\delta_i t)\right\}^{-1/\beta} \tag{3}$$

called the Richards curve (Lindsey, 2004; Seber & Wild, 2003). For $\beta>0$ this curve describes initial exponential growth that is increasingly damped as the population density increases until it eventually stops. The parameter β changes the position of the inflection point and, hence, the shape of the curve (3). The determination of the inflection point by a free parameter makes the Richards growth model relatively flexible and inclusive of the other sigmoidal growth models.

If $\beta=1$, the Richards curve becomes the well-known logistic growth that is symmetrical about the inflection point. For $\beta>1$, the most density dependent change occurs at a high population level (close to the carrying capacity). According to both theory and empirical information, this is characteristic for species with a life history typical of large mammals (Fowler, 1981). The reverse is true for species with life history strategies typical of insects and some fishes, with $0<\beta<1$ (Fowler, 1981).

Although self-regulation models with $\beta>0$ are useful in modelling many actual communities, there are some biologically important systems, such as bacterial populations, where population growth could be modelled better by the Gompertz law with a growth rate

$$f_i(x) = -\delta_i \ln\left(\frac{x}{K_i}\right). \tag{4}$$

Model (4) is a special case of the generalized Verhulst self-regulation with the exponent $\beta \to 0$. To show that one must take the intrinsic growth rate in (2) of the form δ_i / β.

In Paper IV we analysed the generalized Verhulst model with a large exponent $\beta > 1$ (GVLB), and in (II) the models with Gompertz self-regulation and the generalized Verhulst model with a small exponent $0 < \beta < 1$ (GVSB) were studied.

Environmental parameters vary over time, and so do carrying capacities. This is the reason why environmental noise should be modelled by the inclusion of an additive noise term for the carrying capacity K_i. For the sake of mathematical simplicity, it is useful to look for types of coloured noise such that enable, in the case of the mean-field theory at least, the stationary probability density to be evaluated exactly for any value of the correlation time. The simplest noise of this kind is the dichotomous (two-state) Markovian noise, also known as the random telegraph signal (Horsthemke & Lefever, 1984). Such noise switches back and forth between two values, and the jumps follow in time according to a Poisson process. Dichotomous noise is often a good representation of actual environmental fluctuations, such as the alternating decades with low and high precipitation in southern Africa; the removal of vegetation by large, migrating herbivores and subsequent recovery; or the cyclic and vertical currents in water that transport algae in regions of high and low light availability (Wichmann et al., 2003).

Thus motivated, in our study the fluctuations of the carrying capacity for GVLB were modelled as

$$K_i = K\left[1 + a_0 Z_i(t)\right], \tag{5}$$

where the coloured noise $Z_i(t)$ is assumed to be a dichotomous Markovian stochastic process (Horsthemke & Lefever, 1984; Hänggi & Jung, 1995) with state values $z = -1, 1$. The values occur with the stationary probability 1/2 and the transition probabilities between the states $Z(t) = \pm 1$ can be obtained as follows:

$$P(\pm 1, t+\tau \mid \mp 1, t) = \frac{1}{2}(1 - e^{-\nu\tau}), \quad \tau > 0, \quad \nu > 0.$$

The mean value of $Z_i(t)$ and the correlation function are $\langle Z_i(t) \rangle = 0$, $\langle Z_i(t), Z_j(t') \rangle = \delta_{ij} \exp(-\nu \left| t - t' \right|)$, where the switching rate ν is the reciprocal of the noise correlation time, $\nu = 1/\tau_c$. The parameter a_0 can be interpreted as the noise amplitude and obviously, Model (1) with Eqs. (2) and (5) is biologically meaningful only if $\left| a_0 \right| < 1$ (the carrying capacity K is nonnegative).

In the case of Gompertz self-regulation (4) and GVSB an additional adaptation parameter $\varepsilon > 0$ is required:

$$K_i = K\left(1 - \frac{\varepsilon}{N} \sum_{j \neq i} X_j(t)\right)[1 + a_0 Z_i(t)]. \tag{6}$$

The factor $[1 - (\varepsilon / N) \sum X_j(t)]$ in Eq. (6) mimics the decrease of the carrying capacity caused by adaptive competition of populations for common resources, such as food or living space (see also (Dimitrova & Vitanov, 2001; Sprott, 2004)). A need for the consideration of inter-species adaptive competition in models with Gompertz self-regulation of biological relevance arises from the following circumstance: In the absence of adaptation (ε=0), for all $J_{ij} > 0$ the corresponding deterministic model (without noise) is characterized by instability; it means that within a finite time the site average $\bar{X} = (1/N) \sum X_i(t)$ grows to infinity (Rieger, 1989; Ciuchi et al., 1996). For biologically relevant models any growth of an expanding population must eventually be stopped by shortage of resources. Addition of adaptation to the model would regulate the behaviour of the system so that an unstable state of the system will be replaced by a new stable stationary state. A qualitatively analogous situation takes place in models with general Verhulst self-regulation with $0<\beta<1$ (II). The adaptation parameter ε is assumed to be independent of the species, i.e., the populations adapt themselves with respect to the total number of individuals of all populations.

We must point out that the same technique, an additive noise term for the carrying capacity, is used by the authors of (Ripa & Lundberg, 1996; Petchey et al., 1997; van Nes et al., 2004). In comparison with (Mankin et al., 2002), where the immediately fluctuating quantity is the reciprocal of the carrying capacity, such approach is more natural.

2.2. MEAN-FIELD APPROXIMATION AND THE MASTER EQUATION FOR LOTKA-VOLTERRA SYSTEMS

The basic Lotka-Volterra model deals with interaction between a pair of species. As most populations are embedded in rich communities and affected by numerous interspecific interactions, low-dimensional models involving one or just a few species cannot capture the patterns of fluctuations. To analyse a community of many species by the general Lotka-Volterra model (1), we need take into account the interaction coefficients between each pair of the species involved. For example, in a system of 10 species a total of 90 interaction coefficients and 10 carrying capacities would have to be determined to be able to use the model. Clearly, in this way analytical calculations can be applied only to very simple systems.

The simplest approach is to assume that all individuals in a system are homogeneous, evenly mixed in space and they interact equally – what in physics is termed a mean-field. Such assumptions are the basis of most *N*-species community models (Ciuchi et al., 1996; Rieger, 1989; McKane et al., 2000; McKane & Newman, 2004; Bastolla et al., 2005; Mombach et al., 2002). The advantage of mean-field models is that, on the one hand, they can often be solved with relatively little effort and, on the other hand, they account for subsystem-subsystem interactions of many-body systems.

To proceed with the analytical examination of Model (1) with the self-regulation (4) we follow the mean-field approximation scheme described in (Mankin et al., 2002). We are interested in the case of infinitely many interacting species, $N \to \infty$. The mean-field approximation can be reached by replacing the site average $(1/N)\sum_{j(\neq i)} X_j(t)$ by the statistical average $\langle X \rangle$. On the basis of (Mankin et al., 2002; Rieger, 1989; Ciuchi et al., 1996) we consider all species to be equivalent, so that the characteristic parameters of the ecosystem (or metapopulation) are independent of the species, i.e., $\delta_i = \delta, K_i = K > 0.$ Interspecies interaction is characterised by the coupling constant $J>0$, so that in Model (1) $\sum_{j\neq i} J_{ij} X_j = (J/N)\sum_i X_i$, and consequently the growth rate depends on the average species concentration.

The natural time scale in Model (1) is given by the growth rate parameter δ and it is useful to absorb it into the time scale. The population density can be scaled by the carrying capacity. By applying a scaling of the form

$$\tilde{X} = \frac{X}{K}, \quad \tilde{t} = \delta t, \quad \tilde{J} = \frac{KJ}{\delta}, \quad \tilde{\nu} = \frac{\nu}{\delta}, \quad \tilde{\varepsilon} = \varepsilon K. \tag{7}$$

we get dimensionless variables. For brevity’s shake, we shall omit tilde throughout this study.

In the case of general Verhulst self-regulation we get a stochastic differential equation of the form

$$\frac{dX(t)}{dt} = X(t)\left\{1 + J\left\langle X(t)\right\rangle - \gamma X^{\beta}(t)[1 + aZ(t)]\right\}, \tag{8}$$

in which we have introduced

$$\gamma = \frac{1}{2(1-a_0^2)^{\beta}}\left[(1+a_0)^{\beta} + (1-a_0)^{\beta}\right], \tag{9}$$

and the amplitude of the dichotomous fluctuations

$$a = \frac{(1+a_0)^{\beta} - (1-a_0)^{\beta}}{(1+a_0)^{\beta} + (1-a_0)^{\beta}}. \tag{10}$$

We can see that as a result of the mean-field-type interaction the original many-body problem has been reduced to a one-body problem.

The corresponding composite master equation is

$$\frac{\partial P_n(x,t)}{\partial t} = -\frac{\partial}{\partial x}\left\{x[r(t) - x^{\beta}\gamma(1+a_n)]P_n(x,t)\right\} + \sum_m U_{nm}P_m(x,t) \tag{11}$$

with $r(t) \equiv 1 + J\left\langle X(t)\right\rangle$, P_n (x,t) denoting the probability density for the combined process $(x, a_n, t);\ n, m = 1, 2;\ -a_1 = a_2 = a$; and

$$\mathbf{U} = \frac{\nu}{2}\begin{pmatrix} -1 & 1 \\ 1 & -1 \end{pmatrix}. \tag{12}$$

For the model with Gompertz self-regulation the corresponding stochastic differential equation is

$$\frac{dX(t)}{dt} = X(t)\left[-\ln\left(\frac{X(t)}{\sqrt{1-a_0{}^2}\,[1-\varepsilon\left\langle X(t)\right\rangle]}\right) + \ln\sqrt{\frac{1+a_0}{1-a_0}}\,Z(t) + J\left\langle X(t)\right\rangle\right], \tag{13}$$

and the composite master equation can be expressed as

$$\frac{\partial P_n(x,t)}{\partial t} = -\frac{\partial}{\partial x}\left[x\left(-\ln x + q(t) + z_n \ln\sqrt{\frac{1+a_0}{1-a_0}}\right)P_n(x,t)\right] + \sum_m U_{nm}P_m(x,t), \tag{14}$$

with $q(t) \equiv J\left\langle X(t)\right\rangle + \ln\left[\sqrt{1-a_0{}^2}\,(1-\varepsilon\left\langle X(t)\right\rangle)\right]$.

The behaviour of a stationary system can be analytically studied by means of a standard mean-field theory procedure (García-Ojalvo & Sancho, 1999). For a stationary state we can solve Eqs. (11) and (14), taking as the boundary condition that there is no probability current at the boundary. This way we get the stationary probability distribution in the *x* space, $P(x,r) = \sum_n P_n^s(x)$, where $P_n^s(x)$ is the stationary probability density for the state (x, a_n) (IV). The self-consistency equation for the Weiss mean-field approach, whose solution yields the dependence of $\left\langle X \right\rangle$ on the system parameters, is

$$\left\langle X \right\rangle = \int_{x_2}^{x_1} xP(x,r)dx. \tag{15}$$

For GVSB the corresponding self-consistency equation takes the following form

$$\rho - \lambda m = m^{1-\frac{1}{\beta}}\,{}_2F_1\left(\frac{1}{2\beta}, \frac{1}{2\beta} + \frac{1}{2}; m + \frac{1}{2}; a^2\right), \tag{16}$$

where ${}_2F_1$ is the hypergeometric function, the "order parameter"

$$m := \frac{\nu}{2\gamma\beta}\left\langle \frac{1}{X^{\beta}} \right\rangle = \frac{\nu}{2\beta(1+J\langle X \rangle)}, \tag{17}$$

and the parameters ρ and λ are defined as

$$\rho = \left(\frac{2\gamma\beta}{\nu}\right)^{1/\beta} \frac{\nu}{2\beta J}, \quad \lambda = \left(\frac{2\gamma\beta}{\nu}\right)^{1/\beta} \frac{1}{J}. \tag{18}$$

For the model with Gompertz self-regulation the corresponding self-consistency equation is

$$\langle X \rangle = (1-\varepsilon\langle X \rangle)F(\nu, a_0)\exp\left(J\langle X \rangle\right), \tag{19}$$

where

$$F(\nu, a_0) := (1-a_0)\,\Phi\left(\frac{\nu}{2}, \nu; \ln\left|\frac{1+a_0}{1-a_0}\right|\right),$$

and Φ is the confluent hypergeometric function.

The results that we got from analysing the different solutions of Equations (16) and (19) are presented in (II, IV) and in Section 3.

For the model with $\beta>1$ the mean-field solution $\langle X \rangle$ was also compared with a computer simulation with a finite number of interacting species, $N = 500$, using the numerical methods described in (Van den Broeck et al., 1997; García-Ojalvo & Sancho, 1999). The mean value of the population densities $\bar{X}$ was computed by

$$\bar{X} = \frac{1}{TN}\int_{t_0}^{t_0+T} \sum_{j=1}^{N} X_j(t)\,dt.$$

The averaging time T was chosen to be sufficiently longer than the correlation time (for example, $T \approx 1$ near the coexistence region) and the time evolution of the average value was carefully monitored until the stationary state was reached ($t_0 > 5$).

2.3. BROWNIAN PARTICLES IN A TILTED SYMMETRIC SAWTOOTH POTENTIAL

Within the past two decades a number of stochastic ratchets (or Brownian motors) have been proposed to induce continuous directional motion of small particles (Reimann, 2002). In these models a system has a periodic structure with local symmetry breaking and particles are submitted to some local ‘shaking’, so that the asymmetric structure rectifies into a net macroscopic transport along the structure. Recently, two interesting basic one-dimensional models for a single Brownian particle exhibiting absolute negative mobility have been presented in (Cleuren & Broeck, 2003; Jiménez de Cisneros et al., 2003). The authors of the referred works analysed models where switching between different potential configurations (states) can take place in certain specific positions of the particle. By contrast with them in our approach the transitions between different potential configurations are not localized at discrete points.

We have considered the motion of Brownian particles in a one-dimensional (1D) spatially periodic potential $\tilde{V} = \tilde{V}(\tilde{x}+L)$ of a period L and barrier height $\tilde{V}_0 = \tilde{V}_{max} - \tilde{V}_{min}$. The applied force consists of an additive static force $\tilde{F}$ and of a noise term composed of thermal noise $\tilde{\xi}(\tilde{t})$ with a temperature T and a coloured three-level Markovian noise $\tilde{Z}(\tilde{x},\tilde{t})$. As thermal fluctuations play a notable role in very small systems, the inertial forces are negligible and the dynamics is overdamped. The system is described by the following stochastic differential equation:

$$\kappa \frac{d\tilde{X}}{d\tilde{t}} = -\frac{d\tilde{V}(\tilde{X})}{d\tilde{X}} + \tilde{F} + \tilde{\xi}(\tilde{t}) + \tilde{f}\tilde{Z}(\tilde{X},\tilde{t}), \tag{20}$$

where κ is the friction coefficient and $\tilde{f}$ is a constant force. The thermal fluctuations $\tilde{\xi}(\tilde{t})$ are modelled by a zero-mean Gaussian white noise with the correlation function $\left\langle \tilde{\xi}(t_1)\tilde{\xi}(t_2) \right\rangle = 2\kappa k_B T \delta(\tilde{t}_1 - \tilde{t}_2)$, where k_B is the Boltzmann constant, $2\kappa k_B T$ is the thermal noise intensity, and $\delta(t)$ is Dirac's delta function. The term $\tilde{Z}(\tilde{X},\tilde{t})$ represents a three-level Markovian stochastic process and is assumed to be spatially non-homogeneous, so that transitions between the states $\tilde{z}_1 = -1$, $\tilde{z}_2 = 0$ and between the states $\tilde{z}_2 = 0$, $\tilde{z}_3 = 1$ can take place only in the left half-period and in the right half-period of the potential, respectively. The probabilities $W_n(t)$ that $\tilde{Z}(\tilde{X},\tilde{t})$ is in the state n at the time $\tilde{t}$ evolve according to the master equation

$$\frac{d}{d\tilde{t}} W_n(\tilde{t}) = \sum_{m=1}^{3} \tilde{U}_{nm} W_m(\tilde{t}), \tag{21}$$

where

$$\tilde{\mathbf{U}} = \frac{\tilde{\nu}}{2} \begin{pmatrix} -\tilde{a}_1(\tilde{x}), & \tilde{a}_1(\tilde{x}), & 0 \\ \tilde{a}_1(\tilde{x}), & -1, & \tilde{a}_2(\tilde{x}) \\ 0, & \tilde{a}_2(\tilde{x}), & -\tilde{a}_2(\tilde{x}) \end{pmatrix}, \tag{22}$$

with $\tilde{a}_1(\tilde{x}) = \Theta(\tilde{x} - L/2)$, $\tilde{a}_2(\tilde{x}) = \Theta(L/2 - \tilde{x})$, and $\Theta(x)$ is the Heaviside function.

By applying a scaling of the form

$$X = \frac{\tilde{X}}{L}, \quad V(x) = \frac{\tilde{V}(\tilde{x})}{\tilde{V}_0}, \quad t = \frac{\tilde{t}}{\tilde{t}_0}, \quad \xi = \frac{L\tilde{\xi}}{\tilde{V}_0}, \quad F = \frac{L}{\tilde{V}_0}\tilde{F}, \quad f = \frac{L}{\tilde{V}_0}\tilde{f}, \tag{23}$$

we get a dimensionless formulation of the dynamics with the potential V with the property $V(x) = V(x-1)$. By the choice of $\tilde{t}_0 = \kappa L^2/\tilde{V}_0$ the dimensionless friction coefficient turns to unity. The rescaled noises are given by

$$\nu = \frac{\kappa L^2 \tilde{\nu}}{\tilde{V}_0}, \quad a_1(x) = \Theta\left(x - \frac{1}{2}\right), \quad a_2(x) = \Theta\left(\frac{1}{2} - x\right), \quad D = \frac{k_B T}{\tilde{V}_0}, \tag{24}$$

where $2D$ is the strength of the rescaled zero-mean Gaussian white noise $\xi(t)$. For brevity's sake, from now on we shall call D temperature. The dimensionless dynamics reads

$$\frac{dX}{dt} = -\frac{dV(X)}{dX} + F + \xi(t) + fZ(X,t), \tag{25}$$

where the rescaled nonequilibrium noise $Z(X, t)$ is characterized by the transition matrix $\mathbf{U}$ of the form

$$\mathbf{U} = \frac{\nu}{2} \begin{pmatrix} -a_1(x), & a_1(x), & 0 \\ a_1(x), & -1, & a_2(x) \\ 0, & a_2(x), & -a_2(x) \end{pmatrix}$$

The process $Z(X, t)$ can be presented as the sum of two kangaroo processes $Z(X,t) = Z_0(t)\delta_{0,1} + Z_1(t)\delta_{1,i}$ (van Kampen, 1987). If the kangaroo processes $Z_0(t)$ and $Z_1(t)$ are statistically independent, which is the case addressed in the present study, then the two-dimensional process $\{x(t), z(t)\}$ is Markovian and its joint probability density $P_n(x,t)$ for the position variable $x(t)$ and the fluctuation variable $z(t)$ obeys the master equation of the form (van Kampen, 1987)

$$\frac{\partial}{\partial t}P_n(x,t) = -\frac{\partial}{\partial x}\left[\left(h(x)+F+z_n f - D\frac{\partial}{\partial x}\right)P_n(x,t)\right] + \sum_m U_{nm}P_m(x,t) \tag{26}$$

with $m,n = 1,2,3$; $z_1 = -1$, $z_2 = 0$, $z_3 = 1$; $h(x) = -dV(x)/dx$. More precisely, in the interval (0,1) the master equation (26) splits up into two differential equations $\mathbf{P}_i(x,t) = (P_{1i}, P_{2i}, P_{3i})$ ($i = 0,1$), defined in the intervals $(0,\frac{1}{2})$ and $(\frac{1}{2},1)$, respectively.

The stationary current J is then evaluated via the current densities

$$j_n(x) = \left(h(x) + z_n f + F - D\frac{\partial}{\partial x}\right)P_n^s(x), \quad J = \sum_n j_n(x), \tag{27}$$

where $P_n^s(x)$ is the stationary probability density for the state (x, z_n). It follows from Eq. (26) that the current J is constant. In the stationary case, the total net probability flux between the states $n = 1,2,3$ must vanish, implying

$$\int_0^{1/2} P_2^s(x)dx = \int_0^{1/2} P_3^s(x)dx, \quad \int_{1/2}^{1} P_1^s(x)dx = \int_{1/2}^{1} P_2^s(x)dx. \tag{28}$$

To derive an exact formula for J, we present an analysis of the system of Eq. (25) for a piecewise linear sawtooth-like symmetric potential

$$V(x) = \begin{cases} -(2x-1), & x \in (0,1/2) \mod 1, \\ (2x-1), & x \in (1/2,1) \mod 1. \end{cases} \tag{29}$$

The force $h(x) = -dV(x)/dx$ being periodic, the stationary distributions $P_n^s(x)$ as solutions of Eqs. (26) are also periodic and it suffices to consider the problem in the interval [0, 1). The force corresponding to the potential of Eq. (29) is

$$h(x) = \begin{cases} h_0 := 2, & x \in (0,1/2) \mod 1, \\ h_1 := -2, & x \in (1/2,1) \mod 1. \end{cases} \tag{30}$$

A schematic representation of the three configurations assumed by the "net potentials" $V_n(x) = V(x) - Fx - z_n f x$ associated with the right hand side of Eq. (25) is shown in Fig.1. The lines depict the net potentials with $z_1 = -1$, $z_2 = 0$, and $z_3 = 1$. Unbiased transitions with a switching rate ν can take place between the discrete states, but only at specific positions, namely, in the interval $x \in (0,\frac{1}{2})$, modulo 1 between V_2 and V_3, and in the interval $x \in (\frac{1}{2},1)$, modulo 1 between V_2 and V_1. Regarding the symmetry of the dynamical system (25), we notice that $J(-F) = -J(F)$. Thus, we may confine ourselves to the case $F \geq 0$. Obviously, for $F = 0$ the system is effectively isotropic and no current can occur.

As the force $h(x)$ is piecewisely constant Eq. (26) splits up into two linear differential equations with constant coefficients for the two vector functions $\mathbf{P}_i^s(x) = (P_{1i}^s, P_{2i}^s, P_{3i}^s)$ ($i = 0,1$), defined on the intervals $(0,\frac{1}{2})$ and $(\frac{1}{2},1)$, respectively. The solution includes ten constants of integration and for the probability current J it can be determined at the points of discontinuity, by requiring continuity and periodicity for the quantities $\mathbf{P}_i^s(x)$ and $j_{ni}(x)$, i.e.

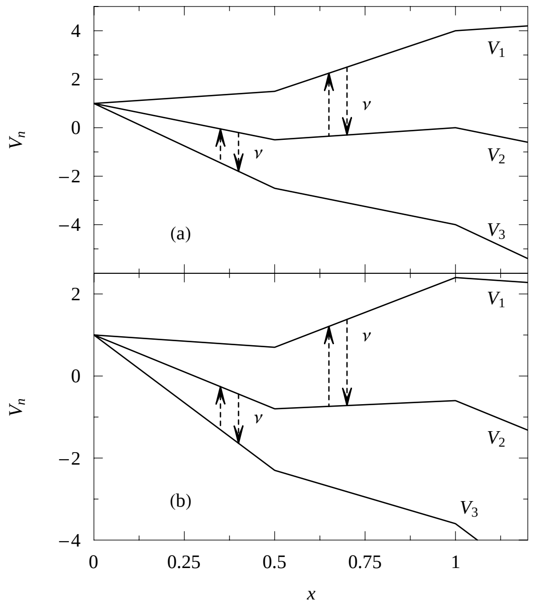

Figure 1. Schematic representation of different states and their transitions in the model (25) with the sawtooth potential (29) at low temperatures. (a) The case of $F=1$, $f=4$. (b) The case of $F=1.6$, $f=3$.

$$P_{n0}^{s}\left(\frac{1}{2}\right)=P_{n1}^{s}\left(\frac{1}{2}\right),\quad P_{n0}^{s}(0)=P_{n1}^{s}(1),\quad j_{n0}\left(\frac{1}{2}\right)=j_{n1}\left(\frac{1}{2}\right),\quad j_{n0}(0)=j_{n1}(1),\quad n=1,2,3. \tag{31}$$

As it follows from Eq. (26) that J = const [see also Eq. (27)], the system of linear algebraic equations (31) contains only ten linearly independent equations. By including an eleventh (normalization) condition,

$$\sum_{n=1}^{3}\int_{0}^{1}P_{n}^{s}(x)dx=1, \tag{32}$$

a complete set of conditions is obtained for the ten constants of integration and for the probability current J. This procedure leads to an inhomogeneous set of eleven linear algebraic equations. Now, J can be expressed as a quotient of two determinants of the eleventh degree. The exact formulae are presented in the Appendix of (III). It will be used to find the dependence of the current J on the tilting force F and the dependence of the mobility $m=dJ/dF$ on the switching rate. All numerical calculations are performed by using the software MATHEMATICA 4.1.

3. RESULTS AND DISCUSSION

3.1. COLOURED-NOISE-INDUCED TRANSITIONS IN SYMBIOTIC ECOSYSTEMS

3.1.1. A system with generalized Verhulst self-regulation

The presence of coloured fluctuations of the carrying capacities of populations in N-species symbiotic ecological systems with generalized Verhulst self-regulation with an exponent $\beta>1$ is analysed and discussed in (IV). We have found that:

- For symbiotic ecological systems with generalized Verhulst self-regulation, coloured fluctuations of the environment can cause bistability and abrupt transitions of mean population densities.

- The hysteresis for the mean field and related discontinuous transitions can be found as functions of noise parameters as well as of the coupling constant.
- For $\beta>1$ abrupt changes of mean population densities appear only if the noise amplitude is greater than the threshold value a_{0c} and the critical noise amplitude depends on the exponent β, only: a_{0c} increases relatively rapidly if β increases.

Discontinuous transitions can occur by a gradual change of the coupling strength J. Figure 2 shows different solutions of the self-consistency equation (16) for the mean field m as a function on the coupling constant J and the noise correlation time τ_c at the amplitude parameter $a_0^2 = 0.980$. The solid and dashed lines are stable and unstable solutions of Eq. (16), respectively. The existence of alternative stable states (Fig. 2, the curve $\tau_c = 0.5$) indicates that there is a coexistence region, $J_1 < J < J_2$, where two stable phases are possible. Notably, coexistence does not mean that the two phases are present simultaneously, however, either is possible depending on the initial distribution. If the value of the mean field m lies on the upper branch of the curve $\tau_c = 0.5$ close to the point F, a slight growth of the coupling parameter J induces a catastrophic transition of the system to another stable state with the value of the mean field corresponding to the point G. The opposite shift occurs, when the coupling parameter decreases below the value J_1. The situation described represents a typical case of first-order phase transitions. As the coupling-induced two-phased coexistence region does not exist in the system without noise, it is a coloured noise effect. The results indicate that the effect of noise is not merely restricted to the shift of the mean population density, but the whole nature of the dynamics changes.

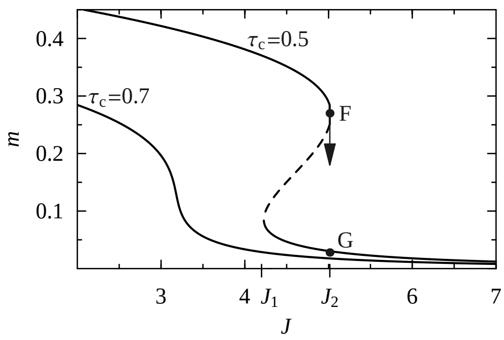

Figure 2. Stationary mean-field m vs coupling strength J at different correlation times τ_c. The solid and dashed lines are stable and unstable solutions of the self-consistency equation (16), respectively.

This interesting circumstance demonstrates that both agents – the symbiotic coupling of species and the coloured fluctuations of the carrying capacities – act in unison to generate discontinuous transitions of the mean population density. Moreover, as in scaling (7) the growth rate δ and the deterministic carrying capacity K of species have been absorbed into the time scale and into the coupling strength $\tilde{J}$, thus, in the original (unscaled) set-up, discontinuous transitions can occur also by a gradual change of the parameters δ and K.

From Figure 2 one can see that the coexistence region of the two phases exists only for sufficiently large values of the correlation time τ_c. Hence, there is an upper limit τ_c^* for the correlation time τ_c, at greater values of which the system is monostable. In Fig. 3 we have plotted the critical correlation time τ_c^* as a function of the parameters a_0^2 and β. In the case of fixed values of β the critical parameter τ_c^* increases monotonically from zero to infinity if the noise amplitude a_0 increases from $a_{0c}(\beta)$ to 1.

Perhaps the most important new result, in an ecological context, is the existence of the critical noise amplitude. We emphasize that for $\beta > 1$ abrupt changes of mean population densities appear only if the noise amplitude exceeds the threshold value a_{0c}. In Fig. 3 the filled dots on the a_0^2 axis correspond to different values of the critical noise amplitude $a_{0c}(\beta)$. It should be pointed out that the threshold amplitude a_{0c} depends only on the exponent β describing generalized Verhulst self-regulation. Therefore, an increase of noise amplitude or a decrease of noise correlation time can under certain conditions cause a catastrophic fall in the size of populations. As the critical noise amplitude increases relatively rapidly if β increases, it seems reasonable to assume that in symbiotic ecosystems with generalized Verhulst self-regulation abrupt transitions appear with a greater probability if the exponent β is lower.

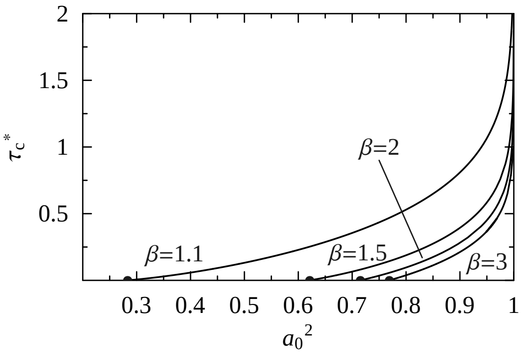

Figure 3. The critical correlation time τ^*_c vs the noise amplitude a_0^2 for some values of the system parameter β.

Hysteresis can also occur in the case of either noise parameter, τ_c or a_0, being chosen as the control parameter. For example, in Fig. 4 hysteresis is exposed for the mean value of the population densities $\langle X \rangle$ if the noise correlation time τ_c is considered as the control parameter. It can be seen that a jump from a state with a bigger number of individuals to that with a lesser one occurs at smaller correlation times than the opposite jumps.

The mean-field results considered correspond to an infinite number of globally coupled species. Bearing in mind the results of computer simulations (the squares in Fig.4), one can assume that this scenario is not much different from more realistic ecosystems, where the number of species is finite, at least in the case when the number of species is large enough.

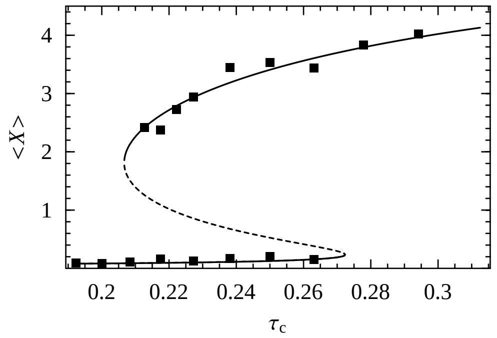

Figure 4. Plot of the mean value of the population density $\langle X \rangle$ as a function of the noise correlation time τ_c at a_0^2 =0.939, β=2, and J=6. The solid and dashed lines correspond to the stable and unstable solutions of Eq. (16), respectively. The squares are obtained by means of computer simulations of the system with N=500.

It is worth emphasizing that the deterministic counterpart of most ecological models exhibiting noise-induced discontinuous transitions is able to display transitions similar to those induced by noise for a certain range of parameters values (Scheffer et al., 2001; Vandermeer & Yodzis, 1999; May, 1977; Rinaldi & Scheffer, 2000; Rozenfeld et al., 2001; Pascual & Caswell, 1997; Antal & Droz, 2001; Abramson, 1997). In our model, however, these transitions occur only if coloured noise is present.

We believe that the obtained results are of interest also in other fields where symbiotic interaction and generalized Verhulst self-regulation are relevant, e.g. in the dynamics of human world population (Johansen & Sornette, 2001), coupled chemical reactions, some laser systems (Horsthemke & Lefever, 1984), and in business (Bouchaud, 2002; Trimper et al., 2002).

3.1.2. A system with Gompertz self-regulation

The presence of coloured fluctuations of the carrying capacities of populations in N-species symbiotic ecological system with Gompertz self-regulation is analysed and discussed in (II).

We have established two types of noise-induced discontinuous transitions – doubly unidirectional transitions (DUT) and single unidirectional transitions (SUT) – and given the necessary and sufficient conditions for the appearance of such effects. Single unidirectional transition means that an increase in noise amplitude can cause a catastrophic fall in the size of populations, while by decreasing the noise amplitude no opposite transitions can occur. To our knowledge, the appearance of a noise-induced SUT in models of ecosystems without extinction is a new noise-induced effect.

When investigating the dependence of $\langle X \rangle$ on the correlation time τ_c, five different types of the graph $\langle X \rangle$ versus switching rate υ emerge (Fig 5). We interpret these five qualitatively different shapes of the graphs as different ”phases” in the phase space (ε, J), where ε is the adaptation parameter and J is the strength of symbiotic interactions [the phases (a)–(e) in Fig. 6]:

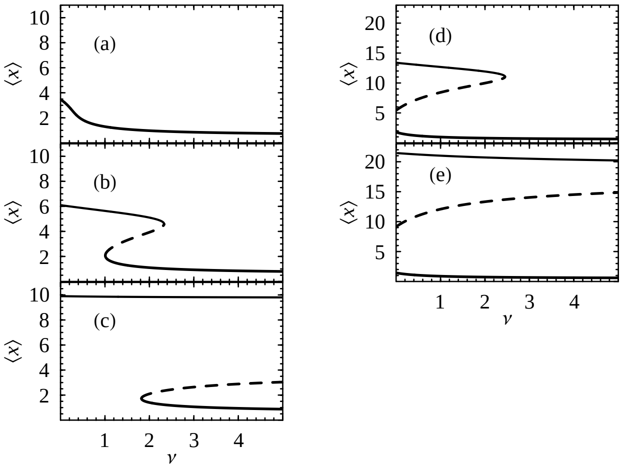

Figure 5. The shape of the function $\langle X \rangle$ vs. ν for the different domains in Fig. 6.

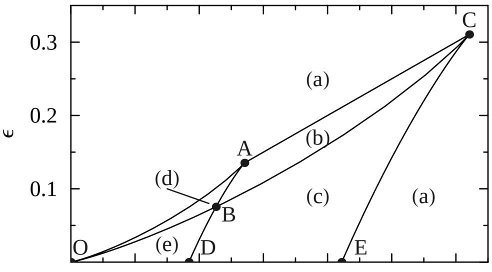

Figure 6. (ε, J) phase diagram for the dependence of the population density $\langle X \rangle$ on ν in the case of a_0=0.9. The phases (a) - (e) correspond to Fig. 5 (a) - (e), respectively.

(a) The system is monostable for all values of ν.
(b) The phenomenon of doubly unidirectional transitions appears.
(c) The system exhibits single unidirectional transitions from a lesser number of individuals to a bigger number.
(d) The system also exhibits SUT, but from a bigger number of individuals to a lesser one.
(e) In this case, the system is bistable for all values of ν, no transitions between stable states occur.

We must note that the coordinates of points B, C, and E in Fig.6 depend on the noise amplitude a_0. As a_0 increases from 0 to 1, the points C and E move away from the origin O and this will increase the region of the phase space (ε, J), where discontinuous transitions are possible. Moreover, the point B moves from A to D, which causes an increase of the domain (d), where a SUT from the stable state of a bigger number of individuals to a lesser one takes place.

In the case considered here, an increase in noise amplitude can, under certain conditions, cause a catastrophic fall in the size of populations, while by decreasing the noise amplitude an opposite transition cannot be brought about. This novel feature of symbiotic ecosystems can provide a possible scenario for some catastrophic shifts of population sizes observed in nature (Scheffer & Carpenter, 2003), e.g. in the case of coral reefs, where symbiosis is essential (McCook, 1999).

The next interesting finding is that the critical noise amplitudes (the amplitudes at which discontinuous transitions appear) decrease if noise correlation time decreases. On the basis of this result, one may formulate the conjecture that in symbiotic ecosystems with Gompertz self-regulation discontinuous transitions appear with a greater probability if the noise correlation time is shorter. Weakly stable ecosystems will be prone to species extinctions and thus could sustain less diverse biotas. Therefore, it is important that any impacts on the stability of ecosystems be considered when designing environmental management plans.

Finally, we believe that the model and results discussed here are also of interest in other fields where Gompertz self-regulation is relevant in system modelling, e.g. in oncology (Sullivan & Salmon, 1972; Michelson et al., 1987), bioeconomics (Pradhan & Chaudhuri, 1998; Kar, 2004), and sociology, in particular in the theory of cultural diffusion (Hamblin et al., 1979).

3.2. NOISE-INDUCED TRANSPORTATION EFFECTS IN THE STUDIED BROWNIAN RATCHET

Overdamped motion of Brownian particles in a 1D periodic system with a simple symmetric sawtooth potential subjected to both unbiased thermal noise and a spatially nonhomogeneous three-level coloured noise are considered analytically in (I, III).

For the stationary case, the dependence of the current J on the tilting force F enables us to establish the following four effects characterizing anomalous behaviour of the resistance (or mobility):

- A resonant-like behaviour of anomalous mobility occurs: the particles move in the direction opposite to a small external force F (the region $0 < F < 1$ in Fig.7).
- The curve exhibits intervals of F where particle speed decreases as the applied drive is increased – an effect that is termed negative differential resistance.
- For large values of the switching rate υ and a low temperature D the current is, at some values of the tilting force F (in Fig.7 at F=1 and $F\approx 2$), very sensitive to a small variation of F – a phenomenon called hypersensitive differential response (HDR).
- At a low temperature and a large switching rate ν the current exhibits characteristic „disjunct windows“ of the tilting force, where the value of the current is very small (the interval $2 < F < 3.5$ in Fig.7).

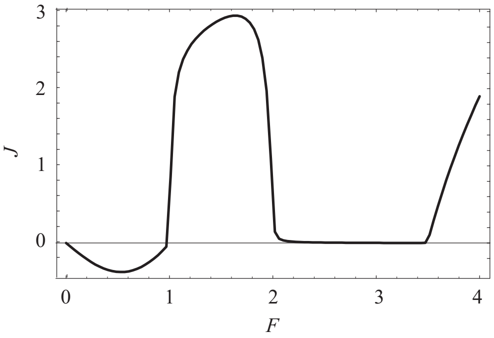

Figure 7. The current J vs the applied force F in the region of anomalous mobility. $D=10^{-7}$, $\upsilon=10^{3}$, and $f=3$.

For both slow and fast fluctuating forces, and for low temperatures, we have presented analytical approximations that agree with the exact numerical results. Figure 8 shows the mobility m_0 as a function of the temperature D for four different values of the noise amplitude f in the case of a low switching rate limit. In this figure, one can also observe absolute negative mobility at small and intermediate temperatures, which apparently gets more and more pronounced as the noise amplitude $f>2$ increases. The tendency apparent in Fig. 8, namely, an increase of the critical temperature D_c (the temperature at which the phenomenon of ANM disappears) as the amplitude f grows, also takes place in the case of a large f, e.g. if $f>6$. It is remarkable that the phenomenon of ANM also occurs at high temperatures, if only the noise amplitude f is large enough.

Our major result is a resonance-like enhancement of absolute negative mobility at intermediate values of the switching rate of a non-equilibrium noise. Two circumstances should be pointed out. (i) A resonant-like behaviour of ANM can occur in a system parameters domain where the characteristic distance of thermal diffusion $\sqrt{D/\nu}$ is comparable with typical deterministic distances for the driven particles during the noise correlation time. (ii) There is an upper limit temperature D_c beyond which the phenomenon of ANM disappears. Notably, at increasing the noise amplitude f the critical temperature D_c grows as $D_c \sim \sqrt{f}$. It is obvious that the presence and intensity of ANM can be controlled by thermal noise or by the nonequilibrium noise amplitude f. The advantage of this model is that the control parameter is temperature, which can easily be varied in experiments. Moreover, as in Eq. (24) the friction coefficient κ is absorbed into the time scale, so, in the original (unscaled) set-up, the particles of different friction coefficients are controlled by different switching rates. This can lead to an efficient mechanism for the separation of different types of particles (Reimann, 2002; Bier & Astumian, 1996).

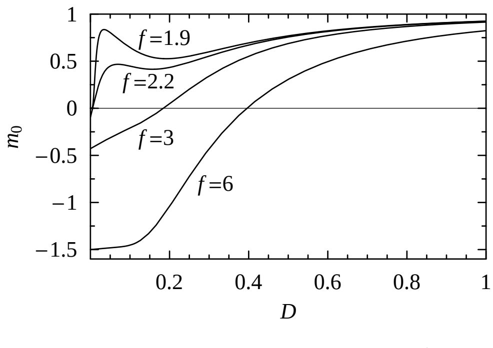

Figure 8. The mobility m_0 vs temperature D at various noise amplitudes f in the case of an adiabatic limit.

Our other result is the establishing of the effects of both HDR and a “disjunct window” at large values of the switching rate ν and low values of the temperature D. We emphasize that here the mechanism of HDR is of a qualitatively different nature from the mechanism of hypersensitive response considered in (Ginzburg & Pustovoit, 2001; Bena et al., 2002; Mankin et al., 2003). It should be pointed out that in the present model the effect of HDR is pronounced in the case of fast switching of the nonequilibrium noise, while in the models in (Ginzburg & Pustovoit, 2001; Bena et al., 2002; Mankin et al., 2003) hypersensitive transport is generated by low or moderate values of the switching rate. Surprisingly enough, at a low temperature and a large switching rate, $D\nu << 1$, the current is very small in the finite interval of the tilting force $2 + (f/2) > F > \max\{2, f-2\}$. This novel feature for a Brownian particle is, so far, mainly of theoretical interest while applications are not clearly identifiable yet.

3.3. SOME OPEN PROBLEMS

Any study can find answers or explain only some problems, leaving most of them unsolved. Before concluding, we should mention some issues for future research.

1. In this study we have considered symbiotic ecosystems. But how may coloured environmental noise affect the ecosystems with interspecies interaction other than symbiotic? Of particular interest is the influence of environmental noise on oscillating population densities as in predator-prey communities.
2. The populations dynamics described by Eq. (1) contains no time delay effects, that is, the growth rate at a time t can be completely determined by the values of variables at the present time t. But many processes in ecology surely involve time delays. It is known that a delay can bring about a qualitative change in the dynamical behaviour of systems. More realistic and interesting models should take into account both the fluctuating environment and the effects of time delays.
3. In Sec. 3.1 and in Papers (II, IV) we have presented the critical values and regions in phase diagrams (IV, Fig. 4; II Figs. 2 and 3) for the noise and system parameters where discontinuous transitions in the population densities appear. What is the probability the occurrence of these values in nature? One important problem is the linking of the mathematical models to empirical data.
4. Examination of the studied stochastic ratchet system should be continued from the energetical viewpoint, especially with more extensive analysis of the efficiency with which the ratchet converts fluctuation to useful work.
5. Although there are different physical mechanisms in the analysed ecosystems and the stochastic ratchet system, they have similar effects such as catastrophic shifts in population densities and hypersensitive differential response in the case of particles transport. Further investigations of interacting ratchet systems may reveal a closer connection between the above effects mentioned.

3.4. CONCLUSIONS

In this thesis we have analysed two kinds of non-linear systems – communities with symbiotic interaction and Brownian particles in a tilted symmetric sawtooth potential – in a fluctuating environment. The main question was whether coloured environmental noise with interaction of nonlinearity could generate new states and forms of behaviour of these systems, which do not appear in the noise-free limit.

In the case of N-species generalised Lotka-Volterra model of symbiotic ecosystems the external environmental noise was modelled as dichotomous fluctuations of the carrying capacity and two models of self-regulation were used: generalised Verhulst and Gompertz. The analytical examination of the respective self-consistency equations gave the following major results:

- In symbiotic ecological systems coloured fluctuations of the environment can cause bistability and abrupt transitions of mean population densities. Therefore, an increase of noise amplitude or a decrease of noise correlation time can, under certain conditions, cause a catastrophic fall in the size of populations. Moreover, we emphasize that for the model with the exponent $\beta>1$ abrupt changes of mean population densities appear only if the noise amplitude is greater than the threshold value, which increases relatively rapidly if β increases. In the models with $0<\beta<1$ as well as with the Gompertz law such a restriction is absent. Hence, catastrophic shifts appear with a greater probability in those communities where the exponent β is lower. It remains to be seen whether such a trend has a meaning for problems in natural sciences. (II, IV).
- In the ecosystems with the exponent $0<\beta<1$ as well as with the Gompertz law an increase of noise amplitude can cause a catastrophic fall in the size of populations, while by decreasing the noise amplitude an opposite transition cannot be brought about. To our knowledge, the appearance of noise-induced single unidirectional transitions in models of ecosystems without extinction is a new noise-induced effect. (II).
- Critical noise amplitudes (the amplitudes at which discontinuous transitions appear) decrease if noise correlation time decreases. Consequently, in symbiotic ecosystems discontinuous transitions appear with a greater probability if the noise correlation time is shorter. (II, IV).

- Discontinuous transitions can also occur by a gradual change of the coupling strength. This interesting circumstance demonstrates that both agents – symbiotic coupling of species and coloured fluctuations of the carrying capacities – act in unison to generate catastrophic shifts of the mean population density. (II, IV).

Another problem we have addressed is the dynamics of an overdamped Brownian particle in a periodic symmetric, one-dimensional sawtooth potential landscape subjected to a static tilting force and to both thermal noise and a spatially nonhomogeneous three-level coloured noise.

A major virtue of the proposed model is that an interplay of three-level coloured and thermal noises in tilted ratchets with simple symmetric sawtooth potentials can generate a rich variety of cooperating effects, such as absolute negative mobility, negative differential resistance, hypersensitive differential response, and the phenomenon of "disjunct windows" for the tilting force (see Sec. 3.2 and also (I, III)).

Particularly, for the phenomenon of absolute negative mobility we have established that:

- The presence and intensity of ANM can be controlled by thermal noise. There is an upper limit of temperature (critical temperature) beyond which the phenomenon of ANM disappears. Notably, the critical temperature grows as the amplitude of environmental fluctuations increases. The advantage of this effect is that the control parameter is temperature, which can easily be varied in experiments. (I, III).
- A resonant-like behaviour of ANM versus noise correlation time can occur in a system parameters domain where the characteristic distance of thermal diffusion is comparable with a typical deterministic distance for the driven particles during the noise correlation time, i.e., in this case a considerable amplification of ANM occurs at an appropriate value of the correlation time. (I, III).

We believe that the described models may shed some light on the stochastic interaction processes of ecosystems as well as on intracellular molecular motors with nonequilibrium environmental fluctuations and these could be used for the elaboration of some more realistic models for nonequilibrium intracellular transport as well as for the nonequilibrium phase transitions (catastrophic shifts) sometimes occurring in ecosystems. As the nonequilibrium phenomena considered in (I-IV) are robust enough to survive a modification of the coloured noise (i.e. environmental fluctuations) as well as a self-regulation mechanism (or potential landscape), the results of the investigations of the basic Models (1) and (20), belonging to a highly topical interdisciplinary realm of studies, can be applied for a variety purposes, starting from a description of Josephson connections (Majer et al., 2003; Pankratov & Spagnolo, 2004) and ending with a possible explanation of the catastrophic shifts occurring in ecosystems (Mankin et al., 2002; Spagnolo et al., 2004). The possible applications of Model (20) range from superconductors to intracellular protein transport in biology, or to methods of particle separation in nanotechnology (Linke, 2002; Reimann, 2002) as well as of separating biomolecules (Bader, 1999).

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KESKKONNAPARAMEETRITE FLUKTUATSIOONIDE MÕJU MITTELINEAARSETE SÜSTEEMIDE DÜNAAMIKALE

Kokkuvõte

Paari viimase aastakümne jooksul on suurt tähelepanu pälvinud avatud süsteemide käitumise sõltuvus keskkonnaparameetrite fluktuatsioonidest ehk mürast. On selgunud, et mittelineaarsetes süsteemides võib müra tekitada nähtusi, mis deterministlikul juhul puuduvad. Näiteks võib tuua stohhastilise resonantsi, müra poolt indutseeritud faasiüleminekud ja stohhastilise transpordi ruumiliselt perioodilises jõuväljas, sh tükati lineaarse perioodilise potentsiaali korral (nn hammaslattmudelid).

Ökoloogiliste süsteemide uurimisel on keskkonnaparameetrite fluktuatsioonide kirjeldamiseks enamikes töödes kasutatud valge müra mudelit. Aegridade analüüs on aga näidanud, et keskkonnamüra on pigem lõpliku korrelatsiooniajaga ehk värviline müra. Sellest lähtuvalt on antud uurimistöös elukeskkonna muutlikkust modelleeritud keskkonnamahutavusele lisatud dihhotoomse müra abil.

Teine valdkond, kus keskkonnamüra võib tekitada senitundmatuid efekte, on nanoosakeste transport. Hiljutised uuringud on näidanud, et teatud tüüpi hammaslattmudelite korral võib esineda osakeste negatiivne absoluutne liikuvus – kuitahes väikese välise jõu lisamine põhjustab Browni osakeste voo sellele jõule vastupidises suunas. Oma uurimistöö raames analüüsisime Browni osakeste dünaamikat uut tüüpi hammaslattmudelis.

Doktoritöö põhieesmärgid:
1. Analüüsida lõpliku korrelatsiooniajaga keskkonnamüra poolt indutseeritud üleminekuid sümbiootilistes ökosüsteemides, sealhulgas
   a) selgitada välja erineva iseregulatsiooni mehhanismi (üldistatud Verhulst, Gompertz), sümbiootilise vastasmõju ja keskkonnaparameetrite fluktuatsioonide koosmõju vastavates ökosüsteemides;
   b) analüüsida müra ja süsteemi parameetrite mõju ökosüsteemi stabiilsusele ning leida tarvilikud ja piisavad tingimused bistabiilsuse tekkimiseks.
2. Uurida kallutatud hammaslattsüsteemi, kus Browni osakeste ühesuunaline transport on allutatud nii termilisele tasakaalulisele mürale kui ka mittetasakaalulisele lõpliku korrelatsiooniajaga kolmetasemelisele mürale ning
   a) demonstreerida erinevaid müratekkelisi transpordinähtusi;
   b) analüüsida negatiivset absoluutset liikuvust süsteemi parameetrite erinevates väärtuspiirkondades.

Uuritavate mudelite dünaamika kirjeldamiseks kasutasime stohhastilisi diferentsiaalvõrrandeid. Tuginedes erinevate autorite poolt väljatöötatud ja Tallinna Ülikooli teoreetilise füüsika õppetooli juures tegutseva uurimisrühma poolt edasiarendatud metoodikale, analüüsisime seejärel vastavate kineetika põhivõrrandite (*master equation*) lahendeid statsionaarsel juhul.

Järgnevalt doktoritöö olulisemad tulemused.
Sümbiootiliste ökosüsteemide uurimisel selgus:

- Üldistatud Verhulsti iseregulatsioonile alluvates sümbiootilistes ökosüsteemides võivad keskkonnaparameetrite fluktuatsioonid nii amplituudi kui ka sageduse suurenemisel põhjustada katastroofilisi hüppeid populatsioonide arvukuses.
- Kui iseregulatsiooni astmenäitaja $\beta > 1$, siis eksisteerib müra amplituudi jaoks kriitiline piir, millest väiksema müra amplituudi väärtuste korral katastroofilisi üleminekuid ei teki. See kriitiline müra amplituud sõltub üksnes iseregulatsiooni astmenäitajast ja kasvab monotoonselt astmenäitaja kasvades. Kui astmenäitaja $0<\beta<1$ või kui on tegemist Gompertzi mudeliga, sellist kriitilist amplituudi ei esine. Järelikult sümbiootilistes ökosüsteemides toimuvad keskkonnamürast tingitud katastroofilised hüpped suurema tõenäosusega juhul, kui Verhulsti iseregulatsiooni iseloomustav astmenäitaja on väiksem.
- Gompertzi iseregulatsiooniga ökosüsteemide analüüs tõi välja uut tüüpi, mittepöörduvate üleminekute võimalikkuse. See tähendab, et müra amplituudi või sageduse kasv võib põhjustada populatsioonide arvukuse hüppelist vähenemist, vastava parameetri kahanemine aga endist situatsiooni ei taasta, populatsioonide arvukus jääbki väikeseks.

- Väiksematele korrelatsiooniaja väärtustele vastavad väiksemad kriitilise amplituudi väärtused, järelikult sümbiootilistes ökosüsteemides on katastroofilised üleminekud tõenäosemad, kui müra korrelatsiooniaeg on väike ehk müra sagedus suur.
- Katastroofilised hüpped populatsioonide arvukuses võivad tekkida ka sümbiootilise vastasmõju tugevust iseloomustava parameetri väikesel muutumisel. Seega võib väita, et bistabiilsuse teke on analüüsitud mudelites põhjustatud sümbiootilise vastasmõju ja keskkonnamahutavuse fluktuatsioonide koosmõjust.

Browni osakeste transpordi uurimine vaadeldud hammaslattsüsteemis näitas, et esinevad mitmed anomaalsed nähtused: negatiivne absoluutne liikuvus, negatiivne diferentsiaalne liikuvus, ülitundlik diferentsiaalne transport ja "isoleeritud aken" – välisjõu väärtuste vahemik, kus osakeste voog praktiliselt puudub, võrreldes vooga väiksemate või suuremate jõu väärtuste korral.

Lähemalt uurisime negatiivset absoluutset liikuvust, mille korral selgitasime välja järgmist:

- Efekti esinemist ja efektiivsust saab kontrollida temperatuuri muutmisega, kusjuures esineb kriitiline temperatuur, millest kõrgemal negatiivset absoluutset liikuvust ei esine. Kuna temperatuuri muutmine on lihtne, pakub see uusi võimalusi vastavate seadmete loomisel.
- Resonantsisarnane efekt negatiivse absoluutse liikuvuse käitumisel esineb süsteemi parameetrite sellises piirkonnas, kus termilise difusiooni karakteristlik teepikkus on võrreldav deterministlikus süsteemis osakese poolt läbitud teepikkusega müra korrelatsiooniajale vastava aja jooksul.

Usume, et saadud tulemused pakuvad uusi võimalusi looduslikes kooslustes esinevate populatsioonide arvukuse hüppeliste muutuste mõistmiseks ning elusorganismides toimuva rakusisese transpordi modelleerimiseks. Liikide vastasmõju ja keskkonnaparameetrite fluktuatsioonide koostoime väljaselgitamine on oluline ökosüsteemide regeneratsioonil ja stabiilsuseks vajalike tingimuste loomisel. Uut tüüpi hammaslattmudel võib rakendust leida nanoosakeste (sh biomolekulid, aerosooliosakesed) detekteerimise ja separeerimise tehnoloogiates.

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