## DISSERTATIONES PHYSICAE UNIVERSITATIS TARTUENSIS

## COLORED-NOISE-CONTROLLED ANOMALOUS TRANSPORT AND PHASE TRANSITIONS IN COMPLEX SYSTEMS

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## List of publications

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

- I R. Mankin, A. Ainsaar, A. Haljas<sup>1</sup>, and E. Reiter, *Constructive role of temperature in ratchets driven by trichotomous noise*, Phys. Rev. E **63**, 041110 (2001).
- II R. Mankin, A. Ainsaar, A. Haljas, and E. Reiter, Trichotomousnoise-induced catastrophic shifts in symbiotic ecosystems, Phys. Rev. E 65, 051108 (2002).
- III R. Mankin, A. Haljas, R. Tammelo, and D. Martila, *Mechanism of hypersensitive transport in tilted sharp ratchets*, Phys. Rev. E **68**, 011105 (2003).
- IV R. Mankin, A. Sauga, A. Ainsaar, A. Haljas, and K. Paunel, Colored-noise-induced discontinuous transitions in symbiotic ecosystems, Phys. Rev. E **69**, 061106 (2004).
- V A. Haljas, R. Mankin, A. Sauga, and E. Reiter, Anomalous mobility of Brownian patieles in a tilted symmetric sawtooth potential, Phys. Rev. E **70**, 041107 (2004).
- VI A. Rekker, R. Mankin, and R. Tammelo, Noise-flatness-induced hypersensitive transport in tilted periodic sawtooth potentials, Physica E 29, 419-425 (2005).
- VII T. Laas, A. Sauga, R. Mankin, A. Ainsaar, U. Ugaste, and A. Rekker, *Colored-noise-induced anomalous transport in periodic structures*, Nukleonika **51**, 63-69 (2006).

#### Other publications in the relevant area:

- VIII R. Mankin, A. Ainsaar, and A. Haljas, *Trichotomous-noise-induced phase transitions for the stochastic Hongler model*, Proc. Estonian Acad. Sci. Phys. Math. **49**, 28-39 (2000).
  - IX A. Haljas, R. Mankin, and R. Tammelo, A new mechanism of hypersensitive transport in tilted sharp ratchets (In: Third International Workshop and School on "Plasma Physics, Diagnostics and Plasma Related Applications", Kudowa Zdroj, Poland, 438-444, 2003).

<sup>&</sup>lt;sup>1</sup>Haljas is the author's maiden name

- X A. Haljas, R. Mankin, and A. Ainsaar, *Trichotomous noise: applications to noise-induced transitions in nonlinear systems* (In: International Seminar: "Interaction Between Dense Plasma and Materials", Tallinn, Estonia, 87-95, 2003).
- XI A. Haljas, R. Mankin, and R. Tammelo, *Mechanism of hypersensitive transport in tilted sharp ratchets* (In: Satellite of the 20th General Conference of the EPS CMD: "Frontiers of Quantum and Mesoscopic Thermodynamics", Prague, Czech Republic, 80-81, 2004).
- XII A. Sauga, R. Mankin, and A. Haljas, Colored-noise-induced discontinuous transitions in symbiotic ecosystems (In: Joint Conference MPD 7 DeStoBio 3, Computional and Mathematical Population Dynamics, Trento, Italy, 130, 2004).

#### Author's contribution

**Publication I:** The author is responsible for the analysis of asymptotic regimes (the large amplitude limit, the adiabatic limit, the fast noise limit, and the large flatness limit) of the probability current for Brownian particles. She has also done some of the figures.

**Publication II:** The author is responsible for the derivation of the self-consistency equations and for the compilation and analysis of the phase diagram. She has also done some of the figures.

**Publication III:** The author is responsible for the analysis of the asymptotic regimes of the probability current. She has also done most of the figures.

**Publication IV:** The author is responsible for the derivation of the critical values of the noise amplitude and of the coupling parameter. She is also responsible for the compilation of the phase diagram.

**Publication V:** The author is responsible for the analysis of the phenomena of hypersensitive differential response and disjunct windows. She has also done most of the figures and participated in the compilation of the model.

**Publication VI:** The author is responsible for the derivation of the exact formula for the particle current. She has also done all of the figures.

**Publication VII:** The author is responsible for the analysis of the phenomena of hypersensitive transport and hypersensitive differential response. She has also done some of the figures.

## List of abbreviations

ANM - absolute negative mobility

CR – current reversal DW – disjunct window

GVM – generalized Verhulst self-regulation mechanism

HDR – hypersensitive differential response
 NDR – negative differential resistance

VM – Verhulst self-regulation mechanism

## **Preface**

In the last few decades, interest in the influence of environmental fluctuations on the dynamics of complex systems and in the stochastic methods for describing them has grown enormously. Econophysics, new separation techniques for nanoscale objects, a better understanding of Brownian motors active in living cells, stability analysis of ecosystems in fluctuating environment are but a few examples of relevant studies. Models based on stochastic processes, belonging to a highly topical interdisciplinary realm of studies, can be applied for a variety of purposes, starting from a description of quantum-dot ratchets and ending with a possible explanation of the catastrophic shifts that sometimes occur in ecosystems. Such models are now even used outside the realm of natural sciences, in economics and sociology. As for fluctuations-induced phenomena in complex systems, those also present a fascinating subject of investigation since, contrary to all intuition, environmental randomness may induce a more structured behavior of the system. Thus motivated, we have considered two different classes of stochastic model-systems.

One class of the models is concerned with overdamped Brownian particles in a periodic one-dimensional sawtooth potential landscape subjected to both thermal noise and a nonequilibrium colored noise. A major virtue of the proposed models is that an interplay of colored noise, thermal noise and non-linearity of system can generate a rich variety of nonequilibrium cooperation effects, such as multiple current reversals [I, VII], hypersensitive transport [III, VI, VII], absolute negative mobility, hypersensitive differential response, negative differential resistance, etc [V, VII].

Another class of models is concerned with N-species Lotka-Volterra stochastic models of symbiotic ecological systems with the logistic [II] and the generalized Verhulst [IV] self-regulation mechanism. The effect of a fluctuating environment on the carrying capacities of subpopulations was taken into account as colored noise. The results of analysis of the models provide some new possible scenarios for catastrophic shifts of population sizes observed in nature.

The current Thesis consists of two parts. The first is a summary of the studies and the second one consists of published papers.

As most of my contributions to Papers [IV, V, VII] have been done in close collaboration with Ako Sauga, thus for the sake of complete review of the results a few of them presented in subsections 3.1.3 and 3.2.2 coincide with some results of his dissertation [1].

## 1 Introduction

The idea that noise, via its interaction with nonlinearity of the system, can give counterintuitive results has led to many important discoveries: stochastic resonance [2, 3], resonant activation [4], nonequilibrium phase transitions [5], and stochastic ratchets (Brownian motors) [6]-[15], to name but a few.

The main subjects of the present Thesis are colored-noise-induced transport phenomena of Brownian particles and the influence of colored noise on the dynamics of ecosystems.

## 1.1 Noise-induced transport phenomena

Recently, noise-induced anomalous transport phenomena of Brownian particles in nonlinear periodic structures have been the topic of a number of physical investigations. Among such phenomena, we can mention multiple current reversals (CRs), multipeaked current characteristics, hypersensitive response, absolute negative mobility (ANM), negative differential resistance (NDR), and amplification or suppression of diffusion [16]-[19].

A ratchet is a device that can induce unidirectional motion of particles without a net external force or gradient. The recent enthusiasm for the ratchet effect, i.e., a unidirected motion of Brownian particles induced by nonequilibrium fluctuations, with no macroscopic driving applied, in a ratchet-like potential was triggered by Magnasco's theoretical work [7]. Magnasco pointed out that two facts – first, that a ratchet-like periodic potential has no inversion symmetry and second, that symmetric noise is non-white (it is correlated in time) bear joint responsibility for transport in one direction. The motivation in this field has come from cell biology, e.g., from in molecular motors, which are proteins (e.g., kinesin or dynein) responsible for the transportation of various chemicals in cells of living organisms. Powered by hydrolysis of ATP, they move along complementary protein fibers, which are periodically modulated and asymmetric, e.g., acting filaments or microtubules [6]-[8]. Beyond that, it has been suggested that the ratchet mechanism can be used for obtaining efficient separation methods of nanoscale objects, e.g., DNA molecules, proteins,

viruses, etc. [6, 9, 10]. To date, the feasibility of particle transport by man-made devices has been experimentally demonstrated for several ratchet types [10]-[13]. Many different forms of ratchet systems are possible. The classification of different types of ratchets (correlation, flashing, etc.) can be found in [6].

The dynamics in ratchet structures with its inherent spatial asymmetry generally exhibits a rich complexity, such as the occurrence of multiple current reversals (CRs) and multipeaked current characteristics [6, 20]. Also, the combined influence of several different noise sources can cause unexpected behavior in the system [7], [21]-[25]. Two noises acting together can potentially generate a far more organized motion than either of them alone, even though the noise sources are statistically independent [21]. The authors of Ref. [23] have analyzed a correlation ratchet in which directed transport is subjected to both a thermal equilibrium noise and zero-mean asymmetric dichotomous They show that the transport direction of Brownian fluctuations. particles can be controlled by thermal noise, i.e., the presence of an additional thermal noise can cause CR. Moreover, the dependence of the current on temperature is nonmonotonic and there are two other characteristic (optimal) temperatures at which, respectively, the positive and negative currents are maximized.

The models with CRs are potentially very useful, because CRs could lead to a more efficient fluctuation-induced separation of particles [26]-[28]. It has been shown that the effect of CR can be attained by changing the correlation time of non-equilibrium fluctuations as well as the flatness parameter (the ratio of the fourth moment to the square of the second moment) of the noise [27], [29]-[34]. The direction of the current can also be reversed by modifying either the power spectrum of the noise source [35], or the number of interacting Brownian particles per unit cell [36], mass of the particles [37], the temperature in multinoise cases [23], etc.

The motivation to study hypersensitive response has come from numerical, analytical and experimental studies of a nonlinear Kramers oscillator with a multiplicative white noise. Under the effect of intense multiplicative noise, the system is able to amplify an ultrasmall deterministic ac signal [38, 39]. Afterwards, a related phenomenon such as noise-induced hypersensitive transport was found in some other sys-

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tems with a multiplicative colored noise. It was shown that in such a system a macroscopic flux (current) of matter appears under the influence of an ultrasmall dc driving [40, 41].

A characteristic feature of models with ANM is that upon the application of an external static force F, these models respond with a current that always runs in the direction opposite to that of the force (if the force is small enough) [42, 43]. Notably, for F=0, no current appears due to the spatial symmetry of the system. The effect of ANM is distinct from the phenomenon of negative differential mobility (or resistance) which is, for a sufficiently large F, characterized by a decrease of the current as the driving force F increases but the system does not exhibit ANM [28, 44]. Devices that display both ANM and negative differential resistance (NDR) exist and they have important biophysical and technological applications, e.g., semiconductor devices [45, 46], tunnel junction in superconductor devices [47, 48], biological ion channels [28, 44, 49], etc.

Thus motivated to study noise-induced transport phenomena of Brownian particles, such as current reversals, hypersensitive transport, absolute negative mobility, negative differential resistance, we will consider three types of ratchet models with a 1D sawtoowth potential subjected to both thermal noise and a nonequilibrium three-level colored noise: (i) a correlation ratchet, in which directed transport is subjected to an additive trichotomous noise, (ii) a tilted ratchet system driven by a multiplicative trichotomous noise, and (iii) a tilted ratchet system subjected to a spatially nonhomogeneous three-level colored noise.

## 1.2 The influence of noise on the dynamics of ecosystems

Modeling of the dynamics of interacting species is a central problem in ecological theory, and there exists a vast literature describing deterministic and stochastic models for such interactions (for a reference survey see, e.g., [50]-[52]). Usually the processes are so complex that the dynamics of such webs of coevolving species, especially in the case of a great number of interacting species, can be successfully represented by means of a dynamical system with stochastic elements [53]-

[56]. Ecological systems are usually assumed to respond smoothly to gradual changes of environmental parameters. However, studies have shown that smooth changes are interrupted by catastrophic shifts leading to a new state of the ecosystem [57]. Furthermore, recent results exhibit the existence of alternative stability domains in different natural ecosystems [57]-[61]. Such catastrophies have also been noticed in various theoretical models assuming that the effective deterministic potentials are multistable [50, 51, 52, 57]. Typical examples are the models in which a prey-predator relationship dominates [62]-[67], and the models of competing communities [68].

Ecologists have mainly been interested in the dynamical consequences of population interactions, often ignoring environmental variability altogether. Physical environments, however, are rarely static, and variability in important environmental parameters, such as temperature and rainfall, have widely recognized impacts on natural populations of plants and animals. The essential role of environmental fluctuations has recently been recognized in theoretical ecology. Noise—induced effects on population dynamics have been subject to intense theoretical investigations [69]-[80]. Some theoretical investigations suggest that the population dynamics is sensitive to noise color [82]-[86].

Recently, noise-induced nonequilibrium transitions (as well as colored-noise-induced transitions) in spatially extended nonlinear systems with multiplicative noise have been the topic of a number of physical investigations [5]. The initial motivation in this field has come from the studies of phase transitions, in particular from the discovery of a noise-induced reentrant second-order phase transition for an artificial spatially extended model [87]. Afterwards, noise-induced nonequilibrium transitions (either continuous or discontinuous) were found in systems of coupled oscillators [88]-[93] and also in some other systems [94]-[105]. The fact that external multiplicative noise can induce multistability as well as discontinuous transitions in some complex systems (see, e.g., [104, 105]) inspired us to apply an analogous approach to analyzing ecological models. It is of interest, both from theoretical and practical viewpoints, whether the catastrophic shifts sometimes occurring in ecosystems [57]-[61] can be regarded as induced by multiplicative colored noise.

In this study we will consider a broad class of N-species Lotka-Volterra models of symbiotic ecological systems with the generalized Verhulst self-regulation mechanism (GVM) and also with the true Verhulst (logistic) self-regulation mechanism. The effect of fluctuating environment on the carrying capacity of a population is modeled as a multiplicative colored noise.

## 1.3 Objectives

The general aim of the study presented in the current Thesis is to analyze external colored-noise-generated effects in some complex systems, such as ratchet systems and symbiotic ecosystems: particularly focusing on the role of noise flatness.

The main objectives of the Thesis are as follows:

- (1) To find the dependence of the particle current on the system parameters in the case of an overdamped Brownian particle in a piecewise linear spatially periodic potential subjected to both thermal and colored symmetric three-level Markovian noise.
- (2) To establish a mechanism of hypersensitive transport, demonstrating that the flatness of multiplicative noise can generate hypersensitive response to small external adiabatic force in a tilted sharp ratchet system.
- (3) To generalize the 1D "three-layer" basic model, presented in Ref. [43], to the case where the transitions between different potential configurations (different "layers") are not localized at discrete points, i.e., a nonhomogeneous three-level colored noise induces transitions rather in finite intervals. On the basis of the developed model-system, to discuss some novel phenomena where the role of nonhomogeneous noise is crucial, particularly to establish the conditions allowing hypersensitive differential response.
- (4) On the basis of the N-species stochastic Lotka-Volterra model of a symbiotic ecological system with generalized Verhulst self-regulation, to find an answer to the question whether the catastrophic shifts sometimes occurring in ecosystems can be regarded as induced by environmental fluctuations (by multiplicative col-

- ored noise).
- (5) To apply the developed theory on some modifications of the basic model and especially to investigation of the conditions for colored-noise-induced first-order-like phase transitions over extended noise parameters and interaction strengths. The colored-noise-induced transitions in the basic N-species Lotka-Volterra model can be used to provide a possible scenario for catastrophic shifts of population sizes observed in nature.

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## 2 Models and methods

#### 2.1 Three-level noise

The most productive abstraction of noise-like influence from the environment is Gaussian white noise. However, various physical effects are induced by colored noise, which has a non-zero correlation time, and in these cases the white noise approximation represents an oversimplification. In the present study nonequilibrium fluctuations (a colored noise) is modeled as a symmetric three-level telegraph process Z(t) that may be called trichotomous noise (see VIII and [106]). Also, we have modeled spatially nonhomogeneous fluctuations assumed to be a three-level Markovian stochastic process  $Z^{nh}(X,t)$ .

The trichotomous Markovian stochastic process Z(t) consists of jumps among three values  $z_1 = 1$ ,  $z_2 = 0$ ,  $z_3 = -1$ . The jumps follow in time according to a Poisson process, while the values occur with the stationary probabilities

$$p_s(z_1) = p_s(z_3) = q, \quad p_s(z_2) = 1 - 2q.$$
 (2.1)

The probabilities  $W_n(t)$  that Z(t) is in the state n at the time t evolve according to the master equation

$$\frac{d}{dt}W_n(t) = \sum_{m=1}^{3} U_{nm}W_m(t),$$
(2.2)

where

$$\mathbf{U} = \nu \begin{pmatrix} q - 1 & q & q \\ 1 - 2q & -2q & 1 - 2q \\ q & q & q - 1 \end{pmatrix}. \tag{2.3}$$

The transition probabilities between the three values  $z_1 = 1$ ,  $z_2 = 0$ ,  $z_3 = -1$ , can be obtained as follows:

$$P(\pm 1, t + \tau | 0, t) = P(-1, t + \tau | 1, t) =$$

$$= P(1, t + \tau | -1, t) = q (1 - e^{-\nu \tau}),$$

$$P(0, t + \tau | \pm 1, t) = (1 - 2q) (1 - e^{-\nu \tau}),$$

$$\tau > 0, \quad 0 < q < 1/2, \quad \nu > 0.$$
(2.4)

In a stationary state, the mean value and the correlation function are

$$\langle Z(t) \rangle = 0, \quad \langle Z(t_1)Z(t_2) \rangle = 2q \exp(-\nu \mid t_1 - t_2 \mid).$$
 (2.5)

It can be seen that  $\nu$  is the reciprocal of the noise correlation time:

$$\nu = 1/\tau_c. \tag{2.6}$$

The trichotomous process is a special case of the kangaroo process [29] with the flatness parameter  $\varphi$ 

$$\varphi = \langle Z^4(t) \rangle / \langle Z^2(t) \rangle^2 = 1/(2q). \tag{2.7}$$

At large flatnesses the trichotomous noise essentially coincides with the three-level noise used by Bier [27] and Elston and Doering [30]. It is remarkable that for trichotomous noises the flatness parameter  $\varphi$ , contrary to the cases of the Gaussian colored noise ( $\varphi = 3$ ), and the symmetric dichotomous noise ( $\varphi = 1$ ), can be anything from 1 to  $\infty$ . This extra degree of freedom can prove useful at modelling actual environmental fluctuations.

We emphasize that the dichotomous noise [107] is as a specific case of the trichotomous noise, q = 1/2.

In Section 3.1.3, we consider the influence of spatially nonhomogeneous fluctuations  $Z^{nh}(X,t)$  on a motion of Brownian particles in a one-dimensional system with a spatially periodic potential V = V(x+L) of a period L. The random function  $Z^{nh}(X,t)$  represents a three-level Markovian stochastic process and is assumed to be spatially non-homogeneous, so that transitions between the states  $z_1 = -1$ ,  $z_2 = 0$  and between the states  $z_2 = 0$ ,  $z_3 = 1$  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  $Z^{nh}(X,t)$  is in the state n at time t evolve according to the master equation

$$\frac{d}{dt}W_n(t) = \sum_{m=1}^{3} U_{nm}W_m(t),$$
(2.8)

where

$$\mathbf{U} = \frac{\nu}{2} \begin{pmatrix} -a_1(x), & a_1(x), & 0\\ a_1(x), & -1, & a_2(x)\\ 0, & a_2(x), & -a_2(x) \end{pmatrix}$$
(2.9)

and  $a_1(x) = \Theta(x - L/2)$ ,  $a_2(x) = \Theta(L/2 - x)$ ;  $\Theta(x)$  is the Heaviside function (for more details see Paper [V]).

#### 2.2 Ratchet models with a three-level noise

We consider overdamped motion of Brownian particles in a 1D spatially periodic potential of the form  $V(x,t) = V(x)[\alpha + \beta Z(t)]$ , where Z(t) is a trichotomous noise (see Sec. 2.1),  $\alpha$  and  $\beta$  are constants, and V(x) is a spatially periodic function of a period L and barrier height  $V_0 = V_{max} - V_{min}$ . There is an additional force that consists of thermal fluctuations  $\xi(t)$  of temperature T, an external static force F, and a colored three-level spatially nonhomogeneous noise  $Z^{nh}(X,t)$  (see Sec. 2.1). The system is described by the following Langevin equation

$$\kappa \frac{dX}{dt} = [\alpha + \beta Z(t)]h(X) + a_0 Z(t) + F + f Z^{nh}(X, t) + \xi(t), \quad (2.10)$$

where  $h(x) = -\frac{dV(x)}{dx}$ ,  $\kappa$  is the friction coefficient,  $a_0$  is the amplitude of the trichotomous noise and f is the constant force. The thermal fluctuations  $\xi(t)$  are modeled by a zero-mean Gaussian white noise with the correlation function  $\langle \xi(t_1), \xi(t_2) \rangle = 2\kappa k_B T \delta(t_1 - t_2)$ , where  $k_B$  is the Boltzmann constant. By applying a scaling of the form

$$\tilde{X} = \frac{X}{L}, \quad \tilde{V}(\tilde{x}) = \frac{V(x)}{V_0}, \quad \tilde{t} = \frac{t}{t_0}, \quad \tilde{Z} = \frac{L}{V_0}Z, \quad \tilde{\xi} = \frac{L}{V_0}\xi,$$

$$\tilde{F} = \frac{L}{V_0}F, \quad \tilde{f} = \frac{L}{V_0}f, \quad \tilde{a_0} = \frac{L}{V_0}a_0, \quad (2.11)$$

we get a dimensionless formulation of the dynamics with  $\tilde{V}(\tilde{x}) = \tilde{V}(\tilde{x} - 1)$ . By the choice of  $\tilde{t}_0 = \kappa L^2/V_0$  the dimensionless friction coefficient turns to unity, i.e.,  $\tilde{\kappa} = 1$ . The rescaled noises are given by

$$\tilde{\nu} = \frac{\kappa L^2 \nu}{V_0}, \ \tilde{D} = \frac{k_B T}{V_0}, \ \tilde{a}_1(\tilde{x}) = \Theta\left(\tilde{x} - \frac{1}{2}\right), \ \tilde{a}_2(\tilde{x}) = \Theta\left(\frac{1}{2} - \tilde{x}\right),$$

where  $2\tilde{D}$  is the strength of the rescaled zero-mean Gaussian white noise  $\tilde{\xi}(t)$ . For brevity's sake, we shall call  $\tilde{D}$  temperature. From now on we shall use only dimensionless dynamics and omit the tildes.

On the basis of the Model (2.10) we study three types of ratchets with a sawtoowth potential, which are subjected to both thermal noise and a nonequilibrium three-level colored noise: (i) a correlation ratchet, in which directed transport is subjected to an additive trichotomous noise, i.e.,  $\beta = F = f = 0$  (Papers [I, VII]); (ii) a tilted ratchet system driven by a multiplicative trichotomous noise, i.e.,  $\alpha = a_0 = f = 0$  (Papers [III, VI, VII]); (iii) a tilted ratchet system subjected to a spatially nonhomogeneous three-level colored noise, i.e.,  $\beta = a_0 = 0$  (Papers [V, VII]).

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) of the three-level noise obeys the master equation of the form

$$\frac{\partial P_n(x,t)}{\partial t} = -\frac{\partial}{\partial x} j_n(x,t) + \sum_m U_{nm} P_m(x,t), \quad n, m = 1, 2, 3, \quad (2.12)$$

where

$$j_n(x,t) = \left[\alpha h(x) + \eta(x)z_n + F - D\frac{\partial}{\partial x}\right] P_n(x,t)$$
 (2.13)

are the current densities in the state  $(x, z_n)$ . In the case of the trichotomous noise [f = 0 in Eq. (2.10)] the function  $\eta(x) \equiv a_0 + \beta h(x)$  and the matrix elements  $U_{nm}$  are given by Eq. (2.3). In the case of the spatially nonhomogeneous noise  $[\beta = a_0 = 0 \text{ in Eq. } (2.10)]$  the function  $\eta$  is constant, namely  $\eta \equiv f$ , and the matrix elements  $U_{nm}$  are given by Eq. (2.9).

The stationary current J is evaluated via the current densities

$$J = \sum_{n} j_n^s(x), \quad j_n^s(x) = \left[\alpha h(x) + \eta(x)z_n + F - D\frac{\partial}{\partial x}\right] P_n^s(x),$$
(2.14)

where  $P_n^s(x)$  is the stationary probability density for the state  $(x, z_n)$ . It follows from Eq. (2.12) that the current J is constant.

To derive an exact formula for J, we present an analysis of the system of Eq. (2.10) for a piecewise linear sawtooth-like potential  $V(x,t) = [\alpha + \beta Z(t)]V(x)$ , namely,

$$V(x) = \begin{cases} -(x-d)/d, & x \in (0,d) \text{ mod } 1, \\ (x-d)/(1-d), & x \in (d,1) \text{ mod } 1, \end{cases}$$
 (2.15)

where  $d \in (0,1)$  determines the asymmetry of the potential, which is symmetric if d = 1/2. We may confine ourselves to the case  $d \le$ 

1/2. The "force" h(x) = -dV(x)/dx being periodic, the stationary distributions  $P_n^s(x)$  as solutions of Eqs. (2.12) are also periodic and it suffices to consider the problem in the interval [0,1). The "force" corresponding to the potential of Eq. (2.15) is

$$h(x) = -\frac{dV(x)}{dx} = \begin{cases} h_0 := 1/d, & x \in (0, d), \\ h_1 := -1/(1 - d), & x \in (d, 1). \end{cases}$$
 (2.16)

As the "force" h(x) is a piecewise constant in the open intervals  $(0,d)(mod\ 1)$  and  $(d,1)(mod\ 1)$  Eq. (2.12) splits up into two linear differential equations with constant coefficients for 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,d) and (d,1), respectively.

The exact form of the solution depends on the model of the ratchet system. For example for the model of a tilted ratchet system driven by a multiplicative trichotomous noise and an additive white noise, namely  $\alpha = a_0 = f = 0$  and  $\beta = 1$  in Eq. (2.10), the solution of the master equation reads

$$P_{ni}^{s}(x) = p_{s}(z_{n}) \left[ \frac{J}{F} + \sum_{k=1}^{5} C_{ik} A_{nik} e^{\lambda_{ik} x} \right],$$
 (2.17)

where  $C_{ik}$  are constants of integration,  $A_{nik} = [\lambda_{ik}(D\lambda_{ik} - z_nh_i - F) - \nu]^{-1}$ , and  $\{\lambda_{ik}, k = 1, ..., 5\}$  is the set of roots of the algebraic equation

$$D^{3}\lambda_{i}^{5} - 3D^{2}F\lambda_{i}^{4} + D(3F^{2} - 2D\nu - h_{i}^{2})\lambda_{i}^{3} + F(4D\nu - F^{2} + h_{i}^{2})\lambda_{i}^{2} + \nu(D\nu - 2F^{2} + 2qh_{i}^{2})\lambda_{i} - \nu^{2}F = 0.$$
 (2.18)

Ten independent conditions for the ten constants of integration  $C_{ik}$ , and for the current J can be determined at the points of discontinuities, by requiring continuity and periodicity for the quantities  $P_i^s(x)$  and  $j_{ni}^s(x)$ , that is

$$P_{n0}^{s}(d) = P_{n1}^{s}(d), P_{n0}^{s}(0) = P_{n1}^{s}(1)$$
  
 $j_{n0}^{s}(d) = j_{n1}^{s}(d), j_{n0}^{s}(0) = j_{n1}^{s}(1), n = 1, 2, 3.$  (2.19)

As it follows from Eq. (2.12) that J = const, the system of linear algebraic equations (2.19) contains only ten linearly independent equa-

tions. By including the following eleventh (normalization) condition:

$$\sum_{n=1}^{3} \int_{0}^{1} P_{n}^{s}(x)dx = 1, \qquad (2.20)$$

a complete set conditions is obtained for the ten constants of integration and for the current J. This procedure leads to an inhomogeneous set of eleven linear algebraic equations. Now, the current J can be expressed as a quotient of two determinants of the eleventh degree. The exact formula, being complex and cumbersome, will be not presented here (see Paper [VI]).

Following an analogous procedure, the current J can also be determined for the other ratchet systems considered in this study (see Papers [I, V]).

# 2.3 Lotka-Volterra stochastic model of a symbiotic ecosystem

The models is based on the N-species generalized Lotka-Volterra equation with generalized Verhulst self-regulation

$$\frac{d}{dt}X_i(t) = X_i(t) \left[ \delta \left( 1 - \left( \frac{X_i(t)}{K_i} \right)^{\beta} \right) + \frac{J}{N} \sum_{j \neq i} X_j(t) \right], \qquad (2.21)$$

where  $X_i(t)$  (i = 1, ..., N) is the population density of the *i*-th species at time t (clearly  $X_i(t) \ge 0$ ),  $\delta$  is the growth rate parameter of species and the coupling parameter  $J \ge 0$ , i.e., the *i*-th species is in a symbiotic relationship with the *j*-th species. The carrying capacity  $K_i$  is a limiting factor on the *i*-th population growth, which is imposed by environmental factors, basically food and space limitations.

In Paper [II] we analyzed the generalized Lotka-Volterra model (2.21) with the Verhulst self-regulation mechanism (VM), i.e., we took the exponent  $\beta = 1$ . In Paper IV we analyzed the Model (2.21) with the generalized Vehulst self-regulation mechanism (GVM), i.e., the exponent  $\beta \geq 0$ , focusing mainly on the case  $\beta > 1$ .

The effect of fluctuating environment on the growth of a population is modeled by using colored noise.

For VM random interaction with the environment is taken into account by exploiting a trichotomous noise into the carrying capacity  $K_i$ :

$$\frac{\delta}{K_i} = \frac{\delta}{K} + a_0 Z_i(t), \tag{2.22}$$

where the colored noise  $a_0Z_i(t)$  is assumed to be a trichotomous noise (see Sec. 2.1) with an amplitude  $a_0$ . The Model (2.21) with VM and with Eq. (2.22) is biologically meaningful only if  $a_0 < \delta/K$ .

In order to investigate the presence of a possible hysteresis induced by the noise we modified the above model [Eqs. (2.21)-(2.22)] introducing an adaptation into the carrying capacity  $K_i$ :

$$\frac{\delta}{K_i} = \delta/K + \frac{\epsilon \delta^2}{NK^2} \sum_{j \neq i} X_j(t) + a_0 Z_i(t), \qquad (2.23)$$

where the adaptation factor  $\epsilon > 0$  is assumed independent of the species, i.e., the populations adapt themselves with respect to the total number of individuals of all populations.

The term with the factor  $\epsilon$  in Eq. (2.23) mimics the decrease of the carrying capacity caused by adaptive competition of populations for common resources, such as food or living space [108]. A need for the consideration of inter-space adaptive competition in models with Verhulst self-regulation of biological relevance arises from the following circumstance: In the absence of adaptation ( $\epsilon = 0$ ), for all J > 0 the corresponding deterministic model (without noise) is characterized by instability; it means that within a finite time the site average  $(1/N) \sum_{j(\neq i)} X_j(t)$  grows to infinity. For biologically relevant models any growth of an expanding population must eventually be stopped by shortage of resources. Addition of adaptation of the model would regulate the behaviour of the system so that an unstable state of the system would be replaced by a new stable stationary state.

For GVM we used

$$K_i = K [1 + a_0 Z_i(t)],$$
 (2.24)

where the colored noise  $a_0Z_i(t)$  is assumed to be a dichotomous noise (see Sec. 2.1) with an amplitude  $a_0$ . The Model (2.21) with Eq. (2.24) is biologically meaningful at the condition  $a_0 < 1$ .

Since one of the characteristic quantities of an ecosystem, perhaps the most fundamental one, is its average species density  $\bar{X}$ , we consider average species density as the state parameter of an ecosystem. We study the model using the mean-field approach, focusing on the behavior of the explicit self-consistency equation for the stationary states.

To proceed with analytical examination of the Models (2.21) with different self-regulation mechanisms [Eqs. (2.22)-(2.24)] we assume that  $N \to \infty$ . This means we are interested in the case of infinitely many interacting species. Following Shiino [109], the mean-field approximation can be obtained by replacing the site average  $(1/N) \sum_{j(\neq i)} X_j(t)$  by the statistical average  $\langle X(t) \rangle$  in Eq. (2.21). Hence, each stochastic differential equation Eq. (2.21), where Eqs. (2.22)-(2.24) are assumed, can be reduced to an independent and identical stochastic differential equation of the form

$$\frac{dX(t)}{dt} = X(t)[\delta + J\langle X(t)\rangle - \gamma X^{\beta}(t)(1 + aZ(t))]. \tag{2.25}$$

For the Models (2.21) with VM and with Eqs. (2.22)-(2.23), the parameter  $\gamma \equiv \delta \langle 1/K_i \rangle$  and a is the amplitude of the trichotomous noise  $a \equiv a_0/\gamma$ . For the Model (2.21) with GVM and with Eq. (2.24)

$$\gamma = \frac{\delta}{2(1 - a_0^2)^{\beta} K^{\beta}} \left[ (1 + a_0)^{\beta} + (1 - a_0)^{\beta} \right]$$
 (2.26)

and

$$a = \frac{(1+a_0)^{\beta} - (1-a_0)^{\beta}}{(1+a_0)^{\beta} + (1-a_0)^{\beta}}$$
 (2.27)

may be called the amplitude of the dichotomous noise.

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

$$\frac{\partial P_n(x,t)}{\partial t} = -\frac{\partial}{\partial x} \{x[r(t) - \gamma x^{\beta}(1+a_n)]P_n(x,t)\} + \sum_m U_{nm}P_m(x,t)$$
(2.28)

with  $r(t) \equiv \delta + J\langle X(t)\rangle$ . For the models with trichotomous noise  $n, m = 1, 2, 3; a_1 = a, a_2 = 0, a_3 = -a$  and the matrix **U** is given

by Eq. (2.3). For the models with dichotomous noise [Eq. (2.21) with Eq. (2.24)]  $n, m = 1, 2; a_1 = a, a_2 = -a$  and the matrix **U** is given by

$$\mathbf{U} = \frac{\nu}{2} \begin{pmatrix} -1, & 1\\ 1, & -1 \end{pmatrix}. \tag{2.29}$$

The behavior of a stationary system can be analytically studied by means of a standard mean-field theory procedure [5]. For a stationary state we can solve Eq. (2.28), 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  $(x, z_n)$  (see Papers [II, IV]). The self-consistency equation for the Weiss mean-field approach, whose solution yields the dependence of  $\langle X \rangle$  on the system parameters, is

$$\langle X \rangle = \int_{x_1}^{x_2} x P(x, r) dx. \tag{2.30}$$

For example for the Model (2.21) with VM and with Eq. (2.22) we obtain the following dimensionless formulation of the self-consistency equation

$$\delta^* m = 1 - J^* {}_{3}F_2(1, \frac{1}{2}, 2qm; m, m + \frac{1}{2}; \alpha), \tag{2.31}$$

in which the "order parameter"

$$m := \frac{\nu}{2\gamma} \left\langle \frac{1}{X} \right\rangle = \frac{\nu}{2(\delta + J\langle X \rangle)}$$
 (2.32)

and a scaling of the form

$$\delta^* = 2\delta/\nu, \quad J^* = J/\gamma, \quad \alpha = a_0^2/\gamma^2 \tag{2.33}$$

is used;  $_3F_2$  is the hypergeometric function.

Analogous self-consistency equations, usable for the other models of symbiotic ecosystems, have been considered above, obtained in Papers [II, IV].

## 3 Results and discussion

#### 3.1 Colored-noise-induced anomalous transport

#### 3.1.1 Multiple current reversals

In this subsection the results for the model (2.10) with  $\beta = F = f = 0$  and  $\alpha = 1$ , i.e., the model of a correlation ratchet in which directed transport is subjected to both a trichotomous noise and a thermal noise, are given. Here we will briefly review the behavior of the current J at the different limits. More details are presented in Paper [I].

In the case of a large noise amplitude  $(a_0 \to \infty)$  with a fixed flatness  $\varphi$ , the noise correlation time  $\tau_c$ , and temperature D, the current saturates to a finite negative value. This somewhat surprising result is due to both an effective inhomogeneous diffusion, which becomes more homogeneous at an increasing  $a_0$ , and the so-called flashing barrier effect as stated in [27, 32]. The dependence of the current on the temperature and the switching rate  $\nu = 1/\tau_c$  is illustrated in Fig. 1. As the temperature grows, the current decreases monotonically to zero at any values of  $q = 1/2\varphi$ ,  $\nu$  and the potential asymmetry parameter d.

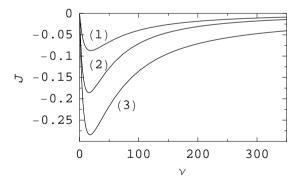


Figure 1: The current J vs the switching rate  $\nu$  in the case of the large-amplitude limit. The curves have been computed for the flatness parameter  $\varphi = 1/2q = 2$ , the potential asymmetry parameter d = 0.25, and temperatures: (1)D = 0.2, (2)D = 0.07, (3)D = 0. The current is negative and its absolute value decreases monotonically as D increases.

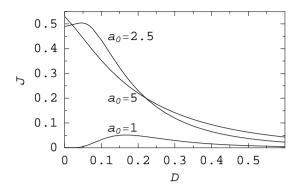


Figure 2: The current J vs the temperature D at various noise amplitudes  $a_0$  in the case of an adiabatic limit. The flatness parameter  $\varphi = 1.5$  and the potential asymmetry parameter d = 0.25. Note that for  $a_0 < h_0 = 1/d$  the current exhibits a bell-shaped extremum; if  $a_0 > h_0$ , then J decreases monotonically. The temperature which maximizes the current decreases monotonically as  $a_0$  increases.

In the case of the adiabatic limit  $\nu \to 0$  the current is positive and changes with temperature as follows: in case the trichotomous fluctuations induce transitions forth and back over the potential barrier, i.e., if  $a_0 > h_0 = 1/d$ , J decreases monotonically as the temperature increases. On the other hand, if the trichotomous transitions do not induce transitions in both directions over the barrier, i.e., if  $a_0 < h_0$ , the net current exhibits a bell-shaped extremum (see Fig. 2). Hence, if  $a_0 < h_0$ , there is an optimal temperature  $D_m$  maximizing the current. As the noise amplitude  $a_0$  increases, the temperature  $D_m$  decreases monotonically to zero at  $a_0 = h_0$ .

In the case of the adiabatic limit  $\nu \to 0$  with small noise amplitudes  $a_0 \ll \min\{1/(1-d), D\}$ , the optimal temperature  $D_m \approx 0.216$ . It is remarkable that in this case the characteristic temperature  $D_m$  depends neither on the shape of the ratchet potential nor on the parameters of the trichotomous noise. It seems reasonable to assume that for overdamped ratchet models with an additive thermal noise and with an additive low-amplitude nonequilibrium noise the same value of the optimal temperature in the adiabatic limit occurs.

In the fast noise limit we allow  $\nu$  to become large, holding all other parameters fixed, and use  $\nu^{-1/2}$  as a smallness parameter. Thus, if

the temperature  $D \neq 0$ , in the large  $\nu$  limit the current is positive and decays algebraically to zero in  $\nu^{-5/2}$ . In the case of a dichotomous noise (q=1/2) such a formula for J has been found in [21]. The thermal noise has a strong effect on the current in the small correlation time  $\tau_c$  limit: in the presence of thermal noise fluctuations the current exhibits exponential growth from  $J \sim \pm \exp(-C/\tau_c)$  with a positive constant C that depends on  $a_0, q$ , and d, to  $J \sim \tau_c^{5/2}$ . It looks like in this model the two noises acting together are able to generate a considerably more organized motion than either one of them alone, even though they are generated by statistically independent sources. The authors of [21] have reached an analogous conclusion for the case of  $\varphi > 2$  and D = 0 there can occur one current reversal (CR) caused by variation of  $\nu$ , in the case of  $\varphi > 2$  and  $D \neq 0$  there can occur either two reversals or none.

In the case of a large flatness parameter,  $\varphi \gg 1$ , we expanded the current as  $J = qJ^{(1)} + q^2J^{(2)} + \dots$  Drawing on the asymptotic expressions of  $J^{(1)}$  we can reach the following results: (i) For variations of the amplitude  $a_0$  an odd number of CRs occur. At large asymmetries  $d \ll 0.5$  we have observed up to three CR-s. Still, in most cases there is one CR. (ii) At variations of the correlation time  $\tau_c$  the number of CRs is even or zero. At numerical calculations and at large asymmetries, we have even observed four CRs (see Paper [I] and [33]). (iii) As for changes of the temperature D there is an upper limit  $\tau_1(a_0)$  for the correlation time  $\tau_c$ , at greater values of which there is no CR (see also Fig. 3). For  $a_0 > h_0 |h_1|$ , where  $h_0 = 1/d$  and  $h_1 = -1/(1-d)$ are the forces corresponding to the sawtooth potential [see Eq. (2.15)], another critical value of the correlation time  $\tau_2(a_0) < \tau_1(a_0)$  occurs. In case  $\tau_2 < \tau_c < \tau_1$  there are two CRs, but at  $\tau_c < \tau_2$  there is only one CR. For  $a_0 < h_0|h_1|$  and  $\tau_c < \tau_1(a_0)$  two or no CRs appear. They can be absent only at the values of the noise amplitude  $|h_1| \ll a_0 \ll h_0$ , which is possible only at large asymmetries of the potential d < 0.01. Then the current exhibits disjunct characteristic "windows" of the correlation time where the temperature-controlled CRs take place (see also [34]).

For example Fig. 3 represents the current J vs temperature D in the case of a large flatness and  $a_0 < h_0|h_1|$ . If the correlation time

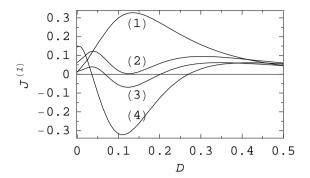


Figure 3: The current  $J=qJ^{(1)}$  vs the temperature D in the case of large flatness at d=0.25. In the limit of high temperature, J is positive and decays to zero. Curves (1)-(4) correspond to the following parameters: (1):  $a_0=1.5$ ,  $\nu=1$ ; (2):  $a_0=3.5$ ,  $\nu=16$ ; (3):  $a_0=3.5$ ,  $\nu=21$ ; (4):  $a_0=4.5$ ,  $\nu=21$ . If  $\tau_c<\tau_1(a_0)$ , then two current reversals occur [curves (3) and (4)]. No current reversals occur when  $\tau_c>\tau_1(a_0)$  [curve (1)].

 $\tau_c > \tau_1(a_0)$ , then there is no CR [curve (1)]. If  $\tau_c < \tau_1(a_0)$ , then there occur two CRs: curves (3), (4). The concrete value  $\tau_1(a_0)$  for a given  $a_0$  and the asymmetry of the potential can be found by numerical methods.

Our major result is that in sawtooth ratchet structures the direction of the transport of Brownian particles driven by symmetric trichotomous fluctuations can be controlled by thermal noise (see Fig. 3). The necessary condition is that the flatness parameter exceeds one.

The advantage of this model is that the control parameter is temperature, which can be easily varied in experiments (see also [23]). Note that the friction coefficient of the particle has been absorbed into the time scale. Thus, in the original (unscaled) setup particles with different friction coefficients are controlled by different effective  $\nu$ -s and can move in either direction in the same ratchet potential and the same fluctuating environment, which has interesting biological and technological implications (see [10, 11, 20, 110, 111, 112]).

#### 3.1.2 Noise-flatness-induced hypersensitive transport

In this subsection the results for the model (2.10) with  $\alpha = a_0 = f = 0$  and  $\beta = 1$ , i.e., the model of the tilted ratchet system driven by a multiplicative trichotomous noise and additive thermal noise, are given. We have analyzed the behavior of the current J, which can be expressed by using Eqs. (2.17)-(2.20), and the mobility m = J/F. More details are presented in Papers [III, VI, VII].

At low temperatures the phenomenon of hypersensitive transport exists, i.e., the enhancement of current is very sensitive to the applied small tilting force. For example Fig. 4 shows the induced current J as a function of the external force F for four different values of the temperature D with fixed values of noise flatness  $\varphi = 1/2q = 3$ , noise correlation time  $\tau_c = 1/\nu = 3/8$ , and the asymmetry parameter d = 0.5. In this figure, one observes the hypersensitive response at very low forcing, which apparently gets more and more pronounced as the thermal noise strength D decreases. For the case  $D \to 0$ , the mobility m = J/F tends to infinity at F = 0, i.e., the current J jumps from the zero level to the macroscopic level with  $J = 32\nu q(1 - 2q)/(\nu + 8)^2 = 1/12$  at the infinitesimally small force F.

To explain the physical mechanism of hypersensitive transport a schematic representation of the three configurations assumed by the "net potentials"  $V_n(x) = z_n V(x) - Fx$  associated with the right hand

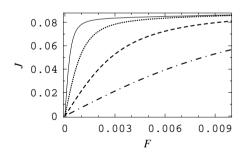


Figure 4: The current J vs. the applied force F in the region of hypersensitive response at the values of the flatness parameter  $\varphi = 3$ , the switching rate  $\nu = 8/3$ , and the asymmetry parameter d = 1/2. Solid line:  $D = 4 \cdot 10^{-8}$ . Dotted line:  $D = 4 \cdot 10^{-7}$ . Dashed line:  $D = 4 \cdot 10^{-6}$ . Dashed-dotted line:  $D = 4 \cdot 10^{-5}$ .

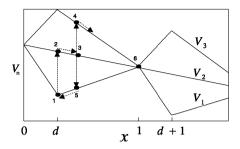


Figure 5: The mechanism of hypersensitive transport in tilted sharp ratchets. The lines represent the three states of the total potential  $V_n(x) = z_n V(x) - Fx$ , where  $z_1 = 1$ ,  $z_2 = 0$ , and  $z_3 = -1$ . An unforced particle cannot move along the potentials  $V_1$  and  $V_3$ . However, if one allows switching between the three states of the total potential  $V_n$ , n = 1, 2, 3, the particle will move downhill along the trajectory 1:2:3:4:6.

side of Eq. (2.10) is shown in Fig. 5. For F=0 the system is effectively isotropic and no current can occur. In the case of zero temperature both the noise levels  $z_n = \pm 1$  in the Langevin equation Eq. (2.10), where  $F \leq \min\{(1/d, 1/(1-d))\}$ , give zero flux. However, if one allows the switching between three dynamic laws  $V_n(x)$ , n=1,2,3,the resulting motion will have a net flux which can be much greater that the flux by dynamic  $V_2 = -Fx$ . If the rate of reaching the minimal energy in each well considerably exceeds the switching rate  $\nu$ , the leading part of the net flux is achieved in the following way: a particle locked in the potential minimum 1 switches to point 2, then slowly moves to point 3, switches to point 4 (or to 5, with equal probability), and rapidly slides down to point 6 (or from 5 back to 1), etc. (see Fig. 5). As a result, macroscopic transport appears. In this case hypersensitive transport is possible and can be intuitively understood. The described picture is valid only in the absence of additive noise. Otherwise, the system is able to pass by a thermally activated escape across potential barriers in both directions, however moving right predominantly, and hypersensitive transport still occurs (at least at a sufficient low temperature).

Our major result is that at low temperatures noise flatness can induce hypersensitive transport.

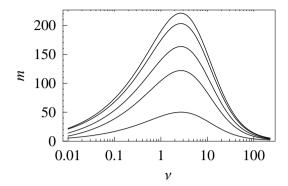


Figure 6: The mobility m vs the switching rate  $\nu$  at d=1/2,  $D=4\cdot 10^{-8}$ , and  $F=10^{-5}$ . The curves correspond, from top to bottom, to the following values of the flatness parameter:  $\varphi=3$ ,  $\varphi=2$ ,  $\varphi=10$ ,  $\varphi=20$ ,  $\varphi=1,1$ . Note that the maximum of the mobility lies at  $\nu=8/3$ .

For example Fig. 6 shows a plot of mobility m vs noise correlation time  $\tau = 1/\nu$  at various noise flatnesses  $\varphi = 1/2q$ . Notably, for fixed low values of temperature, the optimal system parameters at which the mobility is maximized are determined as follows: the flatness parameter  $\varphi \approx 3$ , the correlation time  $\tau_c \approx 3/8$ , and the asymmetry parameter d = 1/2. For sufficiently low values of temperature,  $D \ll \min\{1, 2q\nu, 8q/\nu\}$ , the mobility is given by

$$m \approx \frac{8(1-2q)}{(\nu+8)^2} \sqrt{\frac{2q\nu}{D}} , F < \sqrt{2q\nu D} .$$
 (3.1)

The condition  $F < \sqrt{2q\nu D}$  has a distinct physical meaning: the characteristic distance of thermal diffusion  $\sqrt{D/\nu}$  is larger than the typical distance  $F/\nu$  for the particle driven by the deterministic force F in the state z=0. It can be seen from Eq. (3.1) that the functional dependence of the mobility on the flatness  $\varphi$  and on the correlation time  $\tau_c$  is of a bell-shaped form. Let us note that the formula (3.1) for hypersensitive response is qualitatively valid, i.e.,  $m \sim 1/\sqrt{D}$ , also in case a multiplicative deterministic periodic stimulus replaces the trichotomous noise.

The phenomenon of hypersensitive transport is robust enough to survive a modification of the multiplicative noise (or deterministic

periodic stimulus) as well as the shape of the potential (that is, asymmetric potentials and potentials with several extrema per period). In a general case, if the potential is smooth and the flatness of multiplicative noise is greater than 1, beside of the mechanism described above also another mechanism described in [40] plays an important role and should be taken into account when calculating the mobility. However, in the adiabatic case,  $\nu \ll 1$ , the reported mechanism of generating hypersensitive transport by the flatness of noise induces hypersensitive transport more effectively than the one proposed by Ginzburg and Pustovoit in [40]. Let us look at the latter statement more closely. First, we note that the factor  $\sqrt{\nu/D}$  in Eq. (3.1) is generated by thermal diffusion in the state z=0, while the circumstance that the potential is sharp has no effect on this factor. On the other hand, for adiabatic switching, the mechanism described in [40] generates, in the case of a smooth potential, the mobility  $m \sim \nu/\sqrt{D}$ . Consequently, for sufficiently small switching rates the leading-order term of the mobility is generated by the mechanism described in the Thesis.

It is remarkable that the phenomenon of noise-flatness-induced hypersensitive transport seems to be applicable for amplifying adiabatic time-dependent signals F(t), i.e., signals of much longer periods than the characteristic time of establishing a stationary distribution, even in the case of a small input signal-to-noise ratio  $|F(t)|/\sqrt{D} \ll 1$  (see also [38, 40]). The sensitivity of system response to small input signals can be either enhanced or suppressed by changing the noise parameters (correlation time, flatness, temperature). Moreover, as the friction coefficient  $\kappa$  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. According to the suggestions contained in [6, 9, 10, 113] this can lead to a mechanism for the separation of different types of nanoscale objects (for example, DNA molecules, proteins, viruses, etc.) by exploiting the sensitive dependence of the mobility on the switching rate (see also Fig. 6).

## 3.1.3 Anomalous mobility: hypersensitive differential response, disjunct windows, absolute negative mobility

In this subsection the results for the model (2.10) with  $\beta = a_0 = 0$  and  $\alpha = 1$ , i.e., the model of the tilted ratchet system subjected to both spatially nonhomogeneous three-level colored noise  $Z^{nh}$  (see Eqs. (2.8), (2.9) and Fig. 7) and unbiased thermal noise, are given. We have analyzed the behavior of the current J and differential mobility  $m_d = dJ/dF$  in the case of a linear sawtooth-like symmetric potential, i.e., the asymmetry parameter d = 1/2 in Eq. (2.15). More details are presented in Papers [V, VII].

A major virtue of the proposed model is that an interplay of threelevel colored and thermal noises in tilted ratchets with simple symmetric sawtooth potentials can generate a rich variety of cooperation effects, namely:

- Absolute negative mobility (ANM): upon the application of an external static force F, the Model responds with a current of particles that always runs in the direction opposite to that of the force. Notably, for F=0 no current appears due to a spatial symmetry of the system.
- Negative differential resistance (NDR), which is, for a sufficiently large F, characterized by a decrease of the current as the driving force F increases, but the system does not exhibit ANM.
- Hypersensitive differential response (HDR): the current is, at some values of the tilting force F, very sensitive to small variation of F.
- The phenomenon of "disjunct windows" (DW) for the tilting force: there is a finite interval of the tilting force where the current is very small as compared to that in the surroundings.

Our major result is the establishing of the effects of both HDR and DW at large values of the switching rate  $\nu$  and low values of the temperature D. It seems that the phenomenon of DW is a new transport effect for Brownian particles.

Figure 8 illustrates the behaviour of the current J as a function of a tilting force F in the region of anomalous resistance. It is seen that the curves are highly nonlinear. For the curves (2) and (3), the phenomenon of ANM occurs: the particle moves in the direction

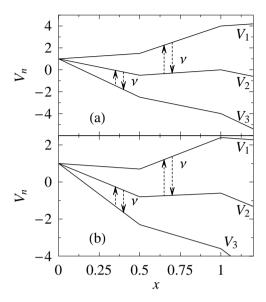


Figure 7: Schematic representation of different states and their transitions in the model (2.10) with a sawtooth-like symmetric potential at low temperatures. The lines depict the net potentials  $V_n(x) = V(x) - Fx - z_n fx$  with  $z_1 = -1$ ,  $z_2 = 0$ , and  $z_3 = 1$ . Unbiased transitions with a switching rate  $\nu$  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  $V_1$ . (a) The case of F = 1, f = 4. (b) The case of F = 1.6, f = 3.

opposite to a small external force F. Moreover, all curves exhibit intervals of F, where the particles' speed decreases with increasing applied drive, an effect that is termed negative differential resistance. The curve (3) demonstrates the effect of hypersensitive response, i.e., the jumps of the current at F=1 and  $F\approx 2$  occur. The effect appears at large values of the switching rate  $\nu$  and low values of the temperature D. In case the noise amplitude f is in the interval 10 of hypersensitive differential response (HDR) occurs at 10 occurs at 11 and 12 occurs at 12 occurs at 13 occurs at 14 and at the low diffusion level 15 occurs at 16 occurs at 17 occurs at 18 occurs at 19 occur

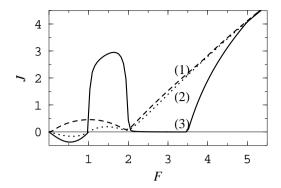


Figure 8: The current J vs an applied force F in the region of anomalous mobility. (1) Dashed line:  $D = 10^{-2}$ ,  $\nu = 10^{-2}$ , and f = 1.9. (2) Dotted line:  $D = 10^{-2}$ ,  $\nu = 10^{-2}$ , and f = 3. (3) Solid line:  $D = 10^{-7}$ ,  $\nu = 10^3$ , and f = 3. Note that in the cases of curves (2) and (3) the phenomenon of absolute negative mobility occurs.

mobility are

$$m_d|_{F=2} \approx -\frac{\nu(4-f)(8+f)}{32(8-f)}, \quad m_d|_{F=f-2} \approx \frac{3\nu(4-f)}{8f}.$$
 (3.2)

The appearance of HDR is not confined to the case described above. If  $\nu \to \infty$  and  $D \to 0$ , the phenomenon can occur, depending on the particular values of the parameters  $\nu D$  and f, at F = 2 + (f/2), 2, f - 2. For example, in the case of 2 < f < 8,  $D\nu \gg 1$ , we have  $m_d|_{F=f-2} \approx f(f-2)/6D(2f-1)^2$ . Note that all these values of F correspond to a change of the net potential configuration. In the case of F = f - 2 and 2 < f < 4 the corresponding change of the net potential  $V_n(x) = V(x) - Fx - z_n fx$  configuration is qualitatively similar to the change from the configuration in Fig. 7(b) to the configuration in Fig. 7(a). A comprehensive description of the physical mechanism for HDR is given in Paper [V].

We emphasize that our mechanism of HDR is of a qualitatively different nature from the effect described in Sec. 3.1.2, where a noise-induced enhancement of the current of Brownian particles in a tilted ratchet system has also been established ([40, 41], and Paper [III]). In the mechanism reported here the hypersensitivity is achieved by a combined influence of fast nonequilibrium noise and a tilt-force-

induced change of the net potentials configuration. It should be pointed out that in the present model the effect of HDR is pronounced in the case of a fast switching of the nonequilibrium noise, while in the models of [40, 41] and Paper [III] the hypersensitive transport is generated by low or moderate values of the switching rate.

Similarly to the case of hypersensitive transport the results of HDR seem also to be applicable for amplifying adiabatic time-dependent signals.

The curve (3) in Fig. 8 also demonstrates the "disjunct windows" effect. At a low temperature and a large switching rate  $\nu$  the current exhibits a characteristic disjunct zone of the tilting force,  $2 + (f/2) > F > \max\{2, f - 2\}$ , in which the current is exponentially small,  $J \sim \nu e^{-\nu d}$ , with d-a constant. The necessary conditions for the emergence of the "disjunct windows" effect are the regime of a small diffusion  $D\nu \ll 1$  and a large  $\nu$ .

As the diffusion is negligible the physical mechanism for DW is simple. For the described interval of F the net potential  $V_1(x)$  exhibits a minimum and the potentials  $V_2(x)$ ,  $V_3(x)$  are monotonic functions. If the correlation time of the noise  $\tau_c = 1/\nu$  is small enough, a particle in the state n=2 cannot, before switching to the state n=1, move to the next spatial period and, consequently, in the stationary state all particles are concentrated at the potential well  $V_1(x)$  and on the right-hand side of the potential  $V_2(x)$ . This is because the absolute value of the deterministic velocity of particles on the right-hand side of  $V_1(x)$  is greater than the velocity on the right-hand side of  $V_2(x)$ . It is obvious that the total current J tends to zero as  $\nu \to \infty$ , since the trapping probability in  $V_1(x)$  and  $V_2(x)$  tends to 1.

Figure 9 shows a plot of differential mobility in the case of the small applied force  $m_0 := \frac{dJ(F)}{dF}\Big|_{F=0}$  as a function of the switching rate  $\nu$  at various temperatures. There occur two important asymptotic regimes in the  $D \neq 0$  situation: first, the regime of low diffusion levels  $D\nu \ll 1$ , for which the characteristic distances of thermal diffusion  $\sqrt{D\tau_c}$  are much smaller than the typical deterministic distances for the particles driven during the noise correlation time  $\tau_c = 1/\nu$ , and second, the regime  $D\nu \gg 1$  for which thermal diffusion dominates. In the regime of low diffusion, if the temperature is small enough,  $D < D_c \approx \sqrt{f}/6$ , the phenomenon of ANM appears, contrary to the case of  $D\nu \gg 1$ ,

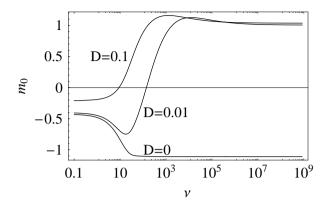


Figure 9: The mobility  $m_0$  vs the switching rate  $\nu$  at various temperatures D and at the noise amplitude f = 3. Note that at the finite value  $\nu = 18$  with the temperature D = 0.01 a resonant-like enhancement of ANM occurs.

where the mobility is positive. Finally, we note that a most salient intermediate regime occurs in which the ANM exhibits a resonant-like enhancement at finite values of  $\nu$ . For example, in Figure 9, the curve  $m_0(\nu)$  with D=0.01 shows amplification of ANM at  $\nu=18$ .

It is obvious that the presence and intensity of ANM can be controlled by thermal noise. Notably, the phenomenon of ANM also occurs at high temperatures, if only the noise amplitude f is large enough (see also [V] and [1]).

# 3.2 Colored-noise-induced catastrophic shifts in symbiotic ecosystems

## 3.2.1 Trichotomous-noise-induced discontinuous transitions in symbiotic ecosystems

In this subsection the mean-field results for the generalized Lotka-Volterra model [Eq. (2.21)] with the Verhulst self-regulation mechanism (VM), i.e., the exponent  $\beta = 1$ , and with a fluctuating carrying capacity [Eq. (2.22)], are given. Also the results for a modified Model (2.21) with VM and with adaptation [Eq. (2.23)] are considered. More details are presented in Paper [II].

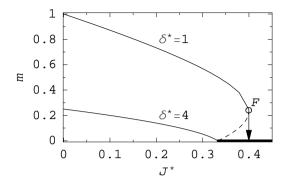


Figure 10: Stationary mean field m vs coupling strength  $J^*$  at different growth rates  $\delta^*$ . The flatness parameter equals  $\varphi = 2$ , the amplitude parameter  $\alpha = 0.8$ , and the critical parameters  $J_1 = 1/3$  and  $J_2 \approx 0.3998$ . The bold line depicts an unstable phase. The dashed lines depict the unstable solutions of Eq. (2.31). If m lies on the upper branch close to the point F, a slight growth of  $J^*$  induces a catastrophic transition of the system to an unstable state.

Next we will discuss the Model (2.21) with the VM and Eq. (2.22). From the self-consistency equation (2.31) the following three characteristic regions can be discerned for the coupling parameter  $J^*$  (see also Fig. 10). (i) There is just one solution of Eq. (2.31) – if  $J^* < J_1$ , the solution is stable. (ii) There is no solution – if  $J^* > 1$ , the system is unstable, as in a finite time the statistical average  $\langle X(t) \rangle$  grows to infinity. (iii) In the case of  $J_1 < J^* < 1$  there are two possible situations in the long time limit. There is an upper limit  $\delta_c^*$  for the growth rate parameter  $\delta^*$ , at greater values of which there is no solution and the system is unstable. For  $\delta^* < \delta_c^*$  another critical value of the coupling parameter  $1 > J_2 > J_1$  occurs. In the case  $J^* > J_2$  the system is unstable, but at  $J_1 < J^* < J_2$  there are two solutions. The bigger one  $(m_1)$  is stable and the smaller one  $(m_2 < m_1)$  is unstable.

The characteristic coupling parameter  $J_1$  is expressed as

$$J_1 = \frac{1 - \alpha}{1 - \alpha(1 - 2q)},\tag{3.3}$$

where  $\alpha$  is the noise amplitude parameter [see Eq. (2.33)] and the noise flatness  $\varphi = 1/2q$ . The presence of colored noise has a profound

effect on an ecosystem described by Eqs. (2.21)-(2.22) with  $\beta = 1$ , rearranging its parameter space so that in a certain region the system can be either in an unstable phase or in a stationary stable one, while abrupt transitions occur. For example Fig. 10 shows different solutions of the self-consistency Eq. (2.31) for the mean field m [Eq. (2.32)] as a function of the coupling constant  $J^*$  and the growth rate parameter  $\delta^*$ . The existence of an unstable solution (Fig. 10, the lower branch of the curve  $\delta^* = 1$ ) indicates that there is a coexistence region,  $J_1 <$  $J^* < J_2$ , where two phases of the system – one stationary stable and the other unstable – are both possible. Notably, coexistence does not mean that the two phases are present simultaneously, however, either is possible depending on the initial distribution. In the case of  $J^* > J_1$ an unstable phase really exists. The situation described represents a typical case of first-order phase transitions. If the value of the "order parameter" m (describing the stationary state of the system at  $J^* < J_2$ close to the point  $J_2$  corresponding to point F in Fig. 10) is different from zero, a slight growth of the coupling parameter may bring it beyond the bifurcation point  $J_2$  and induce a discontinuous transition to the unstable state of the system.

Figure 11 shows a phase diagram in the plane  $J^* - \delta^*$  at the noise amplitude parameter  $\alpha = 0.8$  and flatness  $\varphi = 2$ . The dashed region in the figure corresponds to the coexistence region of the two phases. As  $\delta^*$  increases, the multiphase region narrows down and disappers at the value of the growth rate parameter  $\delta_c^* = 2.68852$ . It should be noted that the critical coupling parameter  $J_1$  can be described by an exact analytical formula Eq. (3.3), but for  $J_2$  there is no such formula. The latter can be evaluated from the self-consistency equation by numerical methods or by using approximate equations. The critical coupling parameter  $J_2$  depends monotonically on the growth rate parameter  $\delta^*$ : if  $\delta^*$  increases from 0 to  $\delta_c^*$ , then  $J_2$  decreases from 1 to  $J_1$ .

The critical growth rate parameter  $\delta_c^*$  can be expressed as

$$\delta_c^* = \frac{2q\sqrt{\alpha}}{1 - (1 - 2q)\alpha} \ln \left| \frac{(1 + \sqrt{\alpha})^{1 - (1 - 2q)\sqrt{\alpha}}}{(1 - \sqrt{\alpha})^{1 + (1 - 2q)\sqrt{\alpha}}} \right|. \tag{3.4}$$

Note that in the case of fixed values of flatness,  $\varphi = 1/(2q)$ , the critical parameter  $\delta_c^*$  increases monotonically from zero to infinity if the noise amplitude  $\alpha \in (0,1)$  increases.

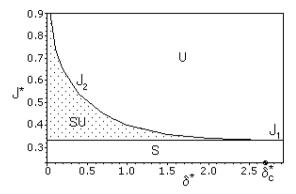


Figure 11: The phase diagram at the flatness parameter  $\varphi = 2$  and the noise amplitude parameter  $\alpha = 0.8$ . The stable phase, the unstable phase, and the coexistence region of the two phases are marked by S, U, and SU, respectively.

As the coupling-induced two-phase coexistence region does not exist in a system without noise, it is a pure colored-noise effect [see also Eq. (3.4)]. From Eq. (2.33) we can find that there is a coexistence region if the noise correlation time  $\tau_c$  satisfies the condition  $\tau_c < \delta_c^*/2\delta$ . Evidently, if the system is in a stationary stable phase in the coexistence region, then a perturbation of the noise parameters can turn the system to the unstable phase. It is remarkable that variations of the noise correlation time can induce only abrupt transitions between the stable and unstable states of the system. In contrast, variations of the noise amplitude (and flatness) can induce both discontinuous and continuous transitions.

In ecological contexts unstable states of a system allow for various interpretations: extinction of populations, presence of additional interaction between species that the model has not taken into account, etc. Therefore we also consider the modified Model (2.21) with VM and with adaptation [see Eq. (2.23)]. In case noise is absent the stationary state is monostable. In the presence of noise, however there is no unstable state of the system and the mean field is characterized by one or two stable stationary solutions for every value of the coupling parameter  $J^* \geq 0$ . Moreover, a hysteresis for the mean field and related discontinuous transitions can sometimes be found as functions

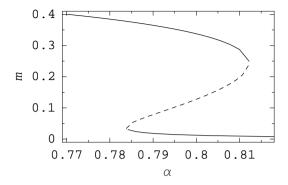


Figure 12: Stationary mean field m vs the noise amplitude  $\alpha$  at  $\varphi = 2$ ,  $J^* = 0.39$ ,  $\tau_c = 0.5$ ,  $\epsilon = 10^{-4}$  with the time scaling  $\delta = 1$ . The solid and dashed lines depict, respectively, the stable and unstable solutions of the self-consistency equation. Hysteresis of the mean field appears.

of the noise parameters as well as of the coupling constants. This is because colored noise can induce bistability of the ecosystem. For example in Fig. 12 the hysteresis is exposed for the mean field m vs the noise amplitude  $\alpha$ . It can be seen that the jump from a state with a bigger number of individuals to that with a lesser one occurs at smaller values of the amplitude than opposite jumps. Therefore a decrease of the noise amplitude (or the correlation time) can under certain conditions cause a catastrophic fall in the size of the population (more details are presented in Paper [II]).

Our major result is that, in the case of ecological systems with a symbiotic interaction between the species, random interaction with the environment can cause discontinuous transitions in ecosystems, even if the system is monostable in the absence of noise (modified model).

Discontinuous transitions can appear in two ways. First, abrupt transitions can be caused by changes of control parameters, for example by variations of the coupling constant or the noise amplitude (see Figs. 10 and 12). Second, some environmental fluctuations can affect the state directly, for example, by wiping out parts of the populations [57]. If there are alternative stable states, rather severe fluctuations may shift the system into the basin of attraction of another state. Such catastrophies have also been noted in different ecological

models assuming that in the absence of noise the deterministic potential is multistable (see [57], [62]-[67]). We would like to emphasize that those models are qualitatively different from the ones considered in our work. In the latter the deterministic potential is monostable and bistability is induced by combined effects of multiplicative colored noise and symbiotic coupling.

#### 3.2.2 Colored-noise-induced bistability

In this subsection we will briefly review the results for the generalized Lotka-Volterra model (2.21) with Eq. (2.24). More details are presented in Paper [IV] (cf. also [1]).

We consider the generalized Verhulst mechanism (GVM) with an exponent  $\beta > 1$ . In this case there is no unstable phase of the system and the deterministic counterpart of the system is monostable, i.e., the present model is qualitatively different from the model with  $\beta = 1$  considered in Section 3.2.1. In the latter an interaction-strength-induced transition from stability to instability takes place, even if the system is deterministic (that is, in the absence of noise), whereas in the present model such transitions are absent. In [IV] we have shown that environmental fluctuations can induce bistability in the model with  $\beta > 1$ , and the system presents abrupt (first-order-like) transitions between the low and high density phases of populations. Hysteresis for the mean field value of the population density  $\langle X \rangle$ , as function of the noise parameters as well as of the coupling constant, appears.

The coexistence region, where two stable phases are possible, exists only at bounded values of the noise correlation time  $\tau_c < \tau_c^*$ . Fig. 13 shows a phase diagram in the  $J - \tau_c$  plane at the noise amplitude  $a_0^2 = 0.980$  and  $\beta = 2$ . The shaded region in the figure corresponds to the coexistence region of the two phases. The boundaries of the coexistence region,  $J_1(\tau_c)$  and  $J_2(\tau_c)$ , can be computed from the self-consistency equation (see [IV]). As the correlation time  $\tau_c$  increases, the multiphase region narrows down and disappears at critical value of the correlation time  $\tau_c^*$ . Hence, there is an upper limit  $\tau_c^*(a_0, \beta)$  for the correlation time  $\tau_c^*$ , at greater values of which the system is monostable. From the self-consistency equation a monotonic dependence of the boundaries of the coexistence region  $J_i(\tau_c)$ , i = 1, 2, on

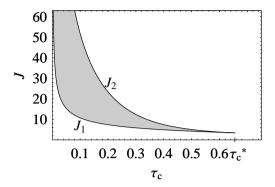


Figure 13: A plot of the phase diagram in the  $J - \tau_c$  plane at  $a_0^2 = 0.980$ ,  $\beta = 2$ . The shaded region in the figure corresponds to the coexistence region of two phases. The critical correlation time  $\tau_c^* = 0.655$ . All quantities are dimensionless with scaling  $\delta = 1$  and K = 1.

 $\tau_c$  follows: if  $\tau_c$  increases from 0 to  $\tau_c^*$  then  $J_i$  decreases from  $\infty$  to  $J^*(a_0, \beta)$ . Notably, the coexistence region exists only if the coupling parameter J is sufficiently large:  $J > J^*$ .

The important new result, in an ecological context, is the existence of a critical noise amplitude  $a_{0c}(\beta)$ . The value of  $a_{0c}(\beta)$  is the lowest value of the noise amplitude for the phenomenon of hysteresis to occur, i.e., discontinuous transitions are possible only if  $a_0 > a_{0c}$ . It should be pointed out that the threshold amplitude  $a_{0c}(\beta)$  depends only on the exponent  $\beta$  describing generalized Verhulst self-regulation. Fig. 14 demonstrates the dependence of  $a_{0c}^2(\beta)$  on  $\beta$ . The critical parameter  $a_{0c}^2$  increases monotonically from zero to  $a_{0c}^2(\infty) \approx 0.9248$  if the parameter  $\beta \in (1, \infty)$  increases. As the critical noise amplitude  $a_{0c}$  increases relatively rapidly if  $\beta$  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  $\beta$  is lower.

If the noise amplitude  $a_0 > a_{0c}$  increases, the critical coupling parameter  $J^*$  decreases monotonically from infinity to the value

12

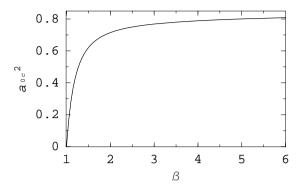


Figure 14: The critical noise amplitude parameter  $a_{0c}^2$  vs the system parameter  $\beta$ . In the case of large values of  $\beta$  the critical noise amplitude saturates up to the value  $a_{0c}^2 \approx 0.9248$ .

$$J^{*}(1,\beta) = \frac{\delta}{K} \left( 1 - \frac{1}{\beta} \right)^{\frac{1}{2}(\frac{1}{\beta} - 1)} \left[ \left( 1 - \frac{1}{\beta} \right)^{\frac{1}{2}} + 1 \right]^{-1/\beta} \times \exp \left[ 1 - \frac{1}{\beta} + \left( 1 - \frac{1}{\beta} \right)^{\frac{1}{2}} \right]$$
(3.5)

at  $a_0 = 1$ . Note that in the case of fixed values of  $\beta$  there is a lower limit for the coupling parameter  $J^*(1,\beta)$ , below which,  $J < J^*(1,\beta)$ , the system is monostable at all values of the noise parameters. It is remarkable that the critical parameter  $\tau_c^*$  increases monotonically from zero to infinity if the noise amplitude  $a_0$  increases from  $a_{0c}(\beta)$  to one.

The circumstance that there exist certain lower limits for the noise amplitude  $a_{0c}(\beta)$  and for the coupling parameter  $J^*(1,\beta)$ , below which discontinuous transitions are not possible, demonstrates that both agents - the symbiotic coupling of species and the colored fluctuations of carrying capacities - act in unison to generate discontinuous transitions of the mean population density. Moreover, as in Eq. (3.5) the growth rate  $\delta$  and the deterministic carrying capacity K of species have been absorbed into the critical coupling strength  $J^*(1,\beta)$ , discontinuous transitions can also occur by a gradual change of the parameters  $\delta$  and K.

Our major results are:

- For symbiotic ecological systems (or metapopulations) with generalized Verhulst self-regulation ( $\beta > 1$ ), colored fluctuations of the environment can cause bistability of mean population densities. Therefore a variation of system parameters can, under certain conditions, cause a catastrophic fall in the size of the populations.
- For  $\beta > 1$ , abrupt changes of mean population densities appear only if the noise amplitude is greater than the threshold value  $a_{0c}(\beta)$  which increases relatively rapidly if the exponent  $\beta$  increases. Therefore, it seems reasonable to assume that symbiotic ecosystems with generalized Verhulst self-regulation are more sensitive to environmental fluctuations if the exponent  $\beta$  is lower.

It is worth to emphasize 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 parameter values [57], [62]-[67]. In our model, however, these transitions occur only when colored noise is present.

### 3.3 Some open problems

Before concluding, we would like to mention some issues for future research.

1. Study of temperature-controlled multiple (more than two) current reversals in the case of intermediate values of noise flatness. The calculations of multiple current reversals in Paper (I) are based on the assumption that the flatness parameter of noise is very large, because the absolute value of the current is very small. The study of this amazing phenomenon should be continued in the intermediate regimes of the system parameters, which is the realm of applications for nano-objects separation. Note that this problem was partly solved in Paper [VII] and in Ref. [81], but some more analysis is needed. We believe that the phenomenon of multiple current reversals will enable us to design continuous two-step separation schemes with a very high selectivity.

- 2. The results of Paper [VII] indicate that variations in the flatness of nonequilibrium noise can sometimes amplify the efficiency with which a ratchet converts energy of fluctuations to useful work. However, how to obtain the best protocol for maximization of efficiency in the case of the ratchet models considered, particularly in the regimes of multiple current reversals, is still an open question.
- 3. Investigation of hypersensitive transport of Brownian particles in tilted ratchets in a general case, if the potential is smooth and the flatness of multiplicative noise is greater than one. In this case both mechanisms, described in Papers [III, VI] and in [40], play an important role and should be taken into account. Possible applications of the phenomenon of hypersensitive transport for concrete physical, biological, and chemical systems should also be continued.
- 4. It seems that the phenomenon of "disjunct windows" for an external force, established in Paper [V], is a new anomalous transport phenomenon for Brownian particles. Future work will further refine the effect, and strive to establish some possible applications.
- 5. The mean-field results considered correspond to an infinite number of globally coupled species. When the number of species is finite, as is true for more realistic ecosystems, the features of the model-system can be different. Although the preliminary results of computer simulations presented in Paper [IV] indicate that the mean-field scenario is not much different from the case of a finite number of species (at least in case the number of species is great enough), further investigations of finite size systems are needed to test them.
- 6. On the basis of the results of Paper [IV], one may formulate the conjecture that in symbiotic ecosystems with generalized Verhulst self-regulation abrupt transitions appear with a greater probability if the exponent  $\beta$  is lower. This conjecture, which may be an important new result in an ecological context, remains to be verified by further studies. A particularly important problem is how to link the mathematical models to empirical data.
- 7. Although our models with symbiotic interaction can be use-

ful in modeling some actual ecological communities (for example, in the case of coral reefs, where symbiosis is essential), in most biologically important ecosystems additional interactions between species, such as competition and prey-predator relationship, should be taken into account. Note that some new results of the influence of environmental fluctuations on the dynamics of predator-prey communities have been recently presented in [80].

#### 4 Conclusions

In this Thesis we studied two subjects: (i) colored-noise-induced transport of Brownian particles in a periodic sawtooth potential, (ii) ecological systems with symbiotic interaction between species in a fluctuating environment.

In the case of Brownian transport we considered three types of ratchets with a sawtoowth potential, subjected to both thermal and nonequilibrium three-level colored noise. The main results and possible applications are the following:

- (a) The correlation ratchet, in which directed transport is subjected to both an additive trichotomous noise and an additive thermal noise [I, VII].
  - 1. The direction of the transport of Brownian particles can be controlled by thermal noise. The necessary condition is that the flatness parameter exceeds one. The advantage of this model is that the control parameter is temperature, which can be easily varied in experiments.
  - 2. The thermal noise has a strong effect on the current in the case of small correlation times. By the absence of thermal noise and in the case of the flatness parameter  $\varphi > 2$  there can occur one current reversal caused by variation of the correlation time, but in the presence of additional thermal noise there can occur either an even number of reversals or none.

The ratchet mechanism with current reversals can be used for obtaining efficient separation methods of nanoscale objects, e.g., DNA molecules, viruses, etc. To date, the feasibility of Brownian particle transport by man-made devices has been experimentally demonstrated for several ratchet types [13].

- (b) The model of the ratchet system subjected to a static tilting force and to both a multiplicative trichotomous noise and an additive thermal noise [III, VI, VII].
  - 1. At low dimensionless temperatures,  $D \ll 1$ , enhancement of the current is hypersensitive to a small static tilting force.

- 2. At low temperatures, the noise flatness can induce the phenomenon of hypersensitive transport.
- 3. The functional dependence of the mobility on correlation time and on flatness is of a bell-shaped form. For fixed low values of the temperature, the optimal parameters of the system, at which the mobility is maximized, are determined as follows: the flatness parameter  $\varphi \approx 3$ , the correlation time  $\tau_c \approx 3/8$ , and the asymmetry parameter d = 1/2, i.e., the potential is symmetric.

The phenomenon of noise-flatness-induced hypersensitive transport seems to be applicable for amplifying adiabatic time-dependent signals F(t), i.e., signals of much longer periods than the characteristic time of reaching a stationary distribution, even in the case of a small input-to-noise ratio  $|F(t)|/\sqrt{D} \ll 1$ . The sensitivity of the system response to small input signals can be either enhanced or suppressed by changing the noise parameters (correlation time, flatness, temperature).

- (c) The model of the ratchet system subjected to a static tilting force and to both a spatially nonhomogeneous three-level colored noise and an unbiased thermal noise [V, VII].
  - A major virtue of the proposed model is that an interplay of three-level colored and thermal noises in tilted ratchets with simple symmetric sawtooth potentials can generate a rich variety of cooperation effects, namely:
    - 1. Hypersensitive differential response (HDR): at some values of the tilting force F, the current is very sensitive to a small variation of F. The effect appears at large values of the switching rate  $\nu$  and low values of the temperature D.
    - 2. The phenomenon of "disjunct windows" (DW) for the tilting force where the current is very small as compared to that in the surroundings. The necessary conditions for the existence of the DW effect are the regime of a small diffusion  $D\nu \ll 1$  and a large switching rate  $\nu$ .
    - 3. Absolute negative mobility (ANM). In the regime of low diffusion  $D\nu \ll 1$ , as temperature D is small enough,  $D < D_c \approx \sqrt{f}/6$ , the ANM appears. Notably, the phenomenon

- of ANM can also occur at high temperatures, if only the three-level noise amplitude f is large enough (cf. [1]).
- 4. Negative differential resistance, i.e., for some intervals of the tilting force F the current decreases as F increases.

In particular we emphasize that the mechanism of HDR reported here is of a qualitatively different nature from the mechanisms of hypersensitive response described in the previous model of (b) and also in the model of [40, 41]. In the model (c) the hypersensitivity is achieved by a combined influence of a fast nonequilibrium noise and a tilt-force-induced change of the net potentials configuration. It should be pointed out that here the effect of HDR is pronounced in the case of a fast switching of the nonequilibrium noise, while in the model of (b) the hypersensitive transport is generated by low or moderate values of the switching rate.

Notably, the results of HDR seem to be applicable for amplifying adiabatic time-dependent signals [see also the previous model (b)]. The phenomenon of "disjunct windows" is a new anomalous transport phenomenon for Brownian particles and is, so far, mainly of theoretical interest, while applications are not clearly identifiable yet. We believe that the present model (c) is particularly suitable for an experimental realization along the lines described in [43], e.g., for particles suspended in a hydrodynamic flow.

Another problem we have addressed is the dynamics of interacting species. We have considered a broad class of N-species Lotka-Volterra models of symbiotic ecological systems with the generalized Verhulst self-regulation mechanism [IV] and also with the true Verhulst (logistic) self-regulation mechanism [II]. The effect of a fluctuating environment on the carrying capacity of a population is modeled as a colored noise, namely for the Model with the Verhulst self-regulation mechanism (VM) a trichotomous noise and for the Model with the generalized Verhulst mechanism (GVM) a dichotomous noise is used. In the framework of mean-field approximation we established the following results.

(a) The model with VM (adaptation is absent; Paper [II]).

- 1. The presence of colored environmental fluctuations has a profound effect on the model of a symbiotic ecosystem, rearranging its parameter space so that in a certain region of noise parameters the system can be either in the unstable phase or in the stationary stable phase, while abrupt (first-order-like) transitions occur. Since the two-phase coexistence region does not exist in the system without noise, it is a pure colored-noise effect.
- 2. The coexistence region of unstable and stable phases exists only at bounded values of the noise correlation time,  $\tau_c < \tau_c^*$ . The critical parameter  $\tau_c^*$  increases monotonically from zero to infinity if the noise amplitude increases. Consequently, a variation of noise parameters can cause catastrophic shifts of an ecosystem from a stable to an unstable phase.
- 3. The variations of the noise correlation time can induce only abrupt transitions between the stable and unstable states of the system. In contrast, variations of the noise amplitude and the flatness can induce both discontinuous and continuous transitions.

In ecological contexts unstable states of a system can variously be interpreted: extinction of populations, presence of additional interaction between species that the model has not taken into account, a catastrophic increase of some population sizes observed in nature, etc. Undoubtedly, an ultimate verification of the phenomenon of pure colored-noise-induced transitions to an unstable state in natural ecosystems lies with experimentally-minded ecologists.

- (b) The model with an adaptation and with VM [II].
  - 1. If noise is absent, the stationary state of this model is monostable. In some cases, the mean field exhibits hysteresis as a function of the noise parameters, i.e., environmental fluctuations can induce bistability of the ecosystem (or metapopulation).
  - 2. A variation of the noise amplitude, as well as of the noise correlation time, can cause a catastrophic fall in the size

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of population under certain condition, i.e., an abrupt jump from a state with a bigger number of individuals to one with a much lesser number.

Such catastrophies have also been noted in different ecological models assuming that the deterministic potential in the absence of noise is multistable [57], but those models are qualitatively different from these considered in our work. In the latter the deterministic model is monostable and bistability is induced by the combined effects of multiplicative colored noise and symbiotic coupling.

- (c) The model with GVM (with an exponent  $\beta > 1$ ; Paper [IV]). The conditions for the appearance of colored-noise-induced bistability and corresponding discontinuous transitions are established.
  - 1. The bistability of mean population densities appear only if the noise amplitude is greater than the threshold value  $a_{0c}(\beta)$ , which increases relatively rapidly if the exponent  $\beta$  increases.
  - 2. In the case of fixed values of  $\beta > 1$  there is a lower limit for the symbiotic coupling intensity, below which the system is monostable at all values of the noise parameters.

Perhaps the most important new result, in the ecological sense, is the existence of the critical noise amplitude  $a_{0c}(\beta) > 0$ . Note that in the case of logistic self-regulation,  $\beta = 1$ , the critical parameter  $a_{0c}(1) = 0$ . This circumstance may, in principle, provide some vital information for maintaining ecosystem stability in a technogeneous environment. Moreover, as  $a_{0c}(\beta)$  increases relatively rapidly if  $\beta$  increases, it seems reasonable to assume that in symbiotic ecosystems with the GVM abrupt transitions appear with a greater probability if the exponent  $\beta$  is lower.

We believe that the obtained results [II, IV] are of interest also in other fields where symbiotic interaction and generalized Verhulst self-regulation are relevant for modeling the system, e.g., in the dynamics of human world population [114], coupled chemical reactions, some laser systems [107], and business [115, 116].

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## Summary in Estonian:

### Värvilise müra tekitatud anomaalne transport ja faasiüleminekud komplekssüsteemides

Viimase aastakümne jooksul on pälvinud suurt tähelepanu keskkonna fluktuatsioonide mõju kompleksetes ja stohhastilistes süsteemides. Ökonofüüsika, uued nanoobjektide separatsioonitehnikad, Browni mootorite mehhanism elusrakkudes, ökosüsteemide stabiilsuse analüüs – on vaid mõned selle uurimisvaldkonna näited.

Antud doktoritöö üldeesmärgiks on analüüsida mittetasakaalulise müra (värvilise müra) poolt genereeritud efekte ja müra tasasusparameetri rolli järgmistes komplekssüsteemides: (i) stohhastiline transport ruumiliselt perioodilises jõuväljas (ratchet-süsteemid), (ii) sümbiootilised ökosüsteemid.

#### Dissertatsiooni põhieesmärgid

- (1) Leida osakeste voo sõltuvus süsteemi parameetritest Browni osakeste kontrollitavas transpordis, mis on indutseeritud mittetasakaalulise kolmetasemelise müra ja soojuslike fluktuatsioonide poolt perioodilise saehambakujulise potentsiaali korral.
- (2) Välja töötada hüpersensitiivse transpordi mehhanism, mis näitaks, et multiplikatiivse müra tasasusparameeter võib genereerida Browni osakeste ülitundliku transpordi kallutatud hammaslatt-süsteemis (ratchet süsteemis).
- (3) Üldistada "kolmetasandilist" mudelit, mis on välja töötatud Cleuren'i ja Van Den Broeck'i poolt (vt [43]), juhule, kus üleminekud erinevate potentsiaali konfiguratsioonide vahel toimuks lõplikes vahemikes. Leida tingimused, mille korral esineb Browni osakeste anomaalne transport, pöörates erilist tähelepanu ülitundliku transpordi nähtusele.
- (4) Kasutades sümbiootilise ökoloogilise süsteemi uurimiseks N-liigi stohhastilist Lotka-Volterra mudelit, leida vastus küsimusele, kas ökosüsteemides teadaolevad katastroofilised üleminekud võivad mõningatel tingimustel olla käsitletavad kui keskkonna fluktuatsioonide poolt põhjustatud nähtused.
- (5) Uurida stohhastilise Lotka-Volterra mudeli erinevaid modifikatsioone ja leida, millistel müra parameetrite ja sümbiootilise vas-

tastikmõju intensiivsuse väärtustel toimuvad mudelsüsteemides esimest liiki faasiüleminekud.

Tööde esimeses [I, III, V, VI, VII] grupis uuriti Browni osakeste transporti saehambakujulise potentsiaali korral, mis on käivitatud mittetasakaalulise kolmetasemelise müra ja soojuslike fluktuatsioonide poolt. Järgnevalt esitame saadud põhitulemused ja võimalikud rakendused.

- (a) Mudel, milles osakeste transport on indutseeritud aditiivse kolmetasemelise müra ja soojuslike fluktuatsioonide poolt [I, VII].
  - 1. Kontrollparameetrite, sealhulgas temperatuuri, reguleerimisega kaasnevad mitmekordsed voolupöörded, kusjuures tarvilik tingimus on, et mittetasakaalulise müra tasasusparameeter  $\varphi > 1$ .
  - 2. Juhul kui müra korrelatsiooniaeg on väike etendab termiline müra olulist rolli osakeste transpordil. Termilise müra lisamine põhjustab tasasusparameetri väärtustel  $\varphi > 2$ , kvalitatiivseid muutusi süsteemi dünaamikas.

Antud ratchet-mehhanismi saab kasutada nanoobjektide (sh DNA fragmentide) separeerimiseks.

- (b) Mudel, milles osakeste transport on indutseeritud konstantse kaldejõu ning multiplikatiivse kolmetasemelise müra ja aditiivse soojusliku müra poolt [III, VI, VII].
  - 1. Müra tasasusparameeter indutseerib osakeste ülitundliku transpordi madalatel temperatuuridel on voolu kasv hüpersensitiivne lisatava konstantse kaldejõu suhtes.
  - 2. Liikuvuse sõltuvus müra korrelatsiooniajast ja tasasusparameetrist on mittelineaarne (Gaussi kõvera kujuline).

Kirjeldatud ülitundliku transpordi mehhanism pakub uusi võimalusi nõrga signaali võimendamise juhtimiseks tugeva müra foonil.

- (c) Mudel, milles osakeste transport on indutseeritud konstantse kaldejõu, ruumiliselt mittehomogeense kolmetasemelise müra ja soojusliku müra poolt [V, VII]. Antud mudelis ilmnevad järgmised anomaalse transpordi efektid:
  - 1. ülitundlik diferentsiaalne vastuvõtlikkus:

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- 2. "isoleeritud akna" fenomen, mille korral osakeste voog on teatavas lõplikus kaldejõu väärtuste vahemikus väga väike võrreldes seda vahemikku ümbritseva piirkonnaga;
- 3. absoluutne negatiivne liikuvus, mis võib ilmneda ka suhteliselt kõrgetel temperatuuridel;
- 4. negatiivne diferentsiaalne liikuvus.

Sarnaselt eelmise mudeliga (b) saab ka antud juhul ülitundliku transpordi efekti kasutada signaalide võimendamiseks. Siin esineb see efekt siiski vaid kõrgetel müra sagedustel, kuna aga juhul (b) ainult väikestel ja mõõdukatel sagedustel.

Tööde teises grupis [II, IV] uuriti sümbiootilist ökoloogilist süsteemi N-liigi stohhastilise Lotka-Volterra mudeli abil, eeldusel, et keskkonna mittetasakaalulised fluktuatsioonid põhjustavad keskkonnamahutavuse fluktueerumise. Keskmistatud välja meetodil saadi järgmised tulemused.

- (a) Logistilise iseregulatsiooniga mudel [II].
  - 1. Müra parameetrite varieerimine võib indutseerida I liiki faasiüleminekud stabiilsest olekust mittestabiilsesse.
  - 2. Süsteem saab olla kas stabiilses või mittestabiilses faasis kahe faasi kooseksisteerimine esineb juhul, kui müra korrelatsiooniaeg on väiksem kriitilisest väärtusest, mis kasvab monotoonselt müra amplituudi kasvades.

Ökoloogilises kontekstis saab mittestabiilset olekut interpreteerida mitmeti: populatsioonide väljasuremine, liikide vaheline lisamõju, mida mudel ei arvesta, katastroofiline populatsiooni arvukuse suurenemine, jms.

- (b) Verhulsti iseregulatsiooniga adaptsiooni arvestav mudel [II].
  - Ilmneb keskmistatud välja hüsterees keskkonna fluktuatsioonid põhjustavad populatsioonide keskmise arvukuse bistabiilsuse.
  - 2. Müra amplituudi ja korrelatsioonia ja muutus võib esile kutsuda katastroofilisi muutusi suurema isendite arvukusega seisundist väiksema arvukusega seisundisse ja vastupidi.

Vastav deterministlik mudel (ilma mürata) on alati monostabiilne. Bistabiilsus on multiplikatiivse värvilise müra ja sümbiootilise vastastikmõju koostoime tulemus.

- (c) Üldistatud Verhulsti iseregulatsiooniga mudel [IV]. On leitud tingimused, mille korral ilmneb müra poolt indutseeritud bistabiilsus ja vastavad I liiki faasiüleminekud.
  - Esinevad müra amplituudi ja sümbiootilise vastastikmõju intensiivsuse kriitilised väärtused, millest madalamatel väärtustel on süsteem monostabiilne. Need kriitilised väärtused sõltuvad ainult iseregulatsiooni iseloomustavast astmenäitajast.

Saadud tulemused [II, IV] pakuvad alternatiivse võimaluse looduslikes kooslustes esinevate hüppeliste muutuste tekkepõhjuste interpreteerimiseks ja ka nende vältimiseks, säilitamaks ökosüsteemide stabiilsust tehnogeenses keskkonnas.

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## Attached original publications

R. Mankin, A. Ainsaar, A. Haljas, and E. Reiter Constructive role of temperature in ratchets driven by trichotomous noise Physical Review E **63**, 2001, 041110

R. Mankin, A. Ainsaar, A. Haljas, and E. Reiter *Trichotomous-noise-induced catastrophic shifts in symbiotic ecosystems* Physical Review E **65**, 2002, 051108

R. Mankin, A. Haljas, R. Tammelo, and D. Martila Mechanism of hypersensitive transport in tilted sharp ratchets Physical Review E **68**, 2003, 011105

R. Mankin, A. Sauga, A. Ainsaar, A. Haljas, and K. Paunel Colored-noise-induced discontinuous transitions in symbiotic ecosystems
Physical Review E 69, 2004, 061106

A. Haljas, R. Mankin, A. Sauga, and E. Reiter Anomalous mobility of Brownian paticles in a tilted symmetric sawtooth potential Physical Review E **70**, 2004, 041107

A. Rekker, R. Mankin, and R. Tammelo Noise-flatness-induced hypersensitive transport in tilted periodic sawtooth potentials Physica E **29**, 2005, 419-425

VII

T. Laas, A. Sauga, R. Mankin, A. Ainsaar, Ü. Ugaste, and A. Rekker Colored-noise-induced anomalous transport in periodic structures
Nukleonika **51**, 2006, 63-69

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