

Invited Talks

Dynamic domains in 3D and 4D community models with prey dispersal and strong Allee effect

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Models accounting migrations among populations are widely investigated. Here we study the dynamics of two-patch communities consisting of a Prey--Predator-Prey system and two Predator--Prey systems whose prey can diffusely migrate. In both cases the interactions are mediated by prey populations. The emphasis is in situations when differences in prey abundance habitats are the drivers of prey dispersal.

In the first model the Prey subsystem is considered as a refuge. It is shown that as dispersal between the prey-refuge and the predator-prey habitats increases, the system experiences transitions from predator-prey extinction (for all initial conditions), to predator-prey oscillatory stable co-existence, to predator-prey stable non-oscillatory coexistence with the outcomes depending on initial conditions. The possibility of bi-stability and tri-stability all leading to distinct outcomes is discussed. It is shown that just the addition of a prey refuge is enough to increase the range of life-history dynamics that can be supported within the standard prey-predator system. It is argued that evolution should favor the existence of such refuges.

Studying the second model we analyze two 4-dimension attracting manifolds. They appear as limit cycles due to supercritical Hopf and heteroclinic bifurcations, respectively. Evolutions under parameter variations lead to appearance of "chaotic" behaviors close to the boundary of their coexistence domain. The system analysis proves its higher level of persistence than a separate predator-prey system and even preys--predator-prey community. Possible interpretations of the model dynamics are discussed.

Towards a unified perspective on the mechanics of social animal groups

Daniel Grunbaum

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Social groups such as schools, swarms, flocks and herds are a common feature of many animal species. Grouping strongly affects the ecological and evolutionary dynamics of these species. However, we lack a theoretical understanding of the mechanics of social groups sufficient to describe and predict their evolutionary causes and ecological consequences. Among the fundamental open questions concerning social grouping are: Which individual behavioral traits elicit specific group characteristics? What spectrum of group types are possible under biologically reasonable constraints? What are the evolutionary trade-offs that favor expression of some group types over others? The concept underlying most quantitative descriptions of social grouping is the zone model, in which individuals move in stereotypic ways depending on their positions relative to nearest neighbors. However, this concept is essentially untested because there have been few efforts to establish close quantitative agreement between zone model predictions and real animal trajectories within groups. We also lack concise and accurate population-level descriptions that implicitly reflect effects of grouping on movement, predator-prey interactions and disease dynamics. This talk will illustrate recent efforts to quantitatively link individual social behaviors, group-level characteristics and population dynamics, with an emphasis on future directions and opportunities for theoretical insights.

The essential role of time and space in ecological understanding

Alan Hastings

Department of Environmental Science and Policy, University of California at Davis

Much of ecological thinking, and especially ecological theory, has focused on long term, or asymptotic, outcomes. Yet, in order to develop an ecological understanding of the impact of global change it will be necessary to focus on a variety of time scales. I will develop ways that time (and necessarily space) scales enter into ecological understanding, and how ecological dynamics plays out over intermediate time and space scales. I will illustrate the concepts with examples drawn from variety of ecological systems ranging from diseases to marine systems including coral reefs and many others. I will illustrate how these concepts can enter into management approaches.

Replicator equations and the principle of minimal production of information

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Many complex systems in mathematical biology and other areas can be described by the replicator equation. We show that solutions of a wide class of replicator equations minimize the production of information, i.e., the KL-divergence of the initial and current distributions under time-dependent constraints, which, in their turn, can be computed explicitly at every instant due to the system dynamics. Therefore, the Kullback principle of minimum discrimination information, as well as the maximum entropy principle, for systems governed by the replicator equations can be derived from the system dynamics rather than postulated. Applications to the Malthusian inhomogeneous models, global demography, the model of early biological evolution, the ecological model of tree stand self-thinning, and the Eigen quasispecies equation are given.

Mathematical modelling of tissue growth

John King

School of Mathematical Sciences, University of Nottingham

Some (macroscale) multiphase models for the growth of biological tissue will be presented, illustrating in particular the competition between aggregation and dispersal. Multiscale aspects will be touched upon and a variety of possible large-time dynamics will be identified.

Adiabatic invariants

Anatoly Neishtadt

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There are many problems that lead to analysis of Hamiltonian dynamical systems in which one can distinguish motions of two types: slow motions and fast motions. Adiabatic invariants are approximate first integrals of such systems. These quantities change by small amounts on large time intervals, over which the variation of slow variables is not small. Adiabatic invariants usually arise as first integrals of the system after having been averaged over the fast dynamics. Adiabatic invariants are important dynamical quantities. In particular, if a system has sufficiently many adiabatic invariants, then the motion over long time intervals is close to regular. On the other hand, the destruction of adiabatic invariance apparently leads to chaotic dynamics.

In the lecture it is planned to consider the following topics: exponential accuracy of conservation of adiabatic invariants in analytic one-frequency systems, jumps of adiabatic invariants at separatrices, destruction of adiabatic invariance due to captures into resonances and passages through resonances.

Invasion using microcorrelations in spatial and network games

David Rand

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I present some new results on the influence of microcorrelations on spatial and network game dynamics and at the same time develop some new techniques that allow one to deduce analytical results about such games. The discussion extends previous work in a number of significant directions. Firstly, the analytical theory applies to the case where the number of neighbours (the so-called *coordination number*) is not constant and varies from site to site. Secondly, a general result will be derived that allows application of these ideas to a very broad range of models including those involving imitation and learning in addition to birth-death ecological processes. Thirdly, a new analytical approach to invasion is presented which sees it as a two-stage process in which firstly the invaders create a local micro-correlated population and then the microcorrelations determine whether or not this local population can invade the resident population.

Fourthly, we will apply these methods to model the Prisoner's Dilemma (PD) game and get exact criteria for when cooperative strategies can invade. In the classical homogeneously mixed PD game it is not possible for cooperative strategies like Tit-for-Tat to invade non-cooperative strategies like Defect because, when they are comparatively rare, the cooperative strategies primarily interact with non-cooperative strategies and in these interactions they lose out.

It has been shown that it is significantly easier for cooperation to evolve from low levels in the PD if the players are distributed on a network and each only interacts with its neighbours. This will happen if the dynamics of the game leads to a significant level of cooperator-cooperator correlation. I will show analytically that when correlations are included invasion by cooperative strategies is possible and we will see that this approach allows one to determine precise conditions for when this will work. The approach developed here will allow us to deduce analytically similar simple invasion laws in a broad range of contexts generalising those previously found by van Baalen and Rand and Ohtsuki *et al.* They are all approximations to the rule $\lambda > 0$ where λ is the invasion exponent introduced in the lecture.

Ecoepidemiology: a more realistic description of populations interactions.

Ezio Venturino

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The first researches of the author in this field date back to the early nineties, sprouting from seminars of H. Hethcote on epidemic models with demographic dynamics, [6, 12] although there is an earlier paper by Haderler and Freedman discussing a disease spreading among interacting populations, [7, 5]. At the same time of the author's first paper on the subject, [13, 14] another paper appeared, modeling the viral diseases in plankton [1].

In the late nineties the name ecoepidemiology was coined [3], and since then the researches have developed, for instance see [8, 9]. In particular, two important applications concern the spread of the Feline Immunodeficiency Virus among wild cats [2, 10] and the harmful algal blooms, [4].

In the presentation we will describe a few models for the spread of epidemics in ecosystems, under various demographic assumptions, emphasizing the differences with classical results in population theory.

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Contributed
Talks & Posters

Spatial pattern formation in ratio-dependent model: moment-based analysis

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The article aims to study the spatio-temporal pattern formation in a Holling-Tanner prey-predator model with ratio-dependent functional response. The conditions for Turing and wave bifurcation are obtained within spatial domain. The conditions for instability and pattern formation in spatio-temporal model beyond the usual linear regime is obtained based upon higher order moment technique. The analysis is also useful to study the formation of spatial patterns in the concerned model driven by spatial additive white-noise. Numerical simulations are carried out to validate the analytical findings.

Swimming micro-organisms in fluid environments are ubiquitous and diverse. Such micro-organisms frequently undergo movement patterns which can be modelled as random walks. The presence of external cues such as light, chemical gradients, or gravity can modify individual-level behaviour resulting in the random walk being biased towards a preferred direction. In still fluid, at the population level, this can mathematically be described as a diffusion process with drift. In many natural environments, swimming occurs in fluid environments undergoing motion. The fluid flow will interact with the swimming behaviour in several ways and alter the spatial distribution of a population, leading to such phenomena as bioconvection and gyrotactic focussing.

Here I present the derivation of a population-level advection-diffusion model for gyrotactic algae which is based on extensive experimental observations of individual swimming cells in still fluid. I will then present theoretical predictions and experimental data describing the behaviour of gyrotactic micro-organisms in 3D flow. Finally I will discuss the effect of flow on the population-level spatial distribution.

A cellular automaton model for two competitive populations with Allee effect and overcrowding effect

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Abstract:

Cellular automata (CA) have shown to be a valuable approach in ecological modelling, in particular when dealing with local interactions between species and their environment. In CA model, a global interesting spatial pattern emerges through the evolution of interaction at a local scale. A cellular automata model for two competing populations with overcrowding effect and Allee effect in a patchy environment have been developed. Having discussed the influence of the two effects on spatial pattern and dynamical complexity of two competitors, four primary results are given. First, overcrowding effect can produce the cricoid waves in space chaos in time as well as single population model. Second, overcrowding effect of a population not only improves the persistence of the population but also reduce the persistence of its opponent. Third, a suitable Allee effect may vary complexity of two populations before extinction. In addition, extinction or invasion of some competitor may affect the dynamical complexity of original system deeply.

Comparing viral infection and predation as controls of harmful algal blooms
N. Lloyd & R. N. Bearon

There is growing experimental evidence that viruses are involved in the termination of phytoplankton blooms. An alternative thought is that grazing by predators is the leading loss factor of phytoplankton.

A set of coupled ordinary differential equations for the mean concentration of phytoplankton (P), viruses (V) and zooplankton (Z) are considered analytically and numerically. Parameter values, found experimentally, for *Heterosigma akashiwo*, its virus HaV and predator *Oxyrrhis marina* are incorporated into the model and numerical simulations are compared with observed populations of these species. For realistic parameter values, the dynamics of the P-V and P-Z systems display damped oscillations towards a stable equilibrium. By the competitive exclusion principle, the P-V-Z system tends to either the P-V or P-Z system depending on the parameters. The simple model for P-V interactions is extended to investigate how the effect of turbulent flow and motility on the contact rate alters the bloom dynamics.

Potential-Growth Indicator Theorem: a Non-Statistical Tool to Tackle Reproductive Uncertainty

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When individuals of a growing population $\mathbf{x}(t+1) = \mathbf{L} \mathbf{x}(t)$ ($\mathbf{L} = \mathbf{T} + \mathbf{F}$ denotes a generalised Lefkovich $n \times n$ matrix) are classified by the stages of their ontogenesis, how much does each stage group contribute to the population recruitment $x_1(t+1) = b_1 x_1(t) + b_2 x_2(t) + \dots + b_n x_n(t)$? The answer is evident if you monitor the size, $x_j(t)$, of each group and if you know all the stage-specific birth rates b_j in the quantitative units. But the latter term often fails in practice. Even when the dataset identifies all individuals (e.g., when monitoring marked perennial plants in a permanent sample plot), the parents of newborns may not be known. The monitoring thereafter provides for direct calculation of the transition matrix \mathbf{T} , but leaves a great deal of arbitrariness in calibration of the fertility matrix \mathbf{F} – a situation that we call *reproductive uncertainty*. Meanwhile, Frobenius eigenvalue $\lambda_1(\mathbf{L})$ of the projection matrix, the intrinsic growth rate of a structured population, is so sensitive to variations in b_j s that it can change from $\lambda_1(\mathbf{L}) > 1$ to $\lambda_1(\mathbf{L}') < 1$, i.e., from a growing population to a vanishing one, even despite the variations (from \mathbf{L} to \mathbf{L}') are bound to the observed recruitment balance as above.

The *potential-growth indicator* (PGI) is, by definition, a calculable scalar function $R(\mathbf{L})$ of the vital rates with the following *indicator property*: $R(\mathbf{L}) >, =, < 1$ if and only if $\lambda_1(\mathbf{L}) >, =, < 1$. Proven recently, the PGI Theorem states an explicit form of $R(\mathbf{L})$ for a wide class of matrix \mathbf{L} patterns that covers any *progressive-stage* life cycle graph. Once matrix \mathbf{T} has been calibrated, the PGI becomes a (quantitatively certain) linear function $R(b_1, b_2, \dots, b_n)$ of the uncertain birth rates. Its maximization over a polygonal defined by the recruitment balance equation plus the biological upper bounds on b_j s plus (any number of) further hypothetical expert inequalities like $b_j \geq b_k$ represents a standard *LP-problem*, with an ever-ready solution. The solution verifies, by the PGI Theorem, whether the expert knowledge be compatible with the data and with $\lambda_1(\mathbf{L}) > 1$, i.e., with an idea of the growing population. The Theorem thus provides a reliable, non-statistical tool for hypothesis testing.

All the constraints however leave still enough space for the uncertain reproductive variations. It is in the spirit of evolution theory to suggest that adaptation results in the maximal possible value of the growth rate, whereby $\lambda_1(\mathbf{L})$ appears to be the (global) solution of a constraint nonlinear maximization problem. Though invoking some technical problems, this approach does eliminate the principal uncertainty in the stage-specific reproduction rates.

Self-organization in models of predating, competing and diffusing populations

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Abstract

The dynamics of spatial and spatiotemporal pattern formation in nonlinear systems far from equilibrium are of continuous interest and many mechanisms of structure generation are not known yet. Here, the fascinating variety of spatiotemporal patterns in such systems and the governing mechanisms of their generation and further dynamics are described and related to plankton communities.

The formation and spread of spatiotemporal structures in a simple predation-diffusion model with Holling type II or III predator is demonstrated. The analysis of the local system yields a number of stationary and/or oscillatory regimes. Correspondingly interesting is the spatiotemporal behaviour, modelled by reaction-diffusion equations. Spatial spread will be presented as well as competition of concentric and/or spiral population waves with non-oscillatory sub-populations for space, and long transients to spatially homogeneous population distributions. Environmental fluctuations are modelled as parametric as well as external multiplicative noise, using stochastic partial differential equations. The noise can enhance the survival of a population that would go extinct in a deterministic environment. Furthermore, noise can induce local and global oscillations as well as local coherence resonance and global synchronization. The results are related to plankton dynamics, partly with viral infections of the prey population and competition of predation and infection [1–3].

The competition of invading and native populations in a variable environment will be considered as well.

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Density or perception of density?

The effect of density-dependent dispersal on aphid population dynamics

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Theoretical studies have shown that when population dynamics are affected by density, the form of the dispersal function strongly affects resulting population dynamics. Nevertheless, arbitrary functions are often used in modelling since the particular form of density dependence is often hard to infer from observations. This problem can be approached from the other end – by formulating models of population dynamics where dispersal is driven by different mechanisms and comparing the result with observed population dynamics.

Deriving a mechanistic model of dispersal starts with a question – how do individuals know their density? Physical contact between individuals was suggested as a possible mechanism of density-dependent dispersal in some aphid species. In addition, crowding in the previous generation(s) can also affect dispersal (maternal effect). Assuming that population dynamics was only governed by intrinsic growth rate and density-dependent dispersal, three models were formulated differing in how dispersal was affected by density: 1) response to density directly (*direct response*), 2) response to the number of contacts between individuals (*behavioural response*), and 3) response to the number of contacts between individuals and the maternal effect (*maternal effect*)¹. When dynamics produced by these models were compared to population dynamics of alder aphid, only the *maternal effect* model was a good fit adequately showing rise and fall of numbers during the season.

The *maternal effect* model shared fast growth at the beginning of the season with *behavioural response* model and low equilibrium value with *direct response* model. Perception of density through the number of contacts delayed the effect at the beginning of the season when density was low while maternal effect amplified the effect later in the season when density-dependent exploitation could appear. Combination of these two perceptive mechanisms might allow producing large number of dispersers in the most effective way.

¹Mashanova, A., Gange, A. C. and Jansen, V. A.A. 2008. Density-dependent dispersal may explain the mid-season crash in some aphid populations. *Population Ecology* 50: 285-292.

Influence of spatial heterogeneity on the type of zooplankton functional response: field studies and mathematical modelling

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Abstract

Food-web ecological models are rather sensitive to parameterization of the functional response in predation terms. Theoretical studies predict enhancing of ecosystems' stability in case when a functional response is of sigmoidal type (Holling type III). This is especially true for modelling stability properties of aquatic eutrophic ecosystems, where the grazing by zooplankton often controls algal blooms. Extensive experiments on zooplankton feeding in laboratories, however, show non-sigmoidal nature of responses for most herbivorous zooplankton species. As a consequence, we cannot implement Holling III type grazing in plankton models. I argue, however, that such an 'evident' claim is just wrong and sigmoidal functional responses in real plankton communities would emerge more often than it was suggested earlier.

I have conducted a rather extensive literature search on data of zooplankton feeding *in situ*. Moreover, I used the real ocean data obtained by my colleagues from the Shirshov Institute of Oceanology (Moscow). Based on the collected data, I demonstrate that vertical heterogeneity in algal distribution as well as active foraging behaviour of zooplankton can modify the type of zooplankton functional response. In particular, the rate of food intake by zooplankton in the water column often exhibits a sigmoidal response, instead of a non-sigmoidal one found previously in laboratory experiments for *the same* species. I show that this conceptual discrepancy is due to the ability of the zooplankton to feed in layers with high algal density and to avoid the depths with lower algal density. I propose two conceptual models (based on systems of ODEs) explaining the observed alterations of type of response. The models predict the crucial role of light attenuation by phytoplankton in the alteration of the functional response.

Determinants of food-web stability

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Since the publication of Robert May's seminal work on the stability of ecological food webs is a topic of intense research and hot debate. Contrary to many field observations, May showed that large, densely connected food webs are *in general* unstable. The only way to reconcile May's proof with observation is to find the special properties that lend natural food webs their unusual stability. It has been pointed out that the identification of such stabilizing network properties could have broad implications beyond the field of ecology. Most recent theoretical work focuses on numerical models based on explicit rate equations. These and empirical studies have revealed that weak trophic links may play an important role for stability.

However, in contrast to May's abstract random matrix model, numerical constraints limit most simulative studies to the investigation of relatively few instances (approx. 10000) of relatively small food webs (approx. 10 species). Recently, generalized modeling, a novel numerical approach for the analysis of stability in families of nonlinear rate equations, has been proposed. Here we utilize this approach to study several billion instances of food webs of up to 50 species with nonlinear interactions. While we find a stabilizing effect of weak links in small food webs, this stabilization is absent in larger webs. Instead, we identify a universal feature in the distribution of links that is important for stability.

Coevolutionary motion in a niche space model of ecological species interactions

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Organisms living in communities are involved in many coevolutionary relationships with their competitors, predators, preys and parasites. In this context, we present a simple model for the coevolution of species in a common niche space, where the fitness of each species is defined via the network of interactions with all other species. In our model, the sign and type of the pairwise interactions (being beneficial, harmful or neutral) is given by a pre-determined community matrix, while the interaction strength depends on the niche-overlap, i.e. the pairwise distances between species in niche space. The evolutionary process drives the species toward the places with the higher local fitness along the fitness gradient. This gives rise to a dynamic fitness landscape, since the evolutionary motion of a single species can change the landscape of the others (the Red Queen Principle). In the simplest case of only two-species we observe either convergence/divergence equilibrium or a coevolutionary arms race. For a larger number of species our analysis concentrates on an antisymmetric interaction matrix describing the evolution of a food-web, where we observe a large range of dynamic behaviour, from regular and quasiperiodic oscillations to chaotic dynamics. In dependence of the value of a first integral of motion we observe either quasiperiodic motion around a central region in niche space or unbounded movement, characterised by chaotic scattering of species pairs. Finally, in a linear food-chain we observe complex swarming behaviour in which the swarm moves as a whole only if the chain consists of an even number of species. Moreover, in some important cases the system can be presented in Hamiltonian form. This allows to understand basic principles inherent in such systems, and to find conditions which select for the different kinds of dynamics. Our results could be an important contribution to evolutionary niche theory.

Non-Diffusive Migration Modelling with Global and Local Information Access

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Modelling of spatially distributed communities faces serious problems. Non-random smart migration pattern is the basic one. Extremely abundant biological data show that beings migrate with an obvious purpose to improve their well-being. Thus, an approach free from diffusion methodology should be implemented to describe such migration.

That is the selection theory by J. B. S. Haldane standing behind the methodology of a smart migration modelling. In brief, smart migration must bring benefits to an individual executing such transfer, in comparison to another ones transferring themselves randomly (i. e. diffusively). The well-being, or a benefit is measured as net reproduction; thus, a non-diffusive migration must maximize the net reproduction of a species realizing such evolutionary optimal strategy of spatial distribution.

Modelling of spatial distribution based on the evolution optimality principle poses several problems, itself. Obviously, the problem of information access necessary to make a decision towards a migration act is the heaviest one. Three types of that former may be identified: global information access, local information access, and complete lack of information. The third case seems to be the closest to a diffusive migration modelling, while it does not coincide with that latter entirely.

Nine models of smart migration are presented. The model of a population inhabiting two stations with global information access is the basic one. Here the dynamics of each subpopulation is supposed to follow Verchulst's equation, if no migration takes place: $N_{t+1} = aN_t - bN_t^2$, $M_{t+1} = cM_t - dM_t^2$, and migration starts when the double inequality

$$p \leq \frac{a - bN_t}{c - dM_t} \leq p^{-1}$$

does not hold true; here p is the transfer cost (measured in fractions of net reproduction). Migration yields the maximization of an average (over two stations) net reproduction; a migration flux determined through the specific values of both net reproduction functions, and the transfer cost means the global information access.

Next model generalizes the basic one representing the situation of local information access. Actually, there is no comprehensive theory towards the modelling of information circulated in a biological community. We proposed a simple model, where no knowledge towards the environmental conditions and/or the transfer cost is available, for beings. Thus, the local information access results here in a threshold migration: it runs as soon, as the abundance in the habitat exceeds some given level. We used the maximal reproduction rate $\max N_{t+1}$ ($\max M_{t+1}$, correspondingly) to determine the level.

Next model described the dynamics of a single population occupying three and more stations. A change of two-station model for three or more station one brings a new problem: there is no natural rule to share an immigration flux between several stations. We pursued the version where the sharing has been changed for a multi-migration with absolute maximization of net reproduction. Also, another version of the model has been studied where the immigration run in majority pattern: the entire flux immigrated into the station with greater net reproduction (with respect to transfer cost). These models have been implemented for global information access case.

Four models have been implemented to simulate the dynamics of two-species community with prey-predator interaction. A migration-free interaction of the species was supposed to follow Volterra equations, and migration again yielded the maximization of average (over two stations) net reproduction of each species, independently. These four models are based on the idea of global information access. The first model was the basic one. Three other ones simulated the dynamics for three cases of reflection in the interspecies interaction. Indeed, prey beings may realize reflexive strategy; on the contrary, predator beings may do that, and, finally, both species may exhibit reflexive strategies. All three cases have been studied. We investigated the situations where each of the strategies combination brings an evolutionary advantage to their bearers.

Numerous biological effects in the dynamics, as well as the biological issues standing behind the smart migration phenomena are provided and discussed.

Travelling Waves in a Lattice of SIR Nodes in Approximation of Small Coupling

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The numerical simulation of spatially distributed epidemic systems gives insight into different scenarios of epidemic spread. Nevertheless, the inclusion of large numbers (potentially many thousands) of interacting nodes can be costly in terms of integrating epidemic evolution in every single node. Especially if the goal is to obtain statistically justified numerical data, it is necessary to run the process many times with different coupling parameters and initial conditions. Therefore, the dynamics in a single node is usually simplified down to a binary model: infected or not.

Another well-developed simulation technique is based on the continuous media formalism under the assumption that time delay between two neighbour centra is small comparing to the characteristic time of epidemic outbreak in every single node, and usually leads to PDEs of the reaction diffusion type. A well-known feature is the existence of the so-called travelling wave solutions, that preserve speed and shape. Analogous patterns are systematically observed in epidemic data sets, sometimes in situations when the continuous limit is not applicable.

In this work we develop an opposite approximation: characteristic epidemic time in a single node is smaller than time delay between outbreaks in every two neighbour nodes that can occur if coupling (i.e. exchange of infective) between nodes is small. This approximation is most applicable when populations are concentrated mainly in their own communities, and the spread of an epidemic has a distinctive time delay caused by a lack of strong mixing in the overall population, and leads to essential simplification of the model. A contamination of a new node by a small number of infective migrated from nodes with outbreaks can be well described by linearized ODEs. But after the outbreak in a single node is already triggered, it becomes nonsensitive to the infective incoming from other nodes and can be described by non-linear but non-coupled ODEs.

First we consider a single SIR model in the limit of small initial number of infectives, and obtain the so-called limiting solution (independent of initial condition but describing well the travelling wave shape in networks with weak coupling). Additionally we obtain simple approximations for outbreak and fade times. Then we consider a network with the simplest topology—a 1D lattice with a large number of interacting nodes. The dynamics within each node is described by a standard SIR model, with additional terms accounting for the interaction between nodes. In approximation of weak coupling, we assume that the interaction is due to migration of a relatively small proportion of the population (including those infective) between nodes, and is proportional to the small share of time this population spends in the neighbouring nodes. Simulating the model numerically, we establish the existence of travelling wave type solutions under deterministic and random coupling and determine its speed of propagation. It is shown that in an interesting parameter range it is impossible to approximate the finite differences by derivatives, i.e. to pass to reaction-diffusion PDEs, and a discrete spatial approach is essential for the analysis. Explicit formulae for the speed of the travelling waves are found and compared with results of numerical simulation in deterministic case and in the case when coupling coefficients are randomly distributed; they allow us to estimate how the average speed in random media is slowed down. Details can be found in:

Sazonov I., Kelbert M., Gravenor M.B The Speed of Epidemic Waves in a One-Dimensional Lattice of SIR Models, *Math. Model. Nat. Phenom.* 3 (2008), No. 4, 28–47.

A Time-Discrete Model for the Epidemic Population Dynamics

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In this work, we present a way of building a time-discrete model, especially related to the epidemic population dynamics, making use of the Royama's framework (Royama 1992; Seno 2007, 2008), which is sometimes called the 'first-principle' modelling, and further we analyze the derived discrete model to make some comparison to some typical ordinary differential equation models.

Especially let us consider an epidemic population dynamics of nonfatal disease transmission, assuming that the total population size can be regarded as constant, say N , according to the epidemic time scale. The susceptible population on the k th day is denoted by S_k , and the infective by I_k . We assume the probability $P_k(i)$ that the number of contacts to other individuals by an individual is i in the k th day, and give the probability that the individual who contacts in j times to some infectives in the k th day successfully escapes from the infection by $(1 - \beta_k)^j$ ($0 < \beta_k < 1$). The parameter β_k corresponds to the probability that the susceptible is infected by a contact to an infective in the k th day. Besides, we assume the recovery probability q_k for an infective in the k th day, additionally with the probability m that the recovery successfully brings the immunity. The immune population on the k th day is denoted by R_k . The immunity is waned with probability θ per day.

With these assumptions, we can derive the following discrete epidemic dynamics model for the susceptible frequency $\psi_k = S_k/N$, the infective $\phi_k = I_k/N$, and the immune $\eta_k = R_k/N$:

$$\begin{aligned}\psi_{k+1} &= \sum_{j=0}^{\infty} (1 - \beta_k \phi_k)^j P_k(j) \psi_k + (1 - m) q_k \phi_k + \theta \eta_k; \\ \phi_{k+1} &= \sum_{j=0}^{\infty} \{1 - (1 - \beta_k \phi_k)^j\} P_k(j) \psi_k + (1 - q_k) \phi_k; \\ \eta_{k+1} &= m q_k \phi_k + (1 - \theta) \eta_k,\end{aligned}\tag{1}$$

where $\psi_k + \phi_k + \eta_k = 1$ for any k . We show that this discrete model has the nature mathematically analogous to that of Kermack–McKendrick model if we assume that $P_k(j)$ follows a Poisson distribution depending on the total population size N . In such case with a rational introduction of the time step size, we can show that the zero time step limit of the system (1) exactly corresponds to Kermack–McKendrick model. As an extension, some variants of models derived from (1) will be considered.

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How do directed movements of animals towards favorable habitats influence the spreading speed in a periodic patchy environment

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Environments for living organisms are often fragmented by natural or artificial habitat destructions. In such heterogeneous environments, some animals are influenced by the senses of sight, hearing or smell to undergo directed movement toward favorable habitats. Here we consider a single-species invasion in a periodically varying environment, in which a favorable patch of size l_1 and an unfavorable patch of size l_2 are alternately arranged in a one-dimensional space. To incorporate the spatial heterogeneity and directed movement, we propose an advection-reaction-diffusion equation in which the advection velocity and the intrinsic growth rate vary depending on habitat properties. In particular, we consider a special case that both advection velocity and the intrinsic growth rate are piecewise constant as given below:

$$\frac{\partial n}{\partial t} = D \frac{\partial^2 n}{\partial x^2} - \frac{\partial u(x)n}{\partial x} + (\varepsilon(x) - n)n, \quad (*)$$

where

$$u(x) = \begin{cases} u & (ml - \frac{l}{2} \leq x < ml) \\ -u & (ml \leq x < ml + \frac{l}{2}) \end{cases} \quad \varepsilon(x) = \begin{cases} \varepsilon_1 & (ml - \frac{l_1}{2} \leq x < mL + \frac{l_1}{2}) \\ \varepsilon_2 & (ml + \frac{l_1}{2} \leq x < ml + \frac{l_1}{2} + l_2) \end{cases}.$$

We first numerically solve (*) with an initial distribution localized at the origin, and found that the population always evolves to a traveling periodic wave, when the invasion condition is satisfied. Thus by using a heuristic method as we presented before (Shigesada et al. 1986), we derive an analytical formula for the speed of the traveling periodic wave. Based on the formula, we examine how the rate of spread is influenced by the advection velocity, u , habitat qualities, ε_1 and ε_2 and the scale of habitat fragmentation, $l_1 + l_2$. Of particular interest is that the advection to the favorable habitat does not always enhance the rate of spread.

The effect of plant species diversity on community productivity: a competition model

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Current and expected changes in biodiversity have motivated number of experiments studying how biodiversity affects ecosystem functioning. Majority of experimentally assembled communities showed positive effect of biodiversity on productivity. However, debate over the applicability of such results on real communities remains. The main reason is that the positive effects are often missing in studies in permanent communities of perennial plants.

In order to study these questions theoretically we constructed simple competition model of plant community based on classical Lotka-Volterra equations. In our analyses we focused on the diversity-productivity relationship and its underlying mechanisms.

Results of our simulations show that all kinds of productivity-diversity are possible (positive, negative, none) depending on the definition of diversity we study (initial species pool vs. diversity of a mature community, i.e. after competitive exclusion) and on the forces operating in the system. In our model, productivity always increased with the size of initial species pool. The relationship with actual species richness of the mature community exhibited all types of relationship, including the negative one, depending on various model parameters. The negative relationships were found in communities dominated by strong competitive relationships. In real communities, these two mechanisms are usually both present and result in a relationship which is either slightly positive or negative but rather weak. Our model thus explains the apparent dichotomy between results obtained from short-term experiments with artificially created assemblages and long-term experiments or studies on natural stands.

* **Talk making author: Terezie Stachová**

Modeling the *in vitro* Population Dynamics of Epithelial Cells

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Abstract

Epithelial tissue is a highly organized cellular system that forms the covering or lining of all internal and external body surfaces. In physiological condition, epithelia are maintained in a dynamic equilibrium, also referred as homeostasis, where the cell number is kept essentially constant and is regulated in function of production rates, death and half-life of cellular population. Studies of epithelial cell lines growing in 2-dimensional filters supports have provided key insights of how the underline structure of epithelial tissue is established and maintained.

The computational model present here was designed to mimic the experimental data obtained from an *in vitro* culture of mouse Y1 adrenocortical cell line. For this purpose we develop a cell population model that includes a two-dimensional lattice-free cellular representation and microenvironment parameters. We applied mathematical morphology techniques to compare *in vitro* and *in silico* results. This model may be use to study several different cell populations, since the parameters are well adjusted. We believe that this approach allows a more realistic and mechanistic description epithelial cells behavior.

Presenting author: Beatriz Stransky

Particle dynamics modelling of cell populations

Vitaly Volpert
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Abstract:

Evolution of cell populations can be described with dissipative particle dynamics, where each cell moves according to the balance of forces acting on it, or with partial differential equations, where cell population is considered as a continuous medium. We discuss here the relation between these two approaches and apply them to some problems of morphogenesis.

Modelling travelling waves and spatial patterns in exploited food chains of a resource-consumer type

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Dynamic models of food chains demonstrate both regular – equilibria and periodic orbits - and irregular structures under their parameters change. Generally, there are two methods for modelling of food chain dynamics: the most popular approach is based on equations of interacting populations connected by predator-prey relations where the first species is usually self-regulated, while another less widespread techniques considers a chain in units of the entering resource with its explicit description (Jorgensen and Svirezhev, 2004). For the last approach a collection of interesting dynamic features on bifurcations of equilibria under the nutrient inflow increase and strange attractor formation was established (Svirezhev, 1987). In this work the method is used to study dynamics of a spatially distributed exploited partially closed trophic chain with explicit nutrient influx considering existing of travelling wave solutions and formation of spatial patterns under harvesting efforts and varying of input nutrient or energy flux. Perturbations of two parameters – external resource input flux and harvesting mortality coefficient for the last species in the chain of even (length $n = 2$) and odd (length $n = 3$) for the corresponding local wave system initiate different types of travelling waves like a regular wave and wave front. Increasing the resource flux can lead to Hopf bifurcation of non-trivial equilibrium in a wave system of ODE corresponding to appearance of wave trains – periodic wave solutions in the initial PDE model. Rising a harvesting mortality coefficient can result in a wave front leading the last species in the chain to rapid decrease to zero and the chain itself to be shortened. We also study impact of migration and taxis on the spatial pattern formation under conditions of diffusive instability for the spatially homogeneous regime and find out a “wave of chaos” (Petrovskii and Malchow, 2001) as a mechanism of non-Turing pattern formation in a trophic chain dynamics with a high level of exploitation.

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Molecular constructions based on double-stranded nucleic acid liquid crystals: formation, properties, practical application.

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Simple thermodynamic model has been proposed to describe a formation of three dimensional molecular constrictions based on linear double stranded natural nucleic acids and synthetic polyribonucleotides forming the particle of cholesteric liquid crystalline dispersion. It has been shown experimentally that such DNA-based constructions can be used as a novel type of biological micro sensors capable of detecting various biologically active components, for example a human metabolite homocystein. The model, which was developed in close collaboration with experimental group, can be used to explain formation of molecular constructions, derive some qualitative characteristics and predict various regimes which are difficult to observe experimentally.

The effect of local competition induced by resource partitioning on population dynamics

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The population dynamics of single species with seasonal reproduction are often modeled using difference equations. The aim of this research is to present an unified view to understand the mechanistic basis of discrete-time population models from the viewpoints of resource partitioning and spatial aggregation of individuals. We present a first principles derivation of a new population model which incorporates both scramble and contest competition using a site-based framework in which individuals are distributed among discrete resource sites. The derived model has two parameters indicating the deviation from ideal contest competition and the degree of spatial aggregation of individuals respectively. Taking various limits with respect to these parameters gives various population models exhibiting either scramble or contest competition. Furthermore, extending the above argument, we also demonstrate that various population models exhibiting the Allee effect are able to be derived if assuming a population of sexually reproducing species.

Potential growth indicator and the net reproductive rate

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In the well-known matrix models for structured population dynamics

$$\mathbf{x}(t+1) = \mathbf{L} \mathbf{x}(t), \quad t = 0, 1, 2, \dots, \quad (1)$$

where column vector $\mathbf{x}(t) = [x_1(t), x_2(t), \dots, x_n(t)]^T$ is the population structure and $n \times n$ -matrix \mathbf{L} is called the *projection* matrix, we consider a general class of projection matrices in the form

$$\mathbf{L} = \begin{bmatrix} b_1 + r_1 & b_2 & b_3 & \Lambda & b_{n-1} & b_n \\ a_{21} & r_2 & & & & 0 \\ a_{31} & a_{32} & r_3 & & & \\ \Lambda & & \Lambda & 0 & & \\ a_{n-1,1} & a_{n-1,2} & \Lambda & & r_{n-1} & \\ a_{n,1} & a_{n,2} & \Lambda & & a_{n,n-1} & r_n \end{bmatrix}, \quad 0 \leq a_{ij} \leq 1 \quad (i > j),$$

with nonzero first row $b_j \geq 0$ (birth rates, $j = 1, \dots, n$) and $0 < r_j + \sum_{i>j} a_{ij} \leq 1$. This general pattern (that we refer to as *Logofet matrix*) expands the classical Leslie and Lefkovich patterns for a wider variety of organisms' life cycles.

It is well known that vector $\mathbf{x}(t) \rightarrow 0, \infty$, or \mathbf{x}^* , when λ_1 , the maximal (in modulus) eigenvalue of \mathbf{L} , meets the condition $\lambda_1 < 1, > 1$ or $= 1$ respectively. This property of practical importance appears to be testable even without calculation of λ_1 for a calibrated projection matrix. Given certain values of demographic parameters, the *potential-growth indicator (PGI)* problem means to find an explicit function (an indicator) of the parameters whose value can indicate whether the model population grows, declines, or remains steady (Logofet, Belova, 2008). A recently proved Theorem (*ibid.*) establishes the PGI as $\mathbf{R}(\mathbf{L}) = 1 - p(1, \mathbf{L})$, where $p(1, \mathbf{L})$ denotes the monic characteristic polynomial of matrix \mathbf{L} .

The *net reproductive rate (NRR)* V_0 was defined earlier as the mean number of offspring by which a newborn individual will be replaced by the end of its life, and thus the rate by which the population increases (decreases, stays in equilibrium) from one generation to the next (Caswell, 2001; Cushing, Yicang, 1994; Cushing et al., 2004). By definition, the NRR is the maximum eigenvalue of matrix \mathbf{Q} , where $\mathbf{Q} = \mathbf{F}(\mathbf{I} - \mathbf{T})^{-1}$ and \mathbf{F} and \mathbf{T} are the *fertility* and *transition* parts of the projection matrix $\mathbf{L} = \mathbf{F} + \mathbf{T}$.

I have found that the NRR V_0 does also possess the indicator property of PGI for any indecomposable Logofet matrix \mathbf{L} .

Although neither \mathbf{R} , nor V_0 can determine how specifically fast the population is growing (Levin et al., 1996), a practical advantage of the PGI is that it is linear w.r.t. the stage-specific birth rates, which is of practical importance in a calibration procedure for matrix \mathbf{L} .

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Mathematical Models of Collective Dynamics in Biology & Evolution

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Modelling the potential outcome of maternal immunisation campaigns

It is the objective of this work to propose and stimulate the discussion of a preliminary set of population level epidemiological models for the study of any potential outcomes and consequences of a public health intervention by means of mass maternal immunisation. Candidate vaccines of this nature are currently being considered for a number of highly prevalent viral infections (such as human Respiratory Syncytial Virus) that cause significant morbidity and mortality among neonate and young infant age classes. Immunisation is typically administered to pregnant women at around 30 weeks of gestation with the primary intention being a significant rise in disease specific neutralising antibody in the newborn infant, subsequently providing additional immune protection in the first 3-6 months of life, hence reducing the incidence of disease below a target age level and raising the average age at primary infection.

The model variations discussed in this work can be derived around a general MSIR type PDE system, where the rate at which individuals lose maternally acquired protection and become fully susceptible is taken to be directly dependent on the population cord antibody distribution that wanes with increasing age. The models have been used for a preliminary, qualitative study of the static (age profile), dynamic (time series) and seasonal (temporally forced) behaviour of the system in response to various applications of a potential campaign. In addition a number of representative age dependent transmission functions and re-infection mechanisms have also been considered in an attempt to identify cases where such an intervention may give rise to any significantly beneficial or undesirable outcomes.

Preliminary analysis of the proposed systems has indicated that in most cases maternal immunisation is unlikely to ultimately reduce (or increase) the overall prevalence of infection within a host population, given that any additional immunity induced is inevitably lost, and typically within a relatively short period of time with respect to average life expectancy. Therefore it is also unlikely to provide significant protection to unvaccinated individuals through herd immunity as is the case with many active childhood vaccine programmes such as that for MMR. The analysis has however suggested some exceptional circumstances where this may not be the case, for example if there exists a rapid change in age related transmission characteristics encompassed by the average increase in duration of protection, perhaps due to some aspect of physiological development.

Given that epidemic behaviour is largely driven by susceptibility it has also been shown that in some cases rapid application of a maternal immunisation campaign can cause sufficient perturbation to the inflow of susceptible individuals to induce large epidemic dynamics throughout the population. In the case of seasonally forced systems it can also be shown that the timing of administration throughout the (annual) inter-epidemic cycle can be equally critical in mitigating potentially disruptive dynamics and optimising the overall efficacy of the intervention.

Impacts of predation in an age-structured population: mathematical modeling and applications

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Predation is a key mechanism of population growth control. Through mathematical models, we explore impacts of generalist predators in a prey population structured into two age classes, juveniles and adults. A specific predation pressure is prescribed for each of the two age classes, by assuming either no predation or Holling type II or type III functional responses in various combinations.

We distinguish two modeling scenarios. First, we seek for potential Allee effects or multiple positive stable states in the prey population, and for conditions for which predation is more effective on juveniles than adults and vice versa. Allee effects arise quite commonly for most functional response combinations. Most interestingly, predators with type II functional response on juvenile prey have been observed to generate predator pit equilibrium, akin to that generated by predators with the type III functional response preying on an unstructured prey that grows logistically in the predator absence. In the second scenario, we assume that the age-structured prey from the first model feeds in addition on a resource and that the resource and the prey undergo outbreak dynamics. For this scenario, we examine possibilities for the outbreak control using age-specific predation.

Modeling of age-structured populations provides a more realistic description of and insight into the predator-prey interactions and hence an important groundwork for applied ecology, such as for a more effective biocontrol of pests or prevention of species extinctions. We discuss some implications of our results for applied ecology.

Modelling competition between two large African carnivores, African wild dogs and spotted hyaenas

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Poster presenting author: Terezie Stachová

African wild dog (*Lycaon pictus*) is one of the most endangered carnivores on the planet today, with only a few thousand individuals remaining despite strong conservation measures. Several explanations have been suggested for this phenomenon, including competition with other large carnivores, mainly lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*). This competition includes exploitative competition for shared prey, intraguild predation on dog pups by lions and food kleptoparasitism by both hyaenas and lions.

To study the question of wild dog survival in competition with hyaenas under different conditions, we constructed a spatially structured, individual-based model for both predators, parameterized and validated by published data. We included specific life history features of wild dogs (dispersal and pack formation and Allee effect due to reproductive suppression) and focused on the role of spatial heterogeneity, i.e. different prey density and/or vegetation cover, which influences the rate of kleptoparasitism by hyaenas.

The two most important factors affecting wild dog numbers in our model are reproductive suppression and mortality during failed dispersal attempts. We have obtained negative correlation between the numbers of wild dogs and hyaenas in individual territories, which has been reported from the wild on both local and large (ecosystem) scales. Analysis of the role of spatial heterogeneity in our model shows that it helps the survival of both predators in critical situations. While hyaenas are directly limited by low prey numbers in poor territories, prey-rich territories turn out to be critical for dogs due to an indirect effect of prey, leading to very high numbers of hyaenas. In both cases, the heterogeneity creates refugia where the “weaker” predator can persist or at least survive for a longer time. Our model indicates that reducing the number of competitors might be required in some areas to save the wild dogs from extinction.

Analysis of asymmetric stable droplets in a fish patterning model

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Soliton like structures called “stable droplets” are found to exist within a paradigm reaction diffusion model which can be used to describe the patterning in a number of fish species. It is straightforward to analyse this phenomenon in the case when two non-zero stable steady states are symmetric, however the asymmetric case is more challenging. We use a recently developed perturbation technique (Gomila et al, 2004 [1]) to investigate the weakly asymmetric case.

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Traveling fronts in a model for vegetation patterns. Effect of cross advection

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Some interactions between species in population dynamics beings when modeled via continuum equations produce *cross-diffusion* terms - individuals prefer to live far from others if these are in a different «social class» or biological group. Further examples include landscape organization in geophysics and spatial ecology given by von Hardenberg et al. [1]. Their model intends to capture vegetation patterns in arid environments and is formulated in terms of two variables, the biomass density and the ground water density. We study bistable reaction-diffusion systems of this type with *cross-advection* terms using a piecewise linear approximation for the nonlinear reaction term. It is shown that a system with double symmetric cross advection produces the same characteristic equation as a system with cross diffusion in only one equation or a system exhibiting double self advection with opposite signs. For systems with cross-advection terms having opposite signs, traveling-wave solutions are derived explicitly. Fronts constructed from these solutions have characteristic *wavy* profiles. A bifurcation of excitation fronts induced by cross advection is discovered. Including cross diffusion, we find front solutions having both an oscillatory leading edge and an oscillating tail.

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