Conference on Mathematical Population Dynamics, Ecoepidemiology and Evolution

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CIRM - LUMINY

ORAL CONTRIBUTIONS

KEYNOTE LECTURES

Cycles, phase analysis, and synchronization in ecological populations - a tale of four case studies.

Bernd Blasius

Institute for Chemistry and Biology of the Marine Environment, University of Oldenburg, Germany
`bernd.blasius@uni-oldenburg.de`

Abstract Cyclic dynamics are one of the most notable phenomena in population biology and are known to occur in many communities both in the wild and the laboratory. Oscillations in biomass often exceed an order of magnitude, with period lengths ranging from days to decades, and may be spatially synchronized over continental scales. Their underlying causes, however, remain a long-standing enigma. In this presentation I will present modelling analysis from my own work for four paradigmatic case studies. These will present a journey from single species laboratory experiments to the world largest population oscillations, both in in period length and in absolute biomass. I will show that the mechanisms driving the cycles and their synchronization to external forcing may be very different in each case (e.g., predator-prey interactions or synchronized life cycles). But despite these idiosyncratic properties, notions from phase analysis and synchronization theory can be applied to capture observed population dynamics, providing a common theoretic framework for understanding these phenomena that have fascinated ecologists for centuries.

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Animal growth in a randomly varying environment with an application to optimization in cattle raising

Carlos A. Braumann

Centro de Investigação em Matemática e Aplicações, Instituto de Investigação e Formação Avançada, Universidade de Évora, Departamento de Matemática, Escola de Ciencias e Tecnologia, Universidade de Évora, Portugal
braumann@uevora.pt

Abstract (*Joint work with Gonçalo Jacinto and Patrícia A. Filipe.*) The effect of random fluctuations of internal and external environmental conditions on the growth dynamics of individual animals is not captured by the regression model typical approach. We use stochastic differential equation (SDE) versions of a general class of models that includes the classical growth curves as particular cases. Namely, we use models of the form $dY_t = \beta(\alpha - Y_t)dt + \sigma dW_t$, with X_t being the animal size at age t and $Y_t = h(X_t)$ being the transformed size by a C^1 monotonous function h specific of the appropriate underlying growth curve model. α is the average transfomed maturity size of the animal, $\beta > 0$ is the rate of approach to it and $\sigma > 0$ measures the intensity of the effect on the growth rate of Y_t of environmental fluctuations. These models can be applied to the growth of wildlife animals and also to plant growth, particularly tree growth, but, due to data availability (data furnished by the Associação dos Produtores de Bovinos Mertolengos – ACBM) and economical interest, we have applied them to cattle growth.

We briefly mention the extensive work of this team on parameter simulation methods based on data from several animals, including alternatives [2] to maximum likelihood to correct biases and improve confidence intervals when, as usually happens, there is shortage of data for animals at older ages. We also mention mixed SDE models, in which model parameters may vary randomly from animal to animal (due, for instance, to their different genetical values and other individual characteristics), including a new approximate parameter estimation method [3]. The dependence on genetic values opens the possibility of evolutionary studies on the parameters.

In our application to mertolengo cattle growth, the issue of profit optimization in cattle raising is very important. For that, we have obtained expressions for the expected value and the standard deviation of the profit on raising an animal as a function of the selling age for quite complex and market realistic raising cost structures and selling prices [1]. These results were used to determine the selling age that maximizes the expected profit. A user friendly and flexible computer app for the use of farmers was developed by Ruralbit based on our results.

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Preparing for Surprise under Global Change: Resilience, Tipping points, and Early-Warnings.

Vasilis Dakos

Institut des Sciences de l'Evolution de Montpellier (ISEM), University of Montpellier, France
`vasilis.dakos@umontpellier.fr`

Abstract Evidence is increasing that large-scale abrupt changes in ecosystems, fisheries, oceanic circulation patterns, or even human physiology are examples of catastrophic transitions between different system states. Such abrupt changes are typically referred to as tipping points. Recent theoretical findings suggest that distinct properties tend to rule system dynamics prior to tipping points. When quantified, these properties may be more generically used as indicators of resilience. As long-term data become increasingly available and experimental approaches are improving, the challenge has been to apply our theoretical metrics on ecological dynamics to anticipate, prepare, or navigate away from tipping points. In this talk, I will present how we can quantify resilience and detect tipping points highlighting examples from ecological and climate systems. Moreover, I will outline challenges and ideas on how we can operationalise such approaches and also how to better understand tipping point responses in a changing but evolving world.

A Mathematical Perspective on Resilience and Sustainability in Climate and Biodiversity.

Michel De Lara

École des Ponts ParisTech, France
michel.delara@enpc.fr

Abstract In this talk, I gather previous works related to mathematical methods for the management of natural resources, and present how they can contribute to tackle questions in resilience and sustainability. For this purpose, I will outline the following items.

- Scan through the vocabulary of sustainability and resilience in the IPCC (climate) and IPBES (biodiversity) international bodies reports: goals, indicators, vulnerability, adaptive capacity, robustness, risk, scenarios, models, etc..

- Address theoretical questions such as how can we formalize sustainability and resilience with tools from control theory (optimal control, viability) and decision under uncertainty (multistage stochastic optimization, risk). For instance, when goals to achieve are formulated as constraints to satisfy — like minimal spawning stock biomass every year in fishery management, or maximal number of infected in epidemics control — we present the notion of viability kernel, and its stochastic and robust variants.

- Present solution methods: how can we tackle the solving of problems, once mathematically formalized? We sketch stochastic and robust dynamic programming in small state dimension.

- Outline examples: biodiversity (fisheries, epidemiology), energy and climate.

- Raise open questions and challenges: numerical methods for large-scale multistage stochastic optimization problems; value of information; insurance value of natural capital; risk measures for random processes; axiomatics for acceptable processes.

Stochastic dynamics for adaptation and evolution of microorganisms.

Sylvie Méléard

Ecole Polytechniques, Palaiseau, France
`sylvie.meleard@polytechnique.edu`

Abstract Understanding the adaptation and evolution of populations is a huge challenge, in particular for microorganisms since it plays a main role in the virulence evolution or in bacterial antibiotics resistances. We propose a general stochastic model of population dynamics with clonal reproduction and mutations. Moreover the individuals compete for resources and exchange genes. We show that the horizontal gene transfer can have a major impact on the distribution of the successive mutational fixations, leading to dramatically different behaviors, from expected evolution scenarios to evolutionary suicide, including cyclic behaviours. We present different approaches to capture mathematically these scenarii.

Towards process-based comparative models for bridging micro and macroevolutionary speciation research.

Hélène Morlon

Institute of Biology, Ecole Normale Supérieure, France
helene.morlon@bio.ens.psl.eu

Abstract Large scale biodiversity patterns result from the historical processes of speciation and extinction. In particular, the balance between speciation and extinction rates determines how species richness varies through time, across species groups, and geographical regions. Phylogenetic diversification analyses, which rely on fitting stochastic birth-death processes to phylogenetic data, can be used to estimate these macroevolutionary rates from the phylogenies of extant species, potentially further informed by paleodata. I will present recent developments that model fine-scale variations in speciation rates and that can combine neontological and paleontological evidence. Applied to empirical data, these models reveal a wide variation in speciation rates across lineages. While several models have been developed to explain these variations by differences in specific traits or abiotic and biotic conditions, models that would help us better understand the actual processes that control diversification rates are lagging behind. Speciation research at the microscale has focused on understanding the establishment of reproductive barriers, but there is increasing evidence that variations in macroevolutionary speciation rates are poorly explained by variations in the rate at which populations acquire reproductive isolation. I will present recent developments that aim at understanding i) how variations in the rates at which reproductive isolation is initiated, at which populations acquire reproductive isolation, and at which incipient species go extinct combine to explain macroevolutionary speciation rate, and ii) how population sizes, mutation rates and the mode of speciation impact this latter relationship.

Biological invasion in the heterogeneous environment.

Natalia Petrovskaya

School of Mathematics, University of Birmingham, UK
n.b.petrovskaya@bham.ac.uk

Abstract Biological invasion of alien species is regarded as one of the major threats to ecosystems all around the world. Invasion in various habitats causes the damage to biodiversity and the economy, the losses across the world being evaluated as billions of dollars each year and at an increasing rate [5].

The conditions for propagation of invasive species are different in different landscapes and the influence of the surrounding landscape on the spread dynamics of invasive species has been well recognised [3]. However, despite significant progress being made in development of the mathematical theory of biological invasion [2], there is still a gap between theoretical and experimental investigation of invasion in the heterogeneous environment. For example, recent experimental evidence [6] suggests that the urban environment with roads and industrial sites can have an important effect on spatial patterns of biological invasion, yet further investigation is required to conclude about the underlying mechanisms responsible for spatio-temporal dynamics of the invasive species in the urban landscape.

In my talk, I will demonstrate how heterogeneity in the landscape (*e.g.*, a road) increases the complexity of the invasion problem. It will be argued in the talk that the presence of a road in the landscape can result in new propagation regimes in comparison with the homogeneous environment. The results of our study in [1] reveal three distinct regimes of propagation where roads can act as barriers to invasion, lead to a formation of a beachhead, or act as corridors allowing the invasive species to invade the domain in front of the road. Analytical and computational findings on how roads can impact the spread of invasive species show that a small change in conditions of the environment favouring the invasive species can change the case for the road, allowing the invasive species to invade the domain in front of the road where it previously could not spread. That gives rise to the question of detection of the invasive species in the early stages of the invasion. I will show that, while the propagation speed cannot be accurately predicted before the invasive species is established in the new homogeneous environment, the unpredictability is amplified by having a heterogeneity in the landscape. It will also be argued in the talk that the same conclusion remains true when topological properties of the invasive regime are analysed [4], *i.e.*, spatial patterns of biological invasion in the urban landscape cannot be predicted unless the invasive species is established, while the transient time required to establish the invasion regime can be longer than the time taken to invade the entire spatial domain where the invasive species is monitored.

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Modelling Phanerozoic Mass Extinctions.

Sergei Petrovskii

School of Computing and Mathematical Sciences, University of Leicester, UK
sp237@leicester.ac.uk

Abstract Mass extinctions is a phenomenon that came into the focus of scientific community in early 1980s [2] and has been attracting an increasing attention ever since. Species get extinct all the time with a certain background extinction rate; this is a normal part of macroevolution. However, several times through the 550 Ma of the recorded history of life on Earth, the extinction rates exceeded the average background rate by more than an order of magnitude, resulting in 50-90% loss in the global biodiversity. Apart from those "Big Five", there were many smaller mass extinctions with the global biodiversity loss ranging between 10-50% [4]. Remarkably, the current extinction rate (over the last 300 years) is estimated to be more than an order of magnitude higher than the background rate, suggesting that we may be witnessing the beginning of the "6th mass extinction" [3].

We mention here that mechanisms of species extinction have long been a focus of mathematical biology. There is, however, a fundamental difference between modelling extinction of a particular species or a local ecological community and that of a mass extinction. How a factor or process that may result in extinction of some particular species at a particular location may be upscaled to lead to extinction on a global, massive scale through a broad variety of taxa and environments remains largely unclear. Given the inherent deficiency of the fossil data [7], statistical analysis alone does not normally allow to distinguish between the effect of different processes. Process-based modeling approaches are needed.

Importantly, species do not only adapt to a climate change, going extinct if the change is too large or too fast [5]. Some taxa, in particular vegetation, can attenuate the change and/or modify the environment according to their needs. This species's active feedback has long been known in the climate science as the Gaia hypothesis [6] but, surprisingly, has been largely overlooked by earlier modelling studies on mass extinctions. In order to bridge this gap, a novel conceptual modeling approach has been recently developed [8] to couple the zero-dimensional global energy budget model (known as the Budyko-Sellers equation) to a generic model of consumer-resource dynamics. Here we present a further development of this approach [1]: a novel model that combines the active feedback of species to a climate change with species evolutionary response. The model also takes into account the dependence of population growth rate on the ambient temperature. Our model shows that species extinction or survival following a climate change depends on the interplay between the magnitude of the climate change and the rate of species's adaptive evolution. The model predicts a distribution of extinction frequencies which is generally consistent

with the fossil data.

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CONTRIBUTED TALKS

PREDATOR-PREY MODELS WITH HERD RESPONSE TO INDIVIDUALISTIC ATTACKS.

Francesca Acotto, Ezio Venturino

Dipartimento di Matematica "Giuseppe Peano", Università di Torino, Italy
`francesca.acotto@unito.it`

Abstract Starting from the Lotka-Volterra model, over the years, different interaction dynamics have been considered, which differ from the classical assumption of biquadratic terms involving prey and predators. Among these, the case of prey grazing in large groups coexisting on common ground with their predators is of interest, [1]. This happens, for example, in the savannah environment, considering herbivores and predators that feed on them. Living in groups is one of the strategies that herbivores use to defend themselves from predator attacks. Aggregation, furthermore, is not only advantageous for prey in terms of defense, but also the benefits it brings increase with the size of the herd. To model this feature, we depart from the Holling type II response function reformulated to account for herding, [2]. We further assume that a sufficiently large set of prey could respond to individualistic attacks, and therefore induce the predators to renounce. The basic idea is described at first in a simple two-population predator-prey system. It is then expanded considering generalist predators to deal with two prey: in the first case, both are gathered in herds, in the second one, one of the two behaves individualistically.

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A MODELLING FRAMEWORK FOR ECO-EVOLUTIONARY DYNAMICS IN NETWORK-STRUCTURED POPULATIONS WITH MIGRATION.

Wajid Ali

University of Liverpool, UK
Wajid.Ali@liverpool.ac.uk

Abstract Mathematical models that consider the effect of network structure on the evolution of population typically assume a population of fixed size and distribution. In this talk, I will present a mathematical model that describes the eco-evolutionary dynamics where population size and distribution can change through birth, death and migration, all of which are separate processes. This allows complex interaction and migration behaviours that are dependent on competition to be considered. This new framework has led to a more realistic version of previous work, including ecology in a fully decoupled way, with separate birth, death and movement processes. New insights include the effect of group tolerance on density dependent migration, which in turn can significantly affect the evolutionary process. I will show simulation results for the success of a mutant in the rare mutation limit for the complete, cycle and star networks.

Long transient dynamics in deterministic and stochastic time-discrete population dynamics models

AlMutairi, Dalal[1,2]   Morozov, Andrew [1]   Petrovskiy, Sergei [1]

[1] *University of Leicester, UK,* [2] *Shaqra University, Saudi Arabia*
dmsa3@leicester.ac.uk

Abstract Traditionally, mathematical modelling of population dynamics has been focused on long-term, asymptotic behaviour (systems attractors), whereas the effects of transient regimes have been largely disregarded. However, currently, there is a growing appreciation of the role of transients both in empirical ecology and mathematical modelling of population dynamics. Among important challenges are the identification of mechanisms of transients in various dynamical systems and the derivation of the corresponding scaling law of the transient's lifetime. Prediction of the lifetime of ecological transients is of vital practical importance for long-term ecological forecasting and regime shift anticipation. In this study, we reveal various patterns of transients occurring in a few simple discrete population models, which are mathematically described by discontinuous maps. We start with a single population model with a logistic (or Ricker function) local growth and a density-dependent dispersal [1]. In this model, we demonstrate the possibility of various types of transient dynamics within a wide range of system parameters. This includes crawl-by dynamics, chaotic saddles, ghost attractors, and various intermittency regimes. For each type of transient, we have investigated the corresponding scaling law of the transient's lifetime. Then we considered a discrete predator-prey model with a discontinuous dispersal of both populations [2]. In this system, we show the possibility of complex patterns occurring as a cascade of transients of different types. We show that the final attractor of the system becomes highly unpredictable from the time series, which is of great importance for ecosystem management. In the space of the key model parameters, we show where particular types of long transients can be expected. Finally, we also explored the situation where some noise is present in the system. In particular, we considered that some model parameters are affected by external noise of various types: we investigated scenarios of non-correlated and correlated noise (based on fractional Brownian motion). We found that noise can largely affect transient dynamics. In particular, noise can suppress transients or create novel types of transients in the system, which depend on the nature and the amplitude of the noise.

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Complex Spatio-Temporal Dynamics in a Model of Social Protests

Alnuaie, Amal[1,2] , Morozov, Andrew[1], Petrovskiy, Sergei[1]

[1] *University of Leicester, UK,* [2] *Taif University, Saudi Arabia*
`asha3@leicester.ac.uk`

Abstract Mathematical modelling of riots and protests is now becoming a powerful tool in providing a better understanding of dynamics of social unrest with the eventual goal to ensure a sustainable development of the human society. Currently, however, most of the existing studies in the considered research area are based on either non-spatial or spatially implicit models, whereas in a large number of cases dynamics of social protests clearly exhibit spatial heterogeneity. To bridge the existing gap, here we explore spatial-temporal patterns of social protests using a reaction-diffusion modelling framework. Our model variables are: the number of protesters and the cumulative amount of damage made as an outcome of the protest. The system has been studied analytically as well as by means of extensive numerical simulation in one dimensional and two-dimensional space. We show that the proposed model exhibits a variety of dynamical regimes including stationary patterns with round hot spots as well as complex labyrinthine-like structures. The system also predicts the various types propagating waves of protests with regular and irregular fronts as well as a patchy spread, where protests spread in space via irregular motion and interaction of separate patches of high numbers of protestors without formation of any continuous front, the number of protestors between patches being nearly zero. We reveal the structure of the parameter space of the model identifying the range of key parameters for which particular dynamical regimes are possible. Along with reaction-diffusion model, considering continuous space, we also consider the model of protests on discrete networks of different nature. We find that Turing instability can lead to pattern formation on networks, which opens up an exciting possibility to explore it as a generation mechanism in a large number of social unrest contexts. The network- based model also shows a variety of non-Turing patterns including both stationary and non-stationary complex dynamics, where different nodes behave differently. Finally, we consider a realistic network to model the yellow vests movement in France.

Steady state behaviour of populations performing "linked" random walks.

Bearup, Daniel

University of Kent, UK
`D.Bearup@kent.ac.uk`

Abstract Random walks are used to approximate the behaviour of a broad range of physical systems. In this talk, I consider the steady state behaviour of a system containing pairs of random walking particles which are linked, or coupled, through a simple symmetric relationship. In particular, the positions, x_1 & x_2, of a pair of particles are constrained so that $f(x_1, x_2) = c$ where $f(\cdot, \cdot)$ satisfies $f(x_1, x_2) = f(x_2, x_1)$. I show that this linkage can produce non-trivial, i.e. non-constant, steady state distributions of the populations.

This work was motivated by a problem in Bayesian identifiability which I will briefly discuss. I have not looked into potential ecological applications of these behaviours as yet. However, given the ubiquity of random walk models in modelling of animal behaviour, it seems likely that such applications exist. In particular, such random walks could describe the behaviour of interacting individuals, for example in flocking/schooling or courtship dances.

Reconstructing SARS-CoV-2 transmission in African countries using a mathematical model integrating immunity data.

Slimane BenMiled, Bechir Naffeti, Walid BenAribi, Amira Kebir, Maryam Diara, Ines Vigan-Womas, Matthieu Schoenhals, Koussay Dellagi

Institut Pasteur de Tunis, Tunisia
`slimane.benmiled@fst.utm.tn`

Abstract For over 3 years, the Covid-19 pandemic caused by SARS COV2 coronavirus has been ongoing. Compared to Europe, America or Asia, Africa has been somehow spared with a lower number of deaths. However contrasted epidemiological situations exist between African countries raising questions on the determinants of disease spread in the African context. Our goal is to better understand the evolution of the epidemic (from its start on early 2020 to October 2022) in three contrasted countries, Tunisia Senegal and Madagascar, located in North, West and East Africa respectively. Our model took into account the impact of Public Health and Social Measures (PHSM) implemented in each country as well as the virus specific immunity acquired after infection, its spontaneous decline over time and its boosting after natural re-infection or vaccination. .

We build an epidemic Susceptible-Exposed-Infected-Recovered mathematical model including death information due to disease, SEIR/DS model, where the recovery class are structured by specific immunity level and are modeled by a partial differential equation taking into account the opposed effects of immunity decline at distance of infection and immunity boosting after re-infection or vaccination. The model was parameterised using data sets acquired in Senegal on the kinetics of antibodies to the receptor binding domain of SARS-CoV-2 Spike protein (S/RBD) and the Nucleocapsid protein (N).

In Senegal and Tunisia, the pandemic went through three main phases: During the first phase, the SARS-CoV-2 cases emerged from the large reservoir of essentially naive individuals and were limited in number by the strong preventive measures implemented by health authorities. The second phase was characterized by the introduction of new variants in a population where a large fraction of individuals has been already infected at least once. During the third phase, successive epidemic waves were driven by the emergence of SARS-CoV-2 variants that escaped the host immunity and were fueled by the reconstitution of a pool of susceptible individuals after the decline of post-infectious or vaccine induced immunity. In Madagascar, the epidemiological profile was different. It was characterized by a longer interval between epidemic waves, longer than the time lapse needed for immunity loss. As a consequence, there was a large reconstitution of the pool of susceptible who already

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have lost their protective immunity.

SARS-CoV-2 has widely spread within the three countries where most people were massively infected with SARS-CoV-2 and its variants. The start of each new wave was conditioned in large part by the loss of immunity induced by the precedent waves.

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Ecoevolutionary dynamics in shallow lakes.

Sirine Boucenna, Vasilis Dakos, Gael Raoul

*Institut des Sciences de l'Evolution de Montpellier & Centre de Mathematiques
Appliquees de l'Ecole Polytechnique, France*
`sirine.boucenna@etu.umontpellier.fr`

Abstract Ecosystems are exposed to increased threat and may shift abruptly from
one state to another contrasting alternative state. This shift occurs when exter-
nal conditions cross a threshold known as a tipping point which mathematically
corresponds to a bifurcation point. In order to understand the effects of evolution
on tipping point responses, we will consider the case of shallow lakes which is one
of the best known bistable ecosystems. We model the eco-evolutionary dynamics
of submerged macrophytes and floating plants in a shallow lake in competition for
nutrients and light and which are characterized by a phenotypic trait that repre-
sents their growth depth and which underlies their competitive ability for the two
resources. We first study the ecological asymptotic behaviours of the system and
investigate whether alternative stable states occur for different phenotypes and envi-
ronmental conditions. We then study the evolution of submerged macrophytes only,
assuming that the floating plants are fixed at the surface, using Adaptive Dynamics
and a structured trait population model. We identify the conditions under which
the population of submerged macrophytes evolves towards a monomorphic state,
diversifies or experiences evolutionary suicide.

OPTIMAL VACCINATION STRATEGY OF COVID-19: A CONSTRAINT-DEPENDANT APPROACH.

Amira Bouhali[*1,4], Amira Kebir[1,2], Walid Ben Aribi[3]

[1]*BIMS (Pasteur Institute of Tunis, Tunis, Tunisia)*
[2]*ENIT (University of Tunis El Manar, Tunis, Tunisia)*
[3]*IPEIT (University of Tunis, Tunis, Tunisia)*
[4]*School of Business, Esprit School of Business, Tunis 2083,9 Tunisia*
amira.bouhali.2893@gmail.com

Abstract After the vaccine implementation, the WHO set a unified vaccination approach to be adopted by all different countries. However, regarding all the various constraints that can be noted such as the vaccine availability, the unlike age distributions and the different control measures that are adopted by different countries, several questions arise about the optimality of the WHO strategy. Thereafter, in this study, we present an epidemic age-structured controlled SEIR model with two compartments: vaccinated and unvaccinated. The aim of this study is to set a model that allows the optimization of vaccination strategies for both Covid-19 and similar-feature-presenting diseases under all the previously mentioned constraints. The model is proven to have two disease-free steady states: one that corresponds to the period before the start of the pandemic and one that corresponds to the end of it, achieved by total collective immunity. Also, a thorough study is conducted in order to compute the basic reproduction number. The numerical simulations were used to solve the optimal control problem and were conducted for the case of Covid-19. The numerical simulations investigated the impact of different maximal vaccination thresholds on the optimal strategy as well as the impact of various control measures and age distributions on it. The results of the numerical simulations reveal that the optimal strategy is tightly tied to the age distribution of the studied population in the first place and then the distancing protocol opted for. The relation to the age distribution is even more obvious with tight constraints. Moreover, the optimal strategy is revealed also to be quite sensitive to the contact matrix parameters. Distancing and protection measures remain important and their absence is hardly replaced by vaccinating 75% of the population.

CROSS-DIFFUSION SYSTEMS: EXISTENCE AND UNIQUENESS OF STRONG SOLUTION

Elisabetta Brocchieri, L. Desvillettes, H. Dietert

Université de Paris Saclay, France
`brocchieri.1590248@studenti.uniroma1.it`

Abstract Cross-diffusion systems are non-linear parabolic systems with relevant applications in biology and ecology. In this talk, we study the existence of strong solutions for a triangular cross-diffusion system with reaction terms which include the Lotka-Volterra type. The main idea consists in analysing an auxiliary system in a non-divergence form which is equivalent to the cross-diffusion system, by introducing a convenient change of variable. Then, we regularize the auxiliary system, we prove the existence of strong solutions by a fixed-point theorem and we pass to the limit.

Moreover, we also investigate the regularity and the uniqueness of the solution. In particular, we prove that the solution is bounded in $L^\infty(0, T \times \Omega)$, with $T > 0$ and the space domain $\Omega \subset \mathbb{R}^N$, provided that $N \leq 3$, and the solution is unique if $N \leq 2$.

An individual-based model for food webs: how can simple biological constraints enforce precise allometric coefficients.

Virgile Brodu, Sylvain Billiard, Nicolas Champagnat, Coralie Fritsch

University of Lorraine, France
virgile.brodu@univ-lorraine.fr

Abstract For a few decades, a lot of papers in the field of evolutionary ecology have stood for a very particular relationship between body mass or length and metabolism, across several orders of magnitude of species size. It is now well-known as an *allometric* relationship, or simply *allometry*, presented in the form $B \propto M^{\alpha}$, where B is the metabolism, M the mass and α the so-called allometric coefficient. Even if these allometries seem to be a key ingredient for modelling the behavior of species, their mass and ecological features, it is still mainly justified by experimental approaches.

We design a simple individual-based model, structured by a trait called *energy*. We study species characterized by a typical energy, consuming a resource maintained at a fixed level. The whole system is ruled by two sorts of mechanisms: random jumps conforming to births and deaths in the population; and a continuous and deterministic evolution of individual energies over time. Importantly, we will allow ourselves to consider the broad range of possible characteristic energy, either really small or high, and thus consider very different species and not one in particular. It means that we design a model focusing on interspecific allometries, rather than intraspecific dynamics with a fixed typical energy.

First, we enforce with basic probabilistic tools sharp values for the allometric coefficients involved in our model, showing that this allometric setting is very restrictive. This idea is also supported by a more complex property of asymptotic pseudotrajectory verified by our underlying stochastic process, leading to precise asymptotic behaviors.

How does residual fertility impact the effectiveness of the sterile insect technique in controlling *ceratitis capitata*?

Marine Courtois[1], Kévan Rastello[1], Frédéric Grognard[2], Ludovic Mailleret[1,2], Suzanne Touzeau[1,2], Louise van Oudenhove[1]

[1] *Université Cote d'Azur, INRAE, ISA, France,* [2] *Université Cote d'Azur, Inria, INRAE, CNRS, Sorbonne Université, BIOCORE, France*
marine.courtois@inrae.fr

Abstract The context of this work is the control of the Mediterranean fruit fly *Ceratitis capitata* in orchards in Corsica (France). It aims at optimizing the deployment of the Sterile Insect Technique (SIT) in an agricultural context. SIT is a biological control technique based on mass rearing, radiation-based sterilization, and releases of sterile males of the pest species targeted for population control. The sterilization process of is subject to a trade-off: radiation doses should be high enough to effectively sterilize the males, but not too high to preserve their ability to attract females and mate. Population control is achieved thanks to the mating of sterile males with wild females, which do not produce offspring. However, among the releases a proportion of the irradiated pupae may lead to non-sterile males.

Our aim in this work was to investigate the impact of the residual fertility of irradiated males on the pest population by a modelling approach. To represent the pest dynamics when sterile males are released, we have built a mathematical model based on differential equations, consisting of three compartments: sterile males, wild males and wild females. With this model, we compared three cases: perfect male sterilisation, contrasted with two situations in which residual fertility is taken into account, associated either with or without a fitness cost. We varied the residual fertility level and the associated fitness cost and studied their influence on the population dynamics by means of analytical studies (equilibria, stability, bifurcations) illustrated with simulations of the model calibrated for *C. capitata*.

We showed that when residual fertility is below a threshold value, wild populations can be driven to extinction by flooding the landscape with sterile males, generalizing the results presented in [1]. As expected, too high a level of residual fertility makes SIT less effective and hinders population control. Finally, the presence of an associated fitness cost, which is very likely, has a significant impact on control efficiency and generates a higher level of acceptable residual fertility.

In practice, with the model calibrated to the biological parameters of *C. capitata* and a 1% residual fertility rate, a realistic value, a minimum of 300 sterile males per day per hectare would theoretically be required to eradicate the pest population.

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THE PROPAGATION OF INVASIVE PLANT SPECIES IN THE LANDSCAPE WITH OR WITHOUT ROADS.

Bradly Deeley, Natalia Petrovskaya

University of Birmingham, UK
`BFD913@student.bham.ac.uk`

Abstract Biological invasion is identified as one of the most serious environmental problems currently facing society. Invasive plant species cause damage to both the ecosystem and the economy [1] at an increasing rate [2]. We have developed a mathematical integro-difference equation based model that incorporates landscape heterogeneity (e.g., a road) in the spatial domain [3]. While our previous work in [3] has been focused on various regimes of propagation of invasive species in the heterogeneous landscape, we now investigate how the propagation speed depends on the presence of a road in a 1-D spatial domain. It will be argued in the talk, both analytically and computationally, that the propagation speed is different when we compare it to the 'no road' case of uniform landscape. We then argue that the propagation speed for short times during the initial stages of invasion are uncertain.

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Fragile backbones of evolved food webs.

Benjamin Girardot

Institut Natura e Teoria en Pyreneus, France
girardotb.contact@gmail.com

Abstract Network motifs have increasingly become a subject of curiosity, originally having been proposed as the signatures of different classes of networks. Food webs don't make exception and appear to be characterized by their own set of network motifs. We study here the fragility of network motifs in food webs built through eco-evolutionary processes. Particularly, we question if/how the fragility of the motifs relates to the fragility of the whole (i.e. the network) or of its parts (i.e. the species). While there is no clear evidence about the former (motif to network), the later seems to provide more interesting discussion (species from motif). More specifically, motif-based indices of species fragility appear to be more reliable predictors than more usual indices of species fragility.

THE EFFECT OF DISPERSAL AND THE ALLEE EFFECT ON THE ASYMPTOTIC TOTAL POPULATION SIZE IN A LOGISTIC CONTINUOUS-TIME TWO-PATCH MODEL.

Carolin Grumbach

Osnabrück University, Germany
`cgrumbach@uni-osnabrueck.de`

Abstract We want to gain an improved understanding of the impact of the Allee effect on population persistence in a fragmented but connected habitat. In the absence of the Allee effect, we found that dispersal can have exactly four qualitatively different effects (referred to as response scenarios) on the asymptotic total population size [1, 2]. Here, I analyse the change of these response scenarios when introducing the predation-driven Allee effect to the logistic two-patch model. A major focus is on the mechanistic biological interpretation of the obtained numerical and mathematical results.

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Species coexistence by competition-dispersal trade-offs in metacommunities with self-organised pattern formation.

Christian Guill

University of Potsdam, Germany
`guill@uni-potsdam.de`

Abstract In the face of accelerated global biodiversity loss, determining mechanisms that allow species to coexist continues to be a central topic in community ecology. In metacommunities, different conceptual frameworks are used to explain coexistence: patch occupancy models that assume identical patches and focus only on colonisation and extinction dynamics have shown that a trade-off between competitive strength and colonisation rate enables coexistence, while models explicitly considering local population densities often evoke environmental heterogeneity in patch quality to enable coexistence via habitat partitioning and source-sink dynamics. Here we study coexistence of two consumer species in a small meta-food web on two patches with identical environmental conditions by accounting for within-patch population dynamics and between-patch dispersal dynamics. Coexistence due to habitat partitioning is not possible because one consumer is the superior competitor for the shared food resource in both patches. However, we show that when static heterogeneous biomass distributions emerge via self-organised pattern formation, coexistence is possible if the superior competitor exports more biomass from the favourable (source) to the unfavourable (sink) habitat than the inferior competitor. When spatio-temporal biomass patterns emerge (here in the form of anti-phase oscillations between the patches), coexistence is possible if a higher dispersal rate enables the inferior competitor to anticipate beneficial changes in resource availability. In both cases, the ability to plastically reduce the emigration rate from a patch with favourable growth conditions further widens the conditions under which the inferior competitor can persist in the system. Additionally, if the competitors differ in their ability to induce pattern formation, a novel coexistence mechanism akin to relative non-linearity emerges, where the temporarily dominant competitor modifies the spatio-temporal variation in the resource biomass in a way that favours the recovery of the currently rare competitor. Self-organised pattern formation thus generically provides mechanisms for supporting diversity in metacommunities without requiring particular environmental conditions.

Spatial spread of infectious diseases with conditional vector preferences.

Frédéric M. Hamelin[1], Frank M. Hilker[2], Yves Dumont[3,4,5]

[1]*Institut Agro, Univ Rennes, INRAE, IGEPP, Rennes, France,* [2], *Institute of Environmental Systems Research and Institute of Mathematics, School of Mathematics/Computer Science, OsnabrÃŒck University, Germany,* [3] *CIRAD, UMR AMAP, F-97410 Saint-Pierre, La Réunion, France,* [4] *AMAP, Univ Montpellier, CIRAD, CNRS, INRAE, IRD, Montpellier, France,* [5] *University of Pretoria, Department of Mathematics and Applied Mathematics, South Africa*
frederic.hamelin@institut-agro.fr

Abstract We explore the spatial spread of vector-borne infections with conditional vector preferences, meaning that vectors do not visit hosts at random. Vectors may be differentially attracted toward infected and uninfected hosts depending on whether they carry the pathogen or not. The model is expressed as a system of partial differential equations with vector diffusion. We first study the diffusion-less model. We show that conditional vector preferences alone (in the absence of any epidemiological feedback on their population dynamics) may result in bistability between the disease-free equilibrium and an endemic equilibrium. A backward bifurcation may allow the disease to persist even though its basic reproductive number is less than one. Bistability can occur only if both infected and uninfected vectors prefer uninfected hosts. Back to the model with diffusion, we show that bistability in the local dynamics may generate travelling waves with either positive or negative spreading speeds, meaning that the disease either invades or retreats into space. In the monostable case, we show that the disease spreading speed depends on the preference of uninfected vectors for infected hosts but not on the preference of infected vectors for uninfected hosts. We discuss the implications of our results for vector-borne plant diseases, which are the main source of evidence for conditional vector preferences so far.

A DISCRETE-TIME HOST–PARASITOID–PREDATOR MODEL WITH MULTIPLE OSCILLATING ATTRACTORS.

Frank M. Hilker, Diomar Cristina Mistro, Luiz Alberto Díaz Rodrigues, and Poliana Kenderli Pacini Selau

Institute of Mathematics and Institute of Environmental Systems Research, Osnabrück University, Germany
`frank.hilker@uni-osnabrueck.de`

Abstract Insects are almost certainly attacked by both specialist and generalist natural enemies [1]. Here, we consider a discrete-time model for the population dynamics of a host/prey species, a specialist parasitoid, and a generalist predator. The generalist predator is assumed to be constant because of alternative food sources such that there are two coupled difference equations. The functional responses for both the parasitoid and the predator are assumed to be of type III.

We analyze the model with regards to how the specialist and generalist act together. Their joint interplay can lead to unexpectedly complex dynamics. Numerical simulations reveal, for instance, the coexistence of invariant loops and at least two cycles with different periods. The basins of attraction reveal some self-similar patterns.

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GLOBAL DYNAMICS FOR A NON AUTONOMOUS MODEL WITH STAGE STRUCTURE AND ADAPTATIVE BEHAVIOR.

Khadidja Aicha Kada

Labo.16: Dynamical Systems and Applications, University of Tlemcen, Algeria
`kadak864@gmail.com`

Abstract Diapause and insecticide resistance, is a pest survival process. To better understand these traits, we discuss a structured model with two life stages, juveniles and reproducing adults. The life cycle of the population is divided in three periods: prediapause, diapause, and post-diapause stage. The overlapping generations is described by delay differential equations. The model is not autonomous. We present a systematic study using monotone systems theory. The dynamics is described in terms of an index R obtained by the spectral radius of the Poincaré operator of the linearized problem around the extinction equilibrium. When $R < 1$, the trivial solution is globally asymptotically stable. When $R > 1$, the positive periodic solution is globally asymptotically stable. Numerical simulations confirm the obtained theoretical results.

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Self-financing model for cabbage crops.

Aurelien, Kambeu[1,3], Suzanne, Touzeau[2,3], Frédéric, Grognard[2], and Berge, Tsanou[1,4]

[1] *University of Dschang, URMA, Cameroon,*
[2] *Université Cote d'Azur, INRIA, INRAE, CNRS, Sorbonne Université, MACBES, France ,*
[3] *Université Cote d'Azur, INRAE, ISA, France,*
[4] *University of Pretoria, South Africa*
aurelienkambeu@gmail.com

Abstract One of the biggest challenges for the farmer is to increase the incomes generated by his farm. This is not always easy because of pests and the scarcity of nutrients in the soil. In this work, we model, analyze and simulate a self-financing nonlinear mathematical model for cabbage crops. The model takes into account the young biomass, the adult biomass, the main cabbage pest (*Plutella Xylostella*) in its most devastating developmental state (larvae), the concentration of biopesticides in the culture, the external efforts and the incomes generated by the crop. We assume that the budget is allocated for purchasing new plants, biopesticides, and increasing the growth rate of crops (external efforts). This budget increases only through the sale of adult biomass. We study several variants of the main model. In these different cases, the condition in which the budget must be spent to keep the system alive is obtained. The model analysis reveals that prophylaxis can eradicate larvae in a cabbage crop. In addition, the impact of the delay in the supply of fertilizers and biopesticides to the culture is studied.

Keywords: pest management, delay model, mathematical analysis, investment.

Replicator equations for structured populations: Hawk-Dove game application.

Amira Kebir

BIMS-IPT, Tunis El Manar University, Tunisia, MTB-BCAM, Bilbao, Spain
`amira.kebir@pasteur.utm.tn`

Abstract The focus of our research is on mixed-symmetry games within structured populations, where an individual's predisposition is influenced by its physiological state or size and its past experiences, including the state and size of opponents. Our goal is to examine a generalized form of replicator dynamics to analyze the behavioral plasticity of a population with n strategies structured by physiological state. We assume that individuals interactions depend on local population conditions and that their strategic profiles result from a game where gains are determined by fitness benefits, plasticity costs, and population structure.

Our model explores the evolutionary dynamics that arise from mixed-symmetry games in structured populations, and how they lead to an ESS where each size class has its own strategy. We investigate how population structure can generate asymmetries in matrix games, with important consequences for social dilemmas like Hawk-Dove or Snowdrift games. Finally, we apply this framework to the Hawk-Dove game, considering symmetric or asymmetric costs associated with playing Hawk, and showing how symmetric competition and assortative interactions increase the probability of promoting state-dependent mixed strategies.

Optimal intervention strategies to control the *Radopholus Similis*: pest of Plantain plant.

Frank Kemayou[2,3], Suzanne Touzeau[1,2],
Frédéric Grognard[1], Samuel Bowong[3]

[1] *Université Cote d'Azur, INRIA, INRAE, CNRS, Sorbonne Université,
MACBES, France ,*
[2] *Université Cote d'Azur, INRAE, ISA, France,*
[3] *Université Cote de Douala, Cameroun*
kemayoufranck00@gmail.com

Abstract Plantain production is one of the most important agricultural activities in many countries around the world. A major constraint to this production is the severe damage caused by a nematode called *Radopholus similis*. This nematode spends most of its life cycle inside the roots of the banana tree, which makes it quite difficult to control and leads to a drop in yield. In this work, a model describing the dynamics of banana-plantain plant-*Radopholus similis* interaction is formulated. The model considered takes into account the penetration of free nematodes into the plant which becomes infecting nematodes and inside it feeds on its roots. We present the theoretical analysis of the model. More specifically, we calculate equilibrium points and study their stability by deriving a threshold that determines the extinction or persistence of nematodes in the plantation. In the second part, the initial model is extended to include a control strategy aiming at reducing the infestation. This control can be modeled by the action of widely used bio-pesticides.

A (very personal) review of non-equilibrium thermodynamics, with theoretical ecology in mind.

Henri Laurie

University of Cape Town, South Africa
`henri.laurie@gmail.com`

Abstract Non-equilibrium thermodynamics is obviously central to ecology, as an ecosystem is maintained far from equilibrium by a flow of energy and matter. However, the details of what this really means are not that clear (to me, anyway), especially as it is not clear to what extent one can consider a system not at steady state. I look at a number of well-known and less well-known items from the literature. It seems that many concepts that are well-defined at equilibrium become vague in non-equilibrium contexts. This applies particularly to entropy, and I consider that literature at greater length. I end with a few remarks on entropy in the context of population dynamics.

Quantifying Cytoskeletal Dynamics and Remodeling from Live-imaging Microscopy Data.

Kairui Li

University of St Andrews, UK
`kl239@st-andrews.ac.uk`

Abstract The shape of biological cells emerges from dynamic remodeling of the cell's internal scaffolding, the cytoskeleton. Hence, correct cytoskeletal regulation is crucial for the control of cell behaviour, such as cell division and migration. A main component of the cytoskeleton is actin. Interlinked actin filaments span the body of the cell and contribute to a cell's stiffness. The molecular motor myosin can induce constriction of the cell by moving actin filaments against each other. Capturing and quantifying these interactions between myosin and actin in living cells is an ongoing challenge. For example, live-imaging microscopy can be used to study the dynamic changes of actin and myosin density in deforming cells. These imaging data can be quantified using Optical Flow algorithms, which locally assign velocities of cytoskeletal movement to the data. Extended Optical Flow algorithms also quantify actin recruitment and degradation. However, these measurements on cytoskeletal dynamics may be influenced by noise in the image acquisition, by ad-hoc parameter choices in the algorithm, and by image pre-processing steps. Existing Optical Flow algorithms do not provide tools to estimate uncertainty on inferred velocity fields or remodeling rates that follow from these dependencies. This hinders our progress on understanding actin and myosin dynamics. To address this, we aim to combine Optical Flow algorithms with Gaussian Process regression. Our new method will not be subject to manual parameter optimisation. It will be able to assign velocity values at higher spatial resolution than previous methods and allow for uncertainty quantification of inferred quantities. We test our methods using data on actin and myosin densities in larval epithelial cells of *Drosophila* pupae. The development of our new method will be a starting point for identifying differences in cytoskeletal movement and remodeling under experimental perturbations. Our method will be applicable to other datasets in which flow fields are present.

The method of lower and upper solutions, applied to a system of Stieltjes differential equations describing the dynamics of an exploited fishery.

Lamiae Maia[1]   Noha El Khattabi[1]   and   Marlène Frigon[2]

[1]*Mohammed V University of Rabat, Morocco,* [2]*Université de Montréal, Canada*
`lamiae.maia@um5r.ac.ma`

Abstract In this work, we consider a fish population subjected to predator species (sharks, dolphins...) and seasonal fishing strategy. This fishing strategy is assumed to be a regulation policy so as to protect the newborns during some hatching periods. Several models were considered to describe such dynamics including the Lotka-Volterra problem, using a classical analysis of dynamical systems. However, since the number of fish individuals presents sudden jumps at each hatching time, and also the fished individuals remain constant during the closed seasons of fishing, we suggest a new approach. In this later, we make use of a system of Stieltjes differential equations in the modeling, and we generalize the existence result established earlier in [3] using the method of the lower and upper solutions, to establish a solution for our model. Moreover, this new framework involves a derivation with respect to an adequate left-continuous nondecreasing function. Therefore, on the one hand, the right-hand side term is more concise. On the other hand, several properties of the derivator are inherited by the solution: the discontinuity jumps and the stationary periods. To make our model more realistic, we include a functional dependence. This takes into account the average of the mature females existing during a certain period before each hatching, which gives an estimation of eggs that will successfully hatch.

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A SEX- AND STAGE-STRUCTURED POPULATION DYNAMICS MODEL FOR PEST CONTROL USING THE STERILE INSECT TECHNIQUE.

Ludovic Mailleret, Crésus Kounoudji, Suzanne Touzeau, Frédéric Grognard, Louise van Oudenhove

Univ. Cote d'Azur, INRAE, ISA, Sophia Antipolis, France
Univ. Cote d'Azur, Inria, INRAE, CNRS, Sorbonne Univ.
BIOCORE, Sophia Antipolis, France
`ludovic.mailleret@inrae.fr`

Abstract The sterile insect technique (SIT) is a biological pest control method based on the introduction of sterilized males in the environment, which compete with wild males for mating with wild females. Since such matings produce no offspring, population growth can be reduced and the population eventually driven to extinction. Initially developed to fight cattle pests, the technique also extends to the control of plant pests. In France, several SIT programs are currently being developed against fruit pest insects such as fruit flies. For these insects, the damaging stage is the larva that hatches and develops inside the fruit. In this context, we developped a sex- and stage-structured model inspired by [1] to assess the impact of SIT on fruit pest dynamics. The model describes the dynamics of 5 compartments: larvae, unmated and mated females, and fertile and sterile males. Depending on the sterile insect release rate, the model admits either 3 or 1 equilibria, with a transition through a fold bifurcation. Stability of equilibria was investigated through cooperative system techniques, especially a result from [2] on Metzler matrices. Biologically meaningful quantities, such as the sterile insect release rate needed for pest eradication, were derived and discussed.

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Regulating food webs by the generalist predator: beyond the classical concept of the functional response.

Andrew Morozov

School of Computing & Mathematical Sciences, University of Leicester, UK
am379@leicester.ac.uk

Abstract In ecological communities, a predator often feeds on a number of food sources. Such predator is known as generalist, and its feeding of is traditionally modelled by a functional response. Here we argue that the conventional classification of predators on specialists and generalists as well as the concept of the functional response can be too simplistic. In particular, this is wrong for species, where individual feeding niches are much narrower than that of the entire predator population. Therefore, the predator population consists of subpopulations of specialists, each of which having its specific diet. Our experiments with the freshwater predaceous snail *Anentome Helena* feeding on non-predatory snails provide an example of a such foraging behaviour. We develop a novel modelling framework to describe a generalist predator consisting of subpopulations of specialised feeders. In the model, in addition to the trophic dynamics, there is switching among specialist subpopulations, governed by variation in profitability of each foraging strategy. We show that structuring within the predator population promotes coexistence of competing prey species, however, the outcome depends on initial configuration of specialist subpopulations within the predator. Moreover, the system shows oscillations of densities of prey for almost a constant level of the predator density.

Modelling plant - nematode interactions to understand plant tolerance.

Joseph Penlap[1,2], Suzanne Touzeau[1,2],
Fréd'eric Grognard[1] and Valentina Baldazzi[1,2]

[1] *Université Cote d'Azur, INRIA, INRAE, CNRS, Sorbonne Université, BIOCORE, France,* [2] *Université Cote d'Azur, INRAE, ISA, France*
joseph.penlap@inria.fr

Abstract Root-knot nematodes (RKN) of the *genus Meloidogyne spp.* cause considerable yield losses in numerous crops worldwide. The dynamics and outcomes of crop–pest interactions depend on the ecological conditions, including the phenotypes of the interacting species, their physiology and the abiotic environment. We are particularly interested in understanding the mechanisms that underlie plant tolerance, that is the ability of plants to sustain RKN infestation with limited yield losses. In theoretical ecology, most mathematical models that describe these interactions either focus on plant physiology and do not consider pest dynamics, or conversely are based on the pest life cycle but neglect plant physiology and defense response.

To address the issue of plant tolerance, we built a mechanistic model of plant–RKN interactions that explicitly links plant physiology and pest demography, including both the effect of pests on crop and crop on pests. The model was calibrated on two plant species, tomato and pepper, and used to study the variability of plant response to pest attacks. We analysed the complex interplay between plant physiological traits and nematode biology that affects the infestation dynamics. Understanding the origin of these phenotypic differences is a key challenge to design, improve and assess pest control strategies, including the selection of new tolerant cultivars.

METACOMMUNITY SIZE AND CONNECTANCE AFFECT LOCAL DIVERSITY ENHANCEMENT FROM SELF-ORGANIZED PATTERN FORMATION.

Louica Philipp

University of Potsdam, Germany
`lophilipp@uni-potsdam.de`

Abstract Habitat destruction and fragmentation are major threats to biodiversity worldwide. In fragmented landscapes, separate populations in local habitats are still connected to each other via dispersal. Understanding how the diversity of these large-scale metacommunities is dependent on the number and connectedness of habitat patches is important for effective landscape management that counteracts further anthropogenic disturbance.

One important driver of biodiversity in metacommunities is spatial heterogeneity of the environment, which can emerge in a self-organized manner as (Turing) pattern formation in the resource concentrations and the biomass densities of the species. Recently it was shown that this mechanism can enhance the local diversity of metacommunities.

Building on this study, I explored how metacommunity size (number of patches) and connectance (number of dispersal links) affects the potential of self-organized pattern formation to enhance functional diversity in a generic food-web model.

I found that local diversity can be enhanced through pattern formation in metacommunities of all tested sizes - small to large - and connectance levels - sparsely to fully connected. Higher connectance levels did however enable stronger enhancement of local diversity, as did a larger size of the metacommunities. Fragmentation processes that reduce the size and connectance of metacommunities might therefore negatively affect local diversity through weakening the effect of self-organized pattern formation.

ANALYSIS OF VIABILITY IN MODELS FOR VECTOR-BORNE DISEASES

Peter Rashkov

Institute of Mathematics and Informatics, Bulgarian Academy of Sciences
`p.rashkov@math.bas.bg`

Abstract In this talk we consider a model for a vector-borne disease with control intervention via use of personal protection (repellents). The model is subject to constraints on the control input variable representing the share of individuals using repellents, and on the phase variable representing the size of the infected human compartment. The task is to describe, in analytical or numerical terms, the viability kernel associated to the constraints, that is, the set of those initial states for which solutions of the model respect these constraints for all future times.

Using results from classical dynamical systems, it is possible to state conditions upon which the viability kernel has either zero or positive Lebesgue measure in the phase space. Furthermore, this set can be approximated numerically following a variational approach, which translates to solving an appropriate equation of Hamilton-Jacobi-Bellman type. Its solution defines the kernel via its sub-zero level set, and can be used to recover the optimal control.

The talk presents the analysis of viability for two models for vector-borne disease with the following compartmental structure: susceptible-infected for the mosquito vector, with a) susceptible-infected-susceptible (a Ross-Macdonald-type model) [2]; and b) susceptible-infected-recovered for the human host [1].

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A HIERARCHICAL MODEL FAMILY FOR CONTROL STRATEGIES OF MOSQUITO SPREAD.

Cordula Reisch

Institute for Partial Differential Equations, Technische Universität Braunschweig, Germany
`c.reisch@tu-bs.de`

Abstract Modeling the spread of mosquitos is relevant for controlling transmitted diseases. The population dynamics of mosquitos in winged and aquatic phase are studied using coupled reaction diffusion equations with nonlinear reaction functions, [1]. The spread of mosquitos can be described as a traveling wave solution of the reaction diffusion equation.

In this presentation, the influence of control strategies on the spread of mosquitos is studied. Mathematically, stopping the spread of the mosquitos is connected to a change of the qualitative long-time behavior of the equation. We compare the influence of different strategies on the solution behavior. Local homogeneous strategies are modeled as a strong Allee effect on the mosquitos in the aquatic phase. On the other hand, spraying pesticides effects the aquatic mosquitos only in certain regions. As a consequence, the system has spatially heterogeneous solutions. We study the hierarchical model family containing the different mechanisms analytically and numerically.

This is joint work with O. Richter and D. Langemann.

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Modelling the impact of no-take zones on yield and the total population size in a two-patch model.

Femke Naemi Reurik

Osnabrück University, Germany
`femke.reurik@uni-osnabrueck.de`

Abstract There is a growing interest in scientific research on protected areas due to the 30% area conservation target at the COP 15 conference [1]. Therefore, we will be discussing a time-discrete two-patch model that incorporates harvesting in one patch and a no-take area in the other. Our goal is to investigate the response scenarios of the asymptotic total population size and yield in relation to varying dispersal intensities, focusing on different harvest strategies (e.g. constant or proportional harvesting). The model will feature homogeneous patches and symmetric dispersal. It is well-known that in two-patch models without harvesting, dispersal can lead to a total population size that is either higher or lower than the sum of the carrying capacities of each patch [2]. We will examine whether these effects can be leveraged or relaxed when harvesting is introduced, and how the catch is impacted by the dispersal intensity.

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A Discrete Model for the Evolution of Infection Prior to Symptom Onset

Jordi Ripoll

Department of Computer Science, Applied Mathematics and Statistics, University of Girona, Campus Montilivi, 17003 Girona, Spain
`jordi.ripoll@udg.edu`

Abstract Ecology and evolution of infectious diseases is a hot topic since at least 20 years already. In recent paper [1] we have studied a between-host model for an epidemic outbreak of an infectious disease. The epidemic model introduced is intended for human or animal populations and for diseases with some sort of infection prior to symptom onset. Examples of diseases with asymptomatic carriers are typhoid, HIV, C. difficile, influenza, cholera, tuberculosis and COVID-19. The system takes the form of a non-linear Markov chain in discrete time where linear transitions are based on geometric (main model) or negative-binomial (enhanced model) probability distributions, and the infection process on a Poisson distribution. The whole system can be reduced to a single non-linear renewal equation with a clear probabilistic interpretation. We focus on two epidemiological indicators, namely, the transmission potential (basic reproduction number) and the severity of the pathogen (virulence). Upon linearization, at least two meaningful definitions of the basic reproduction number R_0 arise: firstly as the expected secondary asymptomatic cases produced by an asymptomatic primary case, and secondly as the expected number of symptomatic individuals that a symptomatic individual will produce. See [2, 3] for a practical approach to R_0 in structured population dynamics. In addition, we study the evolution of infection transmission before and after symptom onset. Provided that individuals can develop symptoms and die from the disease, we take disease-induced mortality as a measure of virulence and it is assumed to be positively correlated with a weighted average transmission rate. According to our findings, transmission rate of the infection is always higher in the symptomatic phase yet under a suitable condition, most of the infections take place prior to symptom onset.

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Biome formation and fragmentation: an analytical approach

Ivan Sudakow

School of Mathematics and Statistics, The Open University, UK
`ivan.sudakow@open.ac.uk`

Abstract In this talk, we present an analytical model describing the nonlinear interaction between the climate system and a biosphere consisting of many ecosystems integrated into biomes where many species compete for a few of the same resources.

First, we extend a conceptual climate model with a biosphere component that arises from coupling between the conceptual zero-dimensional global energy balance model of climate dynamics and a multispecific population system living on multiple food sources [1]. This model now is spatially extended and takes into account species migration. The effects of migration can be described by adding a term to the growth function that is proportional to the time it takes for the species to migrate throughout the entire ecosystem. The main result here is that a complicated spatially heterogeneous biosphere split into a number of small different ecosystems shows high stability with respect to slow climate variations but that the biosphere may be volatile with respect to rapid climate changes.

We also apply this model to describe how environmental temperature warming affects species' habitats and apply analytical results to interpret data on the evolution of the vegetation biomes of Europe from 16 - 4 million years ago (the Neogene period)[2].

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Using hyperparasitization to fight the olive moth in the agroecosystems of Trás-os-Montes region (NE Portugal).

Ezio Venturino

Dipartimento di Matematica "Giuseppe Peano", via Carlo Alberto 10, 10123 Torino, Italy
ezio.venturino@unito.it

Abstract *Olea europaea* L., the common olive tree, is an old and quite widespread crop in the Mediterranean countries, where nowadays Portugal plays a relevant role in oil production. *Prays oleae* (Bernard) (Lepidoptera: Praydidae) represents the most relevant olive pest in the Trás-os-Montes region. It has various phases in its life evolution. In each one of them, this insect damages some part of the tree. Luckily, the larvae of several other insects attack it, together with other generalist and specialist predators. Its most important enemies are *Ageniaspis fuscicollis* (Dalman) (Hymenoptera: Encyrtidae), a specialist parasitoid, and *Elasmus flabellatus* (Fonscolombe) (Hymenoptera: Eulophidae) a facultative hyperparasitoid.

We propose a model for the interactions of these agents, in which we also consider the role of spiders as generalist predators feeding on all these species, [1]. Possible pesticide effects are also included in the model. A complete map of the ecosystem equilibria and their relations through transcritical bifurcations is obtained. A sensitivity analysis accounting for possible climatic variations is performed. It is found that the highest level of natural control is exercised by *A. fuscicollis* but *E. flabellatus* or spiders may also be useful in specific situations.

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Integrating demography into speciation models to understand the microevolutionary processes that control rates of speciation at the macroevolutionary scale.

Pierre Veron[1,2], Hélène Morlon[1], Tatiana Giraud[2]

[1]*Institut de Biologie de l'École Normale Supérieure (IBENS), École Normale Supérieure, CNRS, INSERM, Université PSL, 46 rue d'Ulm, 75005 Paris, France,* [2]*Ecologie Systématique Evolution, IDEEV, CNRS, Université Paris-Saclay, AgroParisTech, 12 route RD128, 91190 Gif−sur−Yvette, France*
pveron@bio.ens.psl.eu

Abstract Speciation rates estimated by fitting stochastic birth-death models to phylogenies of extant species reveal high variability of speciation rates across lineages [5, 3]. Given the admitted process by which speciation occurs in sexually reproducting species (reproductive isolation leading to genetic incompatibilities between populations) one would expect that population characteristics influence speciation rates. However most theoretical predictions of such links are verbal, and empirical evidence is scarce and contradictory [2, 6]. To fill this gap, we develop a realistic model of diversification that accounts for the influence of demographic variations and the fate of mutations on different aspects of the diversification process (formation of populations, incompatibilities between them, extinction). We combine the protracted model of speciation [1] with predictions from logistic individual birth-death processes [4] and population genetics and obtain preliminary predictions on the effect of demographic parameters on macroevolutionary speciation rates.

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Impact of different destocking strategies on the resilience of dry rangelands.

Toyo Vignal

University of Edinburgh, Heriot-Watt University, UK
`tvv2@hw.ac.uk`

Abstract Half of the world's livestock live in (semi-)arid regions, where a large proportion of people rely on animal husbandry for their survival. However, overgrazing can lead to land degradation and subsequent socio-economic crises. Sustainable management of dry rangeland requires suitable stocking strategies. Our goal is to understand how variations in stocking strategies affect the resilience of dry rangelands. We describe rangeland dynamics through a simple mathematical model consisting of a system of coupled differential equations. In our model, livestock density is limited only by forage availability, which is itself limited by water availability. We model processes typical of dryland vegetation as a strong Allee effect, leading to bistability between a vegetated and a degraded state, even in the absence of herbivores. We study analytically the impact of varying the stocking density and the destocking adaptivity on the resilience of the system to the effects of drought. Using dynamical systems theory, we look at how different measures of resilience are affected by variations in destocking strategies. We find that:

1) Increasing stocking density decreases resilience, giving rise to an expected trade-off between productivity and resilience.

2) There exists a maximal sustainable livestock density above which the system can only be degraded. This carrying capacity is common to all strategies.

3) Higher adaptivity of the destocking rate to available forage makes the system more resilient: the more adaptive a system is, the bigger the losses of vegetation it can recover from, without affecting the long term level of productivity.

The first two results emphasize the need for suitable dry rangeland management strategies, in order to prevent degradation resulting from the conflict between profitability and sustainability. The third point offers a theoretical suggestion for such a strategy.