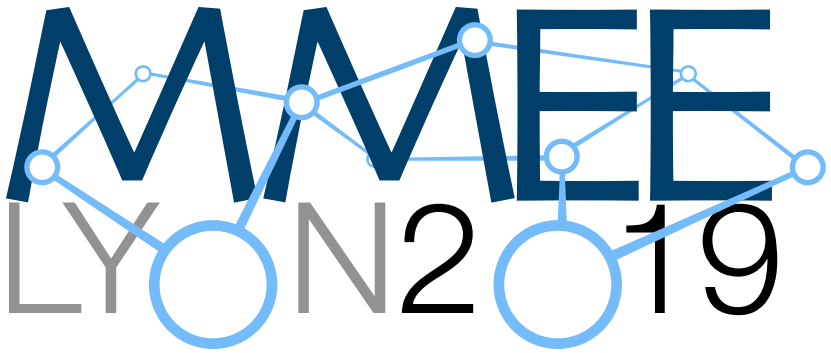

List of abstracts

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Public lecture: Cancer and aging: How our bodies are designed to be reliable and why they fail

Steven Frank [a] [1]

[1] University of California - Irvine – United States

[a] Speaker

Why does cancer occur more often as people grow older? The history of cells in the body provides the answer. Life starts with one cell, when egg and sperm unite. That first cell divides again and again until, as adults, we have about 50 trillion cells. In each year of adult life, many cells die and are replaced. With time, genetic errors accumulate as new cells are made. This ticking clock of errors breaks down the reliability systems built into the cells and tissues. When scientists view the breakdown of reliability in the context of cellular history, they can analyze many puzzles about the age of cancer onset, including: Why do certain cancers happen mostly in children? Why do inherited mutations shift cancer onset to earlier ages? Why does quitting smoking change the subsequent chance of getting cancer?

Keywords: Somatic mutation, carcinogenesis, epidemiology, disease

Keynote 1 – The discrete genetic underpinning of eco-evolutionary dynamics

Joanna Masel [a] [1]

[1] University of Arizona, United States

[a] Speaker

Unravelling the dynamical interplay between ecology and evolution remains one of the great challenges in mathematical biology. Adaptive dynamic models of trait evolution have made important advances in this area, yielding valuable insights into long-term evolutionary outcomes and trait diversification. However, trait-level models tell us little about evolutionary processes at the genetic level. Important eco-evolutionary issues such as how demography and life-history structure might shape patterns of genetic variation remain mysterious. To address such issues, we need to connect population genetics to ecology. But this presents significant modeling challenges: population ecology hinges on abundances, whereas population genetics has historically focused only on relative frequencies — a major simplification. To elucidate some of the issues involved, we present a novel variable-density generalization of the Wright-Fisher model and compare its properties to more familiar treatments of density-dependent selection. We find that traditional population genetic approximations break down when populations are not at demographic equilibrium, and when there is pleiotropy between traits affecting different stages of the life cycle. With this conceptual foundation in place, we turn to a more applied question: the maintenance of genetic variation when both the direction of selection and population density cycle seasonally. We distinguish between two ecological causes of maintenance (protection from selection, frequency-dependence of number of generations needed to rise to carrying capacity) and two genetic causes (cumulative overdominance and reversal of dominance). Only reversal of dominance can stabilize alleles of small effect, but this can preclude reversal of dominance from stabilizing alleles of large effect, which are thus more likely to be stabilized by the other three mechanisms.

Keynote 2 –Evolution of quantitative traits in finite populations

Florence Débarre [a] [1]

[1] Institut d'écologie et des sciences de l'environnement de Paris (iEES Paris) – CNRS UMR 7618 – Sorbonne Université, Paris, France

[a] Speaker

Evolutionary models often consider populations of infinite size – an assumption that is mathematically convenient, but may not always be valid. In this talk, I will present models of phenotypic evolution in finite populations. I will consider different time scales: a short time scale, corresponding to changes occurring over one time step (or generation); an intermediate time step, for which the evolutionary fate of a limited number of variants is considered; and finally a long time scale, where new types can occur by mutation. I will highlight differences between infinite and finite populations, in particular with respect to diversification.

Keynote 3 – Measurement theory and mathematical modeling

Thomas Hansen [a] [1]

[1] University of Oslo – Norway

[a] Speaker

Measurement theory is a branch of philosophy and mathematics that studies how number systems are used to represent empirical objects and their relations. Simply put, measurement theory is the theory of quantification. Some fields, like physics, psychology and economics, have theories of measurement as part of their foundation. Biology, however, lacks a theory of measurement, and biologists generally pay little attention to problems of numerical representation. The result is rampant pseudoquantification, where indices, statistics and models are presented based on intuition without any formal attempt at showing that they represent phenomena of interest. In this talk I will argue that many disciplines of biology could benefit from a theory of measurement and an awareness of measurement issues. In particular, I will take a critical look at mathematical modeling from the perspective of measurement theory.

Keywords: Measurement theory, Statistics, Quantitative genetics, Mathematical modeling

Keynote 4 – Narrow paths to innovation in evolutionary models of stabilizing selection and phenotypic noise

Jeremy Draghi [a] [1]

[1] Brooklyn College, The City University of New York, New York, USA

[a] Speaker

Random processes affect every level of biology. In evolution, stochasticity in reproductive success is called genetic drift and can be an impediment to adaptation or, in cases like Wright's shifting balance model, a vital part of the process by which evolution finds innovative solutions. But randomness also contributes to what an individual looks like, adding uncertainty to how a genotype translates to a phenotype that we can call phenotypic noise. Here I present several models integrating phenotypic noise into models of how populations adapt to produce the right trait value in a given environment. Across several models we find that evolution can sometimes walk a narrow path to higher fitness despite constraints and without a major role for genetic drift. Phenotypic noise contributes in each model as a driver or mediator of change. With cellular-scale phenotypic measurements revealing a new world of microscopic phenotypic noise in biology, these results argue for a new appreciation for the many roles of randomness in evolutionary biology.

Keynote 5 – Coevolutionary dynamics in the immune system

Armita Nourmohammad [a] [1,2]

[1] Max Planck institute of Göttingen, Germany
[2] University of Washington at Seattle, USA

[a] Speaker

Chronic pathogens, such as HIV, are able to persist in a host for extended periods of time. Upon infection, the host immune system and virus engage in an coevolutionary arms race: The immune B-cell receptors diversify to neutralize the virus and HIV evolves to evade the immune response. While it is clear that HIV exerts strong selection on the adaptive immune system, the modes of immune response are still unknown. Here I introduce a non-equilibrium framework to characterize the rapid co-evolution of immune cells and pathogens. By tracing the immune repertoire of HIV patients over time and reconstructing the history of the accumulated mutations within patient, I show evidence for strong co-adaptation of the immune repertoire and HIV. I argue that rapid affinity maturation of the immune system upon viral expansion and a quasi-stationary response during chronic infection characterize the B-cell response to HIV.

Keynote 6 – Sex chromosome degeneration without selective interference

Thomas Lenormand [a] [1]

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[a] Speaker

In many species, the Y (or W) sex chromosome is degenerated. Current theory explains that this degeneration follows the arrest of recombination and results from "selective interference". Selective interference refers to the fact that selection is inefficient in absence of recombination, which results in the accumulation of deleterious mutations on the non-recombining Y (or W). This theory is appealing because it requires very few assumptions (finite population sizes, occurrence of deleterious mutations). Yet, it works best in relatively small populations, and may not easily predict fast erosion of Y (or W) in large populations. In this talk, I will present another mechanism for Y/W erosion that can potentially work fast and in large populations. It is based on the instability and divergence of cis-regulatory sequences in non-recombining regions of the genome and fast coevolution of *cis*- and *trans*-regulators that favors ever-stronger *cis*-regulators on the X (or Z). This process leads simultaneously to rapid Y/W degeneration and dosage compensation in males and females. **Keywords:** Somatic mutation, carcinogenesis, epidemiology, disease

Mini-symposium 1: Discrete and continuous models in evolution

Max Souza [1], Fabio Chalub [2]

[1] Instituto de Matemática e Estatística, Universidade Federal Fluminnse – Brazil
[2] Faculdade de Ciências e Tecnologia, Universidade Nova de Lisboa – Portugal

The different and distinctive features of discrete and continuous evolution models are well known in Evolutionary Dynamics, but this gap has been widening up when considering diverse extensions of the basic and classical models, such as populations that are structured or with stochastic demography. In addition, attempts to obtain equivalent modelling formulations in these two classes has also been proving to be a challenge.

These different topics have been the subject of much intense and recent research, which suggest that large populations might behave very similar to an infinite population in many ways, and still exhibit distinguished features. The aim of this mini-symposium is to bring together researchers that are interested in the fine interplay between these two classes of models under many different modelling assumptions and formulations.

Research topics of interest to this mini-symposium include, inter alia, the behaviour of long term dynamics and fixation probability in these two classes of models; the impact of modelling refinements as demographic heterogeneities (or stochasticity) and age (or stage) structure in these patterns; equivalent modelling formulation across these two classes.

M1.1 – The Variational Formulation of Discrete and Continuous Evolutionary Processes

Fabio Chalub [a]

[1] Centro de Matemática e Aplicações, Faculdade de Ciências e Tecnologia, Universidade Nova de Lisboa – Portugal

The Moran process, the Kimura equation and the replicator dynamics are all processes frequently used to mathematically describe biological evolution.
In this talk, we will show how to reformulate all these models using gradient flow formalism and show that these reformulations are mutually compatible.

Keywords: Moran process, Kimura equation, replicator dynamics

[a] Speaker

M1.2 – Demographic fluctuations and fixation probabilities: disentangling ecological and evolutionary effects

Peter Czuppon [a] [1]

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In evolutionary game theory, models of fixation have typically focused on fixed population sizes and frequency-dependent selection. In population genetics, fixation of traits under frequency-independent selection and in populations with deterministically changing size has been analyzed. We consider a combination of the two ideas, i.e. a model with frequency-dependent selection under stochastic demographic fluctuations. Assuming weak selection the analytical separation of the demographic and evolutionary processes is possible and allows us to approximate the fixation probability of a trait. Interestingly, the fixation behavior resembles the deterministic evolutionary dynamics qualitatively. This is in contrast to findings in the fixed population size scenario, among others the famous 1/3-rule. Furthermore, we are able to extend this two-individual competition to higher order interactions corresponding to a multi-player evolutionary game. We find that as the number of interacting individuals increases the demographic and evolutionary processes become more and more convoluted.

Keywords: demographic stochasticity, fixation probability, diffusion approximation, evolutionary game theory

[a] Speaker

M1.3 – Evolutionary games between newly arising mutants

Arne Traulsen [ab 1]

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Spontaneous random mutations are an important source of variation in evolution. Many evolutionary models consider mutants with a fixed fitness, chosen from a fitness distribution without considering interactions that would drive frequency or density dependence. New interactions between the residents and invading mutants can lead to coexistences or take-over and they can also affect the population size and the extinction risk of populations. Continuous models in this sense are e.g. part of the adaptive dynamics framework, but this framework usually assumes that the types of possible mutants are known from the start. Alternatively, microscopic interactions between individuals can also be modeled by using a dynamic interaction matrix, the dimension of which increases with the emergence of a new mutant and decreases with extinction. Thus, the population size is an evolving property rather than an externally controlled variable. Methods from statistical physics can be applied to calculate the average population size over time and to quantify the extinction risk of the population by the mean time to extinction.

Keywords: evolutionary games, population dynamics, frequency, dependent selection

M1.4 – Diffusion approximation for an age-structured population under viability and fertility selection with application to fixation probability of an advantageous mutant

Cíntia Dalila Soares [ab 1], Sabin Lessard [1]

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In this paper, we ascertain the validity of a diffusion approximation for the frequencies of different types under recurrent mutation and frequency-dependent viability and fertility selection in a haploid population with a fixed age structure in the limit of a large population size. The approximation is used to study, and explain in terms of selection coefficients, reproductive values and population-age-structure coefficients, the differences in the effects of viability versus fertility selection on the fixation probability of an advantageous mutant.

Keywords: Age, structured population. Leslie matrix. Frequency, dependent selection. Diffusion approximation. Fixation probability. Two timescales. Reproductive value. Population, age, structure coefficient.

M1.5 – Analysis of diversity-dependent species evolution using concepts in population genetics

Ingemar Kaj [1], Sylvain Glémin [1], Daniah Tahir [a 1], Martin Lascoux [1]

[1] Uppsala Universitet [Uppsala] – Sweden

[a] Speaker

Models of species richness based on birth-death mechanisms, with constant speciation and extinction rates, suffer from the classical dichotomy of supercritical branching processes, which must either go extinct or grow in size without bound. In reality, however, species numbers tend to vary over long periods of time in a mode of stationarity within a finite range of population sizes. It is, thus, rather natural to implement diversity-dependent regulation in a modeling set-up.
In this work, we present a mathematical framework to address diversity-dependent dynamics for a family of species with a binary trait, for which the rates of creation and extinction of species, and for transition of the trait between species, are trait-dependent. To achieve that, first we investigate the mechanisms in species tree models which are analogous to those of population genetics models - such as mutation, selection, and genetic drift - and later, we apply population genetics concepts and probabilistic methods to explore density-dependent processes. The central technique in our approach is diffusion approximation of a species tree Markov chain, which runs on a suitable time scale of evolutionary time units.
At the core of this study is the interpretation that the fraction of species in the family, which carries one of the traits, evolves in a manner directly comparable with the evolution of allele frequencies in the population genetics framework. The transition of a species of one trait to a species of the other trait resembles mutational change from one allelic type to another. Similarly, various forms of population size dependence may be cast as frequency dependent selection mechanisms. Furthermore, trait-dependent species extinction rates yield frequency dependent genetic drift coefficient. For the analysis of the species dynamics, our main guideline is the systematic use of modeling tools, scaling approaches, and concepts in mathematical population genetics.

Keywords: diversity dependence, binary traits, species evolution, population genetics, mathematical modeling

Mini-symposium 2: Theory in cultural evolution

Anne Kandler [a] [1], Laurel Fogarty [b] [1], Adam Powell [2], Justin Yeh [1]

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Humans are a fundamentally cultural species. We obtain a multitude of knowledge, skills, beliefs or norms from other members of our species culturally, through a large variety of social learning processes. However, the precise dynamics underlying the processes that build such hugely complex cultures are still little understood. Recent advances in the acquisition of (longitudinal) cultural data and the theory of cultural evolution have improved this understanding but empirical and theoretical research frameworks have often been developed in isolation from each other. Therefore, there is an increasing need for theoretical frameworks that may help interpreting cultural data. If culture is defined as "information that can affect an individual's behavior, acquired from other members of ones species through teaching, imitation, or other forms of social learning," cultural evolution is fundamentally the change of culture over time. A core tenet of cultural evolution is that cultural change constitutes an evolutionary process that shares similarities with, but also differs in important ways from, genetic evolution. The formal study of cultural evolution has adapted a number of mathematical models (that originated in e.g. population genetics) to account for processes and dynamics unique to cultural change. In this session we will showcase theoretical cultural evolutionary research with a particular focus on analytical and computational approaches aimed at modelling the evolution of cultural diversity and complexity. We demonstrate how theoretical models of cultural evolution can be linked with anthropological or archaeological data and therefore can help with their interpretation. Importantly, this line of research seeks to understand the "amount of information" about underlying evolutionary processes that can realistically be inferred from sparse, imperfect cultural data. We aim to stimulate discussions about similarities and dissimilarities of cultural and biological evolutionary questions and how and what kind of established biological concepts could be meaningfully applied to cultural evolution.

M2.1 – Packaged transmission of cultural traits generates false signal for selection

Justin Yeh [ab 1], Laurel Fogarty [1], Anne Kandler [1]

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[a] Speaker
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Many cultural traits are not transmitted independently, but together as a package. This can occur through institutions, media that store information, and cognitive mechanisms such as overimitation. Evolutionary biology suggests that physical linkage of genes (being on the same chromosome) allows neutral and maladaptive genes to spread by hitchhiking on adaptive genes. For this reason, it may be difficult to infer whether a gene is adaptive from population survey. Whether the same dynamics occur in cultural evolution is unclear. People do not learn two equal halves of all traits from their two parents at birth, but some traits from each of several people at various time. Furthermore, learned behaviours are not arranged side-by-side on a chromosome. Instead, any two traits can potentially be linked, forming a network of traits. We build an agent-based simulation that allows formation and breakage of such links to explore their effects. The simulation includes 5 traits (loci), each with 4 variants (alleles). Some traits are under selection while others neutral. During transmission, one randomly selected trait, along with all other traits that are directly or indirectly connected to it, are learned together in a package. We compare the evolution of neutral traits and adaptive traits in a system that has links to those in a system that does not allow any links. We find that neutral traits can indeed hitchhike on traits under selection when there are links. Furthermore, even when no trait is under selection, the presence of links alone can lower the diversity of neutral traits as if they are under selection.

Keywords: cultural transmission, selection, linkage

M2.2 – The mechanics and signatures of cultural adaptation

Laurel Fogarty [a 1], Anne Kandler [1]

[1] Max Planck Institute for Evolutionary Anthropology – Germany

[a] Speaker

Literature in cultural evolution often suggests, or explicitly states, that humans have colonised much of the planet because of our unique ability to amass complex culture and to adapt culturally to new environments. However, we understand little about what this process of cultural adaptation might look like. Here we present a mathematical model of cultural selective sweeps that investigates the different roles of existing cultural variation, learning, and innovation in cultural adaptive processes. We examine the probability of adaptation under different circumstances and discuss circumstances under which cultural adaptation might fail. Finally, we discuss ways in which we can use such models to identify cultural selective sweeps in cultural data, exploring the kind of data and analysis needed to infer selection and cultural adaptation.

Keywords: Cultural evolution, cultural adaptation, selective sweeps

M2.3 – Evolving institutions for collective action by selective imitation and self-interested design

Sergey Gavrilets [a] [1,2]

[1] University of Tennessee – United States
[2] Center for the Dynamics of Social Complexity – United States

[a] Speaker

Human behavior and collective actions are strongly affected by social institutions. A question of great theoretical and practical importance is how successful social institutions get established and spread across groups and societies. Here, using institutionalized punishment in small-scale societies as an example, we contrast two prominent mechanisms - selective imitation and self-interested design - with respect to their ability to converge to cooperative social institutions. While selective imitation has received a great deal of attention in studies of social and cultural evolution, the theoretical toolbox for studying self-interested design is limited. Recently we expanded this toolbox by introducing a novel approach, which we called foresight, generalizing standard myopic best response for the case of individuals with a bounded ability to anticipate actions of their group-mates and care about future payoffs. Here we apply this approach to two general types of collective action – "us vs. nature" and "us vs. them" games. Our results show that foresight increases leaders' willingness to punish free-riders. This, in turn, leads to increased production and the emergence of an effective institution for collective action. We also observed that largely similar outcomes can be achieved by selective imitation, as argued earlier. Foresight and selective imitation can interact synergistically leading to a faster convergence to an equilibrium. Our approach is applicable to many other types of social institutions and collective action.

Keywords: cooperation, punishment, leadership, strategy revision, theory of mind, small, scale society

M2.4 – Gene-culture coevolution and cumulative culture in the family

Charles Mullon [a] [1], Laurent Lehmann

[1] University of Lausanne – Switzerland

[a] Speaker

Human evolution depends on the coevolution between genetically-determined behaviours and socially transmitted cultural information. Although vertical transmission of cultural information from parent to offspring is extremely common in hominins, its effects on cultural evolution are not well understood. In this talk, I will report our investigations on gene-culture coevolution in family-structured populations. We derived the invasion fitness of a mutant allele that influences a cultural variable (e.g., amount of knowledge or skill) to which carriers of the mutant are preferentially exposed in subsequent generations due to vertical transmission of culture. We find that this creates preferential associations between genes and culture over multiple generations, allowing kin selection to shape cultural evolution. We then used the invasion fitness we derived to study how genetically-determined learning strategies coevolve with the level of cultural adaptive information they generate. We find that due to kin selection effects, vertical transmission of information favours the evolution of costly learning strategies that lead to greater levels of adaptive information than under pure oblique transmission. Further, vertical transmission prevents the emergence and persistence of cultural cheaters that learn costly information from others. Overall, our analyses suggest that vertical transmission of culture can significantly increase levels of adaptive cultural information, especially under the biologically plausible condition that information transmission between relatives is more efficient than between unrelated individuals.

Keywords: Gene, culture coevolution, Eco, evolutionary dynamics, Social polymorphism, Kin selection

M2.5 – Minimal requirements for the emergence of structured variation

James Winters [a 1], Thomas Mueller [1], Adam Powell [1]

[1] Max Planck Institute for the Science of Human History – Germany

[a] Speaker

Cultural evolutionary models seek to explain both the distribution of cultural variation and how it is organised in space and time. One prominent puzzle concerns the observation that opinion dynamics, fashions and many other cultural domains are structured in a way that maintains diversity globally and forms predictable patterns locally. Many plausible mechanisms have been proposed to explain these patterns of structured variation: From an individual-level conformity bias to the underlying network-topology of a population. Each of these proposed mechanisms have their respective merits and are not necessarily mutually-exclusive. However, given the plurality of explanations, we still know very little about what these different mechanisms share in common and whether generalisable principles can be derived. This talk first approaches the problem of structured variation from an information-theoretic perspective: here, any mechanism that changes the distribution and organisation of variation can be modelled as a function that changes the Shannon entropy over a set of observations. We then use a novel Agent-Based Model, where agents observe and produce cultural variants on a pixel grid, to simulate cultural evolutionary dynamics and investigate under what situations structured variation does and does not emerge. In particular, we manipulate the strength and directionality of amplification by equipping agents with a bias to either increase or decrease the entropy over an observed collection of cultural variants. We show that mechanisms for increasing or decreasing entropy bring about structured variation so long as the dynamics fulfil two minimal requirements: the first is the presence of a regularisation process and the second is a mechanism for mitigating information loss. Whilst our findings corroborate previous insights, they also act as a cautionary tale against simple causal stories. Demonstrating that a specific mechanism can explain a population-level pattern is revealing only to the extent of illuminating one possible causal pathway.

Keywords: cultural evolution, information theory, structured diversity, agent, based modelling

M2.6 – Generative inference for cultural evolution

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[2] Max Planck Institute for Evolutionary Anthropology – Germany

[a] Speaker

Recent methodological advances combined with the increasing geographic and temporal resolution of genetic data have allowed remarkable progress in our understanding of human demographic history. In particular, generative inference frameworks have been developed – often using coalescent-based simulation – to explore the explicit demographic and/or natural selection mechanisms that underlie the observed allele frequency distributions across the globe, and their change through time. This approach, coupled with powerful statistical techniques such as approximate Bayesian computation (ABC), has allowed robust inferences to be drawn on the human past with no a priori assumption of equilibrium. In this talk we review the relevant population genetics literature and demonstrate the applicability and utility of such generative inference approaches to the field of cultural evolution. One of the major challenges in cultural evolution is to understand why and how various forms of social learning are used in human populations, both now and in the past. To date much of the theoretical work on social learning has been done in isolation of data and consequently many insights focus on revealing the learning processes or the distributions of cultural variants expected to have evolved in populations at equilibrium. The generative inference framework advocated here allows us to model non-equilibrium processes, and uses observed population-level data directly to establish the likely presence or absence of particular hypothesized learning strategies. Population-level data describing the usage or occurrence frequencies of different variants of a cultural trait are available in many scientific fields, and in some cases are the only direct empirical evidence about past cultural traditions. Further, especially in historic case-studies the spatial and/or temporal resolution of this kind of data is usually sparse. We show how this data can be used to explore which social learning processes could have been present in past human populations.

Keywords: –

Mini-symposium 3: Effects of within-host interactions and diversity on host-pathogen dynamics

Samuel Alizon [1]

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One of the consequences of next-generation sequencing is the realisation that most infections are caused by multiple strains of the same species and sometimes even of different species. This has direct consequences for an infected host since parasites can interact in many ways, e.g. competing for host resources, producing public goods or eliciting and facing the host immune response. Furthermore, the role of the host microbiota in the course and outcome of the infection is increasingly recognised. At the epidemiological level, these within-host interactions are known to dramatically affect epidemic spread and the evolution of infection traits such as virulence or antimicrobioa resistance. Modelling these processes is a challenge in itself, especially because of combinatorial complexity. In general, models and theories from community ecology can be of a great help to introduce microbial diversity in dynamical systems. On the other hand, data from experimental evolution and clinical settings offer unique opportunities to test long-standing hypotheses regarding evolution accross multiple levels of adaptation.

M3.1 – Nested dynamics and parasite evolution

Mircea T. Sofonea [ab 1], Samuel Alizon [1], Yannis Michalakis [1]

[1] MIVEGEC – Université de Montpellier, Centre National de la Recherche Scientifique, Institut de Recherche pour le Développement – France

In nature, species face a diversity of parasite types. While some evolutionary epidemiology models already incorporate parasite polymorphism, few make the connection between epidemiology and within-host parasite growth. As parasite polymorphism can even occur within the same host, distinct parasite types can interact in various ways and thus interfere with their transmission and therefore their evolution. The combinatorial and dynamical complexity explains why we still lack general predictions regarding parasite evolution in such multiple infection contexts. Seeking for a general trend in virulence evolution, we model each dynamical level on which parasite evolution relies by nonlinear coupled ODEs and random mutations. We notably use fixed point stability analysis to draw a typology of infection patterns that allows us to address virulence evolution under a general framework. As a result, we observe an unavoidable selection bias towards higher virulence when phenotypic mutations are small, wich is confirmed by further stochastic simulations.

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Keywords: evolutionary epidemiology, adaptive dynamics, multiple infections, virulence.

M3.2 – Emergence of drug resistance in HIV: the role of latently infected cells

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[2] University of Oxford – United Kingdom

HIV replicates by integrating into the host cell DNA and using the host machinery to generate multiple copies of itself. However, the virus sometimes remains hidden in the cell DNA and only starts replicating at a later stage, triggered by a mechanisms that is as yet poorly understood: in jargon, we say the virus has entered the *reservoir* of latently infected cells. The hidden virus is invisible to drugs: therefore, in addition to being the main reason why HIV cannot currently be cured, it also escapes the evolutionary pressure imposed by drugs on the 'active' virus. However, the potentially important role of the reservoir on HIV evolutionary epidemiology is often neglected. We consider a model of HIV within- and between-host dynamics involving two drugs, imperfect adherence to treatment, evolution of resistance to either or both drugs, and both a reservoir and an active compartment within the host. We then investigate how the amount of virus transmitted from the reservoir affects the emergence of resistance at the population level. The model consists of a large set of ODEs, but we show how a simplified version of the model and the analysis of the next-generation matrix inspired by a time-since-infection perspective can help shed light on the complexity of the model's behaviour.

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Keywords: HIV, treatment, resistance, reservoir, next generation matrix

M3.3 – Cross-scale modeling of resistance spread in the presence of antibody-mediated bacterial clustering

Florence Bansept [a] [1,2], Loïc Marrec [2], Emma Wetter-Slack [3], Anne-Florence Bitbol [2], Claude Loverdo [2]

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[2] Laboratoire Jean Perrin (UMR 8237), Paris, France – Sorbonne Université UPMC Paris VI, Centre National de la Recherche Scientifique - CNRS – France
[3] Institute of Microbiology, ETH Zürich, Switzerland – Switzerland

[a] Speaker

The body harbors an important and diverse microbiota, most of which is located in the gut. In the gut, the main effector of the adaptive immune response is Immunoglobulin A (IgA), a specific antibody that enchains bacteria upon division. This enchainment results in the formation of clonal clusters of bacteria, prevented from approaching the epithelium and colonizing the rest of the organism. Within host, the interplay between these clusters growth and fragmentation results in the preferential trapping of faster-growing bacteria, the most susceptible to disrupt the gut flora equilibrium. Thus, producing IgA against any bacteria it encounters would be sufficient for the immune system to fight against potentially pathogenic bacteria while preserving the rest of the flora. At the scale of the host population, this mechanism can also impact an epidemic spread if bacteria are transmitted in clonal clusters, for example via the fecal-oral route. We develop a multi-scale model showing that immunity-driven clustering can hinder the evolution and spread of an antibiotic-resistant bacterial strain, and quantify this effect both in the case of pre-existing resistance and in the case where acquiring a new resistance mutation is necessary for the strain to spread in the population. We further show that this effect can be reversed and spread increased when immune hosts are silent carriers, and thus are potentially less treated and/or have more contacts in the population. We check for the robustness of our findings to adding mutations, a fitness cost of resistance and its compensation, and stochastic within-host bacterial growth to the model. Our results highlight the importance of including essential aspects of host immunity to the study of the spread of antibiotic resistance, and argue in favor of vaccine-based strategies to fight it.

Keywords: cross scale modeling, immune response, antibiotic resistance, epidemic spread

M3.4 – Coexistence through co-colonization: how the structure of multi-strain interactions leads to fast and slow epidemiological dynamics in diverse microbial systems

Erida Gjini [a] [1], Sten Madec [2]

[1] Instituto Gulbenkian de Ciência [Oeiras] – Portugal
[2] Université de Tours – Laboratoire de Mathématiques et Physique Théorique – France

[a] Speaker

Understanding the dynamics of polymorphic pathogens remains a challenge, despite advancing molecular technologies for diversity resolution within and between hosts. Analytical approaches are rare, making computationally-intensive simulations the typical way to study the behavior of such systems and their response to perturbations (drugs, vaccines). In this work, we develop an analytical approach to simplify epidemiological dynamics of a multi-strain system with interactions in co-colonization, an example being *Streptococcus pneumoniae* bacteria. Using aggregation methods and the slow-fast dynamics approach, we decompose strain dynamics into fast and slow components. We show that the fast dynamics corresponds to a manifold of neutrally stable equilibria, while the slow stabilizing dynamics result from deviation from symmetry in the co-colonization interaction matrix. Besides computational advantages, this timescale decomposition provides biological insights for multi-strain coexistence and highlights the balance of within- vs. between-strain interactions in frequency-dependent epidemiological competition. More generally, the slow-fast dynamics approach interpolates between a neutral and non-neutral model for diversity and highlights the role of co-colonization processes in the maintenance and stabilization of diversity in bacteria.

Keywords: competition, cooperation, coinfecton, diversity, singular perturbation theory, asymmetry, SIS model

M3.5 – Multiple infection patterns as indicators of contact network properties and cross-immunity

Christian Selinger [ab] [1], Samuel Alizon [a] [1]

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The way hosts interact within a population shapes the spread of infectious diseases. However, such contact patterns are difficult to access. Our idea is to use multiple infections from longitudinal follow-ups to infer these patterns.
The first obstacle was to simulate multiple infections on a contact network in an unbiased way. We address this problem by extending the well-known Gillespie algorithm and implement it for a community of parasites spreading on a network. The second obstacle was to analyse individual infection episodes, which we address by introducing the concept of infection barcodes to represent the infection history in each host. We show that, depending on infection multiplicity and immunity assumptions, it is possible to recover host network properties from barcodes.
In combining our simulation algorithm and barcode analysis of infection histories, we argue that analysing the diversity of parasites in infected hosts can provide insights into global properties of host interaction networks. Finally, we also present results on the converse question, i.e. to which extent it is possible to infer cross-immunity between strains from multiple infection histories on a given host network.

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Keywords: Multiple infections, stochastic approximation algorithms, networks, cross, immunity

M3.6 – High frequencies of environmental disturbance can promote antibiotic resistance in mixed-species communities

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Environmental disturbances are widespread in nature and have a profound effect on the evolution of antimicrobial resistance. Current theory predicts that a lower rate of disturbance will promote resistance: this is supported by single-species empirical studies considering an increase in antibiotic concentration or a switch between different antibiotics as sources of environmental disturbance. However in nature, microbes are rarely found in isolation, rather they exist in multi-species communities where the prevalence of antibiotic resistance is essentially an ecological problem. We demonstrate that the relationship between environmental disturbance and resistance is more complex in mixed-species than single-species communities, this has important consequence for resistance management strategies. Contrary to current understanding, our mathematical model predicts that in mixed species communities a high rate of environmental disturbance introduced in the form of a mortality rate, can support the evolution of resistance. These predictions were verified experimentally using human-pathogenic community of two Candida species.

Keywords: antibiotic resistance, ecological disturbance, mixed species community, resource competition, mathematical models, mixed species community experiments

Mini-symposium 4 – Niche theory

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Niche theory is a conceptual framework at the core of our understanding of species coexistence, species distribution and ecosystem functioning, that recognizes the importance played by the feedback between organisms and their environment. Initially developed in the context of resource competition, classic extensions such as the inclusion of shared predation under the term 'apparent-competition' have broadened the scope of the theory.
Yet, a more general framework of contemporary niche theory that also includes positive interactions, such as facilitation and mutualism, and/or establishes tighter connections with evolutionary theories is necessary. Such a need is reinforced by the recently expanding interest for the study of positive interactions in the contexts of plant and microbial communities.
The aim of this mini-symposium is to bring together researchers working on various aspects of niche theory and present recent advances, syntheses and applications of the theory.

M4.1 – Environmental toxins induce positive interactions in small bacterial communities

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While interactions between species are often assumed to be constant, recent experimental studies have shown that interactions in a microbial community may depend on environmental conditions. Our lab studies interactions between four bacterial species that grow on toxic waste. In experiments, we initially observed only positive interactions between the different species. To explain these observations, we propose a simple model to describe how the interactions between species can occur as a side effect of consumer-resource dynamics. We assume that the bacteria share a substrate containing nutrients and toxins that they can grow on and degrade, respectively. The concentration of nutrients and toxins determine the direction and strength of interactions, so that the same pair of species may show either positive or negative interactions depending on the concentrations. We use the model to show how in co-culture, when one species degrades the toxic substrate, it facilitates growth of other species even in the face of underlying competition for a common pool of nutrients. Additional community members may increase the resource competition or improve detoxification, depending on growth parameters of the species and the concentration of nutrients and toxins. Our model makes clear, qualitative predictions that are supported by further experiments, explaining why we may observe positive interspecies interactions within a bacterial community in a toxic environment. We are now working on fitting the model parameters to our experimental data to make more quantitative predictions. By describing how interspecies interactions may depend on the environment, our results could aid the design of microbial communities with a desired function, such as pollutant degradation.

Keywords: bacterial community, cooperation, competition, coexistence

M4.2 – Patterns of trait diversity in evolved metacommunities of resource competitors

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Ecological models predict that spatial heterogeneity in the supply of different resources can promote regional consumer diversity through e.g. source-sink dynamics or species sorting. But are such - purely ecological - scenarios evolutionarily plausible? When traits are subject to adaptive evolution, will the antagonistic interplay of spatially variable local selection and homogenizing dispersal facilitate or impede regional diversification? We explored this question with a focus on trade-offs in resource-acquisition traits and the degree of resource substitutability. Using a model of competition for two discrete resources, we studied the evolution of resource-uptake specialization as a function of resource type (substitutable to essential) and the shape of the trade-off in resource uptake affinities (generalist- to specialist-favoring). In homogeneous environments, evolutionarily stable coexistence of consumers is only possible for substitutable resources and specialist-favoring trade-offs, yielding one extreme specialist on each resource at the evolutionary endpoint. Under these conditions, spatial heterogeneity cannot promote further evolutionary diversification, because the same two specialists preempt the available niche space everywhere also in a heterogeneous landscape. Instead, in heterogeneous environments, consumer diversity is maximized for intermediate trade-offs and either clearly substitutable or clearly essential resources. Importantly, a regime shift in how niche space can be partitioned occurs at the transition from substitutable to essential resources. When resources are substitutable, different phenotypes are locally most abundant where the supply of their preferred resource is highest. In contrast, when resources are strictly essential, phenotypes are locally most abundant where the supply of their preferred resource is most scarce. As a consequence, a diversity minimum arises at the switch point between these two opposite selection regimes (i.e. when resources are weakly interactively essential). Here, local selection becomes independent of the local resource supply ratio, and a single generalist frequently outcompetes all other strategies.

Keywords: spatial models, adaptive dynamics, coexistence, ESS, resource competition, metacommunity, spatial heterogeneity, niche partitioning, resource ratio

M4.3 – Microbial cross-feeding: well-mixed and spatial dynamics

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Cross-feeding is a type of mutualism where species produce essential resources that other ones need. We first study a non-spatial model with two mutualists that synthesize two micronutrients but compete for a macronutrient that externally supplied. We apply the framework of resource competition theory to we examine the effect of the mutualists' synthesis rates on coexistence and resource limitation. Multiple stable states occur if the synthesis rates are high, and higher synthesis rates increase the possibility that mutualists coexist. However, if a cheater that produces neither resource is present, high synthesis rates promote its invasion, which can collapse the whole community. This leads to the question "how do cross-feeding interactions persist in nature?" Previous attempts to answer it have relied on complex behavior (e.g. cheater punishment) or group selection. Using a stochastic spatial model, we demonstrate two novel mechanisms that can allow cross-feeders to outcompete cheaters, rather than just escape from them. Both mechanisms work through the spatial segregation of the resources, which prevents individual cheaters from acquiring the resources they need to reproduce. First, if microbe dispersal is low but resources are shared widely, then the cross-feeders self-organize into stable spatial patterns. Here the cross-feeders can build up where the resource they need is abundant, and send their resource to where their partner is, separating resources at regular intervals in space. Second, if dispersal is high but resource sharing is local, then random variation in population density creates small-scale variation in resource density, separating the resources from each other by chance. These results suggest that cross-feeding may be more robust than previously expected and offer strategies to engineer stable consortia.

Keywords: resource competition, mutualism, spatial model

M4.4 – A Niche Theory of Positive Interactions

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Niche theory is a central framework to the understanding of species coexistence, species distribution, ecosystem functioning, and the feedback between organisms and their environment. It highlights the dichotomy between the requirement niche, the sensitivity of a population to its environment, and the impact niche, the way this population in turn modifies its environment.
With niche theory, the diversity of ecological interactions found in nature can be organized around a few central concepts, such as population regulation and species competition. However, the theory has so far mostly focused on antagonistic interactions, such as resource-consumer dynamics. Following a recent interest for positive interactions, particularly in the contexts of plant and microbial communities, a more general framework of niche theory that includes facilitation and mutualism is necessary. This talk lays down the theoretical premises of such a niche theory of positive interactions, using nitrogen-fixing plants in terrestrial ecosystems and bacteria in the human gut as illustrative examples.
After defining 'positive interactions', we first address the niche of a single species subject to positive interactions. We show how combining requirement and impact niches gives rise to Holt's invasion and persistence niche dichotomy, a signature of alternative stable states between species' presence and absence. We then describe how a second species affects the niche of the first species, by extending its invasion and/or its persistence niche, and show how such mechanism can drive ecological succession. Finally, we discuss of difference metrics of niche overlap in the context of two-species coexistence involving positive interactions.
To conclude, extending contemporary niche theory to account for positive interactions can lead to new and broader niche concepts, and help us understanding how positive interactions shape ecological communities.

Keywords: niche theory, feedbacks, competition, facilitation, succession

M4.5 – Niche theory, time scales and environmental feedbacks in evolutionary ecology

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[a] Speaker

Evolution is deeply rooted in ecology. Over the last century, a variety of mathematical approaches have been developed to investigate the interplay between ecological and evolutionary processes. In this talk, I will discuss how these various approaches can be unified within a common perspective using the notion of environmental feedback. In particular, I want to stress how this perspective can help us to better understand (1) how the relative time scales of ecological and evolutionary processes affect the eco-evolutionary feedbacks that shape the dynamics of populations and (2) how niche theory fits within this global framework, through the dimension of the environmental feedback.

Keywords: adaptive dynamics, quantitative genetics, feedbacks, time scales

M4.6 – First principles theory for ecological niche

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[a] Speaker

The Hutchinsonian version of niche theory imagines an abstract niche space, which is partitioned between the species; the partitioning is the mechanism to avoid competitive exclusion. It was criticised by biological grounds, citing non-competitive interactions and environmental fluctuations, among others, as reasons for doubting this very intuitive world-view. Also, niche theory was associated by the competitive Lotka-Volterra model. When this model was started to be seen, as oversimplifying and outdated, niche theory inherited the judgement. Leibold's niche theory based on mechanistic modelling became also a victim of the status of theory in ecology: no "model" is supposed to be universally valid, therefore no mathematics is supposed to express a biological world-view.

The first principles theory we propose relies on the Darwinian insight that population growth potentially exponential and necessarily bounded at the same time. Our main proposition is the identification of the ecological niche of a species with its way of regulation: species avoid competition when their growths are checked by different factors. Hutchinson's niche space should be identified by the set of possible regulating factors. The notion of regulating factors/variables is the abstraction that allow us to represent any kind of interactions in the same mathematical framework. Way of regulation is specified by the population's impact on, and sensitivity towards, the regulating factors – a concept inherited from Leibold's niche.

We developed the theoretical ladder connecting the top-level first-principles theory to specific modelling. Among others, connection to Chesson's theory for fluctuation-mediated coexistence will be presented.

The regulation-based theory of ecological niche has a clear mathematical connection to adaptive dynamics, i.e. the theory of frequency-dependent selection and branching evolution. Progress in theoretical and empirical work in speciation research seems to converge to the picture that biological diversity arises, as adaptation to a multitude of ecological niches.

Keywords: ecological niche, fluctuating environment, adaptive dynamics, speciation

Mini-symposium 5 – Plankton dynamics: nonlinear dynamics of individuals, populations and communities

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Careful and creative mathematical descriptions of the dynamics of marine plankton have never been more important. The nonlinear dynamics of plankton communities underpins global primary production and may be central to the stability of complex ecosystems, and has impact at more local scales through the triggering of harmful algal blooms. Recent discoveries point to the importance of individual-level behaviour, and also blur the traditional lines between "predator" and "prey", while remote sensing and new statistical analyses are opening up exciting data-driven opportunities. All these phenomena need to quantified and captured within useful predictive models. This mini-symposium will draw together a broad range of mathematicians and modellers, with the aim of exploring recent advances and developing new collaborations.

M5.1 – Dome patterns in planktonic size spectra reveal strong trophic cascades

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In planktonic communities in the pelagic zones of aquatic ecosystems, certain body-size ranges are often over-represented compared to others. Community size spectra, the distributions of community biomass over the logarithmic body-mass axis, tend to exhibit regularly spaced local maxima, called "domes", separated by steep troughs. Contrasting established theory, we explain these dome patterns as manifestations of cascading top-down effects along aquatic food chains. Combining a compilation of high-quality size-spectrum data, a novel size-spectrum model, and mathematical theory, we test this theory and develop a detailed picture of the mechanisms by which bottom-up and top-down effects interact to generate this phenomenon. Results imply that strong top-down trophic cascades are common in freshwater communities, much more than hitherto demonstrated, and may arise in nutrient rich marine systems as well. Interpreting domes as instances of self-organised spatially periodic patterns, with the size axis replacing physical space, we transfer insights from the general theory of nonlinear pattern formation to domes, thus enabling new interpretations of past lake-manipulation experiments.

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Keywords: Plankton, top down effect, trophic cascade, size spectrum, analytically tractable models, pattern formation

M5.2 – Diversity, dynamics and dominance

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[a] Speaker

For many decades simple ODE-based models have been proposed to explain the diversity of ecological systems. However, in focusing on the properties needed for coexistence, such models may not adequately reflect the essential dynamics which make ecological systems interesting and important. Motivated by models of blooms in plankton communities, but with reference also to examples in biomedicine, I will show that both diversity and temporary dominance can arise quite naturally. I argue that this provides useful insights into the perturbations triggering ecologically important state shifts (dominant infections or harmful algal blooms, for example).

Keywords: plankton bloom, dynamical systems, complexity

M5.3 – Modelling optimal behavioural strategies in structured populations using a novel theoretical framework

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[3] N.I. Lobachevsky State University of Nizhny Novgorod – Russia

[a] Speaker

The conventional paradigm in animal behavior modelling consists of maximisation of some evolutionary fitness function. However, the definition of fitness of an organism or population is generally subjective, and using different criteria can lead us to contradictory model predictions regarding optimal behaviour. Moreover, structuring of natural populations in terms of individual size or developmental stage creates an extra challenge for theoretical modelling. Here we revisit and formalise the definition of evolutionary fitness to describe long-term selection of strategies in deterministic self-replicating systems for generic modelling settings which involve an arbitrary function space of inherited strategies. Then we show how optimal behavioural strategies can be obtained for different developmental stages in a generic von-Foerster age-structured population model with an arbitrary mortality term. We implement our theoretical framework to explore patterns of optimal diel vertical migration (DVM) of two dominant zooplankton species in the north-eastern Black Sea. We parameterise the model using 7 years of empirical data from 2007-2014. Our study demonstrates that it is the depth-dependent variability of the metabolic costs of zooplankton grazers - related to the specific oxygen regime in the Black Sea - rather than trophic pressure by visual predators that determines the choice of the lowest migration depth. The model also predicts that the absence of diel migration of earlier stages of zooplankton might be mostly due to their high mortality rather than due to a high cost of DVM, contrary to what was believed previously.

Keywords: Infinite dimensional traits, evolutionary fitness, diel vertical migration of zooplankton

M5.4 – Why Plankton Modelers Should Reconsider Using Rectangular Hyperbolic (Michaelis-Menten, Monod) Descriptions of Predator-Prey Interactions

Aditee Mitra [a] [1], Kevin Flynn [1]

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[a] Speaker

Rectangular hyperbolic type2 (RHt2) also often referred to as Michaelis-Menten or Monod-like functions are commonly used to describe predation kinetics in plankton models. We present an analysis that indicates that such descriptions are liable to give outputs that are not ecologically or biologically plausible. This is especially so for multi-prey type applications or where changes are made to the maximum feeding rate during a simulation. The RHt2 approach also gives no or limited potential for descriptions of events such as true de-selection of prey, effects of turbulence on encounters, or changes in grazer motility with satiation. We present an alternative, which carries minimal parameterization effort and computational cost, linking allometric algorithms relating prey abundance and encounter rates to a prey-selection function controlled by satiation. The resultant Satiation-Controlled-Encounter-Based (SCEB) function provides a flexible construct describing numeric predator-prey interactions with biomass-feedback control of grazing. The SCEB function includes an attack component similar to that in the Holling disk equation but SCEB differs in having only a single (satiation-based) handling constant and an explicit maximum grazing rate. We argue that there is no justification for continuing to deploy RHt2 functions to describe plankton predator-prey interactions. The means by which the grazing function is related to the description of predator growth will also be discussed.

Keywords: plankton, mixotroph, system dynamics, predator, prey

M5.5 – Niche separation between different functional types of mixoplankton: results from NPZ-style N-based model simulations

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Protist plankton comprise phytoplankton (incapable of phagotrophy), protozooplankton (incapable of phototrophy) and mixoplankton (capable of phototrophy and phagotrophy). Of these, only phytoplankton and zooplankton are typically described in models. Over the last decade, however, the importance of mixoplankton across all marine biomes has risen to prominence. We thus need descriptions of mixoplankton within marine models. Here we present a flexible yet simple N-based model describing any one of the 5 basic patterns of protist plankton: phytoplankton, protozooplankton, and the 3 patterns of mixoplankton: general non-constitutive mixoplankton (GNCM), specialist non-constitutive mixoplankton (SNCM), and constitutive mixoplankton (CM). By manipulation of a few constants, the same model can be used to describe any of these patterns, together with fine tuning of salient features such as the % of C-fixation required for mixotroph growth, and the rate of phototrophic prey ingestion required to enable growth of GNCM and SNCM types. Example outputs are presented showing how the performance of these different configurations accords with expectations (set against empirical evidence). Simulations demonstrate clear niche separations between these protist functional groups according to nutrient, prey and light resource availabilities. This addition to classic NPZ plankton models provides for the exploration of the implications of mixoplankton activity in a simple yet robust fashion.

Keywords: NPZ model, mixotroph, mixoplankton, niche, system dynamics, predator, prey

M5.6 – Physical Flow Effects Can Dictate Plankton Population Dynamics

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[a] Speaker

Oceanic flows do not necessarily mix planktonic species. Differences in individual organisms' physical and hydrodynamic properties can cause changes in drift normal to the mean flow, leading to segregation between species. This physically-driven heterogeneity may have important consequences at the scale of population dynamics. Here, we describe how one form of physical forcing, circulating flows with different inertia effects between phytoplankton and zooplankton, can dramatically alter excitable plankton bloom dynamics. This may have a significant impact on our understanding of the initiation and development of harmful algal blooms (HABs), which have significant negative ecological and socio-economic consequences. We study this system in detail, providing spatio-temporal dynamics for particular scenarios, and summarising large-scale behaviour via spatially averaged bifurcation diagrams. The key message is that, across a large range of parameter values, fluid flow can induce plankton blooms and mean-field population dynamics are distinct from those predicted for well-mixed systems. The implications for oceanic population dynamic studies are manifest: we argue that the formation of HABs will depend strongly on the physical and biological state of the ecosystem, and that local increases in zooplankton heterogeneity are likely to precede phytoplankton blooms. We go on to investigate the effects of mixotrophy on the plankton population dynamics.

Keywords: Harmful algal blooms, inertia, cell density, ecological dynamics

M5.7 – Structural ensemble of an ocean biogeochemical model

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[a] Speaker

Advanced ocean biogeochemical models differ in terms of the number of state variables representing different types of primary producers and grazers. This presentation will deal with some recent results to compare an ensemble of biogeochemical models with a single biogeochemical model, in reproducing observations of phytoplankton biomass and bloom phenology. It will include an example of how an ensemble of multiple biogeochemical models compares with the satellite-derived phenology of large-phytoplankton bloom in the global ocean. A further example will be shown on how a single biogeochemical model can be used to generate an ensemble by perturbing its biological process formulations, and how this ensemble compares with in situ data at site level. The overall results will be discussed in the context of implementing biogeochemical model-ensembles for improved estimation of carbon biomass and phenology of different functional types of producers and grazers, and the potential for interfacing these ensembles with satellite-derived ocean-colour observations.

Keywords: Biogeochemical model, structural ensemble, ocean colour, plankton functional types

Mini-symposium 6 – Finite population size effects in evolution

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Biological populations are finite and their sizes undergo frequent changes. These variations can range from large changes in population size, e.g. population bottlenecks, to small fluctuations around the population's steady state. Dealing with the so introduced stochasticity in population size is a challenge, however the insights obtained are worth the effort. Explicitly studying finite populations can reveal dynamics that differ from the evolutionary outcome predicted by the associated deterministic model that arises from the infinite population size limit. This observation, despite being old, is recently receiving more attention since analytical progress allows to quantify these probabilistic effects on large scale behavior. The study of individual based models and their intermediate to large population size limits have led to new significant insights in various biological systems, e.g. host-pathogen interaction, pathogen diversity, mating type dynamics, public good production, seed banks, etc. The typical quantities of interest are trait fixation or establishment probabilities, mean fixation or extinction times and quasi-stationary distributions of trait frequencies. In this vein the mini-symposium gathers scientists interested in different biological questions but using a similar mindset, i.e. accounting for finite population size effects in their analyses. The aim is to see, learn about and discuss the application of various tools in the context of evolution.

M6.1 – Invasion and extinction properties of mating types in finite populations: uncovering the dynamics of the number of "sexes"

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[a] Speaker

While it is common to view sexual reproduction as intrinsically linked to the two sexes, male and female, in many species this is not the case. Rather than the familiar sperm and egg, isogamous species produce gametes of similar sizes. Although morphologically similar, these gametes are often not interchangeable, but rather fall into a number of self-incompatible gamete classes, termed mating types. Mating types can be crudely viewed as ancestral analogues of the sexes. However without the size dimorphism that defines true sexes, the number of mating types in isogamous species is not restricted to two.

A long-standing question has been what evolutionary pressures control the number of mating types in natural populations, which varies from two to many thousands [1]. While many competing theories have been proposed, here we tackle a simpler question; how much of the observed variation in mating type number is explained simply by finite population size effects? To this end we analyse an infinite allele null model of the system [2] and derive expressions stationary distribution of the number of types [3]. By deriving expressions for the establishment probability of new mutant mating types and the extinction times of residents, we develop deeper insight into their dynamics [3]. Our results indicate that the low number of mating types predicted in certain parameter regimes is driven by low invasion probabilities, with resident alleles being stable over long evolutionary periods.

[1] Kothe, E., Tetrapolar fungal mating types: sexes by the thousands. *FEMS Microbiol. Rev.* **18**:65–87 (1996)

[2] GWAC and Kokko, H., The rate of facultative sex governs the number of expected mating types in isogamous species. *Nat. Ecol. Evol.* **2**:1168-1175 (2018)

[3] Czuppon, P. and GWAC, Invasion and extinction dynamics of a neutral mating type model under facultative sexual reproduction *In Preparation* (2019)

Keywords: stochastic models, population genetics, sexual reproduction, self-incompatibility, balancing selection

M6.2 – Capturing the quasi-stationary distribution within a deterministic framework for stochastic SIS dynamics

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[a] Speaker

The stochastic SIS model represents an important class of epidemic dynamics, and is thought to accurately represent various processes, such as the spread of sexually transmitted diseases and computer viruses.
A feature of this model is the existence of a single absorbing state, corresponding to the disease free state, to which the system will always converge for finite population sizes and disease transmission parameters.
There has been a long history of deterministic representations of the SIS model. Relating these models to the stochastic dynamics frequently makes use of mean-field assumptions, which are derived from the infinite population limit. These models provide useful theoretical insight but do not feature the absorbing state, and therefore it is hard to link the insights back to the stochastic model.
In this work we develop novel methods to account for the absorbing state of the stochastic SIS model within a deterministic framework. We do this by deriving a deterministic approximation to the quasi-stationary distribution (QSD) of the model; i.e. the long-term steady state behaviour conditional on not having reached the absorbing state. In particular, we build a system of population level equations, which when solved provide an accurate and efficient approximate to the QSD of the Markovian network-based epidemic model for a large range of networks and parameter sets.

Keywords: epidemiology, Markov process, network, moment closure, extinction

M6.3 – Pathogen evolution in stochastic epidemics after vaccination

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[a] Speaker

Vaccination is expected to decrease pathogen transmission and to affect dramatically epidemiological dynamics. But vaccination may also have long-term consequences on the evolution of pathogens. Previous attempts to evaluate the evolutionary consequences of vaccination relied on the assumption that pathogen populations are very large and neglected the influence of demographic stochasticity. Here we extend the framework of evolutionary epidemiology theory to explore the effect of vaccination in finite pathogen populations. We show how the short-term epidemiological dynamics driven by vaccination affect the probability of fixation of a pathogen mutant. This probability of fixation depends on (i) the effects of the mutation on pathogen life history traits (transmission and virulence) and (ii) the time at which the mutation is introduced. Right after the start of vaccination, more prudent strategies (low transmission and virulence) have a higher probability of fixation because these strategies are more likely to survive the drop in pathogen incidence consecutive to the vaccination campaign. In contrast, if the mutation is introduced a bit later, more aggressive strategies (high virulence and transmission) may have a higher probability of fixation because they benefit from a transient increase in the density of susceptible hosts. We also discuss the impact of demographic stochasticity on the long-term evolution of the pathogen when mutation are rare and occur near the new endemic equilibrium reached after vaccination. This theoretical framework accounts for the interplay between epidemiology, selection and genetic drift and can be used to explore the short-term and long-term effects of public-health interventions on the evolution of pathogens.

Keywords: epidemiology, virulence, genetic drift, bet hedging, demographic stochasticity

M6.4 – Diversity patterns in parasite populations capable for persistence and reinfection with a view towards the human cytomegalovirus

Cornelia Pokalyuk [a 1], Irene Görzer [2], Anton Wakolbinger [1]

[1] Goethe-University Frankfurt am Main – Germany
[2] Medical University of Vienna – Austria

[a] Speaker

Many parasites like the cytomegalovirus, HIV and Escherichia coli are capable to persist in and reinfect its host. We will investigate a host-parasite model with two parasite types for which these mechanisms are driving the evolution of the parasite population. We consider two variants of the model. In one variant parasite reproduction is directed by balancing selection, in the other variant parasite reproduction is neutral.

In the former scenario we identify parameter regimes for which reinfection and persistence sustain the maintenance of diversity in the parasite population and for which the evolution of the parasite population is asymptotically driven by a (deterministic) dynamical system.

In the neutral scenario reinfection may facilitate the coinfection of a host with both parasite types, but does not enhance the coexistence of both parasite types. Depending on the ratio of the reinfection rate, parasite reproduction rate and host replacement rate we determine the asymptotic distribution of frequencies at which hosts are infected with the two parasite types.

We evaluate the biological relevance of both model variants with respect to the human cytomegalovirus (HCMV), an ancient herpesvirus that is carried by a substantial fraction of mankind and manages to maintain a high diversity in its coding regions.

Keywords: host, parasite model, reinfection, persistence, diversity

M6.5 – Coalescents with demographic bottlenecks

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Modeling populations with varying population size is of great interest, for example to infer the human demographic history. In this work, we model a population of size N that undergoes demographic bottlenecks. A bottleneck is an event that reduces substantially the population size and that may last for one or several generations. We characterize a bottleneck by its intensity (the ratio between the population size during the bottleneck and N) and its duration. We describe the ancestral processes corresponding to different types of bottlenecks.
When the bottlenecks are soft, i.e. when the population size during the bottleneck is small, but still of the order N, the genealogy is described by a time-rescaled Kingman coalescent.
When the bottlenecks are drastic, i.e. when the population size is very small compared to N and remains finite even if N goes to infinity, the genealogy is described by a coalescent with simultaneous multiple mergers.
In particular, if the bottlenecks are short, the genealogy is described by a new type of coalescent with simultaneous multiple mergers that we call the symmetric coalescent.
The symmetric coalescent has some nice geometric properties: it is invariant by the transformation that consists in cutting one branch form a node and retrenching it somewhere else in the tree at the same height. Its transition rates can be characterized by a probability measure in Z+ (which corresponds to the law of the population size during the bottleneck). The family of symmetric coalescents exhibits a large variety of behaviors, in particular regarding the total coalescence rate and the total tree length.

Keywords: Coalescence, Bottlenecks, Demography

M6.6 – Population size changes and extinction risk of populations driven by mutant interactors

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[a] Speaker

Spontaneous random mutations are an important source of variation in populations. Many evolutionary models consider mutants with a fixed fitness, chosen from a fitness distribution without considering microscopic interactions among the residents and mutants. Here, we go beyond this and consider "mutant interactors," which lead to new interactions between the residents and invading mutants that can affect the population size and the extinction risk of populations. We model microscopic interactions between individuals by using a dynamic interaction matrix, the dimension of which increases with the emergence of a new mutant and decreases with extinction. The new interaction parameters of the mutant follow a probability distribution around the payoff entries of its ancestor. These new interactions can drive the population away from the previous equilibrium and lead to changes in the population size. Thus, the population size is an evolving property rather than an externally controlled variable. We calculate the average population size of our stochastic system over time and quantify the extinction risk of the population by the mean time to extinction.

Keywords: Ecology&Evolutionary, Mutation, Stochastic process, Extinction

Mini-symposium 7 – Success and stability in bacterial competition and adaptation

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Bacteria are ubiquitous, playing a central role in ecosystem health and are a dominant force in regulating the global biosphere. Microbial dynamics are complex. Asexual division allows for rapid population growth and collapse. Competitive processes and environmental fluctuations continually drive phenotypic changes in the fight for resource acquisition. Horizontal gene transfer rapidly changes genotypes, whilst slower evolutionary processes shape individuals and communities over longer timescales. As the environment selects for bacteria, bacteria in turn alter their environment. Within this biological context, there may be 10 million bacteria and thousands of species in 1mL of seawater: the complexity of microbial systems makes it challenging or prohibitive to tackle many questions through experimental methods.
One of the aims of microbial ecology is to analyse bacterial interactions and predict the evolution of populations or communities under specific conditions. Bottom-up mechanistic approaches may present contrasting perspectives to a broad, top down philosophy, in experimental or theoretical settings. Modelling can help elucidate which mechanisms may be responsible for emergent phenomena from chaotic systems, answering questions such as: What constitutes winning strategies for individuals versus communities? What drives and limits fitness across bacterial populations? How do stable communities evolve over long timescales?

M7.1 – Directional selection rather than functional constraints can shape the G matrix in rapidly adapting microbes

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Short-term evolution is determined by the **G** matrix, whose covariance terms represent a combination of pleiotropy and linkage disequilibrium, shaped by the population's history. Observed genetic covariance is most often interpreted in pleiotropic terms. In particular, functional constraints restricting which phenotypes are physically possible can lead to a stable **G** matrix with high genetic variance in fitness-associated traits and high pleiotropic negative covariance along the phenotypic curve of constraint. We describe the evolution of **G** when pleiotropy is excluded by design, such that all covariance comes from linkage disequilibrium, which reaches high levels in rapidly adapting microbial populations. To do this, we extended the influential one-dimensional travelling wave model of rapid adaptation of an asexual population into two dimensions, representing two distinct fitness-associated traits in an asexual population. We find that the associated **G**-matrix maintains a stable orientation, but is far less stable in magnitude than predicted by previous models. Different mechanisms drive the instabilities along different principal components of **G**. Their origin is not drift, but rather small amounts of linkage disequilibria generate by mutations on the fittest backgrounds, which are subsequently amplified during competing selective sweeps. By competing one trait with a higher beneficial mutation rate with another with larger mutational effect sizes, we illustrate the range of parameters for which mutation-driven adaptation is possible.

Keywords: clonal interference, polygenic adaptation, stochastic processes, trait correlations, life history traits

M7.2 – A universal genetic topology in bacterial communities

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[a] Speaker

Despite enormous variability at a microscale, microbial communities are remarkably stable at the macroscale, often appearing to be in a fixed point from a taxonomic or functional standpoint. This is counter to what would be expected using classical dynamical modelling techniques. Here, we use methods from metagenomics and data science to construct bipartite taxonomy-protein graphs across multiple environments, and subsequently identify universal topological features in microbial systems. We then use an evolutionary network model of the system to examine the speed at which specific genes can propagate through the community, and the implications this may have for system stability.

Keywords: bacterial communities, microbial systems, network model

M7.3 – Projections of metabolic supply chain models for haploid organisms onto less-dimensional systems

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The investigation of biological systems like the metabolism of an organism, requires the comprehension of the mechanisms in the model. We choose a bottom-up approach to analyze the metabolic resistance of haploid organisms with respect to the geometry of their metabolic supply chain. Therefor, we construct a supply chain under enviromental impacts, and we give a connection to the growth and mortality. Different metabolic paths are related to different fitness properties of a population. Further, a comparison of metabolic resistance and target-site resistance gives us a deeper view into the model mechanisms and a better connection to the biology background.
The study of resistance of a population yields insight, which we consider in more general terms by hands of models including multiple gene loci. We choose an approach of projecting these gene loci to a lower-dimensional selection of them. Different models with unequal amounts of gene loci share common similarities but also have discrepacies, which we discuss.

Keywords: mathematical modeling, supply chains, population dynamics, biological resistance

M7.4 – The survival of microbial communities, taxa and genes

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Despite prokaryotes acting as a driving force in climate, health and industry, there is little information on general principles of how community compositions arise and are maintained. Prokaryotic communities experience poisons, antibiotics, grazers, phage, physico-chemical gradients and heterogeneity that continually select out large fractions of taxa and genes. The rapid re-establishment of survivors offers potential insights for understanding the resilience of all biological systems. However, the dynamics of taxa and gene survival are poorly understood. We discuss the ways in which modelling may help constrain this high variable system to important parameters, and to distinguish what determines survival and resilience.

Keywords: bacteria, resilience

M7.5 – Multi-level selection and the evolution of host microbiomes

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[a] Speaker

Most multicellular animals are associated with a microbiome that provides essential services for their health. For example, hosts often obtain essential nutrients from microbes residing in their gut. The reproductive success of a host will thus depend on the composition of its microbiome, and it is therefore important to understand how the host and their microbiome coevolve. It has recently been suggested that microbiomes could evolve by multilevel selection (MLS): microbiomes that increase their host birth rate could increase in frequency if they are passed on between host generations (vertical transmission). However, this view is controversial: as hosts constantly exchange microbes with their environment (horizontal transmission), the associations between a host and its microbiome might be too weak to allow for MLS. Whether MLS can play a role in the evolution of host microbiomes likely depends on quantitative aspects of the host and microbiome dynamics, yet much of the current debate is based on verbal arguments. Here we present a mathematical model to address these issues. We consider a microbiome consisting of two species: *cooperators* that increase host birth rates, and *defectors* that grow faster than cooperators without affecting host health. In the absence of host-level dynamics defectors always outcompete cooperators, however MLS can maintain cooperators under specific conditions. Specifically, host dynamics has to be fast compared to both the timescale over which defectors outcompete cooperators (which depends on the cost of cooperation) and the timescale over which heritability of the microbiome composition is lost (which depends on the balance of horizontal to vertical transmission). Our model suggests that MLS could play a role in species with fast generation times and strong vertical transmission (e.g. certain insect species), but is unlikely to be of importance in species with long generation times and strong horizontal transmission (e.g. humans).

Keywords: multilevel selection, host microbiome, bacterial communities

M7.6 – Microbial public goods games in a toxic environment: to degrade or to resist?

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Microbial communities provide human society with a variety of benefits including bioremediation. To optimize these benefits, it is necessary not only to maximize process efficiency, but also to stabilize the communities over ecological and/or evolutionary time scales. For example, a few empirical studies of bioremediation show that mutants that do not degrade toxic compounds can spread in the population. Indeed, degrading a toxic compound through the production of an enzyme is regarded as a public goods game, where the invasion of cheaters (non-producers) is predicted. In this study, we constructed an evolutionary game theoretical model, where a microbial population degrades a toxic compound, and used the model to analyze (i) whether cooperators (enzyme producers) can be maintained, and (ii) how to optimize detoxification efficiency by manipulating toxic compound concentration flowing into a chemostat and/or dilution rates. Although cooperators go extinct when cheaters that are equally resistant to the toxin appear, we identified conditions where cooperators with a different level of resistance can invade the population of cheaters and exclude them. However, in the long term, cheaters of the same resistance level are bound to reinvade. To overcome this inevitable outcome, we show that cooperators can be periodically reintroduced to the population to maximize the efficiency and stability of detoxification.

Keywords: bioremediation, environmental feedback, cooperation

Mini-symposium 8 – Mate preferences: impacts on eco-evolutionary dynamics

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Mate preferences, *i.e.* the tendency of some individuals to reproduce with particular phenotypes, are widespread in natural populations. Assortative mating, where individuals with similar phenotypes reproduce more frequently than expected at random, as well as disassortative mating, have been observed in many animal and plant species. Mating preferences often generates frequency-dependent selection on mating cues and therefore shape their evolution. In turn, complex interactions with natural selection acting on mating cues also have a deep impact on the evolution of mate preferences, and these questions have stimulated recent research in ecology and evolution. Furthermore, the choosiness associated with mate preference has also an impact (1) on individual reproductive success, because some individuals might fail finding a suitable partner, and (2) on migration rates among populations, because mate preference can enhance behaviours involved in mate searching. The evolution of mate preferences has thus a profound influence on population dynamics and spatial structure. Depending on the mating cues involved, positive and negative links between sexual selection and speciation have been highlighted by numerous authors, Lande (1981) being the first one to have popularized the idea of sexual selection promoting speciation. Recent empirical data investigating the genetic architecture of mate preferences, and interactions with demography have highlighted new mechanisms involved in the evolution of mate preferences, and explored consequences of mate choices on population divergence. From a mathematical point of view, these questions lead to propose new and difficult models to investigate, notably through the presence of mechanisms of sexual reproduction and of frequency-dependent regulations.
This mini-symposium will gather ecologists and mathematicians to show recent advances in our understanding of the evolution of sexual preferences, and their consequences on population dynamics and speciation.

M8.1 – Coevolution of male and female mate choice can hamper ecological speciation

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Sexual interactions play an important role in generating reproductive isolation, with clear consequences for ecological speciation. In particular, individuals may mate assortatively based on their mate preferences, causing premating isolation. Theoretical developments have focused on the evolution of mate preferences in each sex separately. However, mounting empirical evidence suggests that premating isolation often involves mutual mate choice (e.g. in cichlid fishes or Heliconius butterflies).

Here, using a population genetic model, we investigate how female and male mate preferences co-evolve (phenotype matching rule) and how this affects reproductive isolation. One might expect mutual mate choice to enhance reproductive isolation: if preferences expressed by one sex leads to some isolation, surely preferences in the two sexes must lead to even stronger isolation? We show that this is a naive expectation. Mutual mate choice is unstable because the coevolution of preferences fosters the occurrence of bursts of gene flow which inhibit differentiation. Premating isolation is therefore more reversible than predicted by previous models.

Our theoretical predictions may upturn the way we view the process of speciation, and our empirical appreciation of the stages along the so-called 'speciation continuum'. Cycles of divergence and gene flow, rather than a steady increase in divergence, may in fact characterize ecological speciation.

Keywords: speciation, reproductive isolation, divergence, sexual selection, frequency, dependent selection, genetic drift

M8.2 – Selection-mutation models with asymmetric sexual reproduction kernels

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We review a family of selection-mutation models of a sexual population structured by a phenotypical trait. The main feature of these models is the asymmetric trait heredity or fecundity between the parents: we assume that each individual inherits mostly its traits from the female. Following previous works inspired from principles of adaptive dynamics, we rescale time and assume that mutations have limited effects on the phenotype. Our goal is to study the asymptotic behavior of the population distribution. We derive non-extinction conditions and regularity estimates on the total population. We also show regularity estimates on the solutions of Hamilton-Jacobi equations that arise from the study of the population distribution concentration at fittest traits.

Keywords: adaptive dynamics, non extinction, sexual population, Hamilton Jacobi equation

M8.3 – Can "good genes" maintain male mate choice and female ornaments in polygynous systems?

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[a] Speaker

Empirical studies from recent decades reveal that neither male mate choice nor female ornamentation is as rare as once believed, even in polygynous species. Concurrently, an emergent body of theoretical literature suggests that the common evolutionary processes that are known to drive the evolution of female mate choice-and subsequently maintain it as a mechanism of selection-are unlikely to proceed simply as mirror image processes producing the mirror image pattern of male mate choice and female ornamentation. Therefore, knowledge about the processes driving the evolution of male mate choice and female ornamentation is incomplete and substantial portions of biodiversity are unexplained. One commonly hypothesized scenario that remains unexplored posits that male mate choice and female ornamentation can be maintained by 'good genes' in females. That is, can costly male preferences evolve in response to indirect fitness benefits accrued by choosy males, and-if so-can those male preferences subsequently drive the evolution of a female trait? We interrogate this question with a population genetic model. Furthermore, we examine the extent to which male ability to directly assess female quality ("direct detectability") affects the evolution of male preferences. We conclude that-contrary to common assumptions-"good genes" in females are unlikely to explain the evolution of male preferences, except under very specific conditions. In turn, we show that it is *possible*for these male mate preferences to result in female trait evolution, but that costs on the trait quickly bring this process to a halt. These results cast doubt on the idea that heritable genetic quality in females should be a widespread explanation for the evolution of male mate choice. Moreover, these results suggest that-even once male mate choice alleles come into linkage disequilibrium with alleles for enhanced viability-male mate choice is an ineffective driver of female ornamentation.

Keywords: mate choice, sexual selection, population genetics

M8.4 – Emergence of homogamy in a two-loci stochastic population model

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[a] Speaker

This talk deals with the emergence of a specific mating preference pattern called homogamy in a population. Individuals are characterized by their genotype at two haploid loci, and the population dynamics is modelled by a non-linear birth-and-death process. The first locus codes for a phenotype, while the second locus codes for homogamy defined with respect to the first locus: two individuals are more (resp. less) likely to reproduce with each other if they carry the same (resp. a different) trait at the first locus. Initial resident individuals do not feature homogamy, and we are interested in the probability and time of invasion of a mutant presenting this characteristic under a large population assumption. To this aim, we study the trajectory of the birth-and-death process during three phases: growth of the mutant, coexistence of the two types, and extinction of the resident. We couple the birth-and-death process with simpler processes, like branching processes or dynamical systems, and study the latter ones in order to control the trajectory and duration of each phase.

Keywords: mating preferences, homogamy, evolution

M8.5 – Fitness variability suppresses mating type diversity

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The evolution of sexual reproduction gives rise to a number of intensely debated questions in biology. An often overlooked fact is that sexual reproduction is not always synonymous with the two sexes. Rather than producing sex cells of differing sizes (the familiar egg-sperm system), many species produce sex cells of equal size, a state called isogamy. Much like well-distinguishable sperm and egg cells, isogamous sex cells fall into distinct self-incompatible classes, termed mating types.
A longstanding evolutionary question is what governs the number of mating types in populations? Theoretically, a rare novel type inherently has a selective advantage, because of the large proportion of compatible mating partners in the population. Thus one would expect the number of mating types to grow constantly. However, this is in stark contrast with empirical observation; while many thousands of mating types are possible, most species have only two.
With the presented poster, I will show how this puzzling issue can be addressed with a mathematical approach. We assume that mating types may have a diversity of fitness and model the invasion-extinction dynamics of an isogamous population. We then derive an analytic expression for the expected number of mating types at long times. These results hold for mutants drawn from any arbitrary fitness distribution. We predict that the number of mating types decreases with the rate of sexual reproduction, and is lowered further as the variance of fitness increases. Our analytic results are supported by empirical data and thus provide a potential resolution to this longstanding question.

Keywords: mating types, isogamy, reproduction, facultative sex

Symposium 9 – Evolution of multicellular life cycles

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This mini-symposium intends to bring together researchers studying the emergence and development of the life cycles of primitive multicellular organisms. Even simple species exhibit a wide range of different development and reproduction modes. There are organisms growing from a seed and organisms formed by aggregation of unrelated cells. Some species develop into undifferentiated colonies; a lot more display some form of division of labour. A number of species reproduce via single cell bottleneck; others leave multicellular offspring. Why are these life cycles so different? And do they have at least something in common? We will discuss how evolution shapes formation, development and reproduction of simple multicellularity. This topic captures one of the most fundamental stages of life history on Earth. Being at the intersection of evolution, ecology, and demography, this symposium will provide an opportunity to share the insights coming from various approaches and model systems.

M9.1 – Evolution of the irreversible somatic differentiation

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Many multicellular organisms go through unicellular stage, which lead to the genetically identical cells in an organism. Although, all the cells are genetically identical, only a few of them belong to the germ line, while the majority of cells are irreversibly differentiated into somatic cells and die at the end. From the cell perspective, such an irreversible differentiation is a disadvantageous strategy as this ultimately sacrifices cells' own long-term survival. In principle, soma cells can undergo de-differentiation and give rise to germ cells, however, it happens extremely rarely. How does the irreversible somatic differentiation evolve? Here, we investigate the emergence of irreversible somatic differentiation in a clonal multicellular organism with two cell types. One type (proto-soma) provides benefits to the organism but dies at the end, another (proto-germ) gives rise to new organisms but does not contribute any benefits. The two cell types can give rise to each other with probabilities controlled by stochastic developmental programs with costs. Among all these programs, we seek the irreversible somatic differentiation being the evolutionary optimal, i.e. delivering the largest population's growth rate. Our results show that irreversible somatic differentiation can evolve under the costly differentiation. Moreover, we found that soma contribution patterns also have an effect on the irreversible somatic differentiation.

Keywords: Somatic differentiation, Evolution, Multicellularity

M9.2 – Towards a general theory of reproduction modes evolution

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[a] Speaker

An ability to reproduce is a definitive trait of living systems, as it is a necessary ingredient for the natural selection to operate. But how the reproduction itself is shaped by the evolutionary forces still remains an open question. To approach this problem, we consider reproduction from a mechanistic perspective: as a distribution of the biomass of a single organism among two or more offspring beings. In our model, the rate of biomass accumulation is determined by interactions between the organism and the environment, which evolve at negligibly slow rate. At the same time, natural selection acts on the reproductive strategy: at which size of the parent organism reproduction occurs and what is the pattern of biomass distribution among offspring. We found that in this setup, the evolutionary optimal reproduction mode is always a binary division - fragmentation in two parts. Among binary fragmentation modes, we investigated a number of extreme strategies, such as producing minimally viable propagules, reproduction at the minimal or maximal possible sizes. We outlined conditions, which promote these modes to evolve. For non-extreme cases, we found that the evolutionary optimal strategy is to fragment in way that the combined rate of biomass accumulation is the same immediately before and immediately after reproduction. Finally, combining our approach with the Monod-Michaelis-Menton model of the cell growth, we found that cells of different shapes (spherical or rod-shaped) can evolve completely different patterns of reproduction in the same environment.

Keywords: Asymmetric division, organism size constraints

M9.3 – Eco-evolutionary consequences of imperfect aggregative multicellularity

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[a] Speaker

The life cycle of the social amoeba *Dictyostelium discoideum* includes a multicellular stage in which free-living amoebae aggregate upon starvation to form a multicellular fruiting body. Intriguingly, however, the aggregation process is imperfect, and some cells remain 'out-of-sync' with the majority of the population, thus staying solitary. A compelling question then arises: is this imperfect synchronization ecologically and evolutionarily meaningful, or are these 'loner' cells merely mistakes, with no avenue for selection to shape them? How does this imperfect coordination arise? In this presentation, I will provide empirical evidences that selection can act on these loners and show that they result from a heritable population-partitioning process. Then, using a mathematical model for *D. discoideum* life cycle, I will first propose a mechanistic explanation for such imperfectly synchronized multicellular development and explore its possible implications for strain coexistence in slime mold communities. Our results predict that when strains differing in their level of collective synchronization co-occur, they interact with each other and shift their aggregation behavior, which profoundly impacts strain diversity across spatio-temporal scales. Loners are therefore critical to understanding collective and social behaviors, multicellular development, and ecological dynamics in *D. discoideum*.

Keywords: Multicellularity, microbial ecology, collective behaviors

M9.4 – Evolutionary origins of Darwinian properties during major transitions in individuality

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The evolution of chromosomes, the eukaryotic cell and multicelluar organisms all involved the coming together of separate autonomously reproducing entities to form self-replicating structures. However, the Darwinian nature of those collectives is not granted but involve new mechanisms resulting from ecological and evolutionary dynamics at the level of collectives as well as of their components. We present a simple model in which particles reproduce within collectives, that are in turn subject to a birth-death process. We show that selection acting on population of collectives drives evolution of individual traits toward ecological regimes ensuring the reliable transmission of collective traits across collective generations by canalisation of the ecological dynamics. This can be seen as the emergence of a simple developmental programme, and the closing of a primtive life cycle. Our model establishes an ecological recipe for effecting major transitions in individuality and has implications for top-down engineering of microbial communities.

Keywords: Darwinian Populations, Adaptive Dynamics, Evolutionary Transitions, Individuality

M9.5 – Emergence of diverse life cycles and life histories at the origin of multicellularity

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[a] Speaker

The evolution of multicellularity has given rise to a remarkable diversity of multicellular life cycles and life histories. Whereas some multicellular organisms are long-lived, grow through cell division, and repeatedly release single-celled propagules (e.g. animals), others are short-lived, form by aggregation, and propagate only once, by generating large amounts of solitary cells (e.g. cellular slime molds). There are no systematic studies yet that explore how this diversity in multicellular life cycles has come about. We developed a mechanistic model to examine the primitive multicellular life cycles that emerge from a unicellular ancestor when an ancestral gene is co-opted for cell adhesion. Diverse life cycles readily evolve, depending on the ecological conditions, physiological constraints, and the way by which cells form groups. Among these life cycles, we recapitulate both extremes of long-lived groups that propagate continuously and of short-lived groups that propagate only once, with the latter type of life cycle being particularly favored when groups can form by aggregation. Our results show how diverse multicellular life cycles and life histories could have evolved at the very origin of multicellularity. Beyond multicellularity, this finding has similar implications for other major hierarchical transitions, such as the evolution of social behavior.

Keywords: multicellularity, life cycles, social evolution

M9.6 – Differentiation without aggregation: bet-hedging in unicellular organisms through the exploitation of noise in gene expression

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Bet-hedging strategies consist in minimizing fitness variance in order to promote long-term fitness. They are expected to evolve when the level of environmental stochastic fluctuations overcomes a certain threshold. These strategies are commonly observed across a diversity of taxa, from microorganisms to many multicellular organisms, often in the form of diversified bet-hedging in which a genotype produces two or more phenotypes. However, the mechanism triggering DBH often remains unclear. Here, I introduce an evolutionary model designed to determine under which conditions Evolution may favor genotypes that exploit noise in gene expression to randomly produce distinct phenotypes and study how it in turn influences cell and genome features. Within a cell, the model simulates the lifetime dynamics of gene expression through gene networks subject to noisy gene expression. Fitness emerges from a mechanistic birth-death process: cells feed on two types of nutrients through diffusion processes to produce energy. The energy is then used to grow until the cell reaches a threshold size at which it splits into two daughter cells. The availability of each nutrient may fluctuate stochastically in time, and the capability to exploit any type of nutrients depends on the intracellular concentration of specialized proteins. We also assume that intracellular trafficking is optimal at an intermediate protein content, such that high expressions requires an increase in cell size that, in turn, reduces the surface to volume ratio and the per capita food intake. This framework based on mechanistic assumptions is very appropriate to study cases where transfers of fitness arise, and will be employed to consider various scenarios in the evolution of complexity and multicellularity. We anticipate that the scenario advanced here, where cell differentiation has evolved without (or before) cell aggregation, might challenge the mainstream paradigm according to which multicellularity evolved first through aggregation thenby differentiation.

Keywords: noise, differentiation, bet hedging, stochastic environments, evolution, mechanistic model

Mini-symposium 10 – Models of Cancer Evolution and Ecology

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Cancer is a by-product of somatic evolution, in which asexual cell populations reproduce and dynamically adapt to environmental pressures that can vary in time and space within the host organism. Publicly available multi-omics data analyses of cancer and associated pre-malignancies are increasingly more common due to novel technologies, with the intention to obtain a clearer view of what the cancer ecosystem consists of in vivo.
Indeed, a complex system of regulation and feedbacks are involved in carcinogenesis beyond genetic mutations, such as cell-cell interactions in a shared environment, immune response, and therapeutic reactions. There is therefore a need to understand the processes shaping the observed data, ranging from molecular traits to tissue architectures, which still largely stem from static end point observations.
Quantitative and multiscale models of carcinogenesis incorporating evolutionary mechanisms provide frameworks to test hypotheses of how certain observed data features (mutational spectrums, phenotype diversity, inter-tumour heterogeneity, etc.) could be generated during an organism's life history – questions that cannot be reasonably assessed by simple observational studies.
As the depth of data on cancer genomes and ecology becomes more profound, models are poised to make exciting contributions to the understanding of cancer dynamics and the impact of different components in such a complex system, with the potential to forecast individual disease trajectories and guide clinical decisions.
In particular, we will focus on how tumors arise in the soma (e.g., modeling mutational processes, classifying and identifying driver/passenger mutations, describing the dynamics of mutant cell populations before the appearance of the first neoplastic cell) and evolve during their host's lifetime.
The aim of this mini-symposium is to discuss the challenges, advances and current development of mathematical models of cancer evolution and ecology, that allow the investigation of the unseen evolutionary processes underlying both cancer initiation and its adaption to therapeutic pressures.

M10.1 – Quantifying selection in somatic genomes

Marc Williams [a 1]

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[a] Speaker

There has been long-standing interest in elucidating selection pressures in somatic cells that drive clonal expansions, and ultimately cause malignant cancers. One approach that can be useful in this endeavor is to use information that is encoded in the clone size distribution. That is the distribution of the number or proportion of cells carrying individual mutations. We used a mathematical model based on a branching process framework to elucidate how selection is encoded in these distributions. Then, together with Bayesian inference, we fit the model to data from deep sequencing of bulk cancer samples. This demonstrated that observable subclones under selection have strikingly high selective advantages ($> 20\%$) and emerge early (within the first 15 doublings) during tumour growth. We also develop a similar approach that clarifies the interpretation of the non-synonymous to synonymous ratio (dN/dS) as used in somatic genomes. This enables us to quantify the proliferative bias induced by mutations in cancer driver genes in physiologically normal oesophagus and sking tissue.

Keywords: cancer, evolution, somatic

M10.2 – Modelling the evolution of viral oncogenesis

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Most human oncogenic viruses share several characteristics, such as being DNA viruses, having long (co)evolutionary histories with their hosts and causing either latent or chronic infections. They can reach high prevalences while causing relatively low case mortality, which makes them quite fit according to virulence evolution theory. After analysing the life-histories of DNA oncoviruses, we use a mathematical modelling approach to investigate how the virus life cycle may generate selective pressures favouring or acting against oncogenesis at the within-host or at the between-host level. In particular, we focus on two oncoprotein activities, namely extending cell life expectancy and increasing cell proliferation rate. These have immediate benefits (increasing viral population size) but can be associated with fitness costs at the epidemiological level (increasing recovery rate or risk of cancer) thus creating evolutionary trade-offs. We interpret the results of our nested model in the light of the biological features and identify future perspectives for modelling oncovirus dynamics and evolution.

Keywords: cancer, virus, within, host dynamics, virulence, transmission, life cycle

M10.3 – Cancer evolution in hierarchically-organised tissues

Peter Ashcroft [a 1], Sebastian Bonhoeffer [1]

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[a] Speaker

The hematopoietic system is an archetypal example of a hierarchical population structure: Multipotent stem cells, which have the potential to reconstitute the full complement of blood-based cells, lie at the top of this hierarchy, and then a complex division tree provides diversification and amplification of the progenitor and terminally-differentiated cells. Here we use mathematical models to asses how this tissue structure affects the rate of mutation occurrence and the conditions required for a mutant to be successful. These conditions include the stage of differentiation where the mutant can emerge, the effect of the mutation on the cells proliferative properties, and the role of regulatory mechanisms. Quantifying the probability of mutant establishment is achieved through branching process approximations, while estimating how mutations spread through the system requires more general methods from evolutionary dynamics. Through this work, we show that tissue structures which minimise the cumulative divisional load also minimise the chance of mutation establishment, but the amplification of cell numbers can give delayed-effect mutants an increased chance of survival.

Keywords: Hematopoiesis, Stem cell, Cancer, Evolutionary dynamics

M10.4 – Improving Treatment of Metastatic Cancers through Game Theory

Katerina Stankova [a] [1]

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[a] Speaker

While systemic therapy for disseminated cancer is often initially successful, malignant cells, using diverse adaptive strategies encoded in the human genome, almost invariably evolve resistance, leading to treatment failure. Thus, the Darwinian dynamics of resistance are formidable barriers to all forms of systemic cancer treatment but rarely integrated into clinical trial design or included within precision oncology initiatives.
In this talk, we will investigate cancer treatment as a game-theoretic contest between the physician's therapy and the cancer cells' resistance strategies. This game has two critical asymmetries: (1) Only the physician can play rationally. Cancer cells, like all evolving organisms, can only adapt to current conditions; they can neither anticipate nor evolve adaptations for treatments that the physician has not yet applied. (2) It has a distinctive Stackelberg (i.e. leader-follower) dynamics; the "leader" oncologist plays first and the "follower" cancer cells then respond and adapt to therapy. Current treatment protocols for metastatic cancer typically exploit neither asymmetry. By repeatedly administering the same drug(s) until disease progression, the physician "plays" a fixed strategy even as the opposing cancer cells continuously evolve successful adaptive responses. By changing treatment only when the tumor progresses, treatment failure becomes nearly inevitable.
Using game theory, we will see how physicians can exploit the advantages inherent in the asymmetries of the cancer treatment game, and likely improve outcomes, by adopting more dynamic treatment protocols that integrate eco-evolutionary dynamics and modulate therapy accordingly. Implementing this approach will require new metrics of tumor eco-evolutionary response.

Keywords: game theory, metastatic cancer, Stackelberg game theory, treatment, induced resistance

M10.5 – The Evolutionary Dynamics and Fitness Landscape of Clonal Haematopoiesis

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[a] Speaker

Somatic mutations acquired in healthy tissues as we age are major determinants of cancer risk. Whether variants confer a fitness advantage or rise to detectable frequencies by chance, however, remains largely unknown. By combining blood sequencing data from ∼50,000 individuals, we reveal how mutation, genetic drift and fitness differences combine to shape the genetic diversity of healthy blood ('clonal haematopoiesis'). By analysing the spectrum of variant allele frequencies we quantifty fitness advantages for key pathogenic variants and genes and provide bounds on the number of haematopoietic stem cells. Positive selection, not drift, is the major force shaping clonal haematopoiesis. The remarkably wide variation in variant allele frequencies observed across individuals is driven by chance differences in the timing of mutation acquisition combined with differences in the cell-intrinsic fitness effect of variants. Contrary to the widely held view that clonal haematopoiesis is driven by ageing-related alterations in the stem cell niche, the data are consistent with the age dependence being driven simply by continuing risk of mutations and subsequent clonal expansions that lead to increased detectability at older ages.

Keywords: clonal haematopoiesis, haematopoietic stem cells, evolution, population genetics, acute myeloid leukaemia, mathematical models

M10.6 – Maximum likelihood estimation of single-cell phylogenies

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We have developed a maximum likelihood framework for inferring phylogenetic trees from multilocus NGS genotypes that can be directly applied to single-tumor cells or tumor clones. Our framework is based on a finite-site Markov nucleotide substitution model with 10 diploid states (A/A, A/C,..., G/T), akin to those typically used in statistical phylogenetics. Our model allows for different parameterizations regarding substitution probabilities, nucleotide frequencies, or rate variation among loci. Moreover, our model captures genotype uncertainty using a dedicated error function for single cells that explicitly considers sequencing error and/or allelic dropout. It can also take into account genotype likelihoods from third-party NGS genotype callers. We implemented this model in a widely used open-source phylogenetic inference package (RAxML-NG), that scales particularly well for large phylogenies with hundreds and even thousands of cells. In order to benchmark the accuracy of our implementation, we carried out coalescent simulations of cell samples from an exponentially-growing tumor where the true phylogeny is known. We evolved single-cell diploid DNA genotypes along the coalescent tree under infinite and finite nucleotide mutation models, including trinucleotide mutational signatures, sequencing and amplification errors, allelic dropouts, and doublet cells under different scenarios. These simulations suggest that our method is quite robust to amplification/sequencing errors and to allelic dropout and that it at least matches and often outperforms competing methods (SCITE, SiFit, and TNT) under realistic single-cell NGS scenarios.

Keywords: single cell, somatic evolution, phylogenetics

M10.7 – Modeling the molecular evolution of cancer with scaled selection coefficients and epistasis: a Markov matrix approach

Jeffrey Townsend [a] [1], Stephen Gaffney [1], Vincent Cannataro [2]

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[2] Emmanuel College – United States

[a] Speaker

Since the advent of whole-exome and whole-genome sequencing of tumor tissues, studies of somatic mutations have revealed the underlying genetic architecture of cancer producing ordered lists of significantly mutated genes that imply their relative importance to tumorigenesis and cancer development. Two quantifications have ordered the importance of discovered cancer "driver" genes: the prevalence of gene mutation among tumor tissues sequenced from that tumor type, the statistical significance (P value) of the disproportionality of mutation frequency, or both. However, neither of these metrics provide insight into the evolutionary process. Building on classical population genetics and molecular evolutionary theory, we have developed a data-driven mathematical modeling approach that provides a comprehensive means to evaluate how somatic mutations interact to influence cancer progression in multiple cancer types and that can be projected to provide a genotype-based fitness landscape for tumorigenesis. Using our data-driven model, we have quantified how mutation and selection lead to stage-specific progression and metastasis, in particular revealing the epistatic effects between known somatic mutations and providing probabilistic trajectories of tumor evolution associated with cancer stage progression and therapeutic treatment. Predictions from the model enable better basic research prioritization, faster therapeutic discovery, efficient clinical trial design, and have implications for medical decision-making by precision medicine tumor boards.

Keywords: cancer effect sizes, selection intensity, somatic evolution, epistasis, molecular evolution

M10.8 – Tradeoffs in species coevolution and drug reistance in cancer

Weini Huang [a] [1]

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[a] Speaker

Cancer is an evolving system, where new mutations may lead to advantage or disadvantage in growth and survival and drive their clonal expansion. While trade-off is a fundamental concept in evolution, investigating cancer as an evolutionary process offers new opportunities to tackle the problem of drug-resistance. Biological systems including cancer usually emerge from interactions of individuals with different traits. Often those traits are linked and the optimization of all traits independently is impossible due to the tradeoffs among multiple traits. For example, energy or resources allocated to survival is not available for reproduction. Here, I will present mathematical models and their applications on experiments to understand the role of survival-reproduction tradeoffs in the evolutionary dynamics of a predator-prey system as well as in cancer with chemotherapy resistance. While in the predator-prey coevolutionary system, we found that the shape of tradeoffs also evolves and has an important impact on population diversity level; in the evolution of cancer resistance, the existence of tradeoffs may open an opportunity to control resistant subpopulations with specifically designed evolutionary treatment strategies.

Keywords: Tradeoffs, Cancer Resistance, Predator, Prey systems

M10.9 – Stochastic modeling of the sequential accumulation of driver mutations

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[a] Speaker

It has been recently shown that the lifetime risk of cancer across many different tissues is strongly correlated with the lifetime number of divisions of the normal self-renewing cells in those tissues. We seek to assess the relative contributions to cancer of pure chance on the one hand (cancer as a consequence of normal somatic mutation rates) and of other causes on the other hand (harmful human lifestyles, environmental exposures, inherited genetic defects). For this purpose we propose a stochastic model of carcinogenesis integrating tissue dynamics and its interaction with tumorigenesis to evaluate the distribution of the waiting time until cancer is declared. In this model, we consider each possible sequence of k driver mutations, with k = 2 or 3. Moreover, we steer clear of the classical yet somewhat unrealistic assumption of an exponential tumoral growth. Instead, we take into account the early fluctuations of any newly arising cell population, and assume a logistic growth following the initial stochastic phase.

Keywords: tumor growth, driver mutations, stem cells, birth, and, death process, logistic growth, relative risk

M10.10 – Darwinian immunotherapy: a new approach for cancer treatment?

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[a] Speaker

Today, cancer is the first cause of mortality in Western countries. Despite constant progresses in discoveries of chemotherapy drugs, clinicians are always facing the problem of drug resistance. To overcome this issue, it has been recently proposed to adopt an evolutionary approach for chemotherapy (adaptive chemotherapy) through a carefully designed drug administration in order to keep competition between healthy and cancerous cells. While this approach is extremely encouraging and has shown some very good premises in clinical trials, it is still too early to see in which conditions this approach could be applied safely. In this study, we investigate through mathematical modeling how this kind of evolutionary approach could be applied to immunotherapy as well. While classical chemotherapy is targeting more a cellular phenotype, immunotherapy treatments are targeting a wide range of cellular genotypes. Through considering genotype diversity instead of phenotype diversity, we show that adaptive chemotherapy could generate more genetic diversity within the tumor, yielding potentially more dangerous cancer. On the opposite, Darwinian immunotherapy could decrease both genotype and phenotype diversities and could delay for a longer time the emergence of drug resistance. Finally, we discuss about the conditions required to envision such Darwinian immunotherapy, and compare them to what could be expected with adaptive chemotherapy.

Keywords: –

Session 1-1 – Phylogenies / Population genetics

Wednesday, July 17, 2019 – 10:15-12:15 – Room 1

S1-1.1 – Integration of population genetics theory into phylogenetic methodology and the estimation of the strength of natural selection

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The ratio of non-synonymous over synonymous sequence divergence, dN/dS, is a widely-used estimate of the non-synonymous over synonymous fixation rate ratio ω, which measures the extent to which natural selection modulates protein sequence evolution. Its computation is based on a phylogenetic approach and computes sequence divergence of protein-coding DNA between species, traditionally using a single representative DNA sequence per species. This approach ignores the presence of polymorphisms and relies on the indirect assumption that new mutations fix instantaneously, an assumption which is generally violated and reasonable only for distantly related species. The violation of the underlying assumption leads to a time-dependence of sequence divergence, and biased estimates of ω in particular for closely related species, where the contribution of ancestral and lineage-specific polymorphisms to sequence divergence is substantial. We here use a time-dependent Poisson random field model to derive an analytical expression of dN/dS as a function of divergence time and sample size. We further extend our framework to the estimation of the proportion of adaptive protein evolution α. This mathematical treatment enables us to show that the joint usage of polymorphism and divergence data can assist the inference of selection for closely related species. Moreover, our analytical results provide the basis for a protocol for the estimation of ω and α for closely related species. We illustrate the performance of this protocol by studying a population dataset of four corvid species, which involves the estimation of ω and α at different time-scales and for several choices of sample sizes.

Keywords: population genetics theory, phylogenetic methodology, Poisson random field model, dN/dS, natural selection

S1-1.2 – Fluctuating population size in phylogenetic codon models.

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Mutation, selection and drift in protein-coding sequences can be detected based on multiple sequence alignments using phylogenetic codon models. Mechanistic approaches, grounded on population-genetics first principles, have been recently developed. These so-called mutation-selection models explicitly formalize the interplay between mutation, selection and drift, and return an estimate of the amino-acid fitness landscape, considered static along the phylogeny. They were recently proposed as a null (nearly-neutral) model against which to test for the presence of adaptation (Rodrigue, Lartillot MBE 2016, Bloom, 2016). However, these models rely on the assumption of multiplicative fitness landscapes (no epistasis) and constant population size; they also ignore polymorphism in extant species, with only one sequence representing the whole population. As a result, they return potentially biased estimates. We propose an extended mutation-selection model relaxing some of these assumptions, by accommodating for fluctuating population size and fluctuating mutation rate along the phylogeny, and by modeling polymorphism in extant species. The resulting mechanistic framework allows for a reconstruction of long-term trends in population size along the phylogeny. Simultaneously, it offers a better background for detecting adaptation across large clades, by correcting for local changes in the relative strength of selection and random drift. Finally, our work also points to important theoretical questions about how coding sequences respond to changes in effective population size and to selection.

Keywords: phylogenetic, codon models, mutation, selection, fluctuating population size

S1-1.3 – An MCMC-based method for Bayesian inference of natural selection from time series DNA data across linked loci

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The rapid improvement of DNA sequencing technology has made it possible to monitor genomes in great detail over time, which presents an opportunity for investigating natural selection based on time serial samples of genomes while accounting for genetic recombination. Such time series genetic data allow for more precise estimates for population genetic quantities and hypothesis testing on the recent action of natural selection. In this work, we develop a novel Bayesian statistical framework for the inference of natural selection by capitalising on the temporal aspect of DNA data across linked loci, regardless of whether sampled chromosomes have been phased or not. Our approach relies on a hidden Markov model incorporating the two-locus Wright-Fisher diffusion with selection, which enables us to explicitly model genetic recombination. In the posterior computation, the Wright-Fisher stochastic differential equation is reformulated in a closed form that is amenable to simulation, which enables us to avoid boundary issues and reduce computational costs, and the posterior probability distribution for selection coefficients is obtained by using the particle marginal Metropolis-Hastings algorithm, which also allows for co-estimation of the population haplotype frequency trajectories. The performance of our method is evaluated through extensive simulations, showing that our estimates for selection coefficients are unbiased. Moreover, under certain circumstances, we find that our method can deliver precise estimates for selection coefficients whereas existing single-locus approaches fail, especially for tightly linked loci. The utility of our method is illustrated with an application to the loci encoding white spotting patterns in horses, where we also show that our method can handle missing values.

Keywords: natural selection, genetic recombination, linked loci, Wright, Fisher diffusion, hidden Markov model, particle marginal Metropolis Hastings

S1-1.4 – The effect of epistasis on local adaptation with gene flow

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[a] Speaker

There is little consensus on the importance of epistasis for local adaptation. Here, we investigate the possibility of establishment of weakly locally adaptive de-novo mutations in the face of gene flow, linkage and epistatis.
This process is studied by applying a two-type branching process to the underlying two-locus two-allele model with continent-island migration. The new mutation appears on the island and its offspring distribution depends on the background allele. We use the theory of two-type branching processes to determine the dependence of the establishment probability on the parameters, i.e., selective coefficients of the alleles, migration and recombination rate and epistasis. In general, this establishment probability can not be expressed in closed form, however, we derive an explicit expression that is a good approximation. We use this approximation to predict the average establishment probability over all possible linked mutations. This, in turn, can be used to calculate the approximate size of a genomic island that evolves via the benefit of selection at a linked background locus.

Keywords: local adaptation, gene flow, epistasis, branching process, linked selection

S1-1.5 – Quantifying somatic evolution in human cancers by mathematical modelling and genomic sequencing data.

Benjamin Werner [a 1]

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[a] Speaker

Human cancers usually contain hundreds of billions of cells at diagnosis. During tumour growth these cells accumulate thousand of mutations, errors in the DNA, making each tumour cell unique. This heterogeneity is a major source for evolution within single tumours, subsequent progression and possible treatment resistance. Recent technological advances such as increasingly cheapen genome sequencing allows measuring some of the heterogeneity. However, the theoretical understanding and interpretation of the available data remains mostly unclear. For example, the most basic evolutionary properties of human tumours, such as mutation and cell survival rates or tumour ages are mostly unknown. Here I will present mathematical modelling of the underlying stochastic processes. In more detail, I will construct the distribution of mutational distances in a tumour that can be measured from multi-region sequencing. I show that these distributions can be understood as random sums of independent random variables. In combination with appropriate sequencing data and Bayesian inference based on our theoretical results some of the evolutionary parameters can be recovered for tumours of single patients.

Keywords: Cancer evolution, genomic sequencing data, population genetics, per, cell mutation and per, cell survival rate

S1-1.6 – The effects of epistasis and pleiotropy on local adaptation and the detection of adaptive outlier loci

Reinhard Bürger [ab 1] Adam Jones[c 2], Stevan Arnold [2]

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The search for individual loci underlying local adaptation has become a major enterprise in evolutionary biology. One promising method to identify such loci is to examine genome-wide patterns of differentiation, using an FST-outlier approach. The effects of pleiotropy and epistasis on this approach are not yet known. We modeled two populations of a sexually reproducing, diploid organism with two quantitative traits, one of which is involved in local adaptation. We consider genetic architectures with and without pleiotropy and epistasis. We also model neutral marker loci on an explicit genetic map as the populations diverge. We apply FST outlier approaches to determine the extent to which quantitative trait loci (QTL) are detectable. Our results show, under a wide range of conditions, that only a small number of QTL are responsible for most of the trait divergence between the populations, even when inheritance is highly polygenic. We find that the loci making the largest contributions to trait divergence tend to be detectable outliers. These loci also make the largest contributions to within-population genetic variance. Pleiotropy reduces the extent to which quantitative traits can evolve independently but does not reduce the efficacy of outlier scans. The addition of epistasis, however, reduces the mean FST values for causative QTL, making these loci more difficult to detect.

Keywords: population genomics, local adaptation, migration, quantitative trait loci, F_ST

Session 1-2 – Food web evolution

Wednesday, July 17, 2019 – 10:35-12:15 – Room 2

S1-2.1 – A step toward identifying what really promotes food webs evolution

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In the litterature, several models of food web evolution have been introduced and numerically analysed. In this presentation, we aim at better identifying the key mechanisms and assumptions that promote the emergence of trophic network in a class of eco-evolutionary models previously proposed in the litterature. In particular, some biological conditions of these models seem to be arbitrary and not justified from an ecological point of view. We will show that relaxing strong assumptions of these models can give rise to degenerate trophic network. We will then propose a way to obtain satisfying foodweb topologies, without artificial constrain, modifying the biomass conversion efficiency in accordance with empirical data. Exploring a single family of functions for the biomass conversion efficiency, we will present the emerging foodweb structures w.r.t. the parameters of the family of functions, based on numerical simulations and fitness analysis. Moreover, we will discuss the importance of the relative evolutionary speed of evolving traits in the emerging foodweb structures.

Keywords: food web model, adaptive dynamics

[a] Speaker

S1-2.2 – Achieving minimum time pest eradication by providing the optimal quality of additional food to the predator in a predator-prey system involving type III functional response

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Mathematical modeling of ecological problems to achieve biological control has become an active research area. This field is motivated by the field studies in agricultural entomology and pest control. These problems are modeled as predator-prey systems with pests as prey and their natural enemies as predators. One of the approaches for achieving biological control is to provide additional food to the predators in order to effectively control the pests(prey). However, the effect of additional food provided depends on the quality and quantity of additional food. Type III functional response for predators is a sigmoidal density-dependent response, known to stabilize the ecosystem under low prey densities. A detailed theoretical investigation of predator-prey systems with predator exhibiting type III response was done by the authors. The results convey that, by providing predators with high quality additional food (with specified quantity), one can not onlycontrol pests (prey) but also eradicate them from the system. While this is a reasonable outcome, the major limitation is that the system reaches the required state eventually as an asymptote. This is a major concern for practical implementation of the study. Hence, in this work, we first analyze the controllability of the system by considering inverse of quality of the additional food as the control variable and offer control strategies to steer the system to the desired equilibrium state in minimum time. This is done by formulation of a Time-Optimal ontrol problem with quality of additional food as the control parameter. We observe that the optimal strategy is a combination of bang-bang controls. The properties of the optimal paths are derived from the Maximum Principle. With these results, we conclude that pests can be eradicated in minimum time by providing high quality additional food to the predator.

Keywords: Predator_prey systems, Additional food provision, Biological Control, Pest eradication, Optimal Control Problem, Bang_Bang Controls, Maximum Principle

S1-2.3 – Effects of trait variation on ecosystem function variability and resillience in tritrophic food webs

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Diverse communities can adjust their trait composition to altered environmental conditions, which may strongly influence their dynamics. Previous studies of trait-based models mainly considered only one or two trophic levels, whereas most natural system are at least tritrophic. Therefore, we investigated how the addition of trait variation to each trophic level influences population and community dynamics in a tritrophic model. Examining the phase relationships between species of adjacent trophic levels informs about the degree of top-down or bottom-up control in non-steady-state situations. Phase relationships within a trophic level highlight compensatory dynamical patterns between functionally different species, which are responsible for dampening the community temporal variability. Furthermore, even without trait variation, our tritrophic model always exhibits regions with two alternative states with either weak or strong nutrient exploitation, and correspondingly low or high biomass production at the top level. However, adding trait variation increased the basin of attraction of the high-production state, and decreased the likelihood of a critical transition from the high- to the low-production state with no apparent early warning signals. Hence, we show how trait variation enhances resource use efficiency, production, stability, and resilience of entire food webs.

Keywords: trait, based model, functional traits, phase relationships, compensatory dynamics, food web, alternative stable states

S1-2.4 – Space and migration in an eco-evolutionary food web model

Gavin Abernethy [a] [1]

[1] Sheffield Hallam University – United Kingdom

[a] Speaker

Our understanding of food web functioning has been imbued with renewed significance in recent decades as biodiversity loss, pollution, climate change, and other conservation issues regarding the anthropological impact on natural communities moved to the forefront of the interests of the scientific community. Eco-evolutionary models utilise feedback between evolutionary and ecological processes in constructing an evolving community of species, and can be used to test the response of such ecosystems to perturbations such as extinction waves or habitat destruction. The Webworld model (Drossel et al, 2001) is a well-known example of this class of model, combining foraging, feeding and reproduction, and evolutionary processes (mutation and speciation) on three distinct but interlinked timescales. Species are defined by an allocation of discrete features which determine the strength and direction of feeding relationships. Speciation is modelled by introducing a mutant with a small population that retains all but one of the parent's features, with the other having been randomly replaced, and iterating the model's population dynamics to determine whether or not this new species is able to establish itself in the food web. This presentation will describe a recent extension of the Webworld model to a spatially-explicit community of communities (Abernethy et al, 2018), and explore the impact of allowing migration between different ecosystems constructed and maintained by the model's rules. The role of spatial topology, variation between the habitat's parameters, and different rules governing species migration will be investigated, and we shall consider the impact of habitat destruction and population displacement on the meta-community.

Keywords: Food web model, Spatial model, Meta, community

S1-2.5 – Demographic and evolutionary feedback between selective predation and tolerance evolution

Caterina Vitale [a] [1]

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[a] Speaker

Whether a host defends itself from parasitism through resistance strategies (e.g. lowered transmission, increased recovery) or tolerance strategies (e.g. reduced mortality during infection) changes drastically the possible evolutionary outcomes of defence evolution. Previous work has unravelled how these two different categories of defence induce different ecological feedbacks to parasite prevalence, showing that while resistance decreases parasite prevalence and reduces its own selective pressure, tolerance strategies boost parasite growth and increase selection for tolerance. Thus, theoretical models traditionally predict fixation as the most likely outcome for tolerance.
Here, I will examine how taking into account community interactions can broaden these traditional results. Particularly, I will focus on the impact of including in the system a predator species of the host, which selects to feed preferentially either on healthy or infected prey. Firstly, I will examine how predator selectivity can introduce interesting patterns of bi-stability between co-existence and parasite extinction. Secondly, I will show how the additional ecological feedback induced by the predator allows tolerance branching or non-monotonous trends in the optimal evolutionary strategy.
As the interest for tolerance strategies is increasing in different research the aim of this theoretical study is to identify potential new avenues for further research with closer
integration between modellers and empiricists.

Keywords: tolerance evolution, selective predation, ecoepidemiological model, adaptive dynamics

Session 1-3 – Population dynamics

Wednesday, July 17, 2019 – 10:15-12:15 – Room 3

S1-3.1 – Inferring Mechanisms that Drive Population Dynamics Using Stochastic, Age-Structured Population Models.

Gian Marco Palamra [ab] [1], Stuart Dennis [2], Corinne Haenngi [2], Nele Schuwirth [1], Peter Reichert [1]

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Species with a complex life cycle are common in nature and are widely used as model organisms in different ecological studies. Distinct modelling approaches, with diverse mathematical structures, ranging from individual based models to age-, size- and stage-structured population models have been used to describe such life cycles. Furthermore, different model structures and parameterizations have been used to make inference and test ecological mechanisms affecting population dynamics. We derive a general, density-dependent, stochastic age-structured population model, and build a framework to infer model parameters from time series, using a Bayesian multi-model approach. Using our framework, we infer population parameters for replicated time series data from an experiment with clonal populations of *Daphnia galeata* feeding on *Scenedesmus obliquus*, under different environmental treatments. Daphnia populations are characterized by detectable life stages and a low number of individuals, leading to a highly relevant contribution of demographic stochasticity to population dynamics. We show how to identify the relevant ecological mechanisms affecting Daphnia's fecundity and mortality despite the presence of high demographic noise. Our findings stress the importance of using a multi-model approach to infer relevant model parameters in order to better understand the mechanisms affecting the dynamics of ecological populations. Our modelling approach merges different theoretical perspectives and can be further generalized to include other discrete population models.

Keywords: Structured Populations, Demographic Stochasticity, Bayesian Inference

S1-3.2 – How negatively temporally autocorrelated environments affect natural populations? Wild boar as a case study.

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All natural populations are exerted to stochastic variations in the environment. Such fluctuations commonly cause temporal variation in vital rates of individuals (i.e. survival, growth and reproduction), and thus in population dynamics. In the ecological literature, this stochasticity has most often been modelled as white noise, unrealistically assuming independent and identically distributed environmental conditions. Recent evidence indicate that temporal autocorrelation in demographic processes constitutes an important aspect of population dynamics and thus strongly influences the extent to which the populations are buffered against variations in the environment. Mast-seeding (or masting) characterized by seed production dynamics that are both highly fluctuating and have a pronounced negative temporal autocorrelation provides an ideal context to investigate how environmental autocorrelation influences the stochastic growth rate, as well as the variance in population size of structured consumer populations. Taking advantage of a long-term monitoring of a wild boar (*Sus scrofa*) population, which mainly feeds on mast production, we aim to estimate the effects of the negative temporal autocorrelation characterizing mast seeding on the demography of this population.

Keywords: mast seeding, stochastic growth rate, temporal autocorrelation, transition elasticity, Sus scrofa

S1-3.3 – The dynamics of stress generation determine the migration behavior of phytoplankton in turbulence

Francesco Carrara [ab 1], Anupam Sengupta [2], Lars Behrendt [1], Assaf Vardi [3], Roman Stocker [1]

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Phytoplankton inhabit a dynamic environment where turbulence, together with nutrient and light, shapes species fitness, succession and selection. Many species of phytoplankton are motile and undertake diel vertical migrations to gain access to nutrient-rich deeper layers at night and well-lit surface waters during the day. Disruption of this migratory strategy by turbulence is considered to be an important cause of the succession between motile and non-motile species when conditions turn turbulent. However, this classical view neglects the possibility that motile species may actively respond to turbulent cues. Recently, some phytoplankton species were found to be capable of active responses to turbulence, by altering their direction of vertical migration.

Here, we show that turbulent cues – within only tens of seconds – elicits a bistable stress response in marine phytoplankton and that this bistable response underpins the diversification of their swimming behavior – a split into upward and downward swimmers. The emergent downward-migrating subpopulation accumulated two-fold higher levels of reactive oxygen species, an indicator of stress, and exhibited a 15% lower photosynthetic quantum yield and a 40% smaller growth rate. A mathematical model shows that phytoplankton use mechanical stability to sense the strength of turbulence, and integrate its temporal structure via rapid ROS signaling. The cell's mechanical stability imposes a high-pass filter on a turbulent signal, whereby only the velocity fluctuations faster than the stability timescale can reorient the upward swimming cell, and trigger the emergence of the downward motility. This results in alternating between 'tumbling phases', during which stress is generated, and 'resting phases', where the cell navigates at a fixed orientation and dissipates the accumulated stress. These results show that motile phytoplankton harness the dynamics of ROS-signaling to regulate their migratory behavior in response to turbulence, and provide a mechanistic link between microscale physiology and macroscale population dynamics.

Keywords: Phytoplankton motility, Stress dynamics, Fluid dynamics, Population dynamics

S1-3.4 – The carrying simplex in non-competitive Lotka–Volterra systems

Atheeta Ching [ab 1], Stephen Baigent [1]

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For some competitive Kolmorogov systems, there is an invariant Lipschitz manifold called the carrying simplex which is well studied. It is a global attractor and its convexity affects the behaviour of the system. This manifold exists in competitive Lotka–Volterra population models where it is the boundary of the basin of repulsion of the origin and contains all non-trivial limit sets. It also contains the heteroclinic orbits connecting non-zero steady states. Our research explores non-competitive systems, where we have found an analytic formula for the analogous 'carrying simplex' in the two species case, which we call the balance simplex. Our most recent work looks at the three species system where we have proved the existence of balance simplices and have a method of plotting them as a series solution, whilst matching exactly the known analytic solutions on the two species boundaries. We have also been able to find an exact form for the balance simplex when all species interaction coefficients are equal and competitive.

Keywords: Carrying simplex, invariant manifold, heteroclinic orbit, ODEs

S1-3.5 – Backward prediction in Markov-chain models: a routine or sophistication?

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[a] Speaker

In general, *backward prediction*means the use of the subsequent values of an observed process in order to find the previous ones. The routine substitution of $-t$ for t, which is common for ODEs, does not find an immediate analogue in the system of difference equations $x(t + 1) = Px(t)$with stochastic vectors $x(t)$ and stochastic matrix P as the transition matrix of a Markov chain, neither in theoretical, nor in practical terms. Since the theory suggests global convergence to the single limiting vector x^* for any initial one, $x(0)$, close values in a small vicinity of x^* diverge greatly in the reversed time, depriving the "prediction" of any sense. The practical observation that the one-step backward prediction is algebraically trivial, $x(t - 1) = P\hat{}-\mathbf{1}x(t)$, does not make sense (is useless) already for the next step as the invers matrix, $P\hat{}-\mathbf{1}$, is typically not stochastic.
However, I show how, with what purpose, and with what result the idea of backward prediction can be realized in any finite Markov chain based on real observations, such as a chain that models the fine-scale dynamics of bilberry (*Vaccinium myrtillus*) vs. cowberry (*V. vitis-idaea*) at the mature stages of post-fire succession in a Scots pine boreal forest (Logofet, Maslov, 2019; Ecological Modelling, https://doi.org/10.1016/j.ecolmodel.2018.10.002).
Participation is supported by the RFBR, grant # 19-04-01227.

Keywords: Post, fire succession Fine, scale dynamics, Time, inhomogeneous Markov chain, Matrix average, Limiting distribution, Reversal of data, Backward prediction

S1-3.6 – Using multitrait population projection models to analyze the effects of individual life-history trade-offs on individual fitness

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[a] Speaker

It is increasingly recognized that the incorporation of Life History Trade-Offs (LHTOs) into evolutionary demography models requires the decomposition of the trade-offs into genetic and individual components. This is fundamental to understand how trade-offs are related to fixed and dynamic components of individual heterogeneities and generate variance in individual trajectories. Therefore, embedding such LHTOs into Population Projection Matrices (PPMs) usually requires three traits: a Life-History Determining (LHD) trait (e.g. age or stage), a fixed trait incorporating the genetic trade-off and a dynamic trait modeling the individual component. This has proved a complex exercise until the recent advent of Multitrait Population Projection Matrices (MPPMs). Recent developments of Trait-Level Analysis (TLA) tools for MPPMs now allow studying the demographic and evolutionary consequences of each component of a LHTO. Here, we illustrate this by constructing and analyzing an evolutionary demography model that implements both individual and genetic components of the Costs of Reproduction (CoR), the trade-off between current/early reproduction and future/later fitness. In particular, we explain and describe the use of the TLA to measure the effects of such an LHTO on individual fitness. In order to yield such computations, we provide novel calculations for R0 and its variance for age-structured models with/without fixed and with/without dynamic heterogeneity.

Keywords: multitrait matrices, population projection models, life history trade, offs, lifetime repructive success, R0, individual heterogeneity

Session 1-4 – Evolutionary community ecology

Wednesday, July 17, 2019 – 10:15-12:15 – Room 4

S1-4.1 – Individual-based modelling of cryptic coexistence: understanding the roles of dispersal and competition structure

Aisling Daly [ab 1], Nele De Meester [1], Jan Baetens , Tom Moens [1], Bernard De Baets [1]

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The coexistence of cryptic species (morphologically identical but genetically distinct) has been attributed to several different mechanisms, including differences in their resource use or tolerances to environmental conditions. Recent experimental work has confirmed this type of coexistence in a community of four cryptic *Litoditis marina* (nematode) species. We have developed an individual-based model of this community to help untangle the mechanisms governing its dynamics. This modelling approach was selected in order to capture both the system's individual variability and its spatial heterogeneity, two important features that can support the coexistence of competing species.
The model incorporates the key demographic processes occurring in the community: reproduction, competition, dispersal, and resource use. Data characterizing the cryptic species (in terms of their growth rates, dispersal ability, competitive interactions, and responses to changing environmental conditions) are used to parameterize the model.
Simulation studies and scenario analyses are used to investigate the fundamental mechanisms underlying the coexistence of these cryptic species. Differences in their stress tolerances play an important role in the dynamics of the system, while the persistence of the underlying competition structure is sensitive to biotic changes. In addition, dispersal is found to play a key role in mediating coexistence, with the density-dependent dispersal thresholds varying between the cryptic species. These results provide insights into the functionality of such communities threatened by climate-related abiotic changes.

Keywords: individual-based modelling, competition, dispersal, coexistence, cyclic competition

S1-4.2 – The evolution of trait variance creates a tension between species and functional diversity

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It seems intuitively obvious that species diversity begets functional (trait) diversity: the more plant species there are, the more varied their leaf chemistry will be; more species of crops provide more kinds of food; etc. In this talk I argue that the evolution of trait variance challenges this view. In a trait-based eco-evolutionary model, I show that when species richness is low, individual species evolve large trait variation and therefore broader niches, while in species-rich communities species avoid competition and find their niche by evolving narrow trait breadths. This effect can be so strong that those communities with more but narrower species will cover a smaller fraction of the available trait space than those with fewer but intraspecifically more variable ones. The expected positive relationship between species and functional diversity is thus overhauled, a result which proved extremely robust to changes in model setup and parameterization. I finish by presenting and discussing empirical data consistent with this claim.

Keywords: community ecology, eco evolutionary dynamics, functional diversity, species diversity, trait based ecology

S1-4.3 – How self-regulation, the storage effect and their interaction contribute to coexistence in stochastic and seasonal environments

Coralie Picoche [ab 1], Frédéric Barraquand [1,2]

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Explaining coexistence in species-rich communities of primary producers remains a challenge for ecologists because of their likely competition for shared resources. Following Hutchinson's seminal suggestion, many theoreticians have tried to create diversity through a fluctuating environment, which impairs or slows down competitive exclusion. However, fluctuating-environment models often only produce a dozen of coexisting species at best. Here, we investigate how to create richer communities in fluctuating environments, using an empirically parameterized model. Building on the forced Lotka-Volterra model of Scranton and Vasseur (2016, Theoretical Ecology), inspired by phytoplankton communities, we have investigated the effect of two coexistence mechanisms, namely the storage effect and higher intra- than interspecific competition strengths (i.e., strong self-regulation). We tuned the intra/inter competition ratio based on empirical analyses, in which self-regulation dominates interspecific interactions. Although a strong self-regulation maintained more species (50%) than the storage effect (25%), we show that none of the two coexistence mechanisms considered could ensure the coexistence of all species alone. Realistic seasonal environments only aggravated that picture, as they decreased persistence relative to a random environment. However, strong self-regulation and the storage effect combined superadditively so that all species could persist with both mechanisms at work. Our results suggest that combining different coexistence mechanisms into community models might be more fruitful than trying to find which mechanism best explains diversity. We additionally highlight that while biomass-trait distributions provide some clues regarding coexistence mechanisms, they cannot indicate unequivocally which mechanisms are at play.

Keywords: coexistence, seasonality, competition, phytoplankton, Lotka, Volterra, storage effect

S1-4.4 – Entropy production of microbial communities

Tim Depraetere [ab 1], Aisling Daly , Jan Baetens [1], Bernard De Baets [1]

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Assuming the existence of different species, and an ecological interaction network equipped with competitive, predatory and mutualistic interactions connecting those species, computational ecologists construct differential equations whose dynamics are analyzed in order to find out how species are able to coexist. While this approach has provided us with many insights, its strong assumptions restrict its usability when trying to answer more fundamental questions about the why and how of ecosystems and life in general.

Taking a step back to the basic laws of physics and chemistry, the principle of maximum entropy production stands out as one that might help us explain why ecosystems are structured the way they are. The principle proposes that the sole purpose for the existence of ecosystems is the transformation of high-quality energy, reaching planet earth in the form of sunlight, into low-quality energy, in the form of heat, through the production of entropy. It is thought that ecosystems are structured as to execute this task as efficiently as possible.

We explore the principle of maximum entropy production in the context of differential equations modelling microbial communities by considering a hypothetical reactor which is fed a carbon source at a constant rate. After devising a chemical reaction network which shows how chemical reactions can transform the carbon source into different reaction products, we define different species by their unique ability to take a certain chemical compound and transform it into another, as such harvesting Gibbs free energy that can be invested in the production of new biomass.

Evolving the resulting differential equations, one obtains a steady-state involving a number of species limited by both the competitive exclusion principle and syntrophic interactions. The entropy produced by this steady-state is subsequently calculated, and compared to the maximum entropy the ecosystem could produce under the reigning assumptions.

Keywords: population dynamics, ecological interaction network, principle of maximum entropy production

S1-4.5 – Evolution in interaction space

Farnoush Farahpour [a 1], Mohammadkarim Saeedghalati , Verena Brauer [1], Daniel Hoffmann [1]

[1] Universität Duisburg-Essen [Essen] – Germany

[a] Speaker

Eco-evolutionary models usually consider phenotypic traits as their evolving traits that continuously change and explore the phenotype space to optimize the fitness. In a system dominated by frequency-dependent selection the fate of a phenotypic trait is determined via its interactions and thus phenotypic variations are relevant only when they change the interaction of organisms, otherwise they do not impact ecological dynamics. This suggests that we can study macro-evolutionary dynamics, like emergence of diversity and speciation, using interaction-based eco-evolutionary models. Such a model relies on the assumption that phenotypic evolution can be mapped to the interaction level. This means that regardless of the details of phenotypic variations, we just study the resultant changes in the interaction network. The interaction level is still sufficiently detailed to model macro-evolutionary dynamics that are dominated by ecological interactions. A transition from phenotype space to interaction space requires a mapping from the former to the latter. Here I present the results of our interaction-based model developed to study emergence of diversity in competitive communities. I will explain some advantages and disadvantages of the coarse-graining to the interaction level and some properties of phenotype-interaction map.

Keywords: Eco, evolutionary dynamics, Interaction trait, Phenotype, Interaction map

S1-4.6 – Being indispensable ensures coexistence under shared predation

Michael Raatz [a 1,2], Svenja Schälicke [2], Michael Sieber [1], Ursula Gaedke [2], Alexander Wacker [2,3]

[1] Max Planck Institute for Evolutionary Biology – Germany
[2] University of Potsdam – Germany
[3] University of Greifswald – Germany

[a] Speaker

The investigation of small, artificial food web modules holds the promise of elucidating mechanisms that drive the assembly and functioning of larger, more natural food webs. Among these modules, apparent competition of two prey types mediated by a shared predator has received particular attention in recent years. It was shown that shared predation allows for predator-mediated coexistence of different prey clones of the same species, giving rise to eco-evolutionary cycles, or coexistence of different prey species. At the plant-herbivore interface, this coexistence relies on trade-offs in functional traits that determine the uptake of abiotic resources and the defense against predation or herbivory, i.e. traits that modify vertical interactions across trophic levels. In this presentation, I will present two cases of horizontal interaction between the two prey species that modify the coexistence outcome within this food web module. Especially at the plant-herbivore interface, a mismatch between the biochemical food quality of prey and the requirements of the predator is a strong limiting factor of predator performance. I will show that food quality differences between the two prey species strengthen the formerly partly inferior undefended prey strategy, if it is the only source of essential biochemicals for the predator. Within the same module, different strategies of prey energy acquisition (e.g. autotrophic phytoplankton versus heterotrophic bacteria) may create a horizontal interaction between the two prey species in the absence of other carbon sources. Here, phytoplankton exudation fuels a pool of organic carbon that is essential to the bacteria and therefore prevents out-competition of algae by bacteria. In both of these cases, one prey type delivers essential resources either to its predator or competitor, and, by making itself indispensable, strengthens its persistence within the food web module.

Keywords: Predator prey model, apparent competition, food quality, commensalism, bacterivory, indirect effects, coexistence

Session 2-1 – Epidemiology 1

Thursday, July 18, 2019 – 10:15-12:15 – Room 1

S2-1.1 – Simple cancer model as controlled switched system

Chakib Jerry [a] [1]

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[a] Speaker

We investigate a simple mathematical population model of tumor and non-tumor interactions where the application of chemotherapy is considered as a control variable. The feature thing in this work is that the control variable is not considered continuous by time but piecewise-continuous which is introduced in our work by an impulsive control. This kind of control is motivated by the fact that chemotherapy is not applied continuously (day by day treatment) but piece wisely continuous (a break between two chemotherapy applications). Furthermore, we study an optimal control problem to find the best strategy to minimise the number of tumor cell which mean maximising health state of the treated person. We discuss also numerical results for chemotherapy regimens.

Keywords: chemotherapy, impulsive control, optimal control, Pontryagin's principle

S2-1.2 – Optimal control model of tumor treatment in the context of cancer stem cell

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[a] Speaker
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We consider cancer cytotoxic drugs as an optimal control problem to stabilize a heterogeneous tumor by attacking not the most abundant cancer cells, but those that are crucial in the tumor ecosystem. We propose a mathematical cancer stem cell model that translates the hierarchy and heterogeneity of cancer cell types by including highly structured tumorigenic cancer stem cells that yield low differentiated cancer cells. With respect to the optimal control problem, under a certain admissibility hypothesis, the solution of our problem is the well-known {most rapid approach path} to the equilibrium. In other cases, we use bang bang controls as an optimal solution. These control treatments can retain the entire tumor in the neighborhood of an equilibrium. We simulate the bang bang numerically and demonstrate that the optimal drug scheduling should be administered continuously over long periods with short rest periods. Moreover, our simulations indicate that combining multidrug therapies and monotherapies is more efficient for heterogeneous tumors than using each one separately.

Keywords: Optimal control theory, Pontryagin's Maximum Principle, Cancer stem cell, cancer dynamics, treatment optimization

S2-1.3 – Climate change and urban expansion increase Ae. aegypti density in Brazil

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Background and Methods
The mosquito *Ae. aegypti* is a major vector of arboviruses dengue, chikungunya and Zika which present enormous global health challenges. Climatic suitability for *Ae. aegypti* is associated with arbovirus occurrence because temperature influences the *Ae. aegypti* life cycle. Understanding the effect of climate change on *Ae. aegypti* is therefore crucial for future disease control. We used future climate projections (HadGEM2-ES RCP4.5 and RCP8.5) and urban accessibility in a temperature-driven, stage-structured population dynamics model of *Ae. aegypti* to investigate the effects of climate change on mosquito density in Brazil.
Results and Conclusions
First, we predicted *Ae. aegypti* densities to increase dramatically across Brazil. *Ae. aegypti* density increased by $> 100\%$ in Brazil's five largest cities by 2100; in Rio de Janeiro it was 275%. Even under more conservative RCP4.5 climate projections, the increase was a staggering 111%. Second, we observed *Ae. aegypti* habitat range to be limited by urban accessibility. Despite the climatic suitability of northern and central states, *Ae. aegypti* were limited to urban areas. *Ae. aegypti* densities were highest in northern cities; *Ae. aegypti* density in Manaus was 17 times higher than São Paulo in 2100. Third, we predicted southern states including São Paulo to shift from having seasonal *Ae. aegypti* populations to having large, endemic populations year-round because the climate becomes continuously hospitable.
Crucially, smaller northern cities were especially vulnerable due to highly suitable climates and high rates of urban expansion. *Ae. aegypti* density in Manaus was predicted to increase by _˜170%. This is particularly concerning as these regions include some of the poorest in Brazil, which is in turn associated with arbovirus persistence. Not only is Brazil at risk of experiencing catastrophic increases in *Ae. aegypti* density, the devastating health effects are likely to affect the poorest and most isolated sectors of society.

Keywords: Aedes, mosquito, arbovirus, climate, urbanisation

S2-1.4 – A new perspective on the role of natural enemies in pest management.

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Pest control has become a very interesting research topic because it is closely associated with agricultural and economic loss. There are several biological, physical and chemical control mechanisms. However, the biological control of pest populations by using natural enemies is one of the most important ecosystem services supplied to agriculture around the world. In our research work, we consider an ecological model consisting of prey (pest) and its natural enemy as the predator. We have demonstrated the analytical results through numerical simulations. We observe that in both types of predator-prey models (Truscott-Brindley model and Rosenzweig-MacArthur model), if the killing rate of a natural enemy exceeds a threshold value, then the natural enemy wipes out from the system, and the pest outbreaks can occur. Our results suggest that the natural enemy has an important role in controlling pest population. On the other hand, the role of super predator is not eco-friendly. But in nature, super predator always exists. Naturally, it is essential for the management personnel to control the super predator for better productivity. Therefore, if the full or partial protection (refuge) is provided for the natural enemies, then the biological pest control could be more effective. Accordingly, ecologist and Argo-economist should focus on the conservation of natural enemies for better pest management perspective. It is worthy to mention here that our model can also be applied in the situations when pesticides, other harmful chemicals and/or human activity kill natural enemies from the local ecosystems.

Keywords: Pest, natural enemy interaction, Biological control, Super predator.

S2-1.5 – The ecological and epidemiological consequences of reproductive interference between the vectors Aedes aegypti and Aedes albopictus

Robert Paton [a] [1], Michael Bonsall

[1] Department of Zoology [Oxford] – United Kingdom

[a] Speaker

The arbovirus vectors *Aedes aegypti* and *Aedes albopictus* compete as larvae, but this mechanism is insufficient to explain patterns of species coexistence and exclusion in the wild. Reproductive interference - whereby inviable inter-species copulations diminish reproductive output - has been proposed as an alternative mechanism. Hitherto models of reproductive interference omitted two unique aspects of the *Aedes* case. First, as both species use hosts as beacons to find mates then reproductive interference will only occur if the same host is used. This host choice will be mediated by the functional response of each species to host availability. Second, female mosquitoes can become sterilised after mis-mating with heterospecifics. Our model includes these processes, finding that a species with a strong preference for a shared host will suffer a greater cost from reproductive interference than a less selective competitor. Costs from reproductive interference can be "traded-off" against costs at the larval stage, leading to competitive outcomes difficult to predict from empirical evidence. Sterilisations of a species limited by within-species larval competition can counter-intuitively lead to *higher* densities than a competitor suffering less sterilisation. We identify a concomitant relationship between vector population dynamics and epidemiology, mediated by host functional responses and reproductive interference. When competitors have opposite functional responses, disease can be maintained in systems where human hosts are rare. This is casued by vector coexistence permitted by a diminished cost of reproductive interference. Our work elucidates the relative roles of the competitive processes governing *Aedes* populations and the associated epidemiological consequences.

Keywords: mathematical models, invasion analysis, basic reproductive number, population dynamics, functional response, reproductive interference

Session 2-2 – Evolutionary game theory

Thursday, July 18, 2019 – 10:15-12:15 – Room 2

S2-2.1 – Fitness Optimization in Replicator Systems Evolution

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In this study, we discuss fittness landscape evolution of permanent replicator systems. The hypothesis is that the specific time of the evolutionary adaptation of the system's parameters is much slower than the time of internal evolutionary dynamics. In other words, we suppose that the extreme principle of Darwinian evolution based the Fisher's fundamental theorem of natural selection is valid for the steady-states. Various cases of the evolutionary adaptation for permanent replicator system are considered: versions of the hypercycle system and general replicator system. For the hypercycles, we show that this process of adaptation leads to a system that is sustainable in the presence of parasites. One of the central results is the existence of a phase transition similar to the "error threshold" in the Eigen model: starting from some time moment the mean fitness value increase to a plateau and the hypercycle structure changes.

Keywords: fitness landscape, Fisher's fundamental theorem, replicator system, hypercycle

S2-2.2 – The Stabilisation of Equilibria in Evolutionary Game Dynamics through Mutation

Johann Bauer [a 1], Mark Broom [1], Eduardo Alonso [1]

[1] City, University of London – United Kingdom

[a] Speaker

The multi-population replicator dynamics (RD) has been employed in the game theoretic analysis of coevolving populations with interspecific but with no intraspecific interactions, e.g., in the study of host-parasite systems and of mutualistic systems. Furthermore, it has been related to learning dynamics in games, specifically to Cross-learning. However, not all equilibria of RD are Nash equilibria (NE) of the underlying game, and neither convergence to an NE nor convergence in general are guaranteed, weakening the link between the dynamic and the static properties. Although interior equilibria are guaranteed to be NE, no interior equilibrium can be asymptotically stable in the multi-population RD, resulting, e.g., in cyclic orbits around a single interior NE.

We report on our investigation of a new notion of equilibria of RD, called mutation limits, which is based on the inclusion of a naturally arising, simple form of mutation, but which is independent of the specific choice of mutation parameters. We establish the existence of such mutation limits for a large range of games, and consider an interesting subclass, that of attracting mutation limits. Attracting mutation limits are approximated by asymptotically stable equilibria of the (mutation-)perturbed RD, and hence, offer an approximate dynamic solution of the underlying game, especially if the original dynamic has no asymptotically stable equilibria. Therefore, the presence of mutation will indeed stabilise the system in certain cases and make attracting mutation limits near-attainable, in contrast to the mutation-free system. Furthermore, the relevance of attracting mutation limits as a game theoretic equilibrium concept is emphasised by the relation of (mutation-)perturbed RD to the Q-learning algorithm in the context of multi-agent reinforcement learning. However, in contrast to the guaranteed existence of mutation limits, attracting mutation limits do not exist in all games, raising the question of the conditions of their existence.

Keywords: replicator dynamics, mutation

S2-2.3 – Equilibrium Distributions of Network Structured Populations

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[2] Mathematical Biosciences Institute, Ohio State University – United States
[3] Department of Statistics, Colorado State University – United States

[a] Speaker

Populations of biological species often spread on networks of locations in ways so they can increase their biological or social interactions. The dynamics of the distribution of such a population on a given network can be of great research interest in biological and social sciences such as the studies on fertility selection in genetic evolution, village or tribe development with certain marriage rules, and evolution of social organizations in human societies. Indirectly, it can also be essential for the studies on such topics as sexually transmitted diseases, international trade networks, cultural, religious, or language spreads, etc. We investigate how such populations would distribute over given networks and build a mathematical model for it. More specifically, we formulate the problem as an evolutionary game with the biological or social contacts that an individual can make through the network as the payoff. An equilibrium distribution is reached when every individual's payoff is maximized. We derive network conditions for equilibrium distributions and their evolutionary stabilities, and show in particular that an equilibrium distribution may or may not be on a network clique, where there are complete connections among network sites, but network cliques do support more stable distributions than non-clique sub-networks in general. These results provide theoretical insights into the evolutionary nature of network structured populations and their particular networking and grouping behaviors.

Keywords: Population dynamics, evolutionary games, Nash equilibrium, evolutionary stability, biological and social networks, network cliques

S2-2.4 – From fixation probabilities to d-player games: an inverse problem in evolutionary dynamics

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[2] Centro de Matemática e Aplicações, Faculdade de Ciências e Tecnologia, Universidade Nova de Lisboa – Portugal

[a] Speaker

The fixation probability of a given trait is a central issue in the study of population evolution. Its computation, once we are given a stochastic finite population model without mutations and a (possibly frequency dependent) fitness function, is typically straightforward, and it can be done in many ways. Nevertheless, despite the fact that the fixation probability is an important macroscopic property of the population, its precise knowledge does not give any clear information about the interaction patterns among individuals in the population. Here we address the inverse problem: From a given fixation pattern and population size, we want to infer what is the game being played by the population. This is done by first exploiting the framework developed in FACC Chalub and MO Souza, J. Math. Biol. 75: 1735, 2017., which yields a fitness function that realises this fixation pattern in the Wright-Fisher model. This fitness function always exists, but it is not necessarily unique. Subsequently, we show that any such fitness function can be approximated, with arbitrary precision, using d-player game theory, provided d is large enough. The pay-off matrix that emerges naturally from the approximating game will provide useful information about the individual interaction structure that is not itself apparent in the fixation pattern.

Keywords: Wright-Fisher process, Fixation probability, Game theory, Inverse problems

S2-2.5 – A sequential teamwork dilemma

Jorge Peña [a 1], Georg Nöldeke [2], Arne Traulsen [3]

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[2] Faculty of Business and Economics, University of Basel – Switzerland
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[a] Speaker

We investigate the evolutionary dynamics of a sequential version of the volunteer's dilemma. In our variant of this game-theoretic model, individuals are sequentially recruited by focal groups until a critical number of cooperators needed to provide and/or monopolize a good is reached. This simple rule of group formation leads to a dependence of the effective group size distribution on the level of cooperation in the population and generates predictions that are in stark contrast to those resulting from a standard model without sequential recruitment, including the maintenance of a cooperative equilibrium at arbitrarily high densities of potential interactants. We speculate on the connections between our simple model and key features of situations where individuals join groups and a congestible good is produced or defended, and where the exclusion of newcomers at a personal cost is possible. Examples include collective hunting and confrontational scavenging by social carnivores, superinfection exclusion in bacteriophages, sperm cooperation and competition under functional polyspermy, defensive mutualisms, and host manipulation by parasites. Our model and results highlight the importance of explicitly accounting for priority effects and endogenous processes of group formation in theoretical models of social evolution.

Keywords: evolution of cooperation, collective action, excludability, congestion, group formation

S2-2.6 – Generalised social dilemmas: the evolution of cooperation in populations with variable group size

Mark Broom [ab] [1], Karan Pattni , Jan Rychtar

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Evolutionary game theory is an important tool to model animal and human behaviour. A key class of games are the social dilemmas, where cooperation benefits the group but defection benefits the individual within any group. Previous works have considered which games qualify as social dilemmas, and different categories of dilemmas, but have generally concentrated on fixed sizes of interacting groups. In this talk we discuss a systematic investigation of social dilemmas on all group sizes. This allows for a richer definition of social dilemmas. For example, while increasing a group size to include another defector is always bad for all existing group members, extra cooperators can be good or bad, depending upon the particular dilemma and group size. We consider a number of commonly used social dilemmas in this context, and in particular show the effect of variability in group sizes for the example of a population comprising negative binomially distributed group sizes. The most striking effect is that increasing the variability in group sizes for non-threshold public goods games is favourable for the evolution of cooperation. The situation for threshold public goods games and commons dilemmas is more complex.

Keywords: evolutionary game, cooperation, public goods game, prisoner's dilemma, hawk dove game

Session 2-3 – Evolution in structured populations

Thursday, July 18, 2019 – 10:15-12:15 – Room 3

S2-3.1 – Adaptive dynamics in spatially structured populations

Tadeas Priklopil [a 1], Laurent Lehmann [1]

[1] University of Lausanne – Switzerland

[a] Speaker

In eco-evolutionary theory the formal justification for gradual evolution has been given by a so-called "invasion implies substitution"-principle, which states that upon a successful invasion of a mutant phenotype it replaces its closely similar ancestral phenotype. However, while this principle has been suggested to hold for a wide range of conditions, including demographic and environmental fluctuations under limited dispersal, complete and explicit proofs of the "invasion implies substation" results have been lacking in structured populations. Here, we generalize the "invasion implies substitution"-principle to spatially and group structured metapopulation communities with finite local population sizes, therefore including the effects what indviduals have on their immediate environment. We do this by setting up a continuous-time mutant-resident metapopulation dynamical system and derive a closed expression for a selection gradient. We show that the selection gradient is a function of resident individual growth-rates, class reproductive values and relatedness. Importantly, we show that the selection gradient is frequency independent, from which "invasion implies substitution"-principle directly follows. Our results provide an important step in extending the framework of adaptive dynamics to spatially structured populations.

Keywords: spatial structure

S2-3.2 – Exact fixation probabilities and large population asymptotics for the BD and DB Moran processes on the star graph with frequency dependent fitnesses

Armando Neves [ab 1], Evandro De Souza [1]

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[a] Speaker

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Broom and Rychtar [Proc. R. Soc. A (2008) 464, 2609–2627] have found an exact solution for the fixation probabilities of the Moran process for a structured population, in which the interaction structure among individuals is given by the so-called star graph, i.e. one central vertex and n leaves, the leaves connecting only to the center. We generalize on their solution by allowing individuals' fitnesses to depend on the population frequency, and also by changing the order of reproduction and death draws. In their cited paper, Broom and Rychtar considered the BD (birth-death) process, in which at each time step an individual is first drawn for reproduction and then an individual is selected for death. In the DB (death-birth) process, the order of the draws is reversed. It may be seen that the order of the draws makes a big difference in the fixation probabilities. Our solution method applies to both the BD and the DB cases. As expected, the exact formulae for the fixation probabilities are complicated. We will also illustrate them with some examples and provide results on the asymptotic behavior of the fixation probabilities when the number n of leaves in the graph tends to infinity.

Keywords: Moran process, Structured populations, Evolutionary game theory

S2-3.3 – Eco-evolutionary dynamics under multi-scale density dependence

Koen Van Benthem [a 1], Meike Wittmann [1]

[1] Bielefeld University – Germany

[a] Speaker

Population density directly affects fundamental ecological processes such as resource competition and mate finding. These processes directly influence the fitness, which then feeds back to population density. This makes population density a key factor in eco-evolutionary dynamics. Different life-history processes can be affected by density to varying degrees and potentially by different densities: male-male competition may depend on the density of males, while resource competition is affected by the overall density. Another example is competition for nesting sites that depends on the abundance in the direct vicinity, while foraging grounds and thereby resource competition may cover a much larger area. Here we study how effects of local density and of density in nearby patches can jointly affect eco-evolutionary dynamics.

We analyse a deterministic two-patch model. Both patches have the same fitness function that depends on their own density and the density in the other patch. A phase space analysis reveals that the mutual effect that the patches have on each other can lead to long-term emergence and maintenance of a low and a high density patch. We then include trait values such as aggressiveness, boldness or sociability. We show how the inclusion of density dependent selection pressures can lead to diversification in trait values between these patches. This diversification can simultaneously lead to changes in the long-term population densities: in some systems, the two patches reach the same equilibrium density when the trait value is fixed, but different equilibrium densities when the trait is allowed to evolve. Our results show how, even in the absence of intrinsic differences between patches, interactions between them can lead to differences in long-term population density, and correspondingly to diversification in density-related traits.

Keywords: eco, evolutionary dynamics, population density, emergence of diversity, maintenance of diversity

S2-3.4 – When sinks become sources: adaptive colonization in asexuals.

Florian Lavigne [a 1,2,3], Lionel Roques [1], Guillaume Martin [2], Julien Papaïx [1], Yoann Anciaux [2,4]

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[3] I2M – Aix-Marseille Université - AMU, I2M AMU – France
[4] BIRC – Denmark

[a] Speaker

The establishment success of a population into a new empty habitat outside of its initial niche is a phenomenon akin to evolutionary rescue in the presence of immigration (biological invasions by alien organisms, host shifts in pathogens or the emergence of resistance to pesticides or antibiotics from untreated areas).
We derive an analytically tractable framework to describe the coupled evolutionary and demographic dynamics of asexual populations in a source-sink system. In particular, we analyze the influence of several factors - immigration rate, mutational parameters and harshness of the stress induced by the change of environment - on the success of the establishment in the sink (i.e. the formation of a self-sufficient population in the sink), and on the time until establishment. To this aim, we use a classic phenotype-fitness landscape (Fisher's geometrical model in n dimensions) where source and sink habitats determine distinct phenotypic optima. The dynamics of the full distribution of fitness and of population size in the sink are analytically predicted, under a strong mutation strong immigration limit, where the population is always polymorphic.
The resulting eco-evolutionary dynamics depend on mutation and immigration rates in a non straightforward way. Below some mutation rate threshold, establishment always occurs in the sink, following a typical four-phases trajectory of the mean fitness. The waiting time to this establishment is independent of the immigration rate and decreases with the mutation rate. For a mutation rate greater than the threshold, lethal mutagenesis impedes establishment and the sink population remains so, albeit with an equilibrium state that depends on the details of the fitness landscape. We use these results to get some insight into possible effects of several management strategies.

Keywords: PDE, source, sink model, selection, mutation, migration, Fisher's geometrical model

S2-3.5 – Infinite-patch metapopulation models: branching, convergence and chaos

Philip Pollett [a] [1]

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[a] Speaker

I will describe a stochastic model for populations that occupy several geographically separated patches of habitat, one for which there is no ceiling on the number of patches that can be occupied. Colonisation and extinction events are assumed to occur in distinct successive phases. When the expected number of patches colonised is proportional to the number currently occupied, the occupancy process is a branching process. However, allowing more general dependence on the number currently occupied, and introducing a threshold, permits a degree of regulation in the colonisation process. We present a large of large numbers for the occupancy measured relative to the threshold, which identifies an approximating deterministic trajectory, as well as a central limit law for fluctuations about that trajectory. We shall see that equilibrium behaviour is richer and more interesting than for standard finite-patch models, because now the limiting deterministic model can exhibit the full range of long-term behaviour, including limit cycles, and even chaos.

Keywords: metapopulations, stochastic models, convergence, branching processes

S2-3.6 – Dynamical behaviour of a stage structured predator-prey model for multispecies demography

Frederic Barraquand [a] [1,2], Bachar Tarraf [3]

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[3] Institut de Mathématiques de Bordeaux – Université de Bordeaux – France

[a] Speaker

We introduce a stage-structured predator-prey model in discrete-time, which can be fitted to data using the Integrated Population Model framework that combines different data sources. The species interactions are represented indirectly, through adult predator reproduction that increases with juvenile prey density, while prey survival decreases with the number of adult predators. The model has connections to the single species model of Neubert & Caswell (2000, J Math Biol); apparently small differences in model structure generate structural differences in possible bifurcations. We study which type of dynamical behaviour can be exhibited by the model, for parameters reflecting various pairs of predator-prey systems (carnivorous & herbivorous mammals, seed eating rodents & annual plants). We show that the model can exhibit multiple routes to chaos and resonances. Adding stochasticity further increases the potential for cyclic oscillations. Finally, we compare the periodicities of population cycles produced by this stage-structured model to those classically predicted by predator-prey theory.

Keywords: predator, prey, demography, discrete time, resonances, oscillations

Session 2-4 – Evolution of genetic / physiological architectures

Thursday, July 18, 2019 – 10:15-12:15 – Room 4

S2-4.1 – Evolutionary dynamics of plasticity in a mechanistic gene-network model.

Andréas Odorico [a] [1], Arnaud Le Rouzic

[1] Évolution, génomes, comportement et écologie (EGCE) – IRD : UMR247, Centre National de la Recherche Scientifique : UMR9191, Université Paris-Sud - Université Paris-Saclay – Avenue de la Terrasse, Bâtiment 13, CNRS, 91198 Gif sur Yvette, France, France

[a] Speaker

The ability for a single genotype to produce multiple phenotypes makes it possible for populations to remain adapted to changing environments without new genetic variants. As such, phenotypic plasticity has always be a major point of interest in evolutionary studies. Yet, phenotypic plasticity may hardly be perfect, and theoretical studies addressing the potential costs, limits or mechanisms responsible for the loss of plasticity are central to producing a framework allowing the study and comprehension of complex regulatory systems. Here, I present a mechanistic model, adapted from a classical gene regulation network model, to study the evolution of a response to an environmental signal correlated to a changing fitness function. This framework is used to characterize phenotypic plasticity in a highly pleiotropic and epistatic system, in absence of an explicit cost to plasticity. Notably, we study the processes of acquisition and loss of plasticity in the light of a genetic assimilation heuristic. We show that no mechanism accelerating the loss of plasticity is required to explain a trade-off between generalists and specialists, and that even stabilizing selection actually maintains a non-null reaction norm rather than accelerating its disappearance. More generally we use this study to stress the importance of using mechanistic models to gain a proximal understanding of the evolution of phenotypic plasticity in complex systems and obtain insights not readily available with a causal modelling of evolutionnary processes.

Keywords: plasticity, genetic assimilation, fluctuating selection, gene regulatory network, individual, based simulation

S2-4.2 – Evolution of genetic canalization in complex genetic architectures

Arnaud Le Rouzic [a] [1]

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[a] Speaker

Genetic canalization reflects the capacity of an organism's phenotype to remain unchanged in spite of mutations. As selection on genetic canalization is weak and indirect, whether or not genetic canalization can reasonably evolve in complex genetic architectures is still an open question. Here, we use a quantitative model of gene regulatory network to describe the conditions in which substantial canalization is expected to emerge in a stable environment. Our simulations shows that the complex genotype-phenotype map generated by the gene network model was highly epistatic and made it possible to evolve towards genetic robustness, as predicted by standard population genetics theory. However, we found no mechanism involving specific features of gene networks, excluding that robustness could appear as an emergent property of the complexity of regulations. Our results lead us to propose a two-fold mechanism involved in the evolution of genetic canalization: the shrinkage of mutational target (useless genes are virtually removed from the network) and redundancy in gene regulation (so that some regulatory factors can be lost without affecting gene expression).

Keywords: Genetic canalization, Epistasis, Individual, based simulations, Gene regulatory networks

S2-4.3 – The origin of the central dogma through conflicting multilevel selection

Nobuto Takeuchi [a] [1],
Kunihiko Kaneko [2]

[1] University of Auckland [Auckland] – New Zealand
[2] University of Tokyo – Japan

[a] Speaker

The central dogma of molecular biology rests on two kinds of asymmetry between genomes and enzymes: informatic asymmetry, where information flows from genomes to enzymes but not from enzymes to genomes, and catalytic asymmetry, where enzymes provide catalysis but genomes do not. How did these asymmetries originate? Here we show that these asymmetries can spontaneously arise from conflict between selection at the molecular level and selection at the cellular level. We consider a model consisting of a population of protocells, each containing a population of replicating catalytic molecules. The molecules are assumed to face a trade-off between serving as catalysts and serving as templates. This trade-off causes conflicting multilevel selection: serving as catalysts is favored by selection between protocells, whereas serving as templates is favored by selection between molecules within protocells. This conflict induces informatic and catalytic symmetry breaking, whereby the molecules differentiate into genomes and enzymes, establishing the central dogma. We show mathematically that the symmetry breaking is caused by a positive feedback between Fisher's reproductive values and the relative impact of selection at different levels. This feedback induces a division of labor between genomes and enzymes, provided variation at the molecular level is sufficiently large relative to variation at the cellular level, a condition that is expected to disfavor the evolution of cooperation. Taken together, our results suggest that the central dogma is a logical consequence of conflicting multi-level selection.

Keywords: reproductive division of labor, origin of genetic information, RNA world hypothesis, Price equation

S2-4.4 – The evolution of an allocation trade-off's shape through changes in hormonal pleiotropy

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[2] Laboratoire de Biométrie et Biologie Evolutive – Université Claude Bernard Lyon 1, Centre National de la Recherche Scientifique : UMR5558 – France

The shape of a trade-off is an essential parameter in the study of evolution. Indeed, by restricting the combinations of traits that can be accessed readily by a population, the trade-off relationship sets the optimal position(s) on a fitness landscape. An individual's position on an allocation trade-off depends on how much is allocated to one trait or the other, which is partly heritable. Phenotypic variation in a population may therefore be explained to some extent by standing genetic variation of hormone- and receptor-coding genes, due to the role of the endocrine system in the regulation of resource allocation. Here we investigate whether further upheaval in the endocrine system could be responsible for the evolution of a trade-off's shape. To this aim, we built a model where mutations can impact an hormone or a receptor's expression or conformation, thereby impacting their binding dynamics and thus, resource allocation. We show that the shape itself can evolve, such that the evolutionarily expected shape depends on the environmental and selective context. When no selection is applied (on the traits), trade-offs evolve towards more linear relationships associated with higher standing genetic variation. Under directional selection, however, the trade-off evolves to be concave. Moreover, we show that the evolutionarily expected curvature of the trade-off tends to be higher when storing the resource incurs a higher cost, such that the shape of a trade-off should depend on physiological and ecological parameters known to impact this cost. Our attempt to link variables of the endocrine system to estimate shape parameters has failed, suggesting that a diversity of genotypes can yield a similar evolutionary response in this context.

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Keywords: tradeoffs, resource allocation, hormonal pleiotropy

S2-4.5 – Evolution of enzyme concentrations in metabolic pathways

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The question of the genotype-phenotype relationship is central in biology. Since Wright's pioneer work (1934), the relationship between enzymes and metabolic flux is commonly used as a model, in particular in evolutionary genetics. Whenever selection tends to maximize a flux ("phenotype"), the concentrations of the enzymes ("genotype") evolve according to a dynamics that depends on the constraints of the system. Here, we used mathematical modeling of constraints on enzyme production, namely competition between enzymes for cellular resources and/or co-regulations between enzymes allied with metabolic control theory to formalize this evolution. Based on a system of differential equations close to the adaptive dynamics framework, we have demonstrated the existence of two evolutionary steady states for the relative concentrations of enzymes involved in the same metabolic pathway. The theoretical equilibrium state – the one to which the system tends – may not always be reached given the constraints. Instead, the effective equilibrium state is reached whenever the constraints prevent the flux from exceeding a certain value. Computer simulations confirmed all theoretical predictions. Effective equilibrium state for the relative abundance of enzyme concentrations depends on both enzyme kinetic parameters and regulation patterns of enzyme abundances. Our results suggest that too tight co-regulations between enzymes from the same metabolic pathway may not have a long term adaptive advantage whenever cellular resources are limited.

Keywords: Evolutionary systems biology, Metabolic control theory, Mathematical modeling, Computer simulations, Genotype, phenotype relationship

S2-4.6 – The evolutionary and developmental dynamics of life history

Mauricio Gonzalez-Forero [ab] [1], Andy Gardner [2]

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Many morphological and behavioral traits are built through development and can be subsequently deconstructed as aging proceeds. Such developmental dynamics depend on the developmental history of the trait. Although developmental and evolutionary dynamics may influence each other, developmental and evolutionary dynamics are typically studied separately, where either an evolutionary equilibrium is assumed to study developmental dynamics or developmental dynamics are neglected to study evolutionary dynamics. Here we develop an approach to simultaneously study evolutionary and developmental dynamics by deriving the selection gradient for traits (control variables) that affect the developmental dynamics of associated traits (state variables). The method offers an alternative to dynamic optimization approaches and links costate variables of optimal control theory to selection gradients of developmentally dynamic traits. We find that, while demographic processes diminish the force of selection with age, developmental processes may diminish or increase the force of selection with age. A trait may thus evolve "negative senescence" provided that developmentally early trait values strongly positively affect developmentally late trait values. We illustrate the method by applying it to study the evolutionary dynamics of energy allocation to growth and reproduction, and of brain life history. The method also enables quantification of developmental constraints and finds that developmentally dynamic traits should typically be outside of their optimum even at evolutionary equilibrium, suggesting a ubiquitous role of developmental constraints in shaping adaptation.

Keywords: Life history evolution, adaptive dynamics, function, valued traits, matrix population models, optimal control

Session 3-1 – Evolution of cooperation and sociality

Thursday, July 18, 2019 – 15:00-17:30 – Room 1

S3-1.1 – A Markov Model of Eusociality at its Origin

Hiroshi Toyoizumi [a] [1], Jeremy Field [2]

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[2] University of Exeter, Centre for Ecology and Conservation – United Kingdom

[a] Speaker

To understand advantages and disadvantages of various eusocial strategies, we use a transient Markov arrival process and branching process modelling the group dynamics in a cooperatively-breeding nest and its offspring dispersals.
In a recent theoretical paper, Fu et al. (2015) took a new approach by using Markov chain and branching processes to model colony and population dynamics respectively. We here extend the model of Fu et al. (2015) to include:
1. Worker mortality: we model not only queen but also workers' death rates.
2. Inheritance of nest: instead of queen death causing catastrophic group failure, we assume that if the queen dies a surviving worker can take over as the egg-layer so that the group
continues to produce offspring.
3. Productivity related linearly to group size: rather than productivity increasing only above a
threshold group size, we assume that each worker increases productivity by the same amount.
We show how to derive the basic reproductive number and the extinction probability of various related models including primitively eusocial species, and give some insight to the origin of eusociality. We find that allowing inheritance of nests is particularly important for understanding the origin of eusociality.
Feng Fu, Sarah D Kocher, and Martin A Nowak. The risk-return trade-off between solitary and
eusocial reproduction. Ecology letters, 18(1):74–84, 2015.

Keywords: eusociality, branching process, basic reproductive number, Markov process

S3-1.2 – Origins of human beliefs: a catalyst for cooperation

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Humans and a small number of insects and crustaceans show eusociality. The defining features of eusociality are a reproductive division of labour, overlapping generations and cooperative care of the young. As compared to insects or crustaceans, humans have taken over the world at an astonishing scale. The reason, typically attributed to the ability of humans to cooperate in large numbers. While other animals (e.g. ants) can also work together in large numbers, they do so because their genetics drives them. In a broad sense, cooperation in humans is unconstrained by their genetics. Thus besides cooperating in large numbers, humans are also flexible in their behaviour. How can we explain the evolution of large scale yet possibly unconstrained potential to cooperate? Using evolutionary game theory, we argue that the cognitive revolution in humans and ability to come up with and believe in extraordinary stories helped us establish a social contract. We show how the belief in an extraordinary story can spread in a population and cooperation piggybacks to fixation. Interestingly, the story need not be related to the concept of cooperation itself. After the establishment of the social contract, there is no selection pressure on maintaining the belief itself. Our theory is thus useful in explaining the origin and spread of not just the fictitious constructs such as nations, corporations and money but also radicalising concepts and fake stories.

Keywords: social contract, religion, inter, subjective reality, cultural evolution, neutral dynamics

S3-1.3 – Sex allocation conflict and sexual selection throughout the lifespan of eusocial colonies

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Models of sex allocation conflict are central to evolutionary biology but have mostly assumed static decisions, where resource allocation strategies are constant over colony lifespan. Here, we develop a model to study how the evolution of dynamic resource allocation strategies is affected by the queen-worker conflict in annual eusocial insects. We demonstrate that the time of dispersal of sexuals affects the sex allocation ratio through sexual selection on males. Furthermore, our model provides three predictions that depart from established results of classic static allocation models. First, we find that the queen wins the sex allocation conflict, while the workers determine the maximum colony size and colony productivity. Second, male-biased sex allocation and protandry evolve if sexuals disperse directly after eclosion. Third, when workers are more related to new queens, then the proportional investment into queens is expected to be lower, which results from the interacting effect of sexual selection (selecting for protandry) and sex allocation conflict (selecting for earlier switch to producing sexuals). Overall, we find that colony ontogeny crucially affects the outcome of sex-allocation conflict because of the evolution of distinct colony growth phases, which decouples how queens and workers affect allocation decisions and can result in asymmetric control.

Keywords: life, history, social evolution, sex allocation, genetic conflicts, optimal resource allocation, adaptive dynamics of function valued traits

S3-1.4 – Acculturation drives the evolution of intergroup conflict

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[a] Speaker

Conflict between groups of individuals is a prevalent feature in human societies. A common theoretical explanation for intergroup conflict is that it provides benefits to individuals within groups in the form of reproduction-enhancing resources, such as food, territory, or mates. However, it is not always the case that conflict results from resource scarcity. We show that intergroup conflict can evolve despite not providing any benefits to individuals or their groups. The mechanism underlying this process is acculturation: the adoption, through coercion or imitation, of the victor's cultural traits. Acculturation acts as a cultural driver (in analogy to meiotic drivers) favoring the transmission of conflict despite a potential cost to both the host group as a whole and to individuals in that group. We illustrate this process with a two-level model incorporating state-dependent event rates and evolving traits for both individuals and groups. Individuals can become 'warriors' who specialize in intergroup conflicts but who are costly otherwise. Additionally, groups are characterized by cultural traits, such as their tendency to engage in conflict with other groups and their tendency for acculturation. We show that, if groups engage in conflicts, group selection will favor the production of warriors. Then, we show that group engagement can evolve if it is associated with acculturation. Finally, we study the coevolution of engagement and acculturation. Our model shows that horizontal transmission of culture between interacting groups can act as a cultural driver and lead to the maintenance of costly behaviors by both individuals and groups.

Keywords: Group selection, Multilevel selection, Cultural evolution, Intergroup conflict

S3-1.5 – The Neolithic transition to large-scale societies is favoured by the co-evolution of cooperation and institutions

Claire Guerin [ab] [1], Laurent Lehmann [1]

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From nomadic hunter-gatherers to sedentary agriculturalists, human societies underwent remarkable lifestyle changes during the Neolithic transition. This transition was accompanied by an overturn in social structure, which called into question both the ultimate and proximate causes of cooperation. In small-scale societies of egalitarian hunter-gatherers, cooperation can be explained by kin selection and reciprocity. But in large-scale agriculturalists societies, the increase in population size mitigates these effects.

Here, using computer simulations, we investigate whether cooperation can be sustained even as groups move towards large-scale societies of unrelated individuals, thanks to the coevolution of cooperation and institution. We consider institutions from the game theoretic perspective of game forms that modify the rules of an economic game.

Specifically, we ask how institutions can naturally emerge through cultural evolution of negotiation, and under which conditions it allows cooperation to be maintained in enlarging populations. We further examine the importance of social structure (hierarchy) in facilitating the creation of institutions.

We consider a structured population where agents can increase resource production through investment into a public good. Through a negotiation process, funds can be used to enforce cooperation by policing. Critical to productivity, negotiation time is optimised by delegating decisional power to an elite class.

We illustrate the valuable role of institutions mediated by hierarchy in promoting cooperation during the Neolithic transition to large-scale human societies.

This work contributes to a growing body of academics that has put considerable effort into establishing a formal theoretical framework on the evolution of human societies, striving to bridge the gap between fields.

Keywords: neolithic transition, institution, cooperation, stratification

S3-1.6 – Functional gain and loss in the evolutionary transition from free-living lifestyle to obligate symbiosis

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Symbiosis is such a ubiquitous interaction that no individual on Earth lives its life in solitude. It has been realised that symbiosis is a source of novel morphology and evolutionary innovation. Since, many researches on symbiosis have been conducted, focusing on the ecological interactions. It was realised that symbiosis evolves along a continuum of dependency, from facultative to obligate symbiosis. Obligate symbiosis is suggested to evolve from facultative symbiosis, and may results in more complex organisms through permanent associations of simpler ones. Yet it is not so obvious why facultative symbionts, who are benefiting from both the external environment and their hosts, would give up this best of both worlds. Empirical studies have shown that obligate symbiosis involved functional loss, hence, obligate symbionts lose their independent reproduction, but life in associations surely requires adaptations. Thus, the evolution of obligate symbiosis must involve both functional gain and loss. We use the adaptive dynamics approach to disentangle the pure strategies that a symbiont can adopt: the free-living lifestyle, obligate symbiosis with horizontal transmission, and obligate symbiosis with vertical transmission. We worked out the conditions under which a mutant with small adaptations to symbiosis invades a resident population without any adaptation. We further explored the conditions where a singular strategy of adaptations to symbiosis exists, and whether resident population that has such adaptations forgo its independent reproduction. This singular strategy may be an ESS, which indicates stable obligate symbiosis, but also a branching point, which indicates unstable obligate symbiosis. Unstable obligate symbiosis indicates the evolutionary transition back to facultative symbiosis or the complete breakdown of the symbiotic relationship.

Keywords: obligate symbiosis, facultative symbiosis, functional gain and loss, evolutionary transitions

Session 3-2 – Population genetics

Thursday, July 18, 2019 – 15:00-17:30 – Room 2

S3-2.1 – Dilute and Re-sequence: experimental validation of putative selection targets in the absence of phenotypic variation

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Evolve and re-sequencing studies investigate genomic responses of adaptation during experimental evolution. Because replicate populations evolve in the same controlled environment, selection signatures shared across replicates provide strong support for reliable biological signal. Recent studies noticed that selection signatures are also restricted to one or a few replicate(s). The statistical validation of such signatures is challenging given the large number of tests performed at the genome-wide SNP level. The selected phenotype(s) are unknown which complicates experimental validation of such candidate loci.

We introduce a novel approach to validate candidates by testing for repeatable selection signatures. As candidates increased in frequency during the E&R study, adding founder individuals decreases their frequency. We reason that a genuine selection target will increase in frequency again after such dilution event, exposed to the same environment.

We apply this dilution method to a selection signature identified in one out of 3 *D. simulans* replicate populations evolving for 70 generations in a novel hot temperature environment. By diluting evolved with founder genotypes, we create two replicates evolving for additional 30 generations in the same temperature regime. The marginal probability of a fly to originate from an evolved or founder population or mixture proportion is tuned to allow the frequency of the tested SNPs to be high enough to escape drift. The Cochran-Mantel-Haenszel test identifies the same SNPs increasing in frequency. We showed that the frequency increase is higher than expected by random drift. We confirmed selection candidates and also observed additional targets of selection, not detected in the original E&R study.

We propose that dilution is a good independent confirmation of selection signatures detected in E&R studies. Dilution experiments may be used to validate selection targets before time consuming functional follow-up experiments.

Keywords: experimental evolution, evolve and resequence, repeatability, Drosophila simulans, validation

S3-2.2 – The dynamics of adaptive response under strong selection regime in small populations

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Climate changes are affecting plants at an incredible pace leading to major life-cycle shifts with complex consequences. The capacity of plants to cope with the rate of predicted climate changes will ultimately determine their survival. Here we investigate the rate of life-cycle shifts in maize using two independent divergent selection experiments (DSEs), conducted for more than 20 years under natural conditions in the Plateau de Saclay. Within each DSE, we started from a commercial inbred line seed lot and we applied a strong selection pressure (1%) for phenological shifts by choosing and selfing at each generation the 10 earliest- and 10 latest- flowering genotypes among thousand observed ones. The resulting Early and Late evolved populations exhibit pronounced phenotypic divergence for flowering, while preserving original characteristics of the initial inbreds. Using genetic markers and transcriptomic data, we identified a number of (epi)genetic differences. In order to address questions related to the role of new mutations versus standing variation in the response to selection, and to the rate and limits of adaptation, we have implemented a revised version of the animal model that explicitly accounts for new mutations. In this model, the observed response to selection is treated as a quantitative trait, driven either by shifts in average phenotype or plastic changes. From the dynamics of the selection response, we quantified the input of new mutations over generations, and indicated the most likely mutational events along the pedigrees. In addition, we implemented a population genetic model that describes the fate of a new mutation, in this high selection-high drift design. We discuss how, in these conditions, drift can accelerate fixation of adaptive mutations.

Keywords: divergent selection experiments, maize flowering time, small population size, fast adaptation, selection response, standing variation vs de novo mutation

S3-2.3 – Traveling-Wave Models of Evolution: The Generalized Infinitesimal Limit

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[2] Departments of Physics and of Bioengineering, University of California, Berkeley – United States

[a] Speaker

The evolutionary dynamics of large populations are rather complicated. A large number of distinct adaptive lineages may be present in a population at once, such that the fate of a new mutation cannot be considered in isolation. The dynamics are well-understood in several limiting cases. These can largely be partitioned into cases in which mutations are strong—that is, in which they fix with probabilities differing substantially from that of a neutral mutation—and cases in which mutations are weak, such that they are only subject to selection collectively. Here we extend these approaches to consider the dynamics of populations subject to mutations which are neither entirely strong nor entirely weak. We discuss how quantities such as the overall rate of adaptation and the coalescence timescale depend on the range of potential effects that mutations can confer and other population-genetic parameters. We further identify a few key timescales and fitness scales—the time required for the fittest lineages to deterministically sweep through the population, the range of fitnesses which routinely contribute future common ancestors of the population, and the most-likely effect size of a fixed mutation. We discuss the suitability of different approximation schemes in terms of these scales, and argue that many dynamical quantities of interest depend on these scales in a rather universal way.

Keywords: population genetics, traveling, wave models, genetic diversity, linkage

S3-2.4 – Modeling higher-order genetic interactions

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The outcome of the evolutionary processes depends, in large part, on the structure of the fitness landscape. Accurate reconstruction of complete landscapes based on high-throughput experimental data can greatly benefit the study of evolutionary dynamics and our ability to predict evolution. Here, I will present two principled methods for inferring fitness landscapes from empirical data that are capable of modeling genetic interactions involving any number of sites. The first method is called Minimum Epistasis Interpolation and attempts to infer the smoothest fitness landscape compatible with experimental observations by minimizing the average squared epistatic coefficient between all possible pairs of mutations in all possible genetic backgrounds. This approach results in a model that can behave in a very complicated manner where the data requires it but behaves nearly additively where data is sparse or absent. This method also has a number of desirable mathematical properties including a close relation with the second-order discrete heat equation. The second method is called Empirical Variance Component Interpolation. It can be viewed as an empirical Bayes procedure wherein one first estimates the fraction of variance due to each interaction order (additive, pair-wise, three-way, etc.) and then infers the maximum a posteriori fitness landscape using the inferred variance components as priors in a Gaussian process framework. I will demonstrate the performance and characteristics of the two methods by applying them to several datasets, including high-throughput assays of protein binding and pre-mRNA splicing, and will also compare the evolutionary dynamics induced by the resulting landscapes.

Keywords: fitness landscape, deep mutational scanning, high throughput mutagenesis, combinatorial optimization, Gaussian process, graph Laplacian, Hamming scheme, amplitude spectra, variance components

S3-2.5 – Mutation frequencies in a birth-death branching process

David Cheek [a 1], Tibor Antal [1]

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[a] Speaker

First, we revisit the stochastic Luria–Delbrück model: a classic two-type branching process which describes cell proliferation and mutation. We prove limit theorems and exact results for the mutation times, clone sizes and number of mutants. Second, we extend the framework to consider mutations at multiple sites along the genome. The number of mutants in the two-type model characterises the mean site frequency spectrum in the multiple-site model. Our predictions are consistent with previously published cancer genomic data.

Keywords: Branching processes, mutations, site frequency spectrum

Session 3-3 – Game theory and decision-making

Thursday, July 18, 2019 – 15:00-17:30 – Room 3

S3-3.1 – Consequences of multiple simultaneous discoveries on free riding

Frédérique Dubois [a] [1]

[1] University of Montreal – Canada

[a] Speaker

Social individuals do not all act in the same way and can therefore have different impacts on the productivity of the group to which they belong or the sustainability of the resources they exploit. Typically, some individuals (as referred to as investors or producers) put efforts into producing services or resources while others (as referred to as free riders, exploiters or scroungers) benefit from these services or resources without contributing. The question of how to limit free riding has been addressed by the Producer-Scrounger (PS) game, a classical example of the game-theoretical approach, in which group members have the options to either search for resources (producers) or exploit the efforts of others (scroungers). Although this model has been successful in predicting changes in tactic use in response to changes in resource value, its solution surprisingly is independent on the rate of resource discoveries. This arises because it assumes that only one resource can be discovered and exploited at a time. Furthermore, it considers that the rate of resource discovery is independent on the number of producers and scroungers in a group, though too many producers may reduce their effeciency in producing resources. I then developed a modified version of the PS model, that accounts for multiple simultaneous discoveries and applies to situations where the probability of making a discovery decreases as producer tactic use increases. Although the model converges towards a mixed ESS (Evolutionary Stable Strategy), the best response depends on the number of simultaneous discoveries, which should cause fluctuations in mean tactic use over time because of stochastic effects. Furthermore, it predicts that free riding should decrease as the number of simultaneous discoveries increases, while the effect of group size depends on whether the rate of resource discoveries declines or not as producer tactic use increases.

Keywords: game theory, free riding, producer scrounger game

S3-3.2 – Learning advantages in incompetent evolutionary games

Maria Kleshnina [a 1], Jerzy Filar [1], Cecilia Gonzalez Tokman [1]

[1] University of Queensland – Australia

[a] Speaker

All organisms on this planet live in a dynamic environment that undergoes changes. Thus, the ability to adapt becomes a key to survival and the adaptation of species to a changing environment is a long-standing question in biology. Adaptation is a mutation process which improves survival skills and reproductive functions of species, and usually includes two components: genetic adaptation and learning. We investigate adaptive learning by combining the concept of incompetence with evolutionary population dynamics. In the sense of evolution, incompetence and training are considered as learning processes with a focus on social interactions of individuals. Incompetence as a learning or adaptation function was first introduced in the context of evolutionary games as a fixed parameter. However, live organisms usually perform different nonlinear adaptation functions such as a power law or exponential fitness growth. Here, we demonstrate how the functional form of the learning process may affect the social competition between different behavioral types. Further, we extend our results for the evolutionary games where fluctuations in the environment affect the behavioral adaptation of competing species and demonstrate importance of the starting level of incompetence for survival. Hence, we define a new concept of learning advantages that becomes crucial when environments are constantly changing and requiring rapid adaptation from species. This may lead to the evolutionarily weak phase when even evolutionary stable populations become vulnerable to invasions.

Keywords: replicator dynamics, learning, incompetence, adaptation

S3-3.3 – Collective Action Problem in Heterogeneous Groups with Punishment and Foresight

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The collective action problem can easily undermine cooperation in groups. Recent work has shown that within-group heterogeneity can under some conditions promote voluntary provisioning of collective goods. Here we generalize this work for the case when individuals can not only contribute to the production of collective goods, but also punish free-riders. To do this, we extend the standard theory by allowing individuals to have limited foresight so they can anticipate actions of their group-mates. For humans, this is a realistic assumption because we possess a "theory of mind". We use agent-based simulations to study collective actions that aim to overcome challenges from nature or win competition with neighboring groups. We contrast the dynamics of collective action in egalitarian and hierarchical groups. We show that foresight allows groups to overcome both the first- and second-order free-rider problems. While foresight increases cooperation, it does not necessarily result in higher payoffs. We show that while between-group conflicts promotes within-group cooperation, the effects of cultural group selection on cooperation are relatively small. Our models predict the emergence of a division of labor in which more powerful individuals specialize in punishment while less powerful individuals mostly contribute to the production of collective goods.

Keywords: Cooperation, Conflict, Theory of Mind

S3-3.4 – Plasticity in evolutionary games

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[a] Speaker

The ability to respond appropriately to environmental cues is fundamental to the success of all forms of life. However, previous theoretical studies of the evolution of plasticity make so diverse assumptions that the conditions under which plasticity can emerge in evolving populations are unclear when fitness is frequency-dependent. We study the effect of adding plastic types to symmetric evolutionary games. Since frequency dependence induces an evolutionary change in the environment of players, one might expect that plastic individuals who can adapt their phenotypes to the environment would have a fitness advantage over simpler purely genetically determined phenotypes. In our model, plastic individuals can detect the type of their opponent before an interaction and condition their action on it. Even though it might appear as an outstanding advantage, such an ability cannot guarantee evolutionary success in all games for even the smallest positive plasticity costs. We classify games according to whether plasticity can or cannot invade a population of pure types and become the evolutionarily stable strategy. In games where the standard replicator dynamics converge to a pure state, costly plasticity cannot invade an equilibrium population. Costly plasticity can however be locally stable, but the way to achieve stability is not to play the best response to any possible encountered type. Rather, part of the stability success of plastic types is based on establishing Pareto-efficiency as residents, which leads to the possible co-evolution of plasticity and cooperation in the Prisoner's Dilemma and the Snowdrift game. Zero-sum games always allow for the global stability of plastic types. This study offers a more principled way of thinking about the evolutionary emergence of plasticity in social scenarios and helps demonstrate that such an emergence is strongly dependent on the type of game individuals are faced with.

Keywords: reaction norms, frequency dependence, natural selection, evolutionary games, environmental change, evolutionary stability

S3-3.5 – Run Away!: Optimal predator responses to startle displays

Ian Dewan [a 1], Tom Sherratt [1]

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[a] Speaker

Startle, or deimatic, signals are used by a variety of species as a defence against predation by causing predators to delay or abandon an attack on a prey item. One possible reason for the effectiveness of these signals is that to a predator it is ambiguous whether the signal comes from suitable prey or a danger, such as a disguised ambush predator; in this case both attacking and delaying to examine the potential prey more closely may be costly for a predator. The optimal behaviour for predators is affected by the degree to which the ambiguity in the signal is due to perceptual error, which can be reduced by further examination, and inherent variability in the types of stimuli in the environment, which cannot. We develop a model of predator decsion-making as a multi-step signal detection problem, in which predators faced with a potential prey item can optionally continue to examine it before deciding whether or not to abandon their attack. We examine in which circumstances immediate abandonment is a superior strategy to further examining a potential prey item, and the implications for the evolution of startle signals.

Keywords: predation, startle, anti, predator defence, speed, accuracy trande, off, signal detection

Session 3-4 – Epidemiology 2

Thursday, July 18, 2019 – 15:00-17:30 – Room 4

S3-4.1 – The evolution of antibiotic resistance on multicopy plasmids

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Plasmids play an important role in the evolution and spread of antibiotic resistance. They often exist in multiple copies within a single bacterial cell. This has consequences for the evolution of new resistance on plasmids. First, the mutational target size is multiplied by the plasmid copy number, making the appearance of resistance mutations more likely. Second, the plasmid copy number crucially influences the establishment probability of the resistance mutation, which initially appears in a single plasmid copy in a cell where all other plasmid copies are non-mutated. The segregation of plasmids into the two daughter cells at cell division leads to bacteria with a plasmid composition different from that of the mother cell, ultimately leading to a homozygous mutant cell (or to extinction of the process). Using multitype branching process theory, we analyze the establishment probability of a single non-mobile mutant plasmid. We thereafter determine the probability that resistance evolves de novo before a large population of drug-sensitive bacteria goes extinct ("evolutionary rescue"). We find that in the interplay of potentially antagonistic effects of the plasmid copy number on the mutational input and the establishment probability, a lower or a higher plasmid copy number may maximize the risk of resistance evolution. The outcome crucially depends on the dominance relationship between the wildtype and the mutant plasmid. We finally briefly discuss how the antibiotic concentration may influence the dominance function and hence the plasmid copy number that maximizes the risk of resistance.

Keywords: antibiotic resistance, multicopy plasmids, evolutionary rescue

S3-4.2 – Modelling Evolution of Virulence in Populations with a Distributed Parasite Load

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Modelling evolution of virulence in host-parasite systems is an actively developing area of research with ever-growing literature. However, most of the existing studies overlook the fact that individuals within an infected population may have a variable infection load, i.e. infected populations are naturally structured with respect to the parasite burden. Empirical data suggests that the mortality and infectiousness of individuals can strongly depend on their infection load; moreover, the shape of the distribution of infection load may vary on ecological and evolutionary time scales. Here we will show that distributed infection load may have important consequences for the eventual evolution of virulence as compared to a similar host-parasite system without structuring. Mathematically, we consider a host-parasite system, where the dynamics of the infected subpopulation within host dynamics are described by a von Forster-type model, in which the infection load plays the role of age. We implement the adaptive dynamics framework to predict evolutionary outcomes in this model and demonstrate that for simple trade-off functions between virulence, disease transmission and parasite growth rates, multiple evolutionary attractors are possible. Interestingly, unlike in the case of unstructured models, achieving an evolutionary stable strategy becomes possible even for a variation of a single ecological parameter (the parasite growth rate within the host) and keeping the other parameters constant. We conclude that evolution in disease-structured populations is strongly mediated by alterations in the overall shape of the parasite load distribution.

Keywords: Structured Populations, Infection Load, Evolutionary Attractor, Pairwise Invasibility Plot (PIP), Singular Points, Trade, Off, Stability

S3-4.3 – Evolution of virulence against juvenile and adult hosts

Ryosuke Iritani [a 1]

[1] RIKEN – Japan

[a] Speaker

The impact of infectious disease is often very different in juveniles and adults, but theory has focused on the drivers of stage-dependent defense in hosts rather than the potential for stage-dependent virulence evolution. Stage-structure has the potential to be important to the evolution of pathogens because it exposes parasites to heterogeneous environments in terms of both host characteristics and transmission routes. We develop a stage-structured (juvenile-adult) epidemiological model and examine the evolutionary outcomes of stage-specific virulence under the classic assumption of a transmission-virulence trade-off. We show that selection on virulence against adults remains consistent with the classic theory. However, the evolution of juvenile virulence is sensitive to both demography and transmission pathway with higher virulence against juveniles being favored either when the transmission pathway is assortative (juveniles preferentially interact together) and the juvenile stage is short, or in contrast when the transmission pathway is disassortative and the juvenile stage is long. These results highlight the potentially profound effects of host stage-structure on determining parasite virulence in nature. This new perspective may have broad implications for both understanding and managing disease severity.

Keywords: Adaptive dynamics, Age, structured population, Life, history evolution, Parasite virulence, Senescence

S3-4.4 – Individual vaccination choice and optimal budget allocation for vaccination campaign

Aniruddha Deka [a 1], Samit Bhattacharrya [a]

[1] PhD Scholar – India

[a] Speaker

The paper aims to investigate optimal budget allocation for vaccination campaign when vaccination is voluntary for an infectious disease like seasonal flu. We use evolutionary game theory to build the model of individual vaccination decision, and use optimal control theory to determine. We assume public health program disburse fund over time that works as incentive for individual vaccinations. We use optimal control theory to determine the budget allocated that minimize the cost of disease control. We formulate the above situation as an optimal control problem and the solution using Pontryagin's Maximum Principle.

Keywords: Optimal Control Theory, Evolutionary Game Theory, Free Rider problem

S3-4.5 – Plant virus ecology and evolution: pathogens that modify host plants to influence their own transmission

Ruairi Donnelly [a] [1]

[1] University of Cambridge [UK] – United Kingdom

[a] Speaker

It is well established that plant virus infection can alter plant-vector interactions, and moreover similar pathogen modifications are found in a range of plant and animal systems. In this talk we will introduce two models for analysing the spread of vector-borne plant viruses with a focus on vector behaviour and dynamics. We will present analyses of these two models that yield insight into the ecology and evolution of pathogen modifications. The first of the models is tailored to viruses that are acquired and inoculated through epidermal cells by aphids. Such viruses make up a large proportion of arthropod-transmitted plant viruses. The second model that we present is tailored to plant viruses that are acquired and inoculated from plant veins. This epidemiological interaction broadly applies to the remaining arthropod-borne plant viruses. In both of these cases, we analyse pathogen strategies, whereby they modify the biochemistry of infected plants, allowing them to influence their own transmission.

Keywords: vector manipulation, epidemiology, plant virus, plant disease

S3-4.6 – Larval mosquito habitat reduction and its potential effects on human malaria transmission, a coupled map lattice simulation.

Tony Kiszewski [a] [1]

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[a] Speaker

Environmental management as a malaria intervention tool is rarely advocated due to high perceived costs of implementation and limited evidence base for efficacy. We explore the potential of this more sustainable approach via a hybrid spatially explicit simulation. Our method combines stochastic automata with coupled map lattices to explore the impact of habitat removal and other methods of source reduction on the population dynamics of mosquitoes and the incidence of malaria transmission to humans. We adapted and re-parameterized a model previously used to simulation malaria transmission on the Amazonian frontier by *Anopheles darlingi* to represent a broader community of interacting villages in southern Burkina Faso, West Africa and with *An. gambiae* s.l. as the vector. Within a 200x200 grid, 64 small communities of about 100 households are represented, each with a maximum occupancy. People are represented as discrete agents with the ability to visit neighboring communities and return to their place of origin. Mosquitoes are represented by continuous variables indicating their abundance at each grid location. Dispersal of mosquitoes is weighted by stage of gonotrophic cycle, with gravids more likely to disperse towards the nearest oviposition site and host-seekers dispersing towards human habitations. Larvae in breeding compete for nutrients and experience developmental delays when nutrients are constrained. Preliminary results indicate that at equilibrium (n=30), in the control scenario without interventions, there are 290,673 (sd 6,302) infected mosquitoes on the simulated landscape and a monthly incidence rate of 1,121.3 (sd 18.4) malaria cases in humans. Habitat removal of 50% then leads to a 72.1% drop in infected mosquitoes and an 80.8% decrease in monthly malaria incidence. Thus, environmental management may have the potential for malaria reductions that respond in a non-linear fashion to reductions in habitat.

Keywords: mosquito, malaria, agent, based, automata, individual, based, vector ecology

Session 4-1 – Ecosystems dynamics

Thursday, July 18, 2019 – 15:00-16:20 – Room 1

S4-1.1 – Complex Bog Landscape Model (COMBOLA) for combined dynamic modeling of biotic turnover and peat deposit processes in peatland landscapes of boreal zone

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[a] Speaker

Biotic cycling processes in ecosystems consist of live organic matter producing branch and dead organic matter destructing one. The latter is accompanied by emission of greenhouse gases into the atmosphere. Overall emission is closely connected with generation, transport and consumption of gases accompanying by heat and water transport. In peatlands, the presence of water table depth (WTD) provides both anaerobic destruction with methane generation below WTD, and an aerobic one above it, accompanying by partial consumption of methane by methanotrophic bacteria. Due to complexity of processes in peat deposit and nonlinearity of the biotic turnover functioning, it's necessary to make combined models of them for assessing possible evolution of peatland landscapes under climate change.

COmplex Model of BOg LAndscapes (COMBOLA) is a set of dynamic compartment models of biotic turnover, net ecosystem exchange, water balance, heat and water transport, generation and transfer of CO2 and CH4 in a peat deposit on various time scales. The first main component is a number of biotic turnover models – from mass-balance equations on an annual to the NEE dynamics model on the daily time scales. Another important component is the one-dimensional model of heat, water and gas exchange in the peat deposit. COMBOLA can be characterized by the layer-module structure that provides the selected problem to be solved using a set of programming modules from different layers depending on the modeling goal, selected time scale, and presence of initial data for calibration. A number of interconnected modules constitute an integrated mathematical model of the peatland landscape adopted for given initial information. Such models are designed and calibrated for a number of bogs from the Western-Siberian middle and southern taiga under climate change scenarios.

The work is supported by projects 19-05-00534-a, 19-04-01227-a of Russian Foundation of Basic Research.

Keywords: terrestrial ecosystem, biotic turnover, dynamic compartment model

S4-1.2 – Emergence and Dynamics of Short Food Supply Chains

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[a] Speaker

Through the consideration of a stochastic matching model dependent on a probability function built from the Heron's formula, we analyze the emergence and the dynamics of short agrifood sale circuits in form of time-evolving random hypergraphs. These marketing circuits, which are used as a supportive policy for promoting local food consumption, typify short distribution channels. Although bipartite matching can be easily derived from the framework, we move our focus on the matching of triplets of players representing buyers, retailers and sellers. Their conditional pairing with respect to standard and social preferences are both taken into consideration. Our results show that the emergence of short food supply chains is triggered by a three-dimensional stochastic matching mechanism. Their time evolution is found to be governed by both stable and unstable dynamics, the latter being subject to bounded antiperiodic oscillations. Via the use of a Poisson process, we then redirect our interest toward spatial randomness and the number of circuits attainable in a defined territory. The model unveils a restricted spread of short circuits over the entire territory, which, in expectation, can only be a partial substitute for long supply chains. The outcomes show consistency with the agribusiness patterns currently observable in France.

Keywords: bioeconomics, short food supply chains, stochastic matching, spatial randomness.

S4-1.3 – Exploring the Influence of Phytoplankton Heterogeneity on the Stabilisation of Tri-Trophic Plankton Ecosystems under Eutrophication

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Understanding the impact of increasing eutrophication in planktonic ecosystems is currently a hot topic in the literature and remains a long-term challenge in ecology. Mathematical models generally predict destabilisation of food webs in eutrophic environments and large oscillations of species densities which can result in species extinction. This is often at odds with ecological observations demonstrating stable dynamics even for high degrees of nutrient load. The apparent discrepancy is known as Rosenzweig's 'paradox of enrichment' and various solutions have been proposed to explain the mismatch between theory and observations. In this study, we explore a new mechanism of stabilisation in a tri-trophic plankton model under various levels of eutrophication that occur as interplay between space heterogeneity and ecological stoichiometry. Mathematically, the model is based on a system of integro-differential equations. We consider various scenarios of phytoplankton growth and zooplankton food-dependent vertical movement. We show that vertical gradients in phytoplankton growth and phytoplankton population structuring in terms of their stoichiometric ratio, would result in a postponing of destabilisation of eutrophic systems as compared to a well-mixed system. We demonstrate the complex bifurcation structure of the system when key model parameters (e.g. degree of eutrophication, light shading) are varied. In particular, this involves the coexistence of limit cycles and stable equilibria. We argue that the possibility of multiple attractors in the system can result in hysteresis phenomena when the nutrient load is manipulated and this should be taken into account in lake restoration programs.

Keywords: the paradox of enrichment, ecosystem stability, structured population, food webs, spatial ecology

Session 4-2 – Evolution in varying environments

Thursday, July 18, 2019 – 15:00-16:20 – Room 2

S4-2.1 – Optimal germination times in unpredictable environments: the importance of dormancy for both among- and within-year variation.

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Bet hedging is of crucial important for organisms living in unpredictable environments. One way to deal with uncertainty among growing seasons is dormancy, which spreads the emergence of offspring across multiple years. Proper timing of emergence is not only important among years, but also within the growing season. Here, we study the evolutionary interactions between bet hedging strategies that deal with among- and within-season uncertainty. To do so, we use a modelling approach to study the separate evolution of dormancy and within-season arrival time, as well as their joint evolution, in plants with an annual life cycle. We find that dormancy can compensate for within-season bet hedging, but not the other way around. Because of this compensatory effect of dormancy on within-season bet hedging, we find that with higher among-season dormancy, plants take more risk within the growing season. Our results indicate that when natural environments become more unpredictable, this counterintuitively leads to less within-season bet hedging. Furthermore, we find that strong priority effects select for earlier emergence which in turn increases the need for dormancy.

Keywords: bet, hedging, phenology, dormancy, competition, evolution

S4-2.2 – Mathematical analysis for a multi-scale evolution model in periodic environment

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Adaptative evolution relies on genetic and epigenetic 'mutations' whose time scale are highly different. Indeed, the genetic mutation rate is about 1000 times smaller than the epigenetic 'mutation' rate. In this work, we introduce a multi-scale mathematical model base on a set of ordinary differential equations. In addition to the transfers induced by mutations, the population subgroup evolution laws are non linearly coupled thought a logistic term which allows taking into account competition for resources. Using asymptotic development and mathematical analysis technics we are able to predict which population subgroups emerge in a periodically varying environment. This study is complemented by stochastic and deterministic numerical simulations that illustrate the different possible scenarios. This work is conduct in collaboration with V. Calvez, S. Charlat and E. Rajon.

Keywords: multi, scale model, genetic, epigenetic, mathematical analysis, numerical simulations, evolution

S4.2-4 – The maintenance of polymorphism under fluctuating conditions: the case where alternative phenotypes are beta distributed

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Among the factors explaining the maintainance of genetic polymorphism, the hypothesis of fluctuating selection was seriously considered (Haldane & Jayakar 1963) then discarded for various reasons. The first reason was that the domain where the the parameters of the original model led to this maintenance was too small to occur likely in the real life. The second one was that ultimately, the type leading to the maximum geometric mean of the fitness ratio at long term always eliminate its counterpart. The distribution of fitnesses and their density of probability however was never addressed in this discussion. We examine here the case where the fitness of the two phenotypes is beta distributed in time. The beta distribution is especially fit when the fitnesses depend heavily of mortality rates. We show, partly by analytic demonstration, parly by simulation and qualitative analysis, that this kind of distribution, with some parameters, is susceptible to enlarge considerably the hypervolume of the domain where the polymorphism is maintained.

Keywords: genetic polymorphism, fluctuating selection, Haldand and Jayakar model

Session 4-3 – Evolutionary community ecology 2

Thursday, July 18, 2019 – 15:00-16:20 – Room 3

S4-3.1 – Proximity to collapse: mapping ecosystem biodiversity phase space

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Collapse, stability, and dynamical shifts between these two states are hallmarks of ecological systems. A major goal in ecosystem research is to identify limits of stability in terms of system properties such as diversity, complexity, interaction-topology, and hierarchies. Understanding how these properties affect the phase space boundaries between stable regions and collapse can help ecologists predict ecosystem response to environmental pressures. In this talk I will present a biodiversity complexity ecosystem phase space attained from generalized Lotka-Volterra dynamics and a new measure which places a given system in phase space and quantifies its' proximity to the collapse boundary. In contrast to previous collapse predictions we take into account that species dynamics can lead to single species extinctions. Allowing for extinctions reveals more structure of the complexity-stability phase space introducing an intermediate phase between stability and collapse –Extinction Continuum, which allows a more nuanced view of how an ecosystem can respond to changed internal and external conditions. With the extended phase space and adherence to construct our predictive measure strictly on observable quantities, our measure is applicable to real systems and contains more information–proximity to collapse as well as path through phase-space to collapse – than the canonical measure by May and critical slowdown.

Keywords: ecosystems, stability/complexity, interaction network, phase space, Lotka, Volterra dynamics

S4-3.2 – Signatures of coexistence mechanisms on stability components

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Coexistence mechanisms enable similar species that compete for similar resources to inhabit the same area. Ecologists have identified multiple coexistence mechanisms that could operate in any community, but it is difficult to determine which dynamics are actually operating in a natural community. These coexistence mechanisms not only have a significant influence on the assembly of communities, but they can also influence the temporal stability of these communities. Community stability has been studied from two distinct approaches: applying and analysing process-based models, and decomposing time-series of species abundance data into a suite of statistical indices. Using an exponential fitness model, we simulated the impact of a two distinct coexistence mechanisms on different aspects of community stability. We modelled communities using the storage effect, a fluctuation dependent mechanism, as well as niches to contrast their respective effects on community stability. We subsequently calculated community stability as well as statistics that decomposed from stability using the generated time series datasets. These community statistics were further analysed using classification trees to determine if the simulated coexistence mechanisms have recognizable signatures among the stability components. Our findings not only allowed us to identify coexistence mechanisms with high accuracy, but also indicate that the community statistics serve as an effective diagnostic to identify coexistence mechanisms from time-series data. However, these statistics have complex relationships with both niche and storage effect mechanisms, as evidenced by our classification tree results.

Keywords: ecological stability, coexistence, community assembly, biodiversity, theoretical ecology

S4-3.3 – The way species interaction shapes the evolution of community

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[a] Speaker

Competition is usually used as main factor to explain communities species richness in evolutionary biology. It imposes indeed a limit in the resource availability for species and induces a diversity-dependence on species diversification process. This is observable in phylogenetic trees for instance, in particular with inter-clade competition, network structure and also selection pressure on traits. Nevertheless, competition is not the only type of interaction in natural environments. Positive interactions, such as facilitation, may also modulate the effect of competition on species diversification. With the present study, we want to investigate what is the signature left by ecological processes, such as competition and facilitation, on phylogenetic and network structure. Especially, how network structure can affect phylogenetic evolution, and vise versa. We seek to acknowledge this theoretical questions using a macro-evolutionary niche model. This model gives us access to the evolution of two kind of communities. On one hand, a community where interactions are only competition. On the other hand, a community where interactions are only facilitation. From these communities, we can extract (i) the phylogenetic evolution, tracked with alpha statistic, (ii) the network structure, via the evolution of degree distribution and modularity over time, and (iii) the trait selection. When species number in each community is stable, we expect to have (i) an alpha statistic higher for facilitation than for competition communities, meaning that species diversification happens later within facilitation communities ; (ii) a positive exponential shape for degree distribution of facilitation interactions, and the opposite for competition ; and finally (iii) a balancing selection of traits for facilitation and disruptive selection for competition. All these measures put together allows us to explore the relationship between the three different approaches, which are usually taken separately.

Keywords: species interaction, network structure, phylogenetic structure, traits dispersion

Session 4-4 – Spatial ecology

Thursday, July 18, 2019 – 15:00-16:20 – Room 4

S4-4.1 – Defining biological spread in stochastic spatial simulations, sans mathematical integration

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Spatial simulations of larger (plant) populations often involve the use of artificial divisions; the population is divided into localised sub-populations which blanket the entire area, and are spatially distinct. Competition is assumed to occur primarily within sub-populations, as a localised interaction. In contrast, reproductive functions such as pollen (gamete) and/or seed (zygote) dispersal typically occur over larger spatial scales, across sub-population boundaries.
Measuring and defining this biological spread is important in population dynamics, as it can for example help predict/describe the infestation pattern of invasive species, and the rate of demographic change due to genetic selection. Typically spread is measured linearly in field trials and regression analysis of the data yields a one-dimensional function. However, to define spread between distinct sub-populations, that one-dimensional function must be mathematically integrated to two-dimensions, resulting in a formula which is both less transferable and less intuitive.
We present a study in which an alternative to mathematical integration was used, due to the two-dimensional nature of the initial biological spread records. Here we investigated the regression analysis of seed spread across a two-dimensional area, from multiple release sites, in a longitudinal study. The parameters in the two-dimensional seed spread equation were estimated directly (including an estimation of variability) whilst running within a larger stochastic simulation model, and generated a good fit to the original data.

Keywords: crop, weeds, seed dispersal, population model

S4-4.2 – Metastability as a coexistence mechanism in a model for dryland vegetation patterns

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Vegetation patterns are a ubiquitous feature of water-deprived ecosystems. Despite the competition for the same limiting resource, coexistence of several plant species (e.g. a woody and herbaceous species) is commonly observed. We present a two-species reaction-diffusion model based on the single-species Klausmeier model, to analytically investigate the existence of patterns in which both species coexist. Ecologically, the model predicts that coexistence is facilitated if there is a small difference in the plant species' average fitness, a quantity defined to be the ratio of a species' efficiency to convert water into new biomass to its mortality rate. Mathematically, coexistence is not a stable solution of the system, but both spatially uniform and patterned coexistence states are metastable. In this context, a metastable solution in which both species coexist corresponds to a long transient (exceeding 10ˆ3 years in dimensional parameters) to a stable one-species state. We show that this behaviour is characterised by the small growth rates of spatially uniform perturbations to a coexistence equilibrium. We present that the growth rates yielding the metastability property have the same order of magnitude as the average fitness difference between the two species and that under suitable conditions formation of a coexistence pattern occurs on a much shorter timescale than the transient behaviour to a single-species state. Finally, we discuss some ecological interpretations of our results, such as predictions on a pattern's eventual fate based on its wavelength.

Keywords: metastability, vegetation patterns, species coexistence, pattern formation, reaction, diffusion systems, semi, arid landscapes

S4-4.3 – Morphogenesis of networks in polydomous ants

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Many biological systems are dependent on transportation networks for the efficient distribution of resources and information. Network builders face the challenge of balancing conflicting network properties such as robustness, efficiency and costs. Polydomous ant colonies are split between multiple spatially separated nests. They build and maintain physical trails that connect their nests to each other and to food resources. The resulting transportation network is used to distribute workers, brood, and food. The morphogenesis of these complex networks and in particular the individual mechanisms underlying them have not yet been quantified. There is empirical evidence that networks are organised at the local level between neighbouring nests and not at the colony level. We test this hypothesis in the species *Formica lugubris* with a model developed at the scale of the colony. The model consists of simple rules of interactions between nests based mainly on distance metrics. The model is validated against empirical data collected for 7 years on 9 colony networks in England. We find a good agreement between simulated and empirical data on many emergent quantities such as the number of trails per nests and centrality measures. We infer the mechanisms possibly involved at the scale of the individuals, with a focus on the diffusive behaviour of motion of scouts. This work provides for the first time a model of morphogenesis of networks in polydomous ants quantitatively validated against empirical data. The colony-level scale of description chosen for the model may well be of interest for future research investigating either the individual behaviours underlying the morphogenesis or the coupling between network structure and resource distribution in polydomous ants.

Keywords: ants, collective behaviour, morphogenesis, network, model

Posters

P01 – A model for a population of actin filaments

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[a] Speaker

Many cellular behaviors such as cell division or shape changes stem from mechanical properties of embryonic cells. The cortical actomyosin cytoskeleton is a major determinant of these mechanical properties. Actin is a protein of the cytoskeleton which exists in two forms: monomers and polymers. The creation of actin filaments results from particular and complex dynamics. In order to better understand these dynamics, we model it on different scales.
The aim of this work is to understand the dynamics of a population of actin filaments, the interactions between filaments, and the interactions between filaments and accessory proteins. Also, the distribution of the lengths of the filaments is an important information for biologists since the length of actin filaments directly impacts the mechanical and structural properties of cells. We begin by modeling a single actin filament and then generalize our results to consider a population of actin filaments.
The first scale corresponds to a single actin filament. Using queuing theory and Skorokhod problem, we determine the fluid limit for a system with a random switching state. This fluid limit highlights a mean behavior and the distribution of the ressource - actin monomers - in the system.
The second scale corresponds to a population of actin filaments. Using a classical model for population dynamics, we study a meta-population and determine the large population limit in order to have the distribution of the lengths of the filaments.

Keywords: Actin, Population dynamics, Queuing theory, Random switching state, Fluid limit, Large population limit

P02 – A clustering algorithm for weighted ecological networks

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Microbial association networks represent microbial taxa as nodes and predicted associations as edges. Therefore, they can visualize community structure and help identify drivers of community structure. However, existing clustering algorithms such as the Markov Cluster Algorithm or Louvain Community detection are unable to take advantage of the information contained in negatively weighted edges. To make optimal use of the available information, we developed a clustering algorithm, *manta*, which uses negative edge weights to identify clusters.

Our algorithm uses network flow to assess cluster membership. However, *manta* operates on a matrix of edge weights rather than a stochastic matrix. Therefore, it can identify clusters separated by negatively weighted edges. The algorithm alternates between three processes: expansion, normalization and inflation. It takes the matrix power of the edge weight matrix, normalizes by the largest absolute value and expands through addition of each entry's inverse value. These iterations are repeated until the matrix converges to values of 1 and -1 or until a memory effect is detected. Convergence only occurs on networks consisting of positively weighted intra-cluster edges and negatively weighted inter-cluster edges. In more realistic situations, clusters contain positively-weighted inter-cluster edges; here, the matrix enters a flip-flop state. We expand on our algorithm with a partial iteration strategy that captures stable positions within the matrix. Moreover, we use the flip-flop state to identify nodes that cannot confidently be assigned to any cluster.

We demonstrate on two synthetic datasets that *manta* outperforms existing clustering algorithms and reaches similar performance as WGCNA, a network inference and module detection algorithm for gene regulatory networks. We identify important qualitative differences between WGCNA and *manta* networks, with WGCNA responding more strongly to underlying scale-free topologies. Finally, we show how *manta* is able to distinguish unique functional groups in a co-occurrence network generated from a cheese rind dataset.

Keywords: Microbial ecology, network theory

P03 – Impact of Climate Variability on Malaria Transmission Using a Dynamic Mosquito-Human Malaria Model

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In this study, we develop a climate-based mosquito-human malaria model to study malaria dynamics in the human population over KwaZulu-Natal, one of the epidemic provinces in South Africa, from 1970-2005. We compare the model output with available observed monthly malaria cases over the province from September 1999 to December 2003. We further use the model outputs to explore the relationship between the climate variables (rainfall and temperature) and malaria incidence over the province using principal component analysis, wavelet power spectrum and wavelet coherence analysis. The model produces a reasonable fit with the observed data and in particular, it captures all the spikes in malaria prevalence.

[a] Speaker

Keywords: Climate variability, Mathematical model, Anopheles arabiensis, Malaria incidence, South Africa, Malaria dynamics

P04 – Mathematical modelling of neutral mutations in varying environment

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One of the most interesting topics in biology is the identification of how important certain mutations are, whether they are adaptive, maladaptive or neutral, and how they spread in the population. Many studies have been done on directly detecting strongly selected mutations, e.g. detecting driver mutations in cancer through genetic data. However, we are still missing mechanistic models to step-wisely explain what is the baseline to define driver mutations. Of special interest is how neutral mutations behave in fluctuating populations, as opposed to the classic assumption of constant or exponentially increasing populations. We combine mathematical modeling and bioinformatics analysis to show how sampling size, mutation burden, difference in age and selection intensity lead to different patterns of mutation frequencies among individuals. We also built a coevolutionary model for a host-virus system to see how neutral mutations and host-virus adaptations shape genetic diversity. In both projects, mathematical models are combined with published data e.g. in prostate cancer or data collected by our collaborators (QMUL, BCI and University of Konstanz).

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Keywords: Modelling, Bioinformatics, Neutral, Mutations, Coevolution, Host, Virus, Cancer

P05 – Moving beyond the 'mean growth rate when rare' of the modern coexistence theory

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[a] Speaker

Modern coexistence theory is widely employed in describing the conditions required for the coexistence of species in a community. Its basic principle is that coexistence occurs when each species is able to invade the community when it is at a low abundance and the other species are all at high abundances. This invasibility is quantified by measuring the mean growth rate of each species starting from a small, close to vanishing, abundance. We show that this privileged quantity, the mean growth rate when rare, describes only partially the true invasibility of a species (and, consequently, other properties related to coexistence such as the mean time to extinction). This is because it ignores a crucial element in the process of invasion, the strength of random abundance fluctuations for a species, i.e. the diffusion along the log-abundance axis. To illustrate our argument, we employ numerical simulations of the lottery and the forest dynamics models for two species, and show that in each case, when the strength of environmental fluctuations is varied then the invasibility of a species bears no direct relation to the respective parameter employed by each model based on the mean growth rate when rare. We provide theoretical explanation for why this is the case, and end by suggesting numerics-based metrics to determine the actual invasibility, the mean time to extinction of a species, and other quantities which may relate to the persistence of species and their coexistence in a coommunity.

Keywords: Community ecology, modern coexistence theory, mutual invasibility, lottery model

P06 – Multispecies Interactions as Drivers of Antimicrobial Resistance Dynamics

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The evolution and spread of multidrug-resistant (MDR) bacteria in healthcare institutions is a major public health threat. Control of MDR bacteria has proven particularly challenging among Gram-negative Enterobacteria, which are often commensal, share resistance-encoding genes with other bacteria via horizontal gene transfer (HGT), and potentially interact with other species in their ecological niche. Mathematical models have played an important role in understanding the eco-evolutionary dynamics of MDR bacteria, but have traditionally focused on one species at a time. Here, we develop and analyze a compartmental ODE model of patients in a healthcare setting that accounts for colonization with multiple bacterial species, inter-patient bacterial transmission, antibiotic selection for resistance, and interspecific interactions including HGT. We describe how bacterial fitness depends on multispecies interactions, how disruption of commensal flora can favour the proliferation of resistance, and how HGT can sustain resistance despite its costs. We further incorporate a suite of public health interventions, including hand hygiene, antimicrobial stewardship and oral fecal transplantation, and use probabilistic numerical simulation to estimate the impact of interventions on bacterial colonization. We conclude by discussing which types of interventions may be most effective at limiting different profiles of MDR bacteria.

[a] Speaker

Keywords: antimicrobial resistance, ordinary differential equations, Gram, negative bacteria, multispecies interactions

P07 – Reconstructing tumour growth history using spatial data

Magnus Haughey [a] [1]

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[a] Speaker

Intra-tumour heterogeneity is a major cause of drug resistance and treatment failure in cancer. During the tumour expansion, "clonal" (common to all cells) and "sub-clonal" (unique to a subgroup of cells) genetic mutations are rapidly accumulated in tumour cells. Understanding how these sub-clones, some of which may be drug resistant, arise and evolve is therefore vitally important to the development of effective therapies. It is often infeasible, however, to collect longitudinal samples from the same tumour in patients, and thus difficult to directly measure the growth history of these sub-clones. Instead, mathematical modelling employed in conjunction with the available spatial information of tumours samples taken at a single time-point can be an effective method for studying the growth of tumour sub-clones. We aim to use computational modelling to understand the history of tumour growth and the dynamics responsible to quantify the heterogeneous structure observed *in vivo*. Historically, "bulk-sequencing" methods have been used to study tumour heterogeneity. These methods, however, do not preserve spatial information which could provide a crucial insight into the evolutionary dynamics of these systems. Motivated by the recent development of BaseScope technology – a cellular-resolution, spatially-preserving method of identifying mutant sub-clones in human tumours – we investigate how to utilise the available spatial information to resolve the underlying dynamics. Based on different dynamical rules, we simulate the spatial spread of wild-type and resistant mutations during tumour growth in three dimensions. By taking "slices" of the 3-dimensional data we obtain 2-dimensional samples: mirroring the process used to acquire samples from human tumours. We present the 3-dimensional simulator and some statistical tools developed from fractal geometry, namely fractal dimension and lacunarity, to relate changes in interfaces between clonal and sub-clonal regions to the underlying growth dynamics.

Keywords: cancer, resistance, simulation, fractal analysis, spatial data

P08 – Impact of population demography on allele frequency statistics

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[a] Speaker

Genome-wide polymorphism data of closely related populations can be summarized by different frequency statistics, such as the joint allele frequency spectrum that records the joint frequency distribution of derived alleles in two related populations, the Patterson's D statistic which tests for admixture between populations, and measures of population differentiation (FST and dxy) and divergence. In my research I investigate the impact of population demographies on frequency statistics using the framework of Poisson random fields. I aim for generalizations of some of the existing formulations and study possible patterns of asymmetry that result from different population demographies. In particular, I am interested in how divergence between populations is influenced by various scenarios of fluctuations in population size which for example can arise at a single point in time or periodically.

Keywords: population genetics theory, population demography, allele frequency, Poisson random field model

P09 – Modelling the foraging behaviour of bumblebee using private or social information.

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Plant-pollinator interaction is a strong evolutive force, and bumblebees are model organisms that have shaped much of our current knowledge. Past researches on bumblebees foraging strategies have shown that their efficiency depends on flower spatial distribution, with bumblebees being able to follow routines while visiting flowers, a behaviour is known as traplining and that relies on the use of personal information. Moreover, the presence of the conspecifics may also impact foraging decisions, namely the decision on whether to visit a given flower, a behaviour that relies on the use of social information. We propose to use an individual-based model to examine the impact of floral resources distribution and diversity on bumblebees foraging behaviour integrating the use of both personal and social information. The model simulates the equivalent of a day of bumblebee foraging. We follow the journey of pollinators across a simulated floral landscape. We are particularly interested in their foraging efficiency measured by the difference between the energy obtained during the feeding and the cost of moving in the environment. The agent can make decisions at two different levels: while moving between flowers, and while probing (or not) a flower. We will focus on the information used to make those decisions.

Keywords: individual based model, foraging behaviour, pollinators

P10 – Biases and alternatives to the Recruitment-Mortality equation used to estimate finite rate of increase of populations of boreal caribou

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Population growth rate is a central parameter used to assess status of species and target populations in jeopardy. The finite rate of population increase (λ) can be assessed either from direct estimates of population size or from matrix models including age-structured survival and reproduction rates derived from the Euler-Lotka equation. However, such data can be challenging to obtain and often leads to the use of simplified models derived from this theoretical framework. In North America, a widely used method to estimate λ for ungulate population is the Recruitment-Mortality (R-M) equation. In this method, λ is expressed as the balance between recruitment and mortality of GPS-collared adult females between two time-steps. For example, the R-M equation is peculiar to studies of threatened boreal woodland caribou (*Rangifer tarandus caribou*) where λ estimates are used to inform conservation actions. However, the R-M equation rely on assumptions that are unlikely to be true and almost never verified such as constant survival and recruitment across adult age class despite the fact that senescence processes have now been well documented in mammals. Using data simulation, we are currently assessing the magnitude of suspected biases. We are also working on the development of an integrated population model that could be used to provide more accurate estimates of demographic parameters from data classically collected in caribou monitoring project (i.e., GPS monitoring, aerial surveys, age- and sex-ratio counts). This model will be applied to the study case of an understudied population of boreal caribou living in the Saskatchewan boreal shield (Canada), an environment characterized by very low human activities but extremely high rates of natural disturbances. By presenting our progress, we hope to prompt discussions on how to avoid over-simplification of demographic model in applied conservation biology and how to make more sophisticated method accessible to a broader audience.

Keywords: Boreal caribou, Finite rate of population increase, GPS, collar, Integrated population model, Recruitment, Mortality equation, Rangifer tarandus caribou

P11 – A master equation approach to studying competitive metacommunities

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Most work considering metacommunities has been restricted to studying specific archetypes (special cases) that may arise. Clearly, this limits a complete and general understanding of metacommunity ecology based on fundamental ecological principles. In this study, we move beyond the archetypes and build a general model of a two-species metacommunity. We include a competitive Lotka-Volterra birth-death process, migration within the metacommunity, demographic stochasticity, environmental catastrophes, and patch heterogeneity in our model. We find that stochasticity typically hinders coexistence, lowering the strength of competition at which competitive exclusion becomes more likely than coexistence from the corresponding deterministic system. It also reduces the likelihood of founder control. We also find that increasing the species' carrying capacity and migration rate increases the probability of coexistence. When these are sufficiently high, they can even overwhelm the effects of competition making coexistence more likely than in the corresponding deterministic system. Our model provides a more complete description of a metacommunity than is typically studied and has implications for understanding the niche-neutral interface. Furthermore, it provides the crucial ability to differentiate between coexistence at the patch and metacommunity level.

Keywords: metacommunity, competition, stochastic dynamics

P12 – The International Initiative for Theoretical Ecology (IITE) – one year on

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A year ago at MPDEE'18 (Models in Population Dynamics, Ecology, and Evolution) in Leicester, a few of us came together to create an organization with the goal to actively strengthen the role of theory in ecology, ultimately to make ecological theory more visible and relevant for ecosystem management and conservation policy. And so the International Initiative for Theoretical Ecology (http://iite.info) was born. The idea proved very popular in the scientific community, with now over 50 colleagues publicly declaring their support on the IITE webpage. So, what is IITE doing? We are analysing where the issues are that are holding the field back, and are raising awareness of them in blog posts and opinion pieces in influential journals (with surprising support by the editors); we are organizing activity on Wikipedia and inviting all theorists to present their insights on this platform to encourage cohesion and consistency in the field; and we are preparing a training drive to build capacity. Soon IITE will become registered as a foundation. Then we will start public-facing work to advertise our profession and what it achieves, and to convince the public, funders and donors that investments into theoretical ecology are worth every penny. Come chat with us at the poster or elsewhere.

Keywords: theoretical ecology, conservation ecology, science policy

P13 – An algorithm for inferring sites of interest from high-resolution data

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[a] Speaker

Due to recent advances in tracking technology, we are now able to acquire animal locations at a sub-second resolution, which provides a vast array of opportunities for understanding animal behaviour. However, many of the current mathematical and statistical tools used to analyse animal movement data are computationally too slow, since they were not designed with these datasets in mind.

In this talk I will explain how we adapted a previous algorithm to better cope with such huge datasets. The algorithm itself is used to identify an animal's sites of interest, which will be areas in which they spend a disproportionally long time. I will present results from applying the algorithm to both simulated data (which demonstrates its accuracy and speed) and empirical data on Alpine cattle.

By identifying these sites we can simplify a complex movement trajectory to a simple, Markov-chain description of broad-scale movement decisions. Our new technique will thus help researchers obtain better inference into the key behavioural drivers behind observed animal movements.

Keywords: Movement, Methods, Animals

P14 – Invariant manifolds of the Selection-Recombination model from population genetics

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I have been analysing a continuous-time model in Population Genetics which focuses on two evolutionary forces at play: selection and recombination. After plotting many phase plane diagrams for this system, I (almost) always found a stubborn special surface in my plots, which is called the quasilinkage equilibrium manifold. Using methods from monotone systems theory, I proved the manifold does indeed exist in the model for a certain case.

Keywords: Population genetics, invariant manifolds, selection, recombination model, quasilinkage equilibrium manifold

P15 – E and N Cadherin-Dependent Cell-Cell Adhesion: A Non-Local Model and Its Application to Wound Healing

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Cell adhesion molecules, such as Epithelial (E)-cadherin and Neural (N)-cadherin, have essential importance on the binding of one cell to another at the cell surface. Known also as cell-cell adhesion this process plays a critical role in tissue formation during early embryo development, immune responses and also the healing of wounds. All these biological functions require the coordinated movement of cells in particular ways to specific locations, however, it is unclear how cell junctions control this coordinated migration. Due to this fact, we mainly examine the role of E- and N-cadherins on cell migration phenomena and we particularly investigate how E- and N-cadherins affect cell direction during wound healing assays. In order to understand their impacts on the direction of cell movement from unwounded to wound areas, we develop a new continuous mathematical model consisting of diffusion and adhesion force terms with two different direction functions that represent the effects of E cadherin and N cadherin.

Keywords: Cell cell adhesion, Integro PDE model, E and N cadherins, Wound healing

P16 – Type, strength and target of perturbations determine whether co-adaptation can ensure the robustness of non-stationary predator-prey dynamics

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[a] Speaker

Global change threatens the maintenance of ecosystem functions that are shaped by the persistence and dynamics of populations. It has been shown that the persistence of species increases if they possess larger trait adaptability. Here, we investigate whether trait adaptability also affects the robustness of population dynamics of interacting species and thereby shapes the reliability of ecosystem functions that are driven by these dynamics. We model co-adaptation in a predator–prey system as changes to predator offense and prey defense due to evolution or phenotypic plasticity. We investigate how trait adaptation affects the robustness of population dynamics against press perturbations to environmental parameters and against pulse perturbations targeting species abundances and their trait values. Robustness of population dynamics is characterized by resilience, elasticity, and resistance. In addition to employing established measures for resilience and elasticity against pulse perturbations (extinction probability and return time), we propose the warping distance as a new measure for resistance against press perturbations, which compares the shapes and amplitudes of pre- and post-perturbation population dynamics. As expected, we find that the robustness of population dynamics depends on the speed of adaptation, but in nontrivial ways. Elasticity increases with speed of adaptation as the system returns more rapidly to the pre-perturbation state. Resilience, in turn, is enhanced by intermediate speeds of adaptation, as here trait adaptation dampens biomass oscillations. The resistance of population dynamics strongly depends on the target of the press perturbation, preventing a simple relationship with the adaptation speed. In general, we find that low robustness often coincides with high amplitudes of population dynamics. Hence, amplitudes may indicate the robustness against perturbations also in other natural systems with similar dynamics. Our findings show that besides counteracting extinctions, trait adaptation indeed strongly affects the robustness of population dynamics against press and pulse perturbations.

Keywords: Stability, disturbance, trait adaptation, resistance, resilience, elasticty

P17 – Modeling cell infection via virus-producing cells rather than free infectious virus significantly improves fits of in vitro viral kinetic data

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Chikungunya and Zika viruses are arthropod-borne viruses that pose significant threat to public health. Experimental data show that during *in vitro* infection both viruses exhibit qualitatively distinct replication cycle kinetics. Chikungunya viral load rapidly accumulates within the first several hours post infection whereas Zika virus begins to increase at much later times. We sought to characterize these qualitatively distinct *in vitro* kinetics of chikungunya and Zika viruses by fitting a family of mathematical models to time course viral load datasets. We demonstrate that the standard viral kinetic model, which considers that new infections result only from free virus penetrating susceptible cells, does not fit experimental data as well as a model in which the number of virus-infected cells is the primary determinant of infection rate. We provide biologically meaningful quantifications of the main viral kinetic parameters and show that our results support cell-to-cell or localized transmission as a significant contributor to viral infection with chikungunya and Zika viruses.

Keywords: virus infection, viral kinetics, mathematical model, Zika, chikungunya

P18 – Find your seat at the buffet: Trophic niche partition of sessile cnidarians

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[a] Speaker

Many shallow-water cnidarians are polytrophic as they feed by heterotrophy, while also receiving photosynthetic products from associated algal endosymbionts (Dinoflagellata, Symbiodiniaceae). These symbioses allow animals such as corals and zoantharians to survive in oligotrophic waters. Nevertheless, alteration of environmental conditions at ecological or evolutionary time scales can move the association towards commensalism or parasitism. For instance, increasing sea water temperatures can induce some endosymbiotic species to assimilate more resources from their host, without translocating a higher proportion of photosynthates. Therefore, climate alterations predicted for the next decades will change ocean conditions and impact cnidarian-endosymbiont performances. Sessile cnidarians can ingest particles in the water column ranging from organic matter and picoplankton to macrozooplankton. Here we investigated potential trophic niche partitions among cnidarian species using an extensive literature review and stable isotope analyses. We used the mixing model Stable Isotope Bayesian Ellipses in R (SIBER) to calculate the isotopic niche (carbon and nitrogen stable isotope ratios; proxy of the trophic niche) of both cnidarians and their associated endosymbionts. Among metrics estimated were trophic niches' width, overlap, and placement. Preliminary analyses revealed that sympatric zoantharian species with smaller mouths had lower trophic levels than species with larger mouths (*Palythoa tuberculosa* and *P. mutuki*, respectively). Still, *P. tuberculosa* had a much wider niche than *P. mutuki* and a smaller overlap of niche (5% relative to the niche of the first species, and 58% relative to the second). Additionally, *P. tuberculosa* had a smaller niche overlap with its associated endosymbiont than *P. mutuki* (31% and 42%, respectively). The results indicated that *P. tuberculosa* has a more generalist nutrition strategy compared to *P. mutuki*, and a less mutualistic symbiotic association.

Keywords: Mixing models, Nutrition, Stable isotopes, Symbioses, Trophic niche

P19 – Phenotypic heterogeneity and the evolution of collective function in the genus Dictyostelium discoideum.

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[a] Speaker

Aggregative multicellularity, where differentiated multicellular organisms assemble from sparse and possibly genetically disparate cells, is an evolutionary conundrum. Due to the similarity with the paradox of cooperation, sociobiology has been invoked to understand how multicellular or 'social' organization has emerged in microbes. In this framework, however, evolutionary explanations largely rely on genetic homogeneity within multicellular groups, which is generally hampered when groups form by aggregation. Whereas evolutionary biologists tend to consider that the genetic background primes in determining the role of cells within aggregates, stochasticity in phenotype determination has also been invoked as a mechanism opposing the loss of cooperation. Indeed, cheaters' success would be undermined if cell fate is determined by a 'lottery' run at the onset of aggregation.Using Dictyostelium discoideum as a model organism, we combine developmental biology experiments and biophysics modeling to explore the possible route by which evolution could turn pristine phenotypic plasticity into evolutionarily stable collective division of labor.

Keywords: Collective, Phenotypic heterogeneit, Cooperation, Selection, Evolution

P20 – Sex differences in altruism and the demography of human warfare

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[a] Speaker

Recent years have seen an increasing interest in understanding the possible links between warfare and the high levels of within-group altruism observed in human societies. At the same time, sex has been shown to modulate incentives to express social behaviours in populations characterised by warfare demographies. However, the potential for sex differences in altruism in the context of warfare has been relatively neglected and the possibility that such differences might be driven by sex biases in demography has not been explored formally. Here, we develop a kin selection model to investigate how the sex of the altruist and that of the beneficiary influences patterns of such behaviours in populations that experience between-group conflict. We find that sex is a fundamental modulator of altruism in the context of the demography of warfare: members of the sex that competes more locally and/or is more philopatric are favoured to be more altruistic than the other sex, and both sexes are favoured to be more altruistic towards the sex that competes more globally and/or that disperses at a lower rate.The effects of these two factors may reinforce each other, potentially explaining recently-observed patterns of sex-specific altruism in populations with different post-marital dispersal norms.

Keywords: altruism, warfare, human behaviour, sex differences, demography, kin competition

P21 – Perturbation transmission in metacommunities

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[a] Speaker

Human activities affect organisms through direct perturbations and habitat fragmentation. Thus, depending on the ability of different species to disperse in a fragmented world, perturbations in one locality can propagate and impact in a very different way other connected populations. To tackle this problem, we use a metacommunity model made of two connected food chains and we studied perturbation transmission for (1) different biomass repartition (*e.g.* biomass pyramid or trophic cascade) and (2) different dispersal regimes (*e.g.* increasing dispersal rates, dispersion of specific trophic levels only...). We considered stochastic perturbations directly applied to species populations and we measured the time variability of species from the two connected food chains to assess their response to perturbations. To assess this time variability, we solved analytically the Lyapunov equation linking the output covariance matrix of a dynamic system to its Jacobian matrix and the input covariance matrix of perturbations. We found that the relative importance of dispersal compared to demographic process depends on species biomass. Thus, biomass repartition in food chains determines which trophic levels disperse the most and propagate perturbations from one locality to another. This can lead to contrasting effects in different populations. For instance, a top-down perturbation in a locality is turned into a bottom-up perturbation in another if the basal species disperses the most. Our model gives the fundamental element to understand perturbation transmission in metacommunities and to predict their effect depending on biomass repartition and dispersal among trophic levels.

Keywords: metacommunity, food chain, stability, perturbation, dispersal, top, down, bottom, up, time variability, synchrony

P22 – Identification of Potential Distribution Area for Haloxylon anmodendron by the MaxEnt Ecologic Niche Model

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Haloxylon anmodendron is an excellent species of sand fixation and wind protection in desertification regions. Identifying the potential distribution areas for *Haloxylon anmodendron* can provide an important scientific basis for the introducing, cultivating, protection, utilization, and sustainable management of *Haloxylon anmodendron* resources. Through the environmental data process of existing distribution area of *Haloxylon anmodendron*, the MaxEnt ecologic niche model was used and the main limited factors for *Haloxylon anmodendron* distribution were selected and the potential distribution areas of *Haloxylon anmodendron* in China were identified. Meanwhile, the model precision was tested through receiver operating characteristic curve. The results shows that the optimum distribution areas of *Haloxylon anmodendron* require the climatic conditions of mean annual air temperature of 9.4_˜10°C, an extreme high air temperature of 39.2_˜44°C, an extreme low air temperature of -17_˜-25°C, the annual precipitation of 32.9_˜43.7 mm; and the soil pH-values of 7.9_˜8.5 as well as the altitude around 1000m a.s.l..The total potential distribution area of *Haloxylon anmodendron* in China was 1.7358million km^2, accounting for 18.1% of the total land area of China. The potential distribution areas were Xinjiang Uygur Autonomous Region, Inner Mongolia Autonomous Region, Gansu province, Qinghai province and Ningxia Hui Autonomous Region. The optimum distribution area in Xinjiang is 250,300 km^2, accounting for 73% of the total optimum distribution in China. The main environmental factors affecting *Haloxylon anmodendron* potential distribution are the precipitation of mean temperature of warmest quarter, annual precipitation, annual mean temperature, min temperature of coldest month, temperature annual range.

Keywords: Haloxylon anmodendron; MaxEnt model; Environment variables; potential distribution

P24 – Grazing Altered the Pattern of Woody Plants and Shrub Encroachment in a Temperate Savanna Ecosystem

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Ulmus pumila-dominated temperate savanna is an important tree-grass complex ecosystem in the Otindag sand land, northern China. To date, few investigations have been undertaken on the spatial patterns and structure of this ecosystem and its driving factors under different grazing pressures. The objective of our investigation therefore is to explore the effects of grazing pressure on the population structure, spatial patterns and interactions among *U. pumila* and woody plants in this ecosystem using field observations and point pattern analysis. Results indicate that biodiversity and seedling decreased with increasing grazing pressure (light-high intensity). However, adult-tree density was significantly unchanged with different grazing pressures. The population structure of *U. pumila* showed a declining trend with increasing grazing pressure; an increase in grazing limited the normal regeneration of the *U. pumila* population, further aggravating its decline. *U. pumila* seedlings recorded a more significant aggregated distribution than juvenile or adult trees. The adult and juvenile trees showed small scale aggregation distribution and a large scale random distribution. Shrubs also showed a significant aggregation distribution. No obvious effect on the spatial patterns for the adult trees was recorded; however, an effect was noticeable for juveniles and seedlings under different grazing pressures. The seedling of *U. pumila* had a positive association with their juveniles and *Spiraea aquilegifolia,* but a negative association with *Caragana microphylla.* Shrub encroachment occurred with decreasing grazing pressures. Our results provide important information for rangeland management practices and vegetation restoration of *U. pumila*-dominated temperate savanna ecosystems.

Keywords: Ulmus pumila, dominated temperate savanna, population structures, spatial patterns, spatial association, grazing pressure

P25 – Evolution of Mobility in Predator-prey Systems

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[a] Speaker

We investigate the dynamics of a predator-prey system with the assumption that both prey and predators use game theory-based strategies to maximize their per capita population growth rates. The predators adjust their strategies in order to catch more prey per unit time, while the prey, on the other hand, adjust their reactions to minimize the chances of being caught. We assume each individual is either mobile or sessile and investigate the evolution of mobility for each species in the predator-prey system. When the underlying population dynamics is of the Lotka-Volterra type, we show that strategies evolve to the equilibrium predicted by evolutionary game theory and that population sizes approach their corresponding stable equilibrium (i.e. strategy and population effects can be analyzed separately). This is no longer the case when population dynamics is based on the Holling II functional response, although the strategic analysis still provides a valuable intuition into the long term outcome. Numerical simulation results indicate that, for some parameter values, the system has chaotic behavior. Our investigation reveals the relationship between the game theory-based reactions of prey and predators, and their population changes.

Keywords: Predator, Prey, Evolution of mobility, Evolutionary game theory, Holling II functional response, Chaotic behavior

P26 – T-cell mediated adaptive immunity and the role of antibody in dengue infection

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[a] Speaker

Dengue is the most common mosquito-borne viral disease and causes a significant number of deaths, mostly in the tropical and subtropical regions. It is caused by the four distinct but antigenically related viruses, known as serotypes, which are transmitted to humans through Aedes mosquito. Currently, more than half of the World's population lives in the area where the Aedes mosquito present. Due to climate changing, dengue incidence is increasing day by day, and more countries are reporting their first outbreak. The desire to establish the factors determining the disease severity and the growing need for efficient drugs has prompted extensive research interest in within-host viral dynamics. However, very few mathematical models of within-host dengue dynamics pertaining to secondary dengue infection are presently available. To address this gap in the pertinent literature, we develop both the primary and the secondary dengue infection model with T - cell mediated adaptive immunity and antibody-dependent enhancement was developed by considering the memory cell and heterogeneous antibody as the main factor. In case of secondary dengue infection, both the virus and homogeneous antibody production are enhanced due to the influence of memory cells remaining from the previous dengue infection. Owing to the high model sensitivity, it was possible to establish that, among antibody-dependent enhancement mechanisms, the increased virus replication inside the infected cell, which increases the overall virus burst size, exerts the maximum effect on disease severity during secondary infection. The obtained results concur with the clinical observations and may be helpful in further research on antibody-dependent enhancements aimed at producing schemes relevant for the dengue vaccine design and development.

Keywords: Adaptive immunity, dengue virus, homogeneous antibody, heterogeneous antibody, antibody dependent enhancement, memory cell

P27 – Modelling the effects of cross-immunity on pandemic risk

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[a] Speaker

Over the last century, the world has seen an increase in the long-distance travel of people and goods, partially due to the growth of the tourism industry and in agricultural trade. This could plausibly increase the risk of pandemics by allowing pathogens to travel between distant communities. However, cross-immunity, the phenomenon whereby infection with one strain of a pathogen provides some level of immunity against other strains, could mean that this enhanced pathogen spread also leads to widespread immunity to further strains. In this poster I will illustrate a metapopulation model of disease spread consisting of SIR populations connected on a network representing travel routes between populations. This model was developed to explore the relationship between travel rates and pandemic risk. I will discuss the effects of network structure, co-circulation of pathogens, and varieties of immunity on this relationship, focussing on analytic results where possible. I will also include an explanation of how this model applies to the behaviour of various diseases in the modern world.

Keywords: immunity, pandemic, risk, metapopulation, network

P28 – Effect of population characteristics on population stability in a fluctuating environment: simulation study

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Changes in Earth's climate are already apparent and expected to continue into the next century. The majority of studies investigating effects of climate on populations focus on changes in the mean climatic value. However, it is known that along with changes in mean climate, temporal climatic variation is also changing, and that natural populations are sensitive to such variation. Moreover, there is some evidence that climate effects the populations of plants and animals by affecting their traits, which, in turn, results in changes of demographic rates. Here we study how the effect of climatic variation on traits propagates to effects on population dynamics by using simulations. To this end, we developed a population model in which climate affects traits, traits and climate affect demographic rates and population dynamics emerges from demographic rates. We parameterized the model with empirical data from two model species that differ in their generation time: a lizard (*Zootoca vivipara*) and an albatross (*Thalassarche melanophris*). To investigate how density dependence combines with climatic variation to influence population stability, we implemented two types of density dependence: Ricker and Beverton-Holt. Our expectation was that population size would fluctuate more, for a given magnitude of climatic variation, with Ricker compared to Beverton-Holt density dependence because population fluctuations can also result under a purely deterministic model of Ricker density dependence even in the absence of environmental stochasticity. Contrary to our expectation, the standard deviation of the population size did not differ between the two types of density dependence irrespective to the increase in climatic variation. However, we observed that climatic fluctuation has a stronger effect on species characterized by a long generation time (albatross) than a species with a short generation time (lizard). This study provides an insight into complex effects of climatic variation on population dynamics, depending on their characteristics.

Keywords: population dynamics, global warming, climatic fluctuation, stability, density dependence, trait

P29 – Effect of chemical contamination on a planktonic host-parasite system

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Disease outbreaks are increasingly becoming a major concern for many ecosystems. Chemical contamination due to anthropogenic factors has also garnered considerable attention in the arena of ecosystem health. Although, the link between disease and contamination has been long identified, but the nature of relationship is not yet well established. Contamination can affect disease related traits via changes in not only host behaviour and parasite concentration but also resource density thus making it vital to understand the combined effect of contamination and disease. Additionally, enrichment via metal contaminants, such as copper, which are also essential trace element can complicate the situation even more. Motivated by this, we have modeled the effect of copper on an algae-Daphnia-Metschnikowia system. Our results indicate that very low or high copper enrichment can destabilize the underlying consumer-resource dynamics. Further, model simulations of the diseased system reveal that an intermediate copper concentration can render the system disease-free. At very toxic and deficient levels, there exists vulnerable regimes, where the parasite, when initially abundant, can invade the system for a comparatively lower spore yield. Overall, our study demonstrates that comprehensive understanding of the effect of contamination is essential in order to gain insight into the ecology of disease.

Keywords: copper contamination, Host resource, Daphnia parasite, Hormesis, Bistability

P30 – Species sustainability through optimal harvesting policy and regime shift in stochastic model(s)

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The purpose of this work is to study the optimal harvesting policy for the use of renewable biological resources and to examine the problems of their sustainability. We use the biological reference point namely the maximum sustainable yield (MSY). In many cases, when MSY is difficult to create, we study the optimal harvesting policy through the sustainability of resources. In this article, we will examine two very useful models, such as the theta logistic model and the Allee model. The framework of the birth- death process is used to study the most relevant stochastic dynamic system in a real environment. We combine two types of cultures to know. Proportional or linear harvesting and nonlinear harvesting. When the management time is entered into a catch rate, it is often considered a non-linear catch rate. It should be noted that for the Alley model, the system may undergo a mode change from one stable state to another. A change of regime shift can result in the disappearance of a species if the system moves from a non-zero stable equilibrium to a stable zero equilibrium. This phenomenon can be limited by an increase in processing time at a non-linear harvest rate. The theoretical results are confirmed using two sets of actual data on herring fish populations recognized as being economically important. The data sets are extracted from the Global Population Dynamics database, used by several scientists around the world.

Keywords: Handling time, Maximum sustainable yield (MSY), Theta Logistic model, Allee effect, Potential function

P31 – Combining correlative and mechanistic modelling approaches to characterise the limits and sensitivity of the ecological niche of two benthic Antarctic species

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Species distribution models (SDMs) are correlative models that help characterise the occupied space of a species according to the environmental conditions into which the occurrences are recorded. Once the relationship occurrence-environment is calibrated, the SDM assesses the probability of the species to be distributed in the area, taking indirectly into account the influence of geographic barriers and biotic interactions. Dynamic Energy Budget models are physiological models that explain how organisms use the energy they assimilate to develop during their entire life cycle (with modelling outputs such as for example maximal age reached, growth performances, energetic allocation to somatic maintenance or to reproduction buffer) in a given environment described by two forcing variables: temperature and food resources. DEB models bring therefore some complementary information regarding the species fundamental niche due to the environmental constraints that delineate the energetic boundaries of the species distribution. Combining the two approaches to describe the species ecological niches is a promising method. In the context of this work, the combinaison was tested for the case study of the sea star *Odontaster validus* and the sea urchin *Sterechinus neumayeri*, both distributed all around the Southern Ocean. The convergence between SDMs and DEB models outputs was evaluated and the relevance of the method at such broad scale was discussed. Comparison between species niches and their sensitivity to simulated environmental changes was assessed by comparing models generated with actual and future conditions predicted by the climatic scenarios of the IPCC 5th report (RCP 2.6 and 8.5 scenarios for 2100).

Keywords: Southern Ocean, Dynamic Energy Budget, Species Distribution Model, Ecological niche

P32 – Explicitly Accounting for Resource Supply in Ontogenetic Growth Models and addressing the problem of allometric fecundity scaling

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[a] Speaker

The last century has seen many biologists attempt to successfully capture growth through ontogeny in the form of sophisticated mathematical models. Mechanistic approaches in developing these models have yielded several venerable biological theories which describe growth across different taxa and both determinate and indeterminate growth schedules. These include bottom-up approaches utilising first priniciples such as Metabolic Theory and Dynamic Energy Budget (DEB) theory and arguably more top-down approaches such as Evolutionary Life History Theory and Game Theory. In the former, while the "master" growth equation remains undisputed as a theoretical foundation, we believe there to be a gap in the literature, specifically how energy supply, realised through resource consumption affects ontogenetic growth. To this end, can the dispersal of growth data around the existing models be explained by the differential scaling of resource consumption rates with body mass found in previous studies? In this meta-study we address this gap by using a large consumer-resource dataset and results from a previous study to incorporate energy acquisition via consumption into an existing growth model. Further, we investigate the implications of the hyperallometry of consumption rate mass scaling on the scaling of allocation of energy/mass to reproduction, which was found to scale superlinearly in recent literature.

Keywords: Ontogenetic Growth, Model, Dynamic Energy Budget, Life History, Optimal Foraging, ESS

P33 – tpcfit: A new tool for quantifying the response of metabolic traits to climate change

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Temperature is fundamental in determining biological rates at all levels of organisation, from bio-chemical reactions to the biosphere. In the face of global climate change, it is essential to gain a mechanistic understanding of the how different metabolic rates respond to temperature. The accuracy of analytical tools used in metabolic ecology are paramount to investigating ecological and evolutionary processes. tpcfit is an open source python package for quantifying the response of metabolic traits to climate change. This novel software will allow researchers to easily fit temperature responses of metabolic traits (i.e. respiration, photosynthesis, growth) to alternative mechanistic mathematical models. By incorporating existing models into an easily accessible and widely distributed python package, we hope this tool will be used to drive the search for general mechanisms of thermal performance by theorists and empiricists alike.

Keywords: metabolic theory of ecology, metabolic rate, temperature, python, open source, climate change, ecoinformatics

P34 – Evaluation of the Accuracy of Species Distribution Models Related to Genera of Culicidae

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[a] Speaker

Species distribution models (SDM) are commonly used to predict and study the increasing spread of Culicidae mosquitoes. Many SDM algorithms exist, but there is little guidance on proper algorithm selection. Selection tends to be based on good performance for a species in the same genus or family in a small subset of literature. However, SDM predictions and accuracy are impacted by many conditions which can vary greatly within literature. We conducted a meta-analysis to determine if any SDM was consistently accurate for Culicidae genera across the literature based upon area under the receiver operating curve (AUC) and sensitivity. Fifteen SDMs were compared, however algorithm use was not uniform across genera. SDM accuracy differed overall but not among genera classifications for a single SDM. The most commonly applied SDMs were found to have lower performance overall, suggesting that SDM algorithms should be tested for accuracy for one's modeling conditions. Selection of SDM based on performance over common usage will allow management officials to better design surveillance and intervention strategies, thus managing vector-borne disease risk. Due to the potential bias of the literature and drawbacks of AUC, further comparisons are required to determine the optimal SDM for mosquitoes.

Keywords: Species distribution model, ecological niche model, Culicidae, meta, analysis

P35 – Fit for shredding in a warming world?

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Gammarus pulex, a keystone species among amphipod shredders, is present in the macrozoobenthos of running freshwaters in Germany. Its abundance might be affected by invasive species (e.g. *Gammarus tigrinus* and *Dikerogammarus villosus*) and global warming: We assume that the different species of Gammaridae vary in fitness and that this difference depends on temperature. In this paper, it is looked into the question who will take over the crucial position of shredding in the food web in the medium-range future.

We define fitness as the lifetime reproductive success. We consider five stages (clutch, egg, juvenile, immature, and mature) for *G. pulex*, G. tigrinus and *D. villosus* life-cycles in a matrix population modelling framework. Stage-specific responses are represented by temperature response for development, fertility and mortality. We parameterized our models based on literature review and field work.

Different temperature scenarios were considered and the lifetime reproductive success was derived for each week of the year. The latter allowed us to predict the potential for a) a yearly lifetime reproductive success and b) a shift in phenology. For example, for *Gammarus pulex* lifetime reproductive success is not highest at actual temperatures but at slightly lower ones. The model showes that the peak season of lifetime reproductive success shifts from summer to spring and autumn if annual mean temperatures increase.

Sensitivity analysis and a comparison of shredder species/taxa with different life cycles and strategies like semiaquatic Trichoptera, Plecoptera or Diptera will improve the validity and scope of the model.

Keywords: Lifetime reproductive success, climate change, invasive species, population dynamics, temperature response, shredder (Gammarus pulex)

P36 – Selection-mutation in a fluctuating environment: a Hamilton-Jacobi approach

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We study the long time behavior of a parabolic Lotka-Volterra type equation considering a time-periodic growth rate with non-local competition. Such equation describes the dynamics of a phenotypically structured population under the effect of mutations and selection in a fluctuating environment. We first prove that, in long time, the solution converges to the unique periodic solution of the problem. Next, we describe this periodic solution asymptotically as the effect of the mutations vanish. Using a theory based on Hamilton-Jacobi equations with constraint, we prove that, as the effect of the mutations vanishes, the solution concentrates on a single Dirac mass, while the size of the population varies periodically in time. When the effect of the mutations is small but nonzero, we provide some formal approximations of the moments of the population's distribution. We then show, via some examples, how such results could be compared to biological experiments.

Keywords: Parabolic integrodifferential equations, Time periodic coefficients, Hamilton Jacobi equation with constraint, Dirac concentrations, Adaptive evolution.

P37 – Evolutionary dynamics of phenotypically structured population in time-periodic environments

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We study the long time behavior of a parabolic Lotka-Volterra type equation considering a time-periodic growth rate with non-local competition. Such equation describes the dynamics of a phenotypically structured population under the effect of mutations and selection in a fluctuating environment. We first prove that, in long time, the solution converges to the unique periodic solution of the problem. Next, we describe this periodic solution asymptotically as the effect of the mutations vanish. Using a theory based on Hamilton-Jacobi equations with constraint, we prove that, as the effect of the mutations vanishes, the solution concentrates on a single Dirac mass, while the size of the population varies periodically in time. When the effect of the mutations is small but nonzero, we provide some formal approximations of the moments of the population's distribution. We then show, via some examples, how such results could be compared to biological experiments.

Keywords: Parabolic integro, differential equations, Time, periodic coefficients, Hamilton, Jacobi equation with constraint, Dirac concentrations, Adaptive evolution.