

MMEE 2015 – Abstracts



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Keynote speakers

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Michael Doebeli

University of British Columbia (Vancouver, Canada)

Diversification and co-evolution in high-dimensional phenotype spaces

Adaptive dynamics is a general framework to study long-term evolutionary dynamics. It is typically used to study evolutionary scenarios in low-dimensional phenotype spaces, such as the important phenomenon of evolutionary branching (adaptive diversification). I will briefly recall the basic theory of evolutionary branching and review a well-studied empirical example. Because birth and death rates of individuals are likely to be determined by many different phenotypic properties, it is important to consider evolutionary dynamics in high-dimensional phenotype spaces. I will describe some results about evolutionary branching in high-dimensional phenotype spaces, as well as results about the existence of non-equilibrium evolutionary dynamics, such as chaos. Finally, I will present new results about how the nature of the (co-)evolutionary dynamics changes as diversity evolves in high-dimensional phenotype spaces. This leads to some new perspectives on how micro-evolutionary processes can generate macro-evolutionary patterns, such as diversity saturation and punctuated equilibrium.

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Régis Ferrière

Ecole Normale Supérieure (Paris, France)

Ecological causes and consequences of evolution: Insights from adaptive dynamics

Ecological systems can be conceptualized as networks of biological populations interacting with one another; each population is a collection of phenotypically unique individuals. Historically, mathematical ecologists have sought to relate individual variation to population dynamics by using structured population models, in which individuals can transition between physiological, behavioral, or environmental states. Only relatively recently have genetically-based differences been considered, thus paving the way to exploring the interplay of ecological processes and evolution. Here I review the general mathematical framework that we currently have to model the “adaptive dynamics” of populations in which there is heritable variation in individual traits that have some impact on their demographic performance. I recall that starting from a “microscopic” individual-level stochastic description of the population, seven classes of models can be derived to describe the population’s “macroscopic” dynamics under alternate assumptions; one of them (the “Trait Substitution Sequence”) yields a rigorous definition of Darwinian fitness and selection gradient for general ecological scenarios. Continuity of the selection gradient with respect to the traits is often assumed, but I argue that discontinuity may not be rare. I highlight three remarkable consequences of discontinuity: evolutionary shifts between alternate ecological equilibria, evolutionary sliding along ecological bifurcations, and evolutionary diversification away from so-called branching points. These consequences are of interest to ecologists. Evolutionary shifts sheds light on patterns of rarity and commonness, and raise the possibility of evolution-driven extinction (evolutionary suicide) and rescue. Evolutionary sliding makes us expect critical transition regimes to be common in population dynamics. Evolutionary diversification away from branching points may occur when trait function is context-dependent; when applied to trophic interactions, this diversification process provides a new eco-evolutionary model for large-scale patterns of community functional diversity.

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Eva Kisdi

University of Helsinki (Finland)

Adaptive dynamics from a single strain to saturated polymorphisms

The modelling framework of adaptive dynamics is particularly suited for understanding how ecological interactions facilitate the evolution of diversity. In this talk, I review two recent lines of development in adaptive dynamics. First, I discuss how the gradual splitting of a lineage during evolutionary branching relates to limiting similarity, which generically excludes the coexistence of similar strains, and what role the trade-off functions play in coexistence and in evolutionary branching. This part will conclude that given a sufficiently complex ecological model (with at least two environmental feedbacks and at least as many trade-offs as feedbacks), the particulars can always be chosen (from open sets) such that evolutionary branching occurs. Second, I consider adaptive dynamics in polymorphic populations where the maximum number of strains are already present, and discuss the special characteristics of adaptive dynamics that apply to such saturated systems.

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Joshua Plotkin

University of Pennsylvania (Philadelphia, USA)

On the role of epistasis in molecular evolution

The phenotypic effect of an allele at one genetic site may depend on alleles at other sites, a phenomenon known as epistasis. Epistasis can profoundly influence the process of evolution in populations and shape the patterns of divergence across species. I will discuss the role of epistasis in the evolution of proteins under either directional or purifying selection; and also in the evolution of microorganisms in laboratory conditions. I will highlight examples where the inference of epistasis is possible and has been validated by subsequent experiments. I will also discuss theoretical limitations on our ability to infer epistasis from several types of commonly reported measurements of evolving populations.

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Maria Servedio

University of North Carolina (Chapel Hill, USA)

Patterns of migration, assortative mating, and the effects of sexual selection on speciation and divergence

Theoretical and empirical research on the evolution of reproductive isolation have both indicated that the effects of sexual selection on speciation with gene flow are quite complex. I focus on how two factors, the pattern of migration between incipient species and the mechanism leading to assortative mating, interact to alter the effect that sexual selection through mate choice has on speciation and trait divergence. I concentrate on two commonly-considered patterns of migration: a two-island pattern, as might approximate gene flow between incipient species following a vicariance event, and a continent-island pattern, as might approximate gene flow from a large population to a peripheral one. Similarly, I consider two mechanisms of assortative mating: phenotype matching and separate preferences and traits. I show that both of these factors interact to influence whether sexual selection has a driving, versus inhibitory role in divergence of a locally adapted trait between populations. I also discuss the evolution of assortative mating strength across these scenarios.

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Arne Traulsen

Max Planck Institute (Plön, Germany)

Somatic evolution in hierarchical tissue structures

Cancer can be viewed as an evolutionary process, where the accumulation of mutations in a cell eventually causes cancer. Many tissues such as the blood system, the colon or the skin, are organized hierarchically. This strongly affects the dynamics in these tissues and inhibits the accumulation of mutations. Mutations arising in primitive cells can lead to long lived or even persistent clones, but mutations arising in further differentiated cells are short lived and do not affect the organism. A generic mathematical model for such tissue structures can be used to model the somatic evolution in various cancers, such as certain Leukemias. However, it remains a challenge to fix the parameters of these models from experimental data. In particular, concrete predictions for disease dynamics within an individual typically require repeated measurements - but this is often unfeasible in a medical context. However, certain biomarkers have properties that allow to derive all relevant parameters from a single measurement, leading to dynamical predictions

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Talks

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Matthew Adamson

University of Leicester (Leicester, United Kingdom)

Evaluating structural sensitivity of partially specified models in ecology.

Matthew Adamson & Andrew Morozov

Mathematical models in ecology and evolution are highly simplified representations of a complex underlying reality. For this reason, there is always a high degree of uncertainty with regards to the model specification, not just in terms of parameters, but also in the form taken by the model equations themselves. This uncertainty becomes critical for models in which the use of two different functions fitting the same dataset can yield substantially different model predictions - a property known as structural sensitivity. In this case, even if the model is purely deterministic, the uncertainty in the model functions carries through into uncertainty in our model predictions, and new frameworks are required to deal with this. In this talk, we shall introduce such a framework by considering partially specified models: ODE models in which unknown functions are represented not by a specific functional form, but by an entire data range and constraints of biological realism. We shall show how these partially specified models can be used to rigorously detect when ecological models are structurally sensitive in their predictions concerning the character of an equilibrium point, and we shall see that when only varying parameters of fixed model functions we can miss such sensitivity completely. Finally, we shall discuss how we can introduce notions of probability into the predictions of partially specified models, and use these notions to both quantify structural sensitivity and undertake probabilistic bifurcation analyses of biological models.

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Samuel Alizon

CNRS (Montpellier, France)

Parasite evolutionary emergence: importance of population dynamics feedbacks

Matthew Hartfield and Samuel Alizon

Parasite strains with a low epidemiological fitness can generate small outbreaks before going extinct, thus allowing a mutant strain to emerge and spread. This process is often referred to as “evolutionary rescue”. Models typically assume that such processes take place in populations at equilibrium, that is, that the effect of the first strain on the environment (here the number of susceptible hosts) is negligible. We develop an analytical approximation to capture two biological cases where this assumption falls apart. The first scenario concerns the case where a “weakly adapted” strain (with $R_0 \approx 1$) mutates into a strongly adapted strain (with $R_0 \gg 1$), as observed for the 2005-2006 chikungunya outbreak in La Réunion. The second scenario takes place at the within-host level and investigates the spread of immune escape mutants, as observed in many infections. Our main result is that the spread of the first strain drastically reduces the probability of emergence of the mutant. This work highlights the importance of taking population feedbacks into account when predicting disease emergence. References

- Hartfield M, Alizon S (2014) Epidemiological feedbacks affect evolutionary emergence of pathogens. *Am Nat* 183:E105-17
- Hartfield M, Alizon S (2015) Within-host stochastic emergence dynamics of immune-escape mutants. *PLoS Comput Biol* 11:e1004149

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Korinna Theresa Allhoff

TU Darmstadt (Germany)

Biodiversity and ecosystem functioning in evolving food webs

Korinna T. Allhoff and Barbara Drossel

We analyze an evolutionary food web model where each species is characterized by three traits, namely its own body mass, its preferred prey body mass, and the width of its potential prey body mass spectrum. Population dynamics includes feeding and competition interactions and determines which species are viable and which ones go extinct. On a timescale much slower than population dynamics, new species emerge as modifications of existing species. The network structure emerges according to the interplay between population dynamics and evolutionary rules and shows an ongoing species turnover. The model thus gives insights into how the functional diversity changes during the initial network buildup as well as due to extinction avalanches. We investigate the relation between the functional diversity and five community level measures of ecosystem functioning. These are the metabolic loss of the predator community, the total biomasses of the basal and the predator community and the consumption rates on the basal community and within the predator community.

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Lee Altenberg

The KLI Institute (Klosterneuburg, Austria)

Fundamental Properties of the Evolution of Mutational Robustness

Lee Altenberg

The evolution of genotypes that form neutral networks was shown in van Nimwegen et al (1999) to concentrate on genotypes with high mutational robustness when mutation rates are high, to a degree determined by the topology of the network. The features of the topology that determine the robustness are here identified to be the eigenvalues of the mutation matrix and the alignment of fitnesses with the eigenvectors of the mutation matrix having the largest eigenvalues. The analysis is generalized beyond neutral networks to arbitrary selection. Mutational robustness generically increases with the mutation rate. The genetic load under evolution on a neutral network is shown to correspond to the first Dirichlet eigenvalue of the normalized graph Laplacian of its mutation structure. The nexus to spectral graph theory is explored.

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Yoann Anciaux

Université Montpellier 2 (Montpellier, France)

Eco-evolutionary dynamics of evolutionary rescue in large asexual populations

Anciaux Yoann; Martin Guillaume; Ronce Ophélie; Roques Lionel; Lambert Amaury

Evolutionary rescue occurs when a population genetically adapts to a new stressful environment that would otherwise cause its extinction. Forecasting the probability of persistence under stress, such as emergence of drug resistance or invasion of a new environment is a major concern in ecology and evolution. Most models describing the eco-evolutionary dynamics of evolutionary rescue consider the stochastic apparition of single alleles and their fixation (narrow genetic basis), or deterministically stable genetic variance in a highly polymorphic sexual population (wide genetic basis). Here, we explore an analytical model in between these two extreme scenarios. We model the dynamics of the distribution of fitness in large asexual populations, through their generating function. This allows following the effect of selection among few or many co-segregating types possibly with background-dependent mutation effects (epistasis) and arbitrary form of initial standing variance. We use a deterministic approximation for evolutionary dynamics and a Feller diffusion approximation for demographic dynamics (coupled with evolution) and apply the general framework to a particular model of context-dependent mutation: Fisher's geometrical model. Analytical approximations are confronted with individual based simulation in different scenarios such as adaptation from standing variance and or de novo mutation.

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Krzysztof Argasinski

Institute of Mathematics of Polish Academy of Sciences (Warszawa, Poland)

Selection under limited population growth. Replicator dynamics and the eco-evolutionary feedback

Krzysztof Argasinski, Mark Broom

In this talk we discuss a new approach to the derivation of population dynamic models called “event based modelling,” which relies on the assumption that the trajectory of the process is the aggregated outcome of individual interactions (i.e., “atomic” events) occurring with respective rates. Thus, the methodology resembles that of chemical kinetics where the interaction rate is the analogue of the reaction rate. An important aspect of the presented framework is the explicit incorporation of growth limitations. The regulation of the population size acts through feedback driven by density dependent juvenile mortality. It was shown that at the population size equilibrium, newborns form a pool of candidates from which survivors who will replace dead adults at their nest sites will be drawn. Thus fertility payoffs can be interpreted as the entries of a nest site lottery mechanism. The new approach emphasizes the role of the turnover of individuals. In this case the stable population size is a dynamic equilibrium between different mortality and fecundity factors instead of an arbitrary fixed carrying capacity. This mechanism can be regarded as an example of eco-evolutionary feedback. This seriously alters the predictions of game-theoretic models in comparison to models with unlimited growth. In this case there can be for example two stable manifolds: one for the frequency dynamics and a second for the population size. The global stationary points are intersections of those manifolds. For example in the Hawk-Dove Game, a pure Hawk population can become evolutionarily stable in addition to the stable mixed equilibrium known from the classical theory. This is caused by the fact that the payoff structure is not constant. The most intriguing result is that under the impact of eco-evolutionary feedback, an apparently unstable invasion barrier between two pure-strategy stable equilibria can become stable at the intersection with the stable density manifold.

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Nicolas Bacaer

IRD (Bondy, France)

Le modèle stochastique SIS pour une épidémie dans un environnement aléatoire

Nicolas Bacaer

Dans un environnement aléatoire qui est une chaîne de Markov en temps continu à deux états, le temps moyen jusqu'à extinction du modèle stochastique SIS pour une épidémie croît, dans le cas surcritique, exponentiellement par rapport à la taille de la population si les deux états sont favorables, et suivant une loi de puissance si l'un des états est favorable alors que l'autre est défavorable à la propagation.

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Stephen Baigent

University College London (London, UK)

Geometric approaches to the study of competition

Stephen Baigent

In this talk I will explain how simple geometry can be utilized to determine the global dynamics of many continuous- and discrete-time competitive systems. I will show how certain deformations of surfaces under the flow can determine global stability of interior or boundary equilibria. I will also comment on how this geometry relates to permanence, and when permanence upgrades to stability. The surfaces I consider generically evolve to an invariant surface known as the carrying simplex, and I will discuss how the geometry of this special surface is also useful in studying global dynamics. Apart from applications to continuous-time competitive models from ecology and evolutionary game theory, I will also present the first global stability results obtained with Zhanyuan Hou for some well-known discrete-time competitive May-Leonard models. Finally, with reference to example models, I will discuss how one might link these ideas on stability with notions of fitness, reproductive value or other biological concepts.

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Daniel Balaz

University of Glasgow (Glasgow, United Kingdom)

Do sheep cheat themselves by mounting weak immune responses?

Daniel Balaz, Christina A. Cobbold, Michael J. Stear, Joaquín Prada Jiménez de Cisneros, Rodney Beard, and Louise Matthews

There is substantial heterogeneity in immune response to parasitic infection. For example, in gastro-intestinal nematode infections of sheep, the parasite-specific IgA response is skewed with many animals producing relatively weak responses. As these responses are also highly heritable, genetic theory predicts that evolution will optimise immune responses for maximal fitness, so why many sheep produce weak responses is unclear. Traditional explanations implicate trade-offs between immunity and growth or immunity to different diseases but these are not supported by the data, which suggest that the sheep with strong responses and low parasite loads have the highest growth rates. One potential explanation is that it may be evolutionarily advantageous for sheep to ‘cheat’ by mounting reduced immune responses and allow other sheep to control infection. We used a game-theoretic approach to explore the benefit of mounting a lower immune response as a function of the strategies of other individuals. Our model, parameterised using data on the sheep - *Teladorsagia circumcincta* system, encompasses dynamics on epidemiological and evolutionary timescales. The epidemiological dynamics determine the infection levels and growth rates of the flock for a given set of immune responses, whilst the evolutionary dynamics allow mutations to the strategies that determine the host densities and evolutionarily stable immune strategies. Across a range of costs of infection burden and immune response, the evolutionary dynamics converge on an equilibrium with suboptimal growth rates. This has important consequences for domesticated sheep flocks in which breeding is managed. In contrast to the view that trade-offs may render selection detrimental, our results suggest that it may be possible to achieve higher growth rates in managed sheep flocks by deliberately selecting for enhanced immune responses. In principle, selection procedures that take into account the behaviour of other animals could reduce disease prevalence and enhance growth rates.

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Zoltan Barta

MTA-DE Lendület Behavioural Ecology Research Group (Budapest, Hungary)

Why budding yeast (*Saccharomyces cerevisiae*) produces public goods?

Zoltán Barta, Nóra Szabó, Melinda Szilágyi and Tamás Emri

Disaccharid sugars form a valuable energy and carbon source for yeast. Nevertheless, in order to uptake these resources yeast must produce an extracellular enzyme, invertase, which hydrolyses disaccharides into simpler sugars of glucose and fructose, because the uptake of disaccharides is very uneconomical compared to that of the monosaccharides. There is, however, a problem, in terms of efficiency, with the extracellular disaccharide hydrolysis; the produced monosaccharides can diffuse away from the cell where they were produced by the invertase and hence become available for other cells as well. They can even be utilised by cells which totally lack invertase i.e., by cells not making the costly investment into invertase production. As a consequence, the process of extracellular hydrolysis closely resembles the process of public good production in humans. The question, both in humans and yeast, is how such a costly investment can, in the shadow of free-riders, be maintained by natural selection. Previous studies have suggested that reciprocal cooperation and facilitation of colony growth might explain the public goods production in yeast. Here, by presenting a game theoretic model based on enzyme kinetics and diffusion processes we argue that neither of the above explanations are likely. Our results suggest that producers of invertase could not benefit from public goods made available by others because that would mean the flow of monosaccharides against a concentration gradient. This renders reciprocity impossible. According to our results the laws of diffusion also prevent the build up of high monosaccharide concentration in the intercellular space, a prerequisite for the colony growth facilitation hypothesis. Based on our empirical investigations we offer a solution.

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Nick Barton

IST Vienna (Vienna, Austria)

Linkage and the limits to selection

Nick Barton

Adaptation in a sexual population is ultimately limited by linkage: the maximum rate at which beneficial mutations can be incorporated is proportional to the recombination rate. The same limit applies to our attempts to detect selection in experimental populations or across spatial clines in nature. In experimental populations, the alleles responsible for selection response will be hard to detect if selection is spread over many loci; conversely, though strongly selected alleles can readily be detected, they may be hard to locate precisely on the genetic map. Selection can also be estimated from the width of natural clines, but again, the precision with which causal alleles can be located is limited by linkage. This is illustrated clines around tightly linked flower colour loci in snapdragons (*Antirrhinum*).

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David Basanta

Moffitt Cancer Center (Tampa, USA)

Tumor Heterogeneity: Insights from Game Theory

David Basanta

Cancer is a disease driven by Darwinian evolution. Our increasing understanding of the role of intra-tumour heterogeneity shows that more heterogeneous tumours translate into worse prognoses. Also in cancers that are more likely to evolve resistance to existing and targeted treatments. The interactions between different cell types influence the fitness of the different tumour phenotypes and drive tumour evolution. Understanding these interactions requires the right mathematical tools. Evolutionary Game Theory is an ideal tool in which to model and explore the role of interactions between players. By simplifying the dynamics of cancer to changes in the fitness of interacting cells it is possible to identify the key interactions that explain cancer progression. In this talk I will show some examples of games that tumour cells play and show how the dynamics (using replicator equations) and long term evolution (in the shape of evolutionary equilibria) can yield important cues that are relevant to mathematical oncologists, experimental and clinical researchers alike.

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Franz Baumdicker

Albert-Ludwigs University of Freiburg (Freiburg, Germany)

Population genetics of dispensable genes

Franz Baumdicker, Peter Pfaffelhuber

The number of completely sequenced genomes is growing to an enormous number. For many species, there are already multiple genome sequences available. Especially in procaryotes this brought to light an unexpected amount of genes present only in a subset of the population. These genes are distributed over the population and constitute the pan-genome of the population. For some bacterial populations the total number of genes in the population seems to be an arbitrary large number, while the genome size of any single individual is finite. In addition it is known that bacteria can transfer genes horizontally between individuals of the population either on purpose or by accident. But which influence does horizontal gene transfer have on gene frequencies? I will give an introduction to the neutral evolution of dispensable genes and the corresponding population genetic models. We define the infinitely many genes model, where genes are gained and lost along Kingman's coalescent. In addition each gene can be transferred between any two individuals. The frequency of one dispensable gene can be described by a diffusion. We derive the frequency spectrum of dispensable genes, i.e., the number of genes present in a certain fraction of the sample. Given the gene frequency spectrum, we compute first moments of relevant statistics. If the gene transfer rate is larger than zero the ancestral relationship is no longer represented by one common tree. Instead the large population limit is given by a sequence of graphs, which we call ancestral gene transfer graph. Luckily, it suffices to look at finitely many graphs of this sequence to infer the ancestral history of a sample and approximate higher moments. The derived statistics can be used to detect populations which show signs of non-neutral pan-genome evolution and forecast the number of relevant genes present in the population.

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Abdelkader Behdenna

Collège de France, UPMC (Paris, France)

Testing for independence between evolutionary processes

Abdelkader Behdenna, Joël Pothier, Sophie S Abby, Amaury Lambert, and Guillaume Achaz

Evolutionary events co-occurring along phylogenetic trees usually point to complex adaptive phenomena, sometimes implicating epistasis. While a number of methods have been developed to account for co-occurrences of events on the same internal or external branch of an evolutionary tree, there is a need to account for the larger diversity of possible relative positions of events in a tree. Here we propose a method to quantify to what extent two or more evolutionary events are associated on a phylogenetic tree. The method is applicable to any discrete character, like substitutions within a coding sequence or gains/losses of a biological function. Our method uses a general approach to statistically test for significant associations between events along the tree, which encompasses both co-occurrences in the same branch, and chronologies in different branches. We address this problem from the statistical viewpoint by a linear algebra representation of the distribution of the evolutionary events on the tree. We compute the full probability distribution of the number of paired events occurring in the same branch or in different branches of the tree, under a null model of independence. We then complete this general study with a likelihood framework allowing us to measure the interactions between two selected events. The strengths and weaknesses of the method are assessed via simulations. We then apply the method to explore two biological cases: the loss of cell motility in intracellular pathogens and the coevolution of nucleotides of the bacterial 16S RNA.

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Veronika Bernhauerová

Masaryk University (Brno, Ceska republika)

Evolution of male-killing bacteria

Veronika Bernhauerova, LudaĎk Berec, Daniel Maxin

Male-killing bacteria are maternally transmitted reproductive parasites which kill male offspring who inherit them. Whereas their incidence and prevalence in natural systems have been well documented, characteristics allowing originally non-male-killing bacteria to evolve the male-killing trait remain unclear. Until now within-species horizontal transmission was widely neglected in all theoretical studies involving male-killing bacteria. This paper shows that horizontal transmission is a key mechanism actually enabling already maternally transmitted bacteria to develop and successfully maintain male-killing over evolutionary time. Almost 100% vertically transmitted male-killer may evolve from a predominantly horizontally transmitted non-male-killing bacterium. Our findings strongly support the empirical evidence on current male-killers, explaining their high efficacy in killing infected males, their variability across and within the insect taxa, and supporting the idea that they likely evolved independently in phenotypically distinct species. Implications of these results and their relation to current male-killing bacteria are discussed.

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Jason Bertram

The University of Arizona (Tucson, USA)

A population-genetic model of long-term adaptation and extinction

Jason Bertram, Joanna Masel

Relatively little is known about what determines taxon extinction over long (My) time scales. Although large culls (“mass extinctions”) may simply be caused by severe abiotic catastrophes with little prospect for adaptation, the majority of extinctions in the fossil record (“background extinction”) presumably represent failures of taxa to adapt to the more routine demands of a constantly changing environment (biotic and abiotic). We present a population-genetic model of long-term extinction in which a population is subjected to recurring, stochastic environmental demands, which reduce absolute fitness by increasing mortality. To adapt to these changes (and reduce mortality), new variants must arise and survive to fixation, a process that depends on the demographic properties of the population. Long-term survival of the population depends on creating a “fitness buffer” which counteracts the variability of adaptive variant establishment. Our model predicts that population extinction risk decreases significantly if the population manages to survive an initial high-risk period and goes on to create this buffer. This prediction is consistent with the age-dependent extinction observed in the fossil record and is in contrast to the “Red Queen hypothesis” (age-independent extinction risk). We also compare the dependence of extinction risk on demographic parameters predicted by our model with the dependence of extinction risk on biomass in the fossil record.

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Sylvain Billiard

Lille University (France)

Revisiting clonal interference: from competitive interactions between individuals to population dynamics and adaptation

Sylvain Billiard

Clonal interference, when two or more mutations coexist in a resident population, is frequent in evolving asexual populations such as bacteria, yeasts or cancers. Several theoretical models showed that clonal interference slows down adaptation because of the competition between several beneficial mutations. However, those models assumed transitive fitness and generally do not take into account explicit ecological competitive interactions between individuals. We developed a stochastic continuous-time model with three competing clones (or species), considering all types of competitive interactions, transitive or not. We first show that, under our hypotheses, many different dynamics are possible: the classical deceleration of adaptation, but also its possible acceleration, as well as non-linear and cyclical dynamics. We especially show that the time when the second mutation occurs is crucial to determine the final state of the population. Second, we estimate the likelihood of each dynamics by assuming that the effect of mutations follow some specific distributions. We finally discuss our results in the light of dynamics observed in empirical data.

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Mark Broom

City University London (London, United Kingdom)

A dynamic network population model with strategic link formation governed by individual preferences

Mark Broom, Chris Cannings

Historically most evolutionary models have considered infinite populations with no structure. Recently more realistic evolutionary models have been developed using evolutionary graph theory, which considered the evolution of structured populations. The structures involved in these populations are typically fixed, however, and real populations change their structure over both long and short time periods. In this talk we consider the dynamics of such a population structure. The timescales involved are sufficiently short that no individuals are born or die, but the links between individuals are in a constant state of flux, being actively governed by the preferences of the members of the population. The process is modelled using a Markov chain over the possible structures. We find that under the specified process the population evolves to a closed class of structures, and we show a method to find the stationary distribution on this class. We also consider some special cases of interest. This is joint work with Chris Cannings from the University of Sheffield.

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Reinhard Bürger

University of Vienna (Austria)

Epistasis, mutational architecture, and the response to selection of complex traits

Reinhard Bürger

The evolutionary dynamics of complex traits is constrained by levels of genetic variation as well as genetic correlations among traits. Because the ultimate source of genetic variation is mutation, the distribution of mutations entering populations profoundly affects standing variation and genetic correlations. The talk will focus on results from a recent study [1] that was designed to investigate how natural selection and gene interactions (i.e., epistasis) shape the evolution of mutational processes affecting complex traits, and thus affect the response to selection. We found that the presence of epistasis allows natural selection to mold the distribution of mutations, such that the matrix of mutational effects aligns with that determining the selection surface. Consequently, novel mutations tend to be more compatible with the current forces of selection acting on the population. Counterintuitively, we found that smaller populations can sometimes harbor higher genetic variances than corresponding larger ones. These results suggest that in many cases mutational effects should be seen as an outcome of natural selection rather than as an unbiased source of genetic variation that is independent of other evolutionary processes. Importantly, the resulting G-matrix is then determined both the evolving matrix of mutational effects and by the selective forces.

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Paul Calcraft

University of Sussex (Falmer, United Kingdom)

Group Selection is Not Needed to Explain the Structure of Sub-Social Spider Colonies

Paul Calcraft, Phil Husbands, Andy Philippides, and Jeremy E. Niven

Group selection, the evolution of individual traits through the differential success of groups they form, is a highly controversial extension to the understanding of evolutionary fitness. Most biologists remain sceptical of its occurrence in nature, while a growing number of theorists are taking it for granted in their models. In a recent publication, Pruitt and Goodnight (2014, *Nature* 514, 359-62) performed manipulative experiments on the colonial spider, *Anelosimus studiosus*, in an effort to demonstrate an effect of group selection on colony aggressiveness, and claim to have succeeded. However, their data shows only that some colonies can be more successful than others, failing to establish the link to fitness and actual evolutionary change. We explain their data using an extension of the Hawk-Dove model under resource availability constraints, incorporating biological detail from the spider's natural history. Frequency-dependent individual selection can account for the observed adaptation, leaving the burden of proof on those who wish to infer group selection. We further compute the extraordinary conditions needed for group selection to have caused the shifts in colony aggressiveness using an individual based model.

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Nicolas Champagnat

Inria Nancy - Grand Est (Nancy, France)

The limit of small mutations in a stochastic individual-based model and the canonical equation of adaptive dynamics

Nicolas Champagnat

The goal of this talk is to present a new approach to justify the canonical equation of adaptive dynamics, intermediate between the historical one of Metz, Geritz et al. (1996), based on a limit of rare mutations in a large population, followed by a limit of small mutation, and the PDE approach of Diekmann, Jabin, Mischler, Perthame (2005), based on a limit of small mutations in an infinite population. The canonical equation arises on a very long time scale in the first one, and the second one suffers from an unrealistic influence of very small population densities. Our approach assumes small mutations in a large but finite, stochastic population. The convergence to the canonical equation follows from a decomposition of the population dynamics on slow-fast scales, and from a careful study of the genealogy of the population.

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Luis-Miguel Chevin

CNRS (Montpellier, France)

Stochastic evolutionary demography under a fluctuating optimum phenotype

Luis-Miguel Chevin

Temporal environmental variation in natural systems includes a large component of random fluctuations, the magnitude and predictability of which are modified under current climate change. Environmental stochasticity strongly impacts ecology and population dynamics, notably by decreasing the long-run growth rate of a population, and increasing extinction risk. Environmentally driven fluctuating selection also determines the effect of genetic responses to selection on the mean fitness of a population, and influences the evolution of bet hedging and phenotypic plasticity. The temporal autocorrelation of the environment, which determines its predictability over different time scales, is an important modulator of these demographic and evolutionary effects. However, we still largely lack a theory that integrates these eco-evolutionary processes, accounting for environmental predictability. In particular, we need predictions not only for expectations of the processes, but also for their stochastic variances, which are especially important for extinction risk. I will present results of simple models where stochastic population dynamics arise from environmental fluctuations of the optimum phenotype for a quantitative trait. Assuming frequency- and density-independent selection on a polygenic trait, I will show how evolutionary quantitative genetics can be used to derive analytically the stochastic distribution of the population size at any time. Exact results under density-independent population growth will be compared to approximations under different forms of density-dependent regulation. These results will be illustrated by the scenario of evolutionary rescue in a stochastic environment. Finally, I will discuss how phenotypic plasticity modifies the eco-evolutionary outcomes of fluctuating selection.

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Thomas Churcher

Imperial College London (UK)

The importance of parasite density in malaria transmission

Thomas Churcher

Epidemiologists and mathematical modellers assume that malaria transmission is dependent on the number of infectious hosts or vectors and not on the quantity of parasites they harbor. However there is now an increasing body of evidence which shows that the parasite density is important in both human-to-mosquito and mosquito-to-human transmission. There is also an awareness that transmission is influenced by density-dependent processes, both positive (facilitating) and negative (restricting) which overall increase the resilience of the parasite to control interventions. In this talk we examine some of these processes and investigate how they will influence the effectiveness of pre-erythrocytic and transmission blocking malaria vaccines which are currently under development. The epidemiological importance of parasite density shall be assessed to see how it will change the way we measure transmission and target malaria elimination.

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David Claessen

Ecole Normale Supérieure (Paris, France)

Eco-evolutionary dynamics in spatially complex systems: from agro-ecology to the global ocean

David Claessen, Boris Sauterey, Jonathan Rault, Pierre-Antoine Precigout, Mick Follows, Corinne Robert

In natural systems we commonly find overlapping time scales of population, evolutionary and landscape dynamics. We focus on ocean phytoplankton populations, that are slaves to ocean currents, transporting populations across the globe, submitting them to a range of biotic and abiotic conditions. In this talk I will focus on the problem of how to define fitness, and to simulate trait evolution, in complex structured and non-stationary populations. This is a fundamental issue in adaptive dynamics theory in recent years. It is particularly relevant for the question how to compute fitness and to simulate phytoplankton evolution in global circulation models. Using a size-structured, trait-based approach, we study the pros and cons of different evolutionary algorithms, depending on the level of spatio-temporal complexity (from well-mixed 0D to the role of horizontal ocean currents). We model the (co)-evolution of cell size, zooplankton body size and the zooplankton predation window. Comparing the results to the now commonly used “Everything is everywhere” approach helps identifying the specific importance of Darwinian evolution vs purely ecological species sorting. While the importance of phytoplankton ecology for the global carbon cycle is well established, the role of their evolution is much less so. Adaptation is of particular importance in predicting the system’s response to climate change, since it will modulate the ecological response to environmental change.

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Stephen Cornell

University of Liverpool (Liverpool, UK)

Spatial incoherence in the Maximum Entropy Theory of Ecology

Stephen J Cornell

The Maximum Entropy Theory of Ecology (METE) predicts macroecological patterns such as species abundance distributions (SADs) and species-area curves (SACs), based on the assumption that these are as unbiased as possible and subject to some biologically motivated constraints. It aims to be a universal theory, akin to thermodynamics, that predicts canonical patterns without needing to know the underlying processes that generate these patterns. Since empirical SADs and SACs are derived from spatial point patterns, a theory that predicts SADs and SACs makes statements about the statistics of these patterns. I shall show that there exists no statistical ensemble of spatial point patterns that is consistent with the SADs and SACs that are predicted by METE, and conclude that METE is not a coherent macroecological theory. This is a potential issue with any theory that attempts to model patterns of abundance without reference to an underlying spatial point process.

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Manon Costa

Ecole Polytechnique (Paris, France)

Stochastic eco-evolutionary model of a prey-predator community

joint work with Nicolas Loeuille, Céline Hauzy and Sylvie Méléard.

We are interested in the impact of natural selection in a prey-predator community. We introduce an individual-based model of the community that takes into account both prey and predator phenotypes. Our aim is to understand the phenotypic coevolution of prey and predators. We consider a microscopic community which evolves as a multi-type birth and death process with mutations. Under the classical framework of adaptive dynamics (large population, rare mutations of small effect), we introduce different objects to describe the co-evolution. When mutations are rare, the community evolves on the mutational scale according to a Markovian jump process. This process describes the successive equilibria of the prey-predator community and extends the Polymorphic Evolutionary Sequence to a coevolutionary framework. We then consider the evolution of monomorphic prey and predator populations. The limit of small mutation steps leads to a system of two differential equations which is a version of the canonical equation of adaptive dynamics for the prey-predator coevolution.

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Rémi Crete

The University of Western Australia, School of Plant Biology (Perth, Australia)

Durability and breakdown of resistance to pathogens in crops

Remi CRETE

Phoma stem canker (Blackleg), caused by the fungus *Leptosphaeria maculans*, is one of the most damaging diseases of oilseed rape that exists wherever canola is present. This disease is of major economic importance, causing yield losses of between 5% and 20% of production in some places, and even up to 100% in exceptional situations. Control strategies rely on fungicides, deep tillage of the crop residues, use of resistant cultivars, and crop management (specific sowing period, crop rotations). However, rotation or stacking of genes can potentially cause a super virulent strain to arise because pathogens with a lot of virulence genes are likely to be selected. Strategies to maximize durability of resistance genes in cultivars should therefore both limit the selection of the more pathogenic variants of the pathogen and reduce pathogen population sizes. To address these issues, we built a new model which simulates the population and evolutionary dynamics of different haploid pathogen strains over a number of years, as they interact with different resistant cultivars planted in a field. Through different examples, we will try to address the following questions: i) How do initial levels of pathogen and different proportions between the strains, influence to the selection of 'supervirulent' strains under particular resistant cultivar rotation strategies? ii) What is the best resistant cultivar rotation strategy to delay evolution of virulence and breakdown of cultivar resistance? iii) Is it possible, under certain conditions, to delay the breakdown of resistance indefinitely, even if the same crop is planted every year?

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Jim Cushing

The University of Arizona (Tucson, USA)

Environmental change and life history strategies: cannibalism and reproductive synchrony

Jim Cushing, Shandelle Henson, James Hayward, Amy Veprauskas

Significant changes have been observed in life history strategies of marine birds nesting on Protection Island National Wildlife Refuge due to a decrease in food resource availability caused by a rise in mean sea surface in the Strait of Juan de Fuca (which lies between western Canada and the United States). For example, data from our field observations, taken over the last decade from glaucous-winged gull colonies on Protection Island, have documented strong correlations among mean sea surface temperature, adult gull cannibalism of eggs, and reproductive scheduling (egg laying timing) of female gulls. We formulate and analyze a general class of stage-structured, population dynamic matrix models which are designed to investigate the dynamics that can result from a decrease in environmental food resource availability and from a resulting increase in cannibalism and certain within-population interactions that occur in response to it. The focus is on model predicted extinction versus population persistence. Mathematically, the study involves the stability and bifurcations of equilibria and synchronous periodic cycles and the occurrence of multiple attractors and Allee effects. If time permits, an adaptive evolutionary version of the model will also be presented and analyzed.

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Aisling Daly

Gent University (Gent, Belgium)

The impact of initial evenness on competitive dynamics: an individual-based approach

Aisling J. Daly, Jan M. Baetens, Bernard De Baets

One of the most important aims in ecology is to identify and comprehend the mechanisms that sustain biodiversity - often critically important for the viability of ecosystems. Many theoretical models have shown that species in competition can coexist – and thus maintain the ecosystem’s biodiversity - if ecological processes such as competition and mobility occur on a local scale. This is also true in the case of communities with non-transitive competition between species, of which the classical example is the rock-paper-scissors game. Initial community evenness has been shown to be a key factor in preserving the functional stability of an ecosystem, but has not been accounted for in previous modelling studies, which typically assume maximal evenness. This is despite evidence that highly even communities are not particularly common in nature. Motivated by this oversight, we formulate a model that allows the initial evenness of the community to be varied in order to investigate the consequent impact on ecosystem biodiversity. We consider a system of four interacting bacterial species, and present a stochastic, spatial individual-based model simulating the ecosystem dynamics. Interactions are governed by game-theoretical rules and take place on a two-dimensional lattice. The model incorporates three demographic processes: reproduction, competition and mobility. In addition to variable initial evenness, multiple competition schemes are implemented, modelling various possible communities, which results in diverse coexistence and extinction scenarios. Simulations show that long-term ecosystem behaviour is strongly dependent on initial evenness and competition structure, demonstrating the merit of incorporating variable evenness in contrast to previous modelling approaches. The system is generally unstable; higher initial evenness has a small stabilizing effect on ecosystem dynamics by extending the time until the first extinction. Varying initial evenness can also significantly impact species’ probability of extinction, to the benefit or detriment of system biodiversity.

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Florence Débarre

Collège de France (Paris, France)

Spatial structure and the evolution of altruistic host defence strategies

Florence Débarre

Most models for the evolution of host defence against parasites assume that host populations are not spatially structured. Yet local interactions and limited dispersal can strongly affect the evolutionary outcome, because they significantly alter epidemiological feedbacks and the spatial genetic structuring of the host and pathogen populations. In this talk, I will present a framework to study the evolution of a number of host life-history traits in a spatially structured host population infected by a horizontally transmitted parasite. This analysis teases apart the selective pressures on hosts and helps disentangle the direct fitness effect of mutations and their indirect effects via the influence of spatial structure on the genetic, demographic, and epidemiological structure of the host population. In light of this framework, I will compare the evolution of resistance vs. tolerance defence strategies, and highlight the different consequences of fitness costs in structured vs. unstructured environments.

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John Donohue

NUI Galway (Galway, Ireland)

The effects of predation on a seasonally migrating population

John G. Donohue, Petri T. Piiroinen

Many biological populations respond to seasonal variation in resources by migrating between geographically distinct habitats each year. The resulting seasonal pulses of resources are thought to be important to the functioning of ecosystems as they establish connections between disparate regions [1]. In this work, we consider the effects of seasonal predation on a migratory population in order to elucidate the basic mechanisms behind more complex spatiotemporal behaviour. A piecewise-smooth dynamical-system approach is used to represent the dynamics of species that interact for a short period of time each year. Within this overall framework, we consider the two ends of the specialist-generalist spectrum so that the predators' reproductive dependence on the seasonal pulse is either total or zero. The breeding and survival stages of the prey population are then modelled as separate annual regimes in a time-dependent switching system. When predatory effects are negligible, the size of the migratory population will tend toward a stable limit-cycle with a period of one year. A stability analysis of this steady-state solution illustrates how different types of predation influences the long-term dynamics of the population. A key advantage of this approach is that it allows us to consider the interplay of different seasonal factors both within and between years. In addition to predation, migratory populations are exposed to various other hazards, both natural and anthropogenic, during their annual cycles. The risk associated with these mortality factors may fluctuate significantly from one year to the next. These mortality factors may be coupled, for example via global climatic conditions, or specific to a single habitat. In either case, an appropriate variation of the model parameters allows us to examine the impact of environmental flux on migratory populations. [1] M. F. Willson and J. N. Womble. Vertebrate exploitation of pulsed marine prey: a review and the example of spawning herring. *Rev Fish Biol Fish*, 16:183–200, 2006.

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G. Sander van Doorn

Groningen University (the Netherlands)

Supporting a truce, while fueling the arms race: contrasting effects of intralocus sexual conflict on antagonistic male-female coevolution

Tanya Pennell and G. Sander van Doorn

Disparity between the evolutionary interest of males and females can ignite two forms of sexual conflict (inter- and intra-locus conflict), which have so far been considered separately. However, if genes involved in antagonistic coevolution between males and females (inter-locus conflict) are expressed in both sexes, they are likely to have divergent sex-specific optima as well, implying that they are also subject to intra-locus conflict. We investigate the interaction between the two types of conflict by analyzing a quantitative genetic model of male and female characters subject to sexual selection that is generated by conflict over the mating rate. In addition, the mating characters have pleiotropic effects in both sexes that are subject to stabilizing natural selection. A local stability analysis of the evolutionary equilibria confirms the intuition that such between-sex pleiotropic trait expression stabilizes the dynamic of intersexual arms races, because it causes the mating characters to be subject to an additional source of stabilizing selection. However, this effect is relevant only in the vicinity of equilibria. Far away from equilibrium, pleiotropic trait expression is actually capable of destabilizing arms races by suddenly reversing their direction. As a result, populations cycle through phases of intersexual arms races, alternated by periods dominated by the resolution of intralocus conflict. By systematically varying the intersexual genetic correlation, we show that this complex dynamics unfolds as a consequence of global bifurcations in trait space, which lead to the evolution of unstable cycles that prevent evolution from reaching any of the stable equilibria. These results highlight the importance of a systems perspective for understanding the evolution of sexual conflict, and caution against relying exclusively on local stability analysis.

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Arnaud Dragicevic

Agro ParisTech (Paris, France)

Network Price Identity

Arnaud Z. Dragicevic, Ahmed Barkaoui

We model a closed-loop network of agents distributed among subnetworks and study the conditions that satisfy the time-dependent topological stability of network connectedness in presence of random perturbations. We show that the stability depends on which of the between-subnetwork coupling and the within-subnetwork coupling prevails. Our findings permit to situate the Price theorem, both in its standard and expanded forms, in the context of network evolutionary variational identity.

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Rick Durrett

Duke University (Durham, USA)

Heterogeneity in the Spatial Moran Model and the Cancer Field Effect

Rick Durrett

In this model, individuals of type i have fitness $(1 + s)^i$ and mutations from type $i-1$ to type i at rate u_i . Motivated by cancer progression, the first thing we will discuss is the time to the occurrence of the first type 2 family that does not die out. The answer depends in an intricate way on the mutation rates and selection coefficients. The proofs of these results allow us to quantify tumor heterogeneity, which can be a serious obstacle to treatment. This in turn sheds light on the “field effect in cancer,” the observation made by Slaughter in the 1950s that a malignancy is often surrounded by normal cells that have undergone a premalignant transformation. This work has been done with Jasmine Foo and Kevin Leder at University of Minnesota, and Marc Ryser a postdoc at Duke.

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Rampal S. Etienne

University of Groningen (Groningen, Netherlands)

Equilibrium and non-equilibrium dynamics simultaneously operate in the Galápagos islands

Luis M. Valente, Albert B. Phillimore, Rampal S. Etienne

Island biotas emerge from the interplay between colonisation, speciation and extinction and are often the scene of spectacular adaptive radiations. A common assumption is that insular diversity is at a dynamic equilibrium, but for remote islands, such as Hawaii or Galápagos, this idea remains untested. Here, we reconstruct the temporal accumulation of terrestrial bird species of the Galápagos using a novel phylogenetic method (DAISIE) that estimates rates of biota assembly for an entire community. We show that species richness on the archipelago is in an ascending phase and does not tend towards equilibrium. The majority of the avifauna diversifies at a slow rate, without detectable ecological limits. However, Darwin's finches form an exception: they rapidly reach a carrying capacity and subsequently follow a coalescent-like diversification process. Together, these results suggest that avian diversity of remote islands is rising, and challenge the mutual exclusivity of the non-equilibrium and equilibrium ecological paradigms.

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Farnoush Farahpour

University of Duisburg-Essen (Germany)

Studying the changes in interaction network of an evolving competitive community: a stochastic adaptive dynamics model

Farnoush Farahpour, Mohammadkarim Saeedghalati, Daniel Hoffmann

The interaction network of biological species is dynamic. The changes in network could be a result of ecological dynamics, e.g., finding another prey after extinction or rarity of previous one, or evolutionary dynamics, e.g., being threatened by emergence of a new competitor. Evolutionary dynamics in a community, continuously, changes the phenotype of species in order to search the dynamic fitness landscape for the best solution. By any change in phenotype, the networks of interaction between species changes and the species with the best interaction strategies will survive. Niche partitioning, structured networks and having generalist or specialist species are the examples of this strategy adoption in interaction phase space. In this study we introduce a stochastic adaptive dynamics model in which species are competing for common resources. We define the traits of species as the set of interaction rates of that species and investigate how the community of species with this trait evolves during time. Reproduction, mutation and selection are the main ingredients of any evolutionary dynamic. Here we show that a trade-off between reproduction rates and abilities is necessary in order to have a living and diverse community.

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Robbert Fokkink

TU Delft (Netherlands)

Ambush frequency should decrease over time during optimal predator search for prey

Robbert Fokkink

We apply the mathematical theory of search games to model the problem faced by a predator searching for prey as a two-player win-lose game. The predator has two strategies - cruising search and ambush – and the prey has two strategies as well – run or hide. If the prey runs, it will get away if the predator is searching but it will be caught if the predator is ambushing. As time progresses, the predator will have searched a larger portion of the space and the prey will be pressed to run. However, time runs out for the predator and if the prey is not caught in time, then the predator gives up and the prey gets away. In an earlier study, we considered this game without the time limitation for the predator, and we showed that ambush frequency increases with time (Alpern, Fokkink, Timmer, Casas, 2011). If we impose the time limitation, then the behaviour of the predator changes drastically and ambush frequency decreases with time. This is joint work with Steve Alpern.

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Antoine Frenoy

ETH Zurich (Zurich, Switzerland)

Evolution of second-order cooperation by selection for a high mutation rate at cooperative loci: division of labour and the extended phenotype

Antoine Frenoy, François Taddei, Dusan Misevic

Most mathematical models and computer simulations of biological cooperation feature simple one-locus (cooperate / do not cooperate) genotypes. These models greatly improved our understanding of social evolution, in parallel with socio-microbiology. However the need to go beyond their simplifications is clear if we consider two things. Firstly, the switch between a cooperative and a non-cooperative behavior can happen either by regulation of gene expression (phenotypic switch) or by mutation, and in both cases the parameters of this switch are themselves evolving. Secondly; when discussing eusociality, one of the most studied phenomena in social evolution, Darwin was already emphasizing that workers should be understood as being part of the phenotype of the queen. One can find some parallels in microbial world where examples of cooperative acts include self-sacrifice (eg colicins), leading us to think that simple single locus models obliterate one important aspect of the cooperative dynamics: competition between “cooperator-generating” and “non cooperator-generating” genotypes is as fundamental and sometimes more relevant than competition between cooperators and non-cooperators. We developed a model where individuals can evolve their mutation rate between non-cooperative and cooperative behaviors. We show that the evolution of alleles increasing the mutation rate toward cooperative behavior is a cooperative dilemma that can be understood by spatial assortment (kin and group selection). We find that “second-order cooperators” (individuals not expressing cooperation but having a high mutation rate toward cooperation) dominate over a large parameter range, even when the cost of cooperation is too high for cooperation alleles to spread. The cooperators “generated” by these individuals play an analogous role to a public good. These findings show that second-order evolution is extremely relevant in the context of cooperation. Additionally our model brings new questions on individuality linked to the concepts of extended phenotype, division of labour, and soma/germline distinction.

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Coralie Fritsch

INRIA Nancy (Nancy, France)

Adaptive dynamics of bacterial populations in a chemostat

Fabien Campillo, Nicolas Champagnat and Coralie Fritsch

We are interested in chemostat stochastic models in which bacterial populations are described by mass structured individual based models and the substrate dynamics are modeled by an ordinary differential equation. We obtain Markov processes we describe as random measures. In large population size, the individual based model of chemostat converges in distribution towards a system of deterministic integro-differential equations. We apply this convergence result to a chemostat model with mutations : under rare mutations and large population size hypotheses, the mutant population can be described by a growth-fragmentation-washout model in constant environment. We make the links between the stochastic reduced model and the deterministic one. In particular, we prove that the two approaches lead to the same invasion criteria of a mutant population. We apply this result to a numeric example for which we characterize a stable adaptive trait.

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Tak Fung

National University of Singapore (Singapore)

Species-abundance distributions and species ages from model communities assembled under environmental variance: a master-equation approach

Tak Fung, James P. O'Dwyer, Ryan A. Chisholm

Recent empirical evidence from species-rich bird and forest communities have revealed how random environmental changes can substantially alter species population dynamics. This environmental variance occurs over a wide range of timescales, causing fluctuations in species abundances far exceeding those found in communities with just stochastic drift. Despite the important effects of environmental variance on the dynamics and hence assembly of natural communities, the resulting impact on key aspects of biodiversity, such as species-abundance distributions (SADs) and species ages, remain unclear. Existing studies have typically used dynamic models with diffusion approximations and which represent environmental variance as white noise. However, a major limitation of this approach is that environmental variance is uncorrelated in time, thus precluding examination of environmental events sustained over a period of time, such as droughts and floods. In contrast, we use a master-equation approach to develop a model in which environmental variance exhibits temporal correlation over arbitrary timescales, thus representing coloured noise. This model can be considered as a logical extension of a master-equation version of Hubbell's neutral model, with one extra parameter. We mathematically analyse the model to derive exact formulae specifying predicted SADs as a function of model parameters. Using these formulae, we demonstrate that the main effect of environmental variance is to flatten predicted SADs from their neutral log-series form, such that they more resemble power-laws. We also find that stronger environmental fluctuations and increased temporal correlation in environmental variance increases the flattening effect, resulting in an even greater proportion of highly abundant species. Furthermore, we derive exact formulae specifying expected species ages and use them to show that strong environmental variance can reduce these ages by about a half compared with the neutral case. This offers a partial solution to the overly long species ages predicted by neutral models.

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Shmuel Gal

University of Geneva (Switzerland)

Repeated hide-see and pursuit-evasion games

Shmuel Gal

A predator (searcher) looks for a prey (hider) in a search space consisting of n locations. The hider chooses a location and the searcher inspects k different locations, where k is a parameter of the game (the giving-up time for the continuous version). If the predator visits a location i at which the prey hides, then the game moves into a pursuit-evasion phase. In this phase capture is not certain but occurs with probability p_i : In a previous work we showed that for all k smaller than an easily calculated threshold, it is optimal to hide with probability proportional to $1/p_i$ for each location i : If k exceeds the threshold, then the optimal hiding strategy is always to stay at the location with the smallest p_i . We extend this game to a repeated game. During the k looks among the different locations within a single patch, there can be any of three events. First, if the searcher does not find the hider, then the game ends with zero payoff for the searcher and a payoff of one to the hider. Second, if the searcher finds the hider and catches it, then the game ends with a payoff of one to the searcher and zero to the hider. Finally, if the searcher finds the hider but does not catch it then the hider escapes to another patch and the process restarts. We show that in this game the optimal hiding strategy is to always make all the locations equally “attractive” for the searcher, no matter how large is k : This situation is quite different from the one stage game in which solutions of this type occur only if k is below the threshold. We actually present a general framework of repeated discounted games. We solve a family of games depending on the discount factor β , $0 \leq \beta \leq 1$. The two extreme cases occur for $\beta = 0$ and for $\beta = 1$ in which we get the undiscounted repeated game. We obtain an explicit expression for the discount factor above which the equally attractive solution is optimal. We also analyze the stochastic game version of the game in which the number of looks is reduced by one after each look even if the hider escapes to a different patch. We present a computational scheme for solving this game.

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József Garay

MTA-ELTE (Budapest, Hungary)

Fight between competing predators

József Garay, Zoltán Varga, Manuel Gámez, Tomas Cabello

Fight between predators is a direct competition. It also takes fixed time duration (similarly to the handling of prey), so fight also decreases the number of active predators. First, a generalized version of the Beddington–de Angelis functional response is introduced, considering that all predator activities (searching and handling prey, fight and recovery) have time duration, the probabilities of predator activities depend on the encounter probabilities, and hence on the prey and predator abundance, too. After that we analyse the corresponding dynamics. We consider two-individual (predator–prey, predator–predator) and three-individual (predator–predator–prey) encounters. In the three-individual encounter model there is a relatively higher fighting rate and a lower killing rate. Using numerical simulation, we surprisingly found that when the intrinsic prey growth rate and the conversion rate are small enough, the equilibrium predator abundance is higher in the three-individual encounter case. The above means that, when the equilibrium abundance of the predator is small, coexistence appears first in the three-individual encounter model. Garay J., Varga Z., Gámez M., Cabello T. (2015) Functional response and population dynamics for fighting predator, based on activity distribution. *J.Theor. Biol.* 368: 74-82

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Thomas Garcia

Institut d'écologie et des sciences de l'environnement, iEE (France)

Evolutionary coupling of sociality and cooperation in microbial populations

Thomas Garcia, Silvia De Monte

Collective living include a wide range of behaviors in microbes, from the ability to attach to other cells (thanks to adhesion proteins or chemotaxis) to the participation in collective functions (e.g., collective migration, biofilm production. . .) once aggregates are formed. This distinction is particularly relevant for microorganisms whose life cycles alternate an aggregation phase and a grouped phase, such as dictyostelids or myxobacteria. A trait that encodes the production of a costly extracellular “glue” might then play a twofold role: (1) improve adhesion in the aggregation phase (here coined “sociality”); (2) maintain group cohesion to the benefit of every cell in the group (here coined “cooperation”). Now if cells are able to regulate glue production depending on the phase of their life cycle, opportunistic strategies might arise. With an evolutionary game-theoretical approach, we modeled a population of cells with 4 possible strategies - social-cooperation (SC), social-defection (SD), asocial-cooperation (AC) and asocial-defection (AD) - that refer to the tendency to produce the glue or not during each one of the two phases. The first phase is modeled by a toy algorithm of aggregation, the second phase by a standard social dilemma (the linear Public goods games). We show that, counter-intuitively, SD opportunistic cheaters cannot persist in most cases, even if the cost of switching on/off glue production is null. Rather, depending on parameters one of the two non-switching strategies SC and AD systematically takes over. This work thus highlights how robust coupling between adhesiveness and cooperation could have emerged in microbial societies.

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Fanny Gascuel

Collège de France, UPMC (Paris, France)

How Ecology and Landscape Dynamics Shape Phylogenetic Trees

Fanny Gascuel, Régis Ferrière, Robin Aguilée, Amaury Lambert

Whether biotic or abiotic factors are the dominant drivers of clade diversification is a long-standing question in evolutionary biology. The ubiquitous patterns of phylogenetic imbalance and branching slowdown have been taken as supporting the role of ecological niche filling and spatial heterogeneity in ecological features, and thus of biotic processes, in diversification. However, a proper theoretical assessment of the relative roles of biotic and abiotic factors in macroevolution requires models that integrate both types of factors, and such models have been lacking. In this study, we use an individual-based model to investigate the temporal patterns of diversification driven by ecological speciation in a stochastically fluctuating geographic landscape. The model generates phylogenies whose shape evolves as the clade ages. Results show that biotic factors have a strong and diverse influence on the shape of phylogenies of ecologically saturating clades and create the evolutionary template in which branching slowdown and tree imbalance may occur. However, the contingency of landscape dynamics and resource distribution can cause wide variation in branching tempo and tree balance. Besides, considerable variation in tree shape among simulation replicates calls for caution when interpreting variation in the shape of real phylogenies.

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Sergey Gavrilets

University of Tennessee (Knoxville, USA)

Collective action and the collaborative brain

sergey gavrilets

Humans are unique both in their cognitive abilities and in the extent of cooperation in large groups of unrelated individuals. How our species evolved high intelligence in spite of various costs of having a large brain is perplexing. Equally puzzling is how our ancestors managed to overcome the collective action problem and evolve strong innate preferences for cooperative behaviour. Here, I theoretically study the evolution of social-cognitive competencies as driven by selection emerging from the need to produce public goods in games against nature or in direct competition with other groups. I use collaborative ability in collective actions as a proxy for social-cognitive competencies. My results suggest that collaborative ability is more likely to evolve first by between-group conflicts and then later be utilized and improved in games against nature. If collaborative abilities remain low, the species is predicted to become genetically dimorphic with a small proportion of individuals contributing to public goods and the rest free-riding. Evolution of collaborative ability creates conditions for the subsequent evolution of collaborative communication and cultural learning.

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Chaitanya S. Gokhale

New Zealand Institute for Advanced Study (New Zealand)

Eco-evolutionary dynamics of social dilemmas

Chaitanya S. Gokhale and Christoph Hauert

Social dilemmas are an integral part of social interactions ranging from microbial populations to human societies. Cooperative actions, such as secreting extracellular products or donating blood, are costly to the actor and hence create an incentive to shirk and avoid the costs even though benefits to recipients are potentially of vital importance. Nevertheless, cooperation is ubiquitous in nature. Both costs and benefits often depend nonlinearly on the number and types of individuals involved – as captured by idioms such as ‘too many cooks spoil the broth’ where additional contributions are discounted, or ‘two heads are better than one’ where cooperators can synergistically enhance the group benefit. Interaction group sizes may depend on the size of the population and hence on ecological processes. This results in feedback mechanisms between ecological and evolutionary processes, which jointly affect and determine the evolutionary trajectory. Only recently combined eco-evolutionary processes became experimentally tractable in microbial social dilemmas. Here we analyse the evolutionary dynamics of non-linear social dilemmas in settings where the population fluctuates in size and the environment changes over time. We find that the combination of the two processes routinely reveals highly complex dynamics, which suggests common occurrence in nature. One particularly interesting outcome is the evolutionary feasibility and maintenance of cooperation at high densities in ecologically fluctuating populations.

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Mauricio González-Forero

University of Lausanne (Lausanne, Switzerland)

A mathematical model for brain development

Mauricio González-Forero, Timm Faulwasser, and Laurent Lehmann

Growing and maintaining a large brain entails substantial energetic costs. A large brain can evolve if these costs are compensated by benefits from correspondingly high cognitive abilities. Benefits are thought to arise from ecological and social pressures, and mostly verbal theories have yielded predictions that have received some support. Here we develop a mathematical model for energy allocation into brain growth during ontogeny. We consider a body composed of brain cells, reproductive cells, and somatic cells. In this model, some of the energy spent by the brain is used to maintain and gain skills to solve ecological problems. Problem solving allows the body to obtain energy from the environment. The energy obtained can then be allocated into maintaining and producing one or more of the three cell types. Under standard life-history assumptions, energy allocation maximizes lifetime number of offspring. Performing this maximization, we obtain ontogenetic curves for brain mass. The model depends on measurable metabolic parameters and yields qualitative and quantitative predictions for brain growth when the selection pressure for energy acquisition is ecological rather than social.

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Frederic Guillaume

University of Zurich (Zurich, Switzerland)

Limits of adaptation of multiple characters to shifting environmental gradients

Frederic Guillaume

Rapidly changing environmental conditions are posing a threat to many natural species, potentially limiting their geographical range. How can we evaluate the capacity of a species to resist or track shifting habitat conditions and persist in a given landscape? Most of the current models of the evolution of species' ranges make two strong assumptions. They consider a single quantitative trait under selection with constant genetic variance. Relaxing the assumption of constant genetic variance is known to strongly affect model predictions and the response of selection on multiple phenotypic characters may be limited by the presence of pervasive pleiotropic gene effects. I will here present a multilocus and multivariate quantitative genetics simulation model of the evolution of a species' range under shifting selection gradients that relaxes these assumptions. I will show that the interplay of gene flow and genetic correlations among multiple phenotypic traits may strongly limit the capacity of a species to adapt to temporally and spatially varying habitat conditions. The conditions under which species fail to adapt and evolve limited ranges are then compared to quantitative genetic model predictions, showing that under many conditions species may sustain larger rates of environmental change than usually accepted. Additionally, the simulations show that genetic constraints are more likely to limit adaptation at the rear than the front edge of the range and that the resulting range expansion dynamics is complex and shows patterns unpredicted by analytical models. Finally, I will show how the modelling approach can be applied to predicting the evolution of species' ranges under climate change in existing endemic alpine plant species.

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Onur Gun

Weierstrass Institute (Germany)

The Stochastic Encounter-Mating Model

Onur Gun

We introduce a new model of permanent monogamous pair formation in zoological populations where animals randomly encounter and mate with the members of the opposite sex. We formulate conditions that characterize panmixia for the special cases where the times animals search for mates are given by Poisson and Bernoulli point processes. Moreover, we give a full description of heterogamy/panmixia/homogamy when populations consists of only two types. Next, we study the infinite population limit of the Poisson model. We prove that the stochastic dynamics converges to a deterministic system governed by coupled ODEs. We relate the limiting ODEs to the well-known replicator equations and solve them for panmictic populations. Finally, we give explicit formulas of the resulting mating pattern for the two types case. (Joint work with Atilla Yilmaz)

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Penelope Hancock

University of Oxford, Department of Zoology (Oxford, United Kingdom)

Density-dependent population dynamics in *Aedes aegypti* slow the spread of wMel Wolbachia

Penelope Hancock, Vanessa Linley-White, Ashley Callahan, Charles Godfray, Ary Hoffmann, Scott Ritchie

The transmission of infectious organisms can depend on heterogeneity in their hosts' fitness driven by density-dependent population growth. The spread of endosymbiotic Wolbachia bacteria in *Aedes aegypti* mosquitoes is important to biocontrol of dengue, but natural variation in mosquito fitness due to density-dependent competition for limited food resources may influence Wolbachia invasion. We know little about these effects, largely because our understanding of density-dependent dynamics in mosquito populations is limited. We develop an empirical model of *A. aegypti*-Wolbachia dynamics where food resources available to the developing larvae are limited. We assess the extent of density-dependent regulation in our *A. aegypti* population using a Bayesian statistical model that estimates the temporal variation in mosquito fitness components. We monitor the spread of Wolbachia and assess the effect of the bacteria on larval fitness components. We demonstrate that mosquito population growth is regulated by strong larval density-dependent variation in mosquito fitness components. Wolbachia spread was slowed by this heterogeneity in mosquito fitness, which reduces the capacity of the bacteria to invade. We demonstrate that the extent and form of density-dependent dynamics in the host population can have a major influence on Wolbachia invasion. The success of Wolbachia in biocontrol of dengue will depend critically on Wolbachia releases that attain a high infection frequency in the mosquito population.

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Mathieu Hemery

CNRS, Université Joseph Fourier (Grenoble, France)

Evolution of sparsity and modularity in a model of allosteric protein

Mathieu Hemery, Olivier Rivoire

How much of the sequence of a protein accounts for its current function and how much is the result of its past evolutionary history? Being the product of a long evolutionary process in an ever changing environment, the sequence of current natural proteins may retain the trace of prior selected functions. Or more simply, it may contain elements that are not - or no more - subject to selection. Using a simple physical model previously analysed to study the folding problem, we probe the influence of past evolutionary environments on protein sequences. Simulations of evolutionary dynamics generically leads to non-trivial correlations between temporal fluctuations and geometrical structure, illuminating the link between history, geometry and function.

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Andrew Higginson

University of Bristol (Bristol, UK)

Use of physiological states as a source of information approximates the performance of Bayesian learning

A. D. Higginson, T. W. Fawcett, J. M. McNamara, A. I. Houston

Theoretical approaches to understanding behaviour often assume that animals have perfect information about environmental conditions or are capable of sophisticated learning. If such learning abilities are costly, however, natural selection will favour simpler mechanisms for controlling behaviour when faced with uncertain conditions. Here, we show that in a foraging context, a mechanism based only on current energy reserves often performs almost as well as a Bayesian learning rule that integrates all previous experiences to form an optimal estimate of environmental conditions. This mechanism exploits the fact that reserves are a source of information about recent conditions. When conditions are mostly not challenging or change very frequently, an even simpler rule that does not account for changes in environmental conditions can still be successful. We find that Bayesian learning gives a strong advantage only if fluctuations in the food supply are very strong and reasonably frequent. Studies assuming Bayesian learning are often accused of being unrealistic; our results suggest that animals can achieve a similar level of performance to Bayesians using much simpler mechanisms based on their physiological state. More broadly, our work suggests that the ability to use internal states as a source of information about recent external conditions will have weakened selection for sophisticated learning and decision-making systems.

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Rebecca Hoyle

University of Southampton (Southampton, UK)

Coevolution of maternal effects and within-generation phenotypic plasticity: a quantitative genetics model

Bram Kuijper, Rebecca Hoyle

Maternal effects are the influences of the maternal phenotype on offspring phenotypes by routes other than direct genetic transmission. Potentially they provide an additional means of adaptation to changing environmental conditions over and above that afforded by within-generation phenotypic plasticity. I will present results from a quantitative genetics model of the coevolution of maternal effects and phenotypic plasticity following an abrupt environmental change and during cyclical environmental fluctuations such as seasonal variation. We find that generally the strongest maternal effects occur for traits that experience very strong selection and for which plasticity is severely constrained. For traits experiencing weak selection, phenotypic plasticity enhances the evolutionary scope of maternal effects, but maternal effects attain much smaller values throughout. As weak selection is common, our results suggest that finding substantial maternal influences on offspring phenotypes may be more challenging than anticipated.

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Ryosuke Iritani

Kyushu University (Fukuoka, Japan)

Near-and-far dispersal revisited: evolutionary limits to mating system can explain differential dispersal.

Ryosuke Iritani & Pierre-Olivier Cheptou

Differential seed dispersal, i.e., outcrossed seeds (O-seeds) and selfed seeds (I-seeds) displaying different propensities for dispersal, has been studied in plant evolutionary ecology. I-seeds possess higher dispersal capacity than O-seeds in some species, while others show the opposite pattern. In this context, near-and-far dispersal theory has been conventions, postulating the exposure to maternal environment potentiates differential seed dispersal by local adaptation because of the genetic similarity with maternal plant is higher for I-seeds than O-seeds. However, no theoretical study is available that tackles this problem, leading to the lack of unified explanations for differential seed dispersal. In the present talk, we will investigate the evolutionary consequences for differential seed dispersal in two distinct episodes: (i) selfing rate is fixed because of some evolutionary limits (“fixed selfing episode”), and (ii) selfing can evolve jointly with seed dispersal rates (“joint evolution episode”). We build on adaptive dynamics theory, and develop an island model of meta-population accommodating numbers of patches each with a large carrying capacity. We assume that pollinator availability exhibits heterogeneity among patches and the degrees of inbreeding depression vary across home/away patches. We found that: (i) fixed selfing episode may be plausible for these opposite patterns, but (ii) joint evolution episode necessarily leads to the consequences where I-seeds have (equal or) higher propensity of dispersal than do O-seeds because of traits-syndrome between selfing and O-seeds dispersal. We advocate that different intensities of evolutionary limits and multi-traits syndrome are responsible for the patterns observed in differential seed dispersal.

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Gereon A. Kaiping

University of Southampton (Southampton, United Kingdom)

Structured populations facilitate cooperation in policed Public Goods Games

Gereon A. Kaiping, Guy S. Jacobs and Timothy J. Sluckin

Societies consisting of cooperative individuals seem to require for their continuing success that defectors be policed. The precise connection between punishers and benefits, population structure, and division of labour, however, remains ill-understood. Many models assume costly “peer punishment” to enforce cooperation, but results in the economics literature suggest that this assumption may not be generally valid. In many human and animal societies, there is a division of labour between a purely supportive majority and a dedicated minority of police-like enforcers. Here we present several extensions to the Public Goods Game with punishment which allow for this possibility, and evaluate their influence on the level of cooperative behaviour. We find that a structure of separate subpopulations, which only interact through migration of individuals, can have a strong effect on the evolutionary dynamics of a system and significantly facilitate cooperation. Forcing defectors to contribute and enabling fitness transfers to punishers both have a weak positive effect on cooperation levels. In the presence of group competition, however, evolutionary effects can paradoxically hinder cooperation.

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Yun Kang

Arizona State University (Tempe, USA)

Co-evolutionary dynamics of a host-parasite interaction model: obligate v.s. facultative brood parasitism

Yun Kang and Jennifer Fewell

We present and study a fully co-evolutionary model of a host-parasite system that incorporates (1) ecological dynamics that feed back into the co-evolutionary outcome; (2) parasite that can be obligate or facultative; and (3) Holling Type II functional responses between host and parasite, which are suitable for brood parasitism since parasites need to search for host and spend some time handling resources. We perform both local and global analysis for the co-evolutionary model and the corresponding ecological model. In the absence of evolution, our analysis on the ecological model implies that the extremely small value of the death rate of parasite due to hunting/searching for all potential host species can drive host extinct globally while the extremely large value of the death rate can drive parasite extinct globally. The facultative parasite system can have one, two, or three interior equilibria while the obligate parasite system can have either one or three interior equilibria. Multiple interior equilibria result in rich dynamics with multiple attractors. Particularly, the ecological system can exhibit bistability between the facultative parasite only boundary attractor and the coexistence interior attractor when it has two interior equilibria. Our analysis on the co-evolutionary model provides important insights on how co-evolution can change the ecological and evolutionary outcomes of host-parasite interactions. Most interesting findings suggest that: (a) Host and parasite can select different strategies that result in local extinction of one species. However, these strategies can have convergence stability (CS) but they may not be evolutionary stable strategies (ESS); (b) Host and facultative (or obligate) parasite can have ESS strategies that drive host (or obligate parasite) extinct locally; (c) Trait functions play an important role in the CS of both boundary and interior equilibria as well as their ESS strategies; and (d) The small variance of the trait difference that measures the parasitism efficiency can destabilize the co-evolution system, thus generate evolutionary arms-race dynamics with different host-parasite fluctuating patterns.

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Georgy Karev

National Center for Biotechnological information (Bethesda, USA)

Modeling of natural selection of strategies

G.P. Karev

Consider a large population of individuals which can adopt two different strategies. We propose a generalized framework where individuals can use either strategy at any moment with its own hereditary probability α . Our aim is to study the process of natural selection of mixed strategies formalized as the evolution of the distribution of the parameter α . To this end we apply the reduction theorem (Karev 2010), which allows us reducing the initial infinite-dimensional problem to low-dimensional system of ODE, which can be effectively solved. As a simplest example we consider the selection between r- and K-strategies and show that K-strategy wins at any initial conditions. We consider also more complex model for ecological niche construction and study the natural selection between two different strategies, namely, allocation of resources towards rapid proliferation or towards slower proliferation but increased physiological and environmental maintenance. In contrast with the r/K strategies, the outcome of natural selection in this case may depend on the initial population composition and starting point in phase-parametric space (Kareva et. al., 2012). The developed approach is also applied to natural selection of strategies for some classical evolutionary games, e.g., “hawk-dove” game. Acknowledgement: this research was supported by the Intramural Research Program of the NIH, NCBI. References. G. Karev. 2010. On mathematical theory of selection: continuous time population dynamics. *J. Math. Biol.* 60(1): 107–129. I. Kareva, F. Berezovskaya, G. Karev, 2013. Mixed Strategies and Natural Selection in Resource Allocation. *J. Math. Biosciences and Engineering*, v. 10, 5/6, 1561-1586.

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Bhavin Khatri

Crick Institute (UK)

Evolutionary stochastic dynamics of speciation for a coarse-grained model of protein binding DNA

Bhavin Khatri

Speciation is fundamental to understanding the huge diversity of life on Earth. Current theory does not address how the speciation rate varies with population size in the important weak mutation regime of evolution, despite some evidence that smaller populations develop reproductive isolation more quickly. Here, we address an underlying biophysical basis of speciation by using a simple model of transcription factor-DNA binding and examine how their co-evolution in two allopatric lines leads to incompatibilities. We tackle this using both theory and simulations of sequence evolution. To develop a tractable analytical theory, we derive a coarse-grained Smoluchowski Equation for the dynamics of binding energy evolution due to the co-evolution of protein and DNA sequences; the high dimensionality of sequence evolution is accounted for by defining a Boltzmann sequence entropy for the binding energy of transcription factors, such that the flux of populations go up gradients in Iwasa's free fitness. We find these simple considerations lead to a new prediction for the monomorphic regime of evolution, born out by theory and simulations, that smaller populations should develop incompatibilities more quickly; this arises as the effect of sequence entropy is to poise the common ancestor of smaller populations more closely to incompatible regions of phenotype space, so less substitutions are needed on average for incompatibilities to arise. Overall, these predictions are consistent with observations of large species diversity in small habitats such as Cichlids in the East African Great Lakes, contrasted with the observed smaller rate of developing reproductive isolation in marine animals and birds, which have large ranges and population sizes.

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Christopher Klausmeier

Kellogg Biological Station (Augusta, USA)

ADventures in space and time

Colin Kremer, Elizabeth Miller, Yonatan Natan

As most ecosystems, lakes are heterogeneous in space and time. This presents opportunities for maintaining species diversity, which can be modelled with adaptive dynamics and related techniques. Here I will present some applications to the distribution of phytoplankton species. The primary axis of spatial variation is the vertical, due to steep gradients in the essential resources of light and nutrients. Under weakly mixed conditions, phytoplankton can play a game against conspecifics where to live within the water column, resulting in an aggregation at depth. In turn, this intraspecific aggregation can enable coexistence of multiple species that show a trade-off between light and nutrient competitive abilities. A major source of temporal variability is due to the annual variation in light, temperature, and mixing, which leads to seasonal succession of species. I will describe how this coexistence due to temporal variability can emerge and be evolutionarily robust.

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Thomas Koffel

Laboratoire Eco&Sols (Montpellier, France)

Geometrical envelopes: a natural extension of the graphical theory of competition to the adaptive dynamics framework

Thomas Koffel, Tanguy Daufresne, François Massol, Christopher Klausmeier

Classical resource competition theory is a central framework in theoretical ecology. It allows representing graphically the different competitive outcomes of a consumers-resources system, among which coexistence, competitive exclusion and priority effects as functions of the external resource supplies. Its general formulation, which includes other kind of limiting factors such as parasitism or predation, led to cornerstone concepts such as the competitive exclusion principle. Yet, it is unclear how this picture translates when the consumers can evolve by means of natural selection. Indeed, some recent studies showed that evolution can either destabilize coexistence or lead to sympatric diversification. Those works implemented evolution using adaptive dynamics, a convenient and general approach based on invasion of a rare mutant in a resident population. However, the focus on evolution was usually associated with the discarding of the main advantage of the theory, its graphical approach. The goal of this presentation is to transpose the graphical concepts of the classical resource competition theory in the eco-evolutionary case. We will first present how the notion of geometrical envelope of a family of curves enables to study a continuum of competitors. Then, we will show the fundamental link between local and global properties of this envelope and a central concept of adaptive dynamics, the Evolutionary Stable Strategy (ESS). This will allow summarizing the different possible evolutionary outcomes of the system as functions of the external resource supplies in an evolutionary bifurcation diagram. Each region of this diagram can be associated with its corresponding Pairwise Invasibility Plot (PIP), synthesizing their evolutionary characteristics: adaptation, stable coexistence or evolutionary branching among others. In the end, we will address the question of the role of the invasion range considered, from a local one with infinitesimal mutations to a global one associated with the “everything is everywhere” paradigm.

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Klemen Koselj

Max Planck Institute (Seewiesen, Germany)

Optimisation of sensing for efficient foraging

Klemen Koselj

Every animal uses its species-specific senses to gather information from environment and guide behaviour. While evolutionary consequences of different behaviours like foraging have been extensively studied, the selective pressures that shaped the senses behind them are still poorly understood. I combined the foraging theory and sensing physiology to study the efficiency of alternative sensing strategies. My model species are echolocating bats, which emit ultrasonic vocalisations and analyse their echoes to navigate the environment and find insect prey while flying around in darkness. I investigated whether and how foraging bats tackle physiological and physical constraints and trade-offs of sensing and movement to sample the environment in an economic fashion. First, I used properties of sound transmission and characteristics of bat auditory system for detection of prey echoes to develop the procedure for estimating search volume for flying bats. Accounting for metabolic costs of flight and vocalisation, I then expressed the net energy intake rate as a function of five parameters: flight speed, maximum detection angle, maximum detection distance, call duration and inter-call interval. I then used analytical and numerical optimisation to find the combinations of these parameters that maximise net energy intake rate in different prey abundances. The results matched the pattern of echolocation and movement exhibited by the bats in the wild. In low prey densities experienced by high-flying species it is most profitable to call with high amplitude, broad sound beams, long call durations and pauses between the calls, and to fly at the maximum flight speed. I conclude that economy of foraging is an accurate novel explanation for the sensing strategies of bats. Animal movement is a part of the strategy to sense the environment, not just a way to get around.

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Vlastimil Křivan

University of South Bohemia (Czech Republic)

Competition driven spatial animal distribution

Vlastimil Křivan

In my talk I will discuss the effect of competition on species distribution and population dynamics in heterogeneous environments consisting of two or more patches. I will assume that dispersal is density dependent and in direction of increasing fitness. When the per capita population growth rate is negatively density dependent, this means that individuals disperse to patches where intra-/inter-specific competition is weaker. For a single species the resulting distribution is known as the Ideal Free Distribution (IFD). In fact, the IFD is an evolutionarily stable strategy of the underlying Habitat Selection Game. The single species IFD was extended to two competing species in two patches using a two-species ESS. In contrast to the single species distribution, the resulting two-species distribution may not be unique. At high population densities, it can lead to complete species segregation with species occupying different patches. Such competition driven species separation has been called “ghost of competition past”. Then I will study consequences of the IFD on the Lotka-Volterra population dynamics of two competing species. I will show that fast adaptive animal dispersal can destabilize a stable population equilibrium leading to fluctuations in population densities. I will also discuss apparent competition and I will show that fast directed density-dependent dispersal of consumers among two resource patches promotes species coexistence when compared with density-independent dispersal.

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Bram Kuijper

University College London (London, United Kingdom)

Nongenetic Effects in Age-Structured Populations

Bram Kuijper, Rufus Johnstone

Existing predictions on the evolution of nongenetic effects have focused exclusively on the role of environmental heterogeneity, but have given little attention to the role of individual variation. To overcome this, we model the evolution of nongenetic effects in an age-structured population. Interestingly, we find that the magnitude of nongenetic effects can vary drastically over the lifespan of an individual. Young parents should always produce offspring with phenotypes which match the most frequent environment, whereas older parents are selected to produce offspring that match the local environment, even when this environment is globally rare. The reason for these age differences is that an older parent's phenotype has endured mortality selection, so that it contains information about the local environment. By contrast, the phenotype of young parents contains little information about the local environment, so that offspring play a fixed strategy and always produce the same phenotype. Overall, our model shows that nongenetic effects may vary strikingly with increasing age.

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Klodeta Kura

City University London (London, United Kingdom)

A game-theoretical winner and loser model of dominance hierarchy formation.

Klodeta Kura, Mark Broom, Anne Kandler

Animals that live in groups commonly form themselves into dominance hierarchies which are used to allocate important resources such as access to mating opportunities and food. We develop a model of dominance hierarchy formation based upon the concept of winner and loser effects, where we analyse the temporal dynamic and the average behaviour of hierarchies emerging from different combinations of these effects. We investigate if we can achieve hierarchy linearity and if so, when it is established. We then develop a game-theoretical version of this model, where individuals choose a strategic level of aggressiveness. For different combinations of reward and cost we find the (unique) evolutionarily stable strategy (ESS) and its associated expected payoff by using two different payoff functions. We analyse how the ESS changes when we vary the reward and cost, and the effect of different payoff functions, using both analysis and simulations to get our results.

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Ben Lambert

Oxford University (United Kingdom)

A novel estimation of mosquito longevity using a Bayesian meta-analysis

B Lambert, A North, C Godfray

As the vectors of human malaria, Anopheles mosquitoes are one of the most important species groups to human health, yet there are conspicuous gaps in our knowledge of their ecology. In this paper I will present a meta-analysis of a recently-compiled database of over 100 published Anopheline mark-release-recapture (MRR) experiments. MRR experiments are a central component of field research on mosquitoes yet individual studies often only result in a moderate amount of data. By combining the separate data-sets in a common hierarchical Bayesian framework, we obtain a robust and cohesive estimation of mosquito longevity, a crucial parameter in models of malaria incidence and control. The methodology further allows us to address a number of important issues: which mathematical models of MRR experiments produce better estimates of mortality? What evidence is there for senescence in Anopheles? And are there differences in Anopheles longevity that vary by species?

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Nicolas Lanchier

Arizona State University (Tempe, USA)

Best-response dynamics

Stephen Evilsizor and Nicolas Lanchier

The best-response dynamics is an example of evolutionary game where players are located on the infinite square lattice and update their strategy in order to maximize their payoff. In the presence of two strategies, and calling a strategy selfish or altruistic depending on a certain ordering of the coefficients of the underlying payoff matrix, a simple analysis of the nonspatial mean-field approximation of this process shows that a strategy is evolutionary stable if and only if it is selfish, making in particular the system bistable when both strategies are selfish. The main objective of this talk is to show that, in contrast with the mean-field approximation, only the most selfish strategy is evolutionary stable for the stochastic process. The main ingredients of the proof are monotonicity results and a coupling between the process properly rescaled in space with bootstrap percolation.

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Nicolas Lartillot

CNRS Université Lyon 1 (Lyon, France)

Fitting a Red-Queen model of species diversification to empirical phylogenies.

Guillaume Achaz, Amaury Lambert, Nicolas Lartillot, Veronica Miro Pina, Todd Parsons

Using phylogenies to infer key aspects of the species diversification processes is typically done using likelihood-based approaches. Thus far, most statistical models used in this context, such as the birth-death model or Kingman’s coalescent, are typically exchangeable — all lineages existing at a given time have equal chances of evolutionary success. When explicitly individual-based, these models typically invoke the neutral theory of biodiversity, positing ecological equivalence between all individuals, irrespective of their species. However, exchangeable models do not explain some aspects of empirical phylogenies, such as tree imbalance. Nor do they predict patterns of macro-evolutionary succession, in which clades that were once dominating biodiversity are now extinct or represented by very few ‘living fossils’, coexisting with younger and highly successful clades. Such patterns suggest instead the existence of Red-Queen ecological processes, in which speciation continually produces fitter species benefiting from a competitive advantage over older species, driving them to extinction. Here, a non-exchangeable, individual-based, point mutation model of species diversification will be presented (similar to O’Dwyer and Chisholm, 2014, *Ecology Letters*), which accounts for such Red-Queen like evolutionary arms races. Fitness is implicit, being mediated by the order of appearance of species, via a multitype logistic branching process with asymmetric competition between types (=species), such that individuals from old species experience density dependent competition with individuals belonging to new species, whereas the converse is not true. We show that, for large metapopulation size, and upon rescaling time, the model converges to a non-exchangeable, Markovian species coalescent process called the ‘shift-down/look-up’ coalescent. This model leads to tractable inference using Bayesian Monte Carlo methods, allowing parameter estimation and model testing against empirical phylogenies.

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Laurent Lehmann

University of Lausanne (Lausanne, Switzerland)

Does evolution lead to maximizing behavior?

Laurent Lehmann

A long-standing question in biology and economics is whether individual organisms evolve to behave as if they were striving to maximize some goal function. We here formalize this “as if” question in a patch-structured population in which individuals obtain material payoffs from (perhaps very complex) multi-move social interactions. These material payoffs determine personal fitness and, ultimately, invasion fitness. We ask what goal function, if any, individuals will appear to be maximizing, in uninvadable population states, when what is really being maximized is invasion fitness at the genetic level. We reach two broad conclusions. First, no simple and general individual-based goal function emerges from the analysis. This stems from the fact that invasion fitness is a multi-generational measure of evolutionary success. Second, when selection is weak, all multi-generational effects of selection can be summarized in a neutral type-distribution quantifying identity-by-descent within patches. Individuals then behave as if they were striving to maximize a weighted sum of material payoffs (own and others). At an uninvadable state it is as if individuals would choose their actions and play a Nash equilibrium of a game with a goal function that combines self-interest (own material payoff), group interest (group material payoff if everyone does the same), and local rivalry (material payoff differences).

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Hélène Leman

Ecole Polytechnique (Paris, France)

Adaptive dynamics model for individual-based spatially structured populations

Hélène Leman

The aim is to study the influence of a geographical structure on phenotypic evolution. The interplay between space and evolution and the heterogeneity of the environment are particularly crucial in the emergence of polymorphism and spatial patterns. The model considered is an individual-based model in which the birth and death of each individual are explicitly described. At any time, individuals are characterized by their phenotypic traits and their geographical positions. Migration is modeled by a Brownian motion reflected at the boundaries. At each birth event, a mutation may occur and a new phenotypic trait then appears in the population. As a first step, we assume that all individuals have the same trait and that the population dynamics is close to a stable macroscopic equilibrium. We study the impact of the emergence of a mutant in this monomorphic population. By using tools of large deviations and Freidlin-Wentzell theory, we prove that, as long as the size of the population descended from the mutant is negligible, the dynamics of the resident population stays close to the equilibrium state. Then we consider the dynamics of the mutant population itself and we answer to the following questions by comparing the mutant population to a branching Brownian motion : What characterizes the survival probability of the mutant population? If it survives, how long does it take for its size to be non-negligible compared to the size of the resident population? Those studies will then be used to generalize the model of Trait Substitution Sequence (TSS) to a spatially structured population. It corresponds to a macroscopic approximation of our microscopic model under three main assumptions: mutations are rare, the size of the population is large and a population composed of two traits can not survive for a long time.

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Eric Lewitus

Ecole Normale Supérieure (Paris, France)

A general function of phylogenetic diversification in animals

Eric Lewitus, Helene Morlon

Our understanding of any biological phenomena is guided by our ability to identify what is universal and what is specific. In the particular case of species diversity, identifying features of diversification universal to all clades and specific to certain clades could allow us to derive a general model of the evolution of species richness. Here, we introduce a method based on the spectrum of the graph-Laplacian of phylogenies to identify various algebraic properties of trees and cluster them into meaningful groups. By applying this approach to a broad set of animal phylogenies, we identify five distinct types of phylogenies based on their patterns of diversification. From this, we derive a general function of diversification in animal phylogenies. We explore the degree of heritability of patterns of diversification in birds and mammals.

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Ard Louis

University of Oxford (UK)

Evolutionary dynamics, the structure of genotype-phenotype maps, and the arrival of the frequent

Ard Louis

Evolutionary dynamics arise from the interplay of mutations acting on genotypes and natural selection acting on phenotypes. How does the structure of the genotype-phenotype (GP) map affect evolutionary processes? By using models for RNA secondary structure, the HP model for protein tertiary structure and the polyomino model for protein quaternary structure[1], we investigate the following structural properties: Correlations: Following on an early suggestion by John Maynard-Smith, we show that genotypes are strongly correlated, that is their mutational neighbours are more likely to map to similar phenotypes than expected from random chance. Neutral correlations greatly enhance robustness above the threshold to allow large neutral networks. Non-neutral correlations lower the rate at which novel phenotypes are found by a population, but also lower the probability that a mutation leads to a deleterious phenotype. Thus correlations in GP maps enhance robustness, but have a more complex effect on evolvability. Bias: Many GP maps show a strong bias: the vast majority of genotypes map to an exponentially small set of phenotypes. We develop a population-genetics model that takes the GP map bias into account. This allows us to calculate effects such as the arrival of the frequent, where phenotypes with many genotypes mapping to them can fix in a population even if their fitness is lower than other phenotypes with fewer genotypes mapping to them [2]. Bias may also 1) help explain how evolutionary solutions are found in hyper-astronomically large genotype spaces, 2) provide a non-adaptive mechanism for homoplasy (convergence) and 3) be linked to the spontaneous emergence of modularity and symmetry. [1] A tractable genotype-phenotype map for the self-assembly of protein quaternary structure, Sam F. Greenbury, Iain G. Johnston, Ard A. Louis, Sebastian E. Ahnert, *J. R. Soc. Interface* 11, 20140249 (2014) [2]The arrival of the frequent: how bias in genotype-phenotype maps can steer populations to local optima, Steffen Schaper and Ard A. Louis, *PLoS ONE* 9(2): e86635 (2014)

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Sabiha Majumder

Indian Institute of Science (Bangalore, India)

A method to estimate the threshold of critical transitions in ecosystems using spatial data

Sabiha Majumder, Vishwesh Guttal, Sriram Ramaswamy

vidence from various ecosystems, ranging from lakes to semi-arid ecosystems, suggests that gradually changing drivers can cause abrupt shifts from one stable state to an alternative stable state. Such shifts can often be irreversible and may result in significant ecological and economic losses. Recently, studies have devised early warning signals of abrupt transitions. However, these signals cannot forecast the threshold value of the ecosystem state or the driver at which the transition will actually occur. In this work, we propose a method to analyze discrete spatial data such as data from satellite imagery to estimate this threshold. To do so, we employ a spatially explicit model of vegetation that includes local interactions such as facilitation between nearby vegetation and competition for resources. These models exhibit transitions in ecological state from a vegetated to a bare state. We propose a method to calculate variance of the spatial data at different levels of coarse-graining (smoothing) of data. Analytical arguments suggest that the spatial variance of the coarse-grained data should peak at the value of the state or the driver variable corresponding to a critical point. In contrast, the raw data (which is typically 0 or 1 at each location) exhibits peak of spatial variance at a mean density of half, irrespective of the nature of local interactions. This method could be applied to satellite or other imagery based data of vegetation cover along a gradient of rainfall or related drivers. An important implication of our work is using such relatively easily available data, we may be able to estimate the threshold value of the driver or the state variable at which the threshold is expected. Our future work will involve testing the method with real data and to understand its strengths as well as limitations.

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Guillaume Martin

CNRS (Montpellier, France)

Non-stationary and non-linear: how can we extend the dynamics of adaptation to a moving optimum

G. Martin, Y. Anciaux, L. Roques

A central model of adaptation to gradual environmental change is the (Gaussian) moving optimum model: fitness is assumed to be a Gaussian function of some multivariate phenotype with an optimum that moves over time. The population responds by selection and mutation on phenotype, the latter creates normally distributed phenotypic changes around each parent. These models have only been analyzed for a constant speed optimum movement. In this case, a stationary regime establishes, where the population is either increasingly maladapted (ultimately extinct) or the phenotypic mean lags at constant distance from the moving optimum. But what happens before stationary regime, and what if the optimum moves at non-constant speed? I will present a framework that can hopefully provide analytical insight into this more general situation, imposing that the optimum remains on a straight line in phenotype space and ignoring stochastic forces, as in the original model. The approach is based on deriving a PDE that describes the dynamics of the cumulant generating function of the bivariate distribution of two key additive components of fitness.

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Ricardo Martinez-Garcia

Princeton University (Princeton, USA)

Fitness tradeoffs between spores and non-aggregating cells can explain the coexistence of diverse genotypes in cellular slime molds

Corina E. Tarnita, Alex Washburne, Ricardo Martinez-Garcia, Allyson E. Sgro, Simon A. Levin

The emergence of multicellularity was one of the major transitions in the early evolution of life on earth. Particularly intriguing are those cases where genetically heterogeneous complexes may be formed, among which cellular slime molds are a paradigmatic example. In the absence of food, single cells aggregate into a non-necessarily clonal multicellular fruiting body, where they differentiate into dead stalk cells and reproductive spores. Such division of labor promotes a strong selection to be represented in the reproductive spores and should lead to a reduction in the genotypic diversity, which is inconsistent with the great diversity found in nature. However, not all cells aggregate into the fruiting body and we suggest that these non-aggregating cells provide an additional fitness component that can resolve this inconsistency in two ways [1]. First, apparent reproductive skew in the spores of chimeric (heterogeneous) fruiting bodies could simply be the result of different investments into spores versus non-aggregators induced by different environmental conditions; and second, in an ecosystem with multiple local environments coupled via weak-to-moderate dispersal, coexistence of multiple genotypes can occur.

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Joanna Masel

University of Arizona (Tucson , USA)

Eco-evolutionary fitness? in 3 dimensions: absolute growth, absolute efficiency, and relative competitiveness

Joanna Masel

Competitions can occur on an absolute scale, to be faster or more efficient, or they can occur on a relative scale, to “beat” one’s competitor in a zero-sum game. Ecological models have focused on absolute competitions, in which optima exist. Classic evolutionary models such as the Wright-Fisher model, as well as more recent models of travelling waves, have focused on purely relative competitions, in which fitness continues to increase indefinitely, without actually progressing anywhere. To describe both at the same time, I first correct a long-standing subscript error on K , which has until now prevented r/K -selection theory from being exploited to its full potential in describing the occupation of territory. To this revised r/K model, I then add a third dimension of fitness that is unitless and normalized. This three-dimensional scheme can be seen as a population genetic formalization of Grime’s triangle of reproductive strategies.

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François Massol

Université des Sciences et Technologies de Lille 1 (France)

Joint evolution of dispersal and the allocation of dispersal cost in heterogeneous landscapes

François Massol

Dispersal is an important trait affecting many processes in ecology and evolution, such as the evolution of local adaptation, speciation, extinction risk, invasion success and species coexistence. Understanding the evolution of dispersal is thus of paramount importance to understand these processes at a higher level. Based on a simple, spatially implicit, adaptive dynamics-based model for the evolution of dispersal in heterogeneous environments, I will present some results on the evolution of dispersal when the cost of dispersal is supported by the offspring vs. the mother and on the joint evolution of dispersal and an allocation trait representing the proportion of dispersal cost supported by the offspring. At constant total cost of dispersal, the singular dispersal strategy is decreased by allocating more to maternal rather than offspring costs, while ESS/branching conditions are not affected by the allocation of costs. Depending on whether the trade-off between maternal and offspring costs is more or less convex than the trade-off that would keep total cost constant, I find that the joint evolution of dispersal with the allocation of costs increase or decrease the potential for evolutionary branching.

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Carlos Melian

Eawag (Switzerland)

Eco-evolutionary diversification dynamics

Carlos Melian

Most theoretical and empirical studies show speciation is a complex process involving several biological levels and spatial scales. However, building theory requires simple and testable models of speciation to infer the main mechanisms driving biodiversity patterns from the empirical observations. In this talk, I will discuss the challenges to connect simple and testable models of speciation and biodiversity dynamics with more complex and realistic ones. In the second part of the talk, as an example to join simple and testable with complex and realistic models of speciation, I will introduce a landscape genetic model based on demographic stochasticity with a speciation model that takes into account the evolution of premating incompatibility or assortative mating to map diversification rates in a spatial context. Using this model I will show that landscape structure and the intensity and directionality of gene flow strongly influence the formation of hot and cold spots of diversification and its connection to biodiversity patterns. Finally I will discuss these results in the context of the biogeography of hot and cold spots of diversification both in biological and human systems.

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Robin Mills

University of Groningen (Groningen, The Netherlands)

Evolution of the Stoop of Falcons in a Model of Bird Flight

Robin Mills, Graham Taylor, Hanno Hildenbrandt, Charlotte Hemelrijk

The Peregrine falcon *Falco peregrinus*, among some other predatory birds, intercepts its prey in a fast-speed, controlled dive called a stoop. This stoop has fascinated both laymen and researchers because enormous speeds of over 320 kmh-1 are often reached; the fastest measured speed for any animal. To intercept a prey at this speed, enormous precision in guidance towards the prey, stability, and control of aerodynamic forces is required, as well as fast reactions to the maneuvering prey. Because only a few species can intercept successfully by stooping, it is interesting to examine under what circumstances a stoop will evolve. This is very difficult to investigate, however, because any reductionist model of the interception problem for Peregrine falcons in nature may fail to include crucial constraints. In order to mimic the problem space in natural evolution as accurately as possible, we have built a three-dimensional, agent-based model of (flapping wing) bird flight, in which model-falcons hunt for model-starlings that fly above their roosting site. Using genetic algorithms, the attack strategies (guidance algorithms) of the falcon evolve. The flight dynamics, cognitive constraints and behavioral rules are based on StarDisplay: a model of flocks of starlings. The aerodynamics and the flight control of the model have been improved, because of the precision and accuracy that is needed in modeling an aerial hunt. We have limited our investigation to selection based on how much the predator misses the prey in a single interception attempt. The prey maneuvers unpredictably, without any escape strategies; we model a surprise attack. Despite that we use one selection criterion, while fitness in nature is governed by many criteria, stoops evolve that mimic real Peregrine falcons in terminal velocity, initial altitude, dive angle and guidance parameters. Key to the evolution of a stoop is the unpredictability in the movement of the prey.

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Dusan Misevic

INSERM (Paris, France)

Shape matters: lifecycle of cooperative patches and the evolution of cooperation

Dusan Misevic, Antoine Frénoy, Ariel B. Lindner, François Taddei

When cooperating with others carries a direct fitness cost for the individual, natural selection should act against such behavior. However, cooperation is widespread across natural systems. Here we summarize a recently published work that highlights the importance a previously overlooked factor, the population shape. We used a combination of three *in silico* systems, Aevol (complex genomes, cooperation based on public good secretion), Aevol-lite (one-locus two-alleles, cooperation based on public good secretion) and CAevol (Prisoner's dilemma with two pure strategies, cooperate and defect). In all three systems, higher level of cooperation evolved when populations lived in bulky worlds, a torus created by folding 100x100 quadrilateral grid, rather than slender ones, based on a 4x2500 grid. The result was not intuitive, since we expected that slim populations would facilitate better separation between secretor and non-secretors and select for more cooperation. Instead, in constant competition of cooperators and cheaters, slim populations constrained the expansion and thus decreased the size of cooperator patches. In nature cooperation occurs in systems ranging from effectively 1D cyanobacteria with division of labor, to microbes colonizing complex 3D lung structure. Our result is general and does not depend on the cooperation mechanism; it urges for careful consideration of population shape in natural and computational cooperative systems.

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Olivier Missa

Ecole Normale Supérieure (Paris, France)

The emergence of biodiversity patterns through deep evolutionary time

Olivier Missa, Calvin Dytham & H el ene Morlon

In ecology and evolution there is often a presumption that systems will converge towards an equilibrium or have reached their equilibrium. Surprisingly little attention has been paid to studying the trajectory itself towards equilibrium. In this talk, we are interested in understanding how quickly biodiversity patterns (both macroecological and phylogenetic) reach their equilibrium. Our approach was to simulate large metacommunities of individuals in spatially explicit cellular automata undergoing random population drift (i.e., neutral population dynamics) and stochastic speciation (according to various but always simple rules) and follow how biodiversity patterns emerge through time. Of all biodiversity patterns, species richness takes – as expected – the least amount of time to stabilize. Species abundance distributions and species area relationships take comparatively longer to stabilize and longer still are phylogenetic patterns of biodiversity. However, these trends also show complex and subtle behaviors depending on the particular combination of rules. For instance, when using the rules that most closely mimics Hubbell’s neutral theory with “point mutation” speciation, most biodiversity patterns seem to reach their equilibrium at the same time. This is not the case for other modes of speciation, which take several orders of magnitude longer to reach their equilibrium in terms of phylogenetic structure compared to their equilibrium in terms of species richness. This result reopens the possibility for neutral processes (other than point mutation) to generate realistic patterns of biodiversity including phylogenetic structure, because what matters more is what happens as species richness stabilizes or around the time it stabilizes, not when it has remained stable for a long period of time. Hence, both macroecological and macroevolutionary patterns could be accounted for by neutral stochastic processes.

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Andrew Morozov

University of Oxford (Oxford, UK)

Bifurcation analysis of biological models with uncertain function specification: developing a new framework.

Andrew Morozov; Matthew Adamson

In many biological models the exact shape of the model functions is often unknown, and only some qualitative properties of the functions can be specified: mathematically, we can consider that the unknown functions belong to a specific class of functions, for instance, we may require that the functional response of a predator is of sigmoid type. In this case, classical bifurcation analysis fails to work properly, since it can only be used when all model functions are mathematically specified and the only existing uncertainty is with respect to their parameters. Here we suggest a new framework - based on the ODE paradigm - which allows us to investigate deterministic biological models in which the mathematical formulation of some functions is unspecified, except for some generic qualitative properties. In particular, for these completely deterministic models we propose to define the probability of a bifurcation taking place when there is uncertainty in the parameterisation in our model. As an illustrative example, we consider a generic predator-prey model where the use of different parameterisations of the logistic-type prey growth function can result in different dynamics in terms of the type of Hopf bifurcation through which the coexistence equilibrium loses stability. Using this system, we demonstrate a framework for evaluating the probability of having a supercritical or subcritical Hopf bifurcation. Finally, we introduce the ‘degree of sensitivity’ of these models, which allows us to estimate uncertainty in partially specified biological models, and then show how this degree can be calculated based on optimization research techniques such as the Pontryagin maximum principle.

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Carina Farah Mugal

Uppsala University (Uppsala, Sweden)

The evolution of the allele frequency spectrum during speciation

Carina F. Mugal and Ingemar Kaj

In the study of speciation certain genomic measures are used to assess the patterns of sequence divergence between two recently diverged populations. Several of these measures depend on the allele frequency spectrum of one population in relation to the other. The evolution of such a 2-fold allele frequency spectrum during speciation is therefore of considerable interest for inferences about speciation. Here, we consider an isolation-without-migration scenario of speciation and describe a non-equilibrium allele frequency spectrum for lineage-specific and ancestral polymorphisms in a Poisson random field framework. This enables us to identify a class of functionals that cover lineage-specific and ancestral contributions to relevant measures of population differentiation (such as F_{ST} and d_{xy}), and the number of fixed differences (d_F). Specifically, in the empirical context of the model these measures depend on the information that is contained in a sample of the population. Of particular methodological interest is the possible advantage of increasing sample size. Under the assumption of neutrality we make use of a coalescent approach and obtain explicit solutions. For a scenario that invokes natural selection we present numerical approximations.

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Elma Nassar

I2M (Marseille, France)

Phenotypic Adaptation in the Moving Optimum Model

Elma Nassar, Etienne Pardoux, Michael Kopp

In recent works of Kopp and Hermisson (2009) and Matuszewski, Hermisson and Kopp (2014), the authors treat adaptation of a population to a linear degradation of its fitness respectively in the one-dimensional case (one phenotypic trait) and the multidimensional one (n phenotypic traits). Nevertheless, they couldn't predict survival or extinction. The starting point of this work is to introduce a Poissonian Stochastic Equation that describes the evolution of the phenotype of a population and study whether the solution is recurrent or transient. First, we will explain the moving optimum model. Then, we will present our results concerning the one-dimensional case and some preliminary results in the multidimensional case.

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Ace North

Department of Zoology (Oxford, UK)

Disease invasion in metapopulations: the role of dispersal range

Ace North, H. Charles J. Godfray

When a pathogen is introduced to a metapopulation, the consequence will depend on both its impact within localities and its movement among them. Epidemiological metapopulation models, however, often assume the host populations are equally connected to one another, and the role of movement behaviour remains poorly understood. In this talk I will present a spatially explicit metapopulation model that allows investigation of how the host and pathogen migration kernels jointly influence the probability of pathogen establishment and invasion. I show that a pathogen may be more likely to establish if both the host and the pathogen disperse locally, since the former acts to cluster the host populations among the available habitat while the latter allows exploitation of this structure. By contrast, local pathogen dispersal is likely to restrict the ensuing invasion by causing the segregation of infected and uninfected populations. Both results, however, depend on biological details that determine the likely introduction site and the extent to which the pathogen disperses with, rather than independently of, the host. I show the spatial effects are generally enhanced if the underlying habitat patches have a correlated spatial distribution yet somewhat reduced if the distribution is dynamic as patches are created and destroyed. I briefly discuss the methods I use to study the model, which involves both simulations and the first terms of a perturbation expansion around appropriate spatial moment equations.

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Vicente Luis Jiménez Ontiveros

Centro de Estudios Avanzados de Blanes (Blanes, Espania)

The temporal assembly of microbial communities: Insights from Island Biogeography Theory

V.L. Jiménez-Ontiveros, M. Hartmann, E. O. Casamayor, J.A. Capitán, D. Alonso

Most ecological theory has been developed for plants and animals. However, for the last years, technical progress on several fields, from computers to last generation DNA sequencers, has made it possible to collect large amounts of data on microbes at unprecedented rates. Huge databases are enlarged by hundreds of scientists every day. All these available information makes microbial communities excellent model systems to check general ideas on the function and structure of ecological communities and expand ecological theory. Most recent work on microbial communities describes spatial patterns, such as the species area relationship and beta diversity indexes, or take statistical approaches to describe snapshots of communities that are assumed to be at a steady state. Although temporal variation is fully appreciated and described for microbial communities, few attempts have been done yet to study the leading mechanisms driving community assembly in time. Here, we show the potential of classic island biogeography theory to gain insights into the temporal dynamics of microbial communities. We use the simplest stochastic model formulation of the theory as a way to estimate effective colonization and extinction rates per microbial group. We found a clear colonization/extinction signature that holds across very different habitats, from soils in Switzerland to mountain lakes in Pyrenees. This signature can be described as a positive correlation between colonization and extinction rates, which indicates that different phylogenetic-based groups are organized on a continuum from highly variable, dynamic groups to very stable, persistent groups. We investigate the possible origin of this pattern by using an immigration-birth-death stochastic model which we also use to shed some light on the possible consequences of such organization for the functioning of microbial communities and the maintenance of microbial diversity.

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Ferran Palero

Institut Sophia Agrobiotech, INRA (Sophia Antipolis, France)

Multi-components Reaction Diffusion Systems in Population Genetics

F. Palero and N.H. Barton

Recent theoretical and empirical studies have shown that post-zygotic reproductive isolation results from the build-up of Dobzhansky–Muller (D–M) incompatibilities, caused by negative epistatic interactions between derived alleles. It has been argued that if the negative epistatic interactions evolve by selection, we should find limited genetic variation within populations for D–M incompatibilities, while if the negative epistatic interactions evolve by drift, populations should harbour substantial genetic variation in compatibility. In my talk I will review the use of Reaction Diffusion Systems (RDS) in population genetics and I will focus on a multi-components RDS modelling epistatic interactions in hybrid zones. It will be shown that alleles might introgress across hybrid zones once they recombine onto a genetic background with which they are compatible, allowing for the maintenance of genetic variation for D–M incompatibilities even without drift effects.

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Etienne Pardoux

Aix-Marseille Université (Marseille, France)

Probability of fixation of an advantageous allele in the “Bolthausen-Sznitman model”.

Boubacar Bah, Simona Grusea, Etienne Pardoux

Consider a population of infinite size, which evolves according to the model which is dual to the Bolthausen-Sznitman coalescent, where the population is composed of two distinct alleles, one of them having a selective advantage over the other. This advantage is modelled by introducing a death rate of the less fit allele. We derive an explicit formula for the probability of ultimate fixation (which occurs in infinite time) of the best fit allele, as a function of the selection parameter and the initial proportion of the two alleles. This formula has already been published by two of the authors. We give a new derivation of this formula, inspired by a result by Pokalyuk and Pfaffelhuber, and compare it with the well-known similar formula in the Wright-Fisher model with selection, i.e., in the model dual to the Kingman coalescent. The two formulas agree of course when only one of the two alleles is present at the initial time, but also when the initial proportion of the advantageous allele is exactly $1/2$. The difference between the two quantities has a different sign, depending upon whether the initial proportion of the selective allele is less than or greater than $1/2$.

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Kalle Parvinen

University of Turku (Turku, Finland)

Unifying adaptive dynamics and inclusive fitness: Evolution of dispersal and cooperation in an extended Hamilton-May model

Kalle Parvinen, Hisashi Ohtsuki and Joe Wakano

The model of Hamilton and May (1977) contains infinitely many habitats, which can support one adult individual. Each season, adults get a large number of offspring and die. Some proportion of the offspring stay in the natal habitat, whereas others disperse to other patches, unless they die during dispersal, which happens with probability p . After immigration, the individual to become adult is randomly chosen among the juveniles in the patch. Their classical result is that the ESS dispersal proportion is $1/(2 - p)$. We consider an extended model, so that habitats can support n individuals, and the relative fecundity of individuals depends on their behavioral strategy. Recently, Wakano and Lehmann (2014) investigated the evolution of cooperation in such a model, and used inclusive fitness arguments to give conditions for evolutionary branching. On the other hand, Metz and Gyllenberg (2001) have presented the concept of metapopulation reproduction ratio, which can be used to study adaptive dynamics in metapopulations. Here we will explain how this concept can be applied to the extended Hamilton-May model. Furthermore, we present the fitness gradient, and the second derivative of the metapopulation reproduction ratio with respect to a general strategy in an explicit form, so that detailed analytic investigations are possible. Earlier, the metapopulation reproduction ratio approach has mainly been applied to such complex metapopulation models, that only numerical analyses have been possible. Finally, we apply our result to the model of evolution of cooperation investigated by Wakano and Lehmann (2014), and find perfect agreement of the branching condition. We also apply our result to the evolution of dispersal, and obtain the ESS dispersal strategy in an explicit form, which for $n = 1$ agrees with the classical result of Hamilton and May. Our result thus provides an unifying investigation of the inclusive fitness approach and the adaptive dynamics & metapopulation reproduction ratio approach.

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Karan Pattni

City University London (London, United Kingdom)

A study of dynamics of multi-player games on small networks using territorial interactions

Mark Broom, Charlotte Lafaye, Jan Rychtar, Karan Pattni

Recently, the study of structured populations using models of evolutionary processes on graphs has begun to incorporate a more general type of interaction between individuals [1], allowing multi-player games to be played among the population. This talk is about the work carried out in [2], where a birth-death dynamics is developed for use in such models and considers the evolution of populations for special cases of very small graphs where we can easily identify all of the population states and carry out exact analyses. Two multi-player games are studied, a Hawk-Dove game and a public goods game. The focus is on finding the fixation probability of an individual from one type, cooperator or defector in the case of the public goods game, within a population of the other type. This value is compared for both games on several graphs under different parameter values and assumptions, and some interesting general features of the model are identified. The close relationship between the fixation probability and these variables that either act to enhance or suppress selection is then investigated.

[1] Broom M, Rychtar J (2012) A general framework for analysing multiplayer games in networks using territorial interactions as a case study. *Journal of Theoretical Biology* 302:70–80 [2] Broom M, Lafaye C, Pattni K, and Rychtar J. A study of dynamics of multi-player games on small networks using territorial interactions. *Journal of Mathematical Biology* (Published online 12 March 2015)

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Steven L. Peck

Brigham Young University (Provo, USA)

An ecologically complex agent-based model of tsetse fly suppression programs in Senegal

Steven L. Peck, Jérémy Bouyer

Controlling tsetse fly populations in much of sub-Saharan Africa is one of the great challenges in stopping the spread of trypanosomosis diseases in both humans and domestic livestock. Analytic mathematical models are often too simple to capture the complexity of these ecological systems and do not address spatial or multiple ecological interactions. Agent-based systems are important for understanding these kinds of complex interactions among organisms and their environment. In this talk, we demonstrate a model we have developed that allows emergent behavior to bubble-up from lower-level scales, as is often found in nature. Digital organisms provide a representation that can be used at multiple spatial and temporal scales. However, these types of models present several challenges to scientific investigations and discourse when we try to interpret how simulation represents the real world. Through the use of a spatially structured agent-based stochastic model, we demonstrate how using such models help disclose the implications of metapopulation structure on the outcome of suppression programs. Specifically, using a simulation model we compare programs that use SIT and those that do not, and combinations of these methods, to assess their potential to significantly suppress the tsetse fly population in spatially and ecologically structured environments. The model has been used to look at recent efforts to suppress tsetse populations in Senegal. In this paper, we examine the results of these suppression efforts in light of this simulation.

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Ido Pen

Groningen University (Netherlands)

When is incomplete epigenetic resetting in germ cells favoured by natural selection?

Ido Pen

Resetting of epigenetic marks (e.g., DNA methylation) in germ cells or early embryos is not always complete and epigenetic states may therefore persist, decay or accumulate across generations. In spite of mounting empirical evidence for incomplete resetting, it is currently poorly understood whether it simply reflects stochastic noise or plays an adaptive role in phenotype determination. Here we use a simple model to show that incomplete resetting can be adaptive in heterogeneous environments. Transmission of acquired epigenetic states prevents mismatched phenotypes when the environment changes infrequently relative to generation time and when maternal and environmental cues are unreliable. We discuss how these results may help to interpret the emerging data on transgenerational epigenetic inheritance in plants and animals.

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Jorge Peña

Max Planck Institute for Evolutionary Biology (Ploen, Germany)

Ordering population structures by their potential to promote the evolution of cooperation

Jorge Peña, Bin Wu, and Arne Traulsen

Population structure can crucially affect the evolutionary dynamics of cooperation. For weak selection in two-player games or phenotypically close competing strategies, the effect of population structure can be captured by a single “structure coefficient” or “scaled relatedness coefficient”, with models characterized by larger coefficients being more conducive to the evolution of cooperation. In more general situations, as those arising from non-trivial multiplayer games, the condition depends on several structure coefficients, and a simple comparison between different models of population structure is less straightforward. Here, we propose two ways of ordering population structures by their potential to promote the evolution of cooperation: the containment order and the volume order. Given two population structures, we say that the first is greater than the second in the containment order if all the games for which cooperation is favored in the second are just a subset of the games for which cooperation is favored in the first. Contrastingly, we say that the first population structure is greater than the second in the volume order if the volume of games for which cooperation is favored in the first is greater than the corresponding volume of the second. We make use of tools from computational geometry and stochastic ordering theory to provide sufficient conditions for establishing comparability or incomparability in the containment order, derive general results concerning the volume order, and compare previously studied models of population structure. Our results unify and generalize several existing results on the evolution of cooperation in structured populations.

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Sophie Péniſson

Université Paris-Est Créteil (Créteil, France)

Can excessive mutation prevent adaptive evolution?

Sophie Péniſson, Philip Gerrish

It is perhaps intuitive that excessive mutation could erode genomes and cause a well-adapted population to decline in fitness, perhaps even to the point of causing extinction. It seems less intuitive, however, that excessive mutation could prevent adaptation; after all, an adaptive mutation still has a relative advantage even in a population whose mean fitness is declining. This line of reasoning works fine if the relative fitness of a newly-arising (focal) mutation is completely determined by its own fitness effect and the fitness of the background upon which it appears (background selection). However, it ignores what happens subsequent to the appearance of the focal mutation: it forgets that, going forward in time, the accumulation of deleterious mutations is a stochastic process. It is well-established that the rate of such accumulation is critically affected by population size, being high in smaller populations and very low in large populations. Accumulation of deleterious mutations will therefore happen much faster in a small lineage founded by a single adaptive mutation than in the rest of the population. We investigate this phenomenon with the help of a stochastic model, describing the evolution over time of the population composition regarding the number of accumulated deleterious mutations. The model is a reducible branching process with countably infinitely many types, which enables a thorough study of the demographic and fitness dynamics of individual beneficial lineages within the population. In particular, we consider: 1) the extinction probability of a newly-arising beneficial mutation in an otherwise homogeneous population, as a function of mutation rate, 2) the relative fitness dynamics of the lineage formed by the beneficial mutation, 3) the timing of sequential extinctions of least-loaded classes, and 4) the synergy between accelerating loss of least-loaded classes and decreasing lineage size (mutational meltdown of the beneficial lineage).

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Valeriy Perminov

BioTeckFarm Ltd. (Moscow, Russian Federation)

Agent-based models and ill-posed problems

Perminov V. D., BioTeckFarm Ltd., Moscow, Russian Federation

It is well known that evaluation of parameters for any mathematical model is always a difficult problem. This is especially true for agents-based models (ABMs) because an evaluation of agent's parameters can be made only based on available information from a higher level of a complex system. Because of information at a higher level is an aggregation of data at the agents level such problems can be ill-posed ones. It means a problem under consideration can have a non-unique or unique but unstable solution. In the latter case numerical solution of the problem has to be based on very special algorithms. In this talk I am going to overview problems that arise for ABMs with different numbers of emergent patterns. In particular I am going to tell about new approach to creation of the ABM for an influenza epidemic spreading in cities. The proposed ABM can be used for past epidemics to estimate the efficiency or inefficiency of undertaken interventions, to propose new ones and to reveal its advantages, shortcomings and cost. This ABM is the first one that under some conditions can be used to model the possible dynamics of coming epidemics or pandemics.

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Dmitri Petrov

Stanford University

Population Genomics of Rapid Adaptation

Dmitri Petrov

Organisms can often adapt surprisingly quickly to evolutionary challenges, such as the application of pesticides or antibiotics, suggesting an abundant supply of adaptive genetic variation. In these situations, adaptation should commonly produce ‘soft’ selective sweeps, where multiple adaptive alleles sweep through the population at the same time, either because the alleles were already present as standing genetic variation or arose independently by recurrent de novo mutations. In my talk I will argue that adaptation by soft selective sweeps should be the rule in all organisms with large census sizes and will outline our approaches for quantification of adaptation by soft sweeps using population genomic data and experimental evolution. First, I will describe application of new statistical approaches to *Drosophila* genomic data that allowed us to discover that most recent and strong adaptation in *Drosophila* was driven by soft sweeps. I will argue that this is because population sizes relevant to adaptation in *Drosophila* are orders of magnitude larger than previously thought, profoundly changing the expected dynamics of adaptation. In the second part, I will describe how we quantify the dynamics of adaptation in large experimental populations of yeast using ultra-diverse barcoding system. We use this system to detect adaptive lineages and study their dynamics while they are still extremely rare and to follow them until they start interfering with one another. We use this approach to quantify the rate of adaptive mutagenesis and the distribution of selective effects of the mutations that drive the adaptive dynamics, as well as to determine the precise molecular identity of hundreds of individual adaptive mutations in a single experiment. I will discuss the implications of these findings for the search of signal of adaptation in the genome and for the possibility of predicting the path of adaptation in large populations.

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Phil Pollett

The University of Queensland (Brisbane, Australia)

Metapopulations with dynamic extinction probabilities

Phil Pollett, Jessica Chan, and Ross McVinish

We study a model for a population network that accounts for the evolution over time of landscape characteristics which affect the persistence of local populations. Specifically, we allow the probability of local extinction to evolve according to a Markov chain. This covers the widely studied case where habitat patches are classified as being either suitable or unsuitable for occupancy. Threshold conditions for persistence of the population are obtained using an approximating deterministic model that is realized in the limit as the number of patches becomes large.

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Mikael Pontarp

Institute of Evolutionary Biology and Environmental Studies (Zurich, Switzerland)

The origin of species richness patterns along environmental gradients: uniting explanations based on time, diversification rate, and carrying capacity

Mikael Pontarp & John Wiens

Patterns of species richness, such as the remarkable biodiversity of tropical regions, have been documented and studied for centuries, but their underlying evolutionary and ecological causes remain poorly understood. An increasingly common paradigm is that high richness in some habitats is caused by one of three competing explanations: habitats with higher richness have either (i) higher carrying capacity, (ii) greater time for speciation (earlier colonization), or (iii) foster more rapid diversification rates (faster speciation relative to extinction). However, these three explanations are largely unstudied theoretically, and empirical studies give conflicting results about their relative importance. Here, we use individual-based eco-evolutionary modeling to study the processes that drive richness patterns along environmental gradients. Contrary to the common paradigm, we find that variation in carrying capacity can underlie both diversification rates and time, and is therefore not a competing, alternative explanation. We also find that the time-for-speciation effect dominates richness patterns over short time scales, whereas diversification rates dominate over longer time scales. These observations can help reconcile the seemingly conflicting results of many empirical studies, which find that some patterns are explained by time and others by differences in diversification rates.

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Andrés E. Quiñones

University of Groningen (Groningen, Netherlands)

A unified model of the transition from solitary to eusocial life

Andrés E. Quiñones, Ido Pen

The evolution of eusociality is considered one of the major transitions in evolution. This transition entails changes in many facets of a species biology, thus, many traits are expected to evolve together. Eusociality's hallmark trait is worker behaviour, whereby individuals forgo their own reproduction to work in the parental nest. Worker behaviour is known to be promoted by split-sex ratios, that is, when colonies differ in their sex-ratio strategy. However, it is not clear how and whether split-sex ratios and worker behaviour co-evolve. We present an inclusive fitness model, matched with individual-based simulations, that captures the co-evolution of worker behaviour and sex ratios split in two broods of a reproductive season. We find that evolution changes the sex ratio of the two broods in opposite directions, and the new split sex-ratios favour the emergence of worker behaviour. However, once worker behaviour is present, the direction of selection on sex ratios is reversed. At equilibrium, the population produces a female workforce in the first brood, and both females and male reproductives in the second brood. Thus, the feedback between worker-behaviour and sex-ratios drives the population from a solitary bivoltine life-history to a eusocial univoltine life-history. Our results are in agreement with the patterns of sex-ratios and sociality found in the hymenoptera. I will discuss how several traits found in this taxon favour the evolutionary transition; they can be considered pre-adaptations for eusociality.

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Sonja Radosavljevic

Linköping University (Sweden)

Logistic age-structured population model in a changing environment

Sonja Radosavljevic, Uno Wennergren, Vladimir Kozlov

Population growth is governed by many external and internal factors. Changes in the environment, such as climate changes or pollution, intra-species competition for resources and overcrowding are significant examples of these factors. In order to study their effects on population growth, we develop an age-structured logistic population model. The model is derived from the classical McKendrick-von Foerster model by adding a logistic term in the balance equation. The carrying capacity in the classical logistic model is a positive constant. We however suppose that competition occurs only within age-classes, which implies that the carrying capacity is age and time dependent function. To include environmental factors, we assume that the vital rates are also age and time dependent. With this in mind, we look for boundaries within which population varies with passing of time. To formulate these boundaries, we use the method of lower and upper solutions known from the theory of ordinary differential equations. We prove that the model has a unique nonnegative bounded solution. In addition, we investigate asymptotic behavior of the number of newborns and of the total population. Our results show that if the net reproductive rate is strictly larger than one, the total number of newborns and the total population tend to certain positive constant values. Otherwise, both functions tend to zero. We pay special attention to the case when environment changes periodically. In this case we discover the connection between the period of oscillation and its effect on population growth.

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Gaël Raoul

Ecole Polytechnique (Palaiseau, France)

Effect of a spatial structure in a population facing a climate change

Gaël Raoul

We are interested in a population living in a continuous environment. If the climate changes (for instance if the temperature rises everywhere), we can imagine several dynamics for this population: it could adapt to the warming up, could also modify its range, or follow a dynamics that combines those two possibilities. In this presentation, we will introduce two models that can be used to analyse the dynamics of such populations: a model for asexual populations, and a model for sexual ones. For asexual population, the model is based on a reaction-diffusion equation, and the dynamics of the solution can then be precisely described in the case of an environmental cline. This careful analysis also allows us to investigate some more general environmental heterogeneities, which can lead to qualitatively different (and surprising) predictions. For sexual populations, the model shares some similarities with inelastic Boltzmann equations. This analogy allows us to simplify the model and to discuss existing links with other existing models. The simplified model, in turn, allows us to describe the dynamics of the population's range.

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Irja Ida Ratikainen

NTNU, Centre for Biodiversity Dynamics (Trondheim, Norway)

A general stochastic dynamic model of the differential allocation hypothesis

Thomas R. Haaland, Jonathan Wright and Irja I. Ratikainen

Differential allocation is usually described as the strategy of a parent adjusting its investment according to the perceived attractiveness or general quality of its mate. Differential allocation has been found in a wide range of empirical studies of animals, but both positive, negative and no differential allocation has been found even within a single species, and it has not been clear what causes the variation in observed strategies. The key to understanding differential allocation is in the effect of the mate on either the cost or the benefit to the parent or the offspring. More specifically if the quality of the mate affects the slope or the elevation of the function describing how parental investment affects current offspring fitness or own future fitness. We use a stochastic dynamic optimization model and show that when mate quality only affects the elevation of the offspring fitness function, no differential allocation is predicted. This could be the case if the mate affects the general quality of offspring, and the result is unsurprising as such overall genetic effects do not lead to a change in the marginal fitness returns of any investment decision. If, on the other hand, mate quality affects the slope of the offspring fitness function, which could be the case if offspring of better mates are better at utilizing energy, then our model predicts the classical positive differential allocation pattern with females investing more in offspring sired by better males. With a sigmoid offspring fitness function and additive parental investment we can see both positive and negative optimal differential allocation depending on the energetic state of the focal individual. We also explore how the trade-off between number and size of offspring is affected by differential allocation when the mate affects either the offspring fitness function or the cost of reproduction.

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Michael Renton

University of Western Australia (Perth, Australia)

Simulating the evolution of structural root growth strategies in plants in different environments

Michael Renton, Pieter Poot

Through evolution, plants develop strategies to acquire the limited resources they need to survive, grow and reproduce. In particular, the way that a plant's root structure develops would be expected to have evolved to enable the plant to acquire the water and nutrients it requires. Dynamic functional-structural models of plant growth (FSPMs) can be used to predict the costs and benefits of different growth strategies in terms of resources gained and used in different environments, at a relatively high level of bio-physical detail. These FSPMs can then be linked with evolutionary algorithms to simulate how the rooting strategies of populations of plants will evolve over time in different conditions. This in turn allows us to explore how ecological strategies evolve to best exploit available resources, and how this evolution of ecological strategies may vary with different patterns of resource availability. We illustrate these ideas with a specific example: an FSPM developed to represent root development within a single growing season within a Mediterranean climate where rainfall is relatively plentiful for a period of the year and negligible for the remainder of the year. We show how the model is able to represent a wide range of relevant rooting strategies in a relatively simple and thus computationally efficient way, which allows computational evolutionary optimization algorithms to be applied to the model. This allows us to simulate the evolution of rooting strategies in two contrasting situations: a very shallow soil where the only chance for the plant to survive the drought season is to find rare wet cracks in the underlying bedrock during the wet growth season, and a deep soil where the plant must simply try to maximise growth during the growth season. (I have indicated no mini-symposium but I think the talk could potentially fit into several if desired)

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Marie Rescan

Station biologique de Roscoff (France)

Interactions between genetic and ecological effects on the evolution of life cycles

Marie Rescan, Thomas Lenormand, Denis Roze

Sexual reproduction leads to an alternation between a haploid and a diploid phase, whose relative development varies widely across taxa, with vegetative growth occurring in one phase only (haploidy or diploidy) or in both (biphasic cycles). Previous genetical models showed that either diploidy or haploidy can be favored, depending on the dominance of beneficial/deleterious alleles and on effective recombination rates. By contrast, ecological models showed that niche differentiation between phases stabilizes biphasic life cycles. Here, we explore the interplay between genetical and ecological factors, considering that mutations affects the ecological properties of haploids and diploids, and may have differential effects between phases. We show that selection on a modifier gene affecting the relative length of both phases can be decomposed into a direct selection term favoring the phase with the highest mean fitness (due to ecological differences or to differential effects of mutations), and an indirect selection term favoring the phase in which selection is more efficient. When deleterious alleles occur at many loci and in the presence of ecological differentiation between phases, evolutionary branching often occurs and leads to the stable coexistence of alleles coding for haploidy and diploidy, while temporal variations in niche sizes stabilize biphasic cycles.

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Jörgen Ripa

Lund University (Sweden)

On niche conservatism, niche monopolization and the mechanics of adaptive trait evolution

Jörgen Ripa

Some naturally selected traits consistently evolve slower than others, so called niche conservatism. In some taxa, traits associated with habitat adaptations (“ β -niche traits”) seem to be more conserved than traits linked with local competition and character displacement (“ α -niche traits”) – a pattern described as β -niche conservatism. Other taxa show the opposite pattern, i.e., α -niche conservatism. To shed some light on these patterns, I analyze an eco-evolutionary model of an organism with two evolving traits, one resource utilization trait (α) and one habitat adaptation trait (β). The adaptive radiation of a single ancestral species can in this model result in α - or β -niche conservatism. What pattern evolves is to some extent random and dependent on genetic constraints, but is also dictated by three key ecological parameters: the trade-offs associated with each evolving trait (α and β) and the rate of dispersal between habitats. β -niche conservatism is more likely if the rate of dispersal is low. A strong trade-off promotes conservation of the corresponding trait, but this result can be ascribed to three mechanisms; A strong trade-off i) generates a strong disruptive selection, promoting early divergence in that trait, ii) may create fitness valleys that are rarely crossed, and iii) augments niche monopolization effects. Evolutionary niche monopolization is here put forward as a generalization of habitat monopolization and is defined as the ability of a species to prevent other species from evolving into the same part of niche space. A species or ecotype can monopolize, and diversify within, a section of niche space fenced off by a strong trade-off, thereby creating a pattern of niche conservatism. The monopolization effect extends along other niche axis with weak trade-offs. I demonstrate monopolization of α - and β -niches and discuss examples from natural systems.

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Giulio Valentino Dalla Riva

University of Canterbury (Christchurch, New Zealand)

Randomness and evolutionary histories in food webs.

Giulio Valentino Dalla Riva, Daniel B. Stouffer, Mike Steel

Food webs are the complex ecological networks of who eats whom. Current theoretical models—tailored for capturing global properties—fail to predict food webs structure at the level of single interaction between species. The patterns we notice are the outcome of the interplay between ecology and evolution. In empirical webs we observe species with closely related evolutionary history performing similar roles: they have similar degree and motifs distribution [1] and share a larger than random portion of interactions [2]. However, weighting the effects of evolutionary processes and ecological constraints in the assembly of food webs represents an open challenge. Moreover, neglecting interaction stochasticity impedes the advancement of evolutionary analysis in food webs. In fact, despite the classic framework considering food webs as purely deterministic objects, a growing body of evidence shows that species' interactions are better described in stochastic terms as they depend on local population abundances—determining species' encounter probability—and on the distribution of phenotypes among those populations—determining their interaction propensity [3]. In this talk we will show how modelling food webs as Random Dot Product Graphs enables us to incorporate their inherent stochasticity and to quantify the evolutionary processes imprint. Indeed, our results support the notion that food webs show a stronger phylogenetic signal in their stochastic backbones than in their fine wiring [2]. Finally, acknowledging stochasticity, our simple model outperforms existing food-web models in terms of both fitting and predictive accuracy. [1] D. B. Stouffer et al. *Science* 6075, 335 1489-1492 (2012). [2] G. V. Dalla Riva and D. B. Stouffer. *Oikos* (submitted). [3] T. Poisot et al. *Oikos* 124, 3 (2014).

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Olivier Rivoire

Laboratory for Interdisciplinary Physics (Grenoble, France)

Models of information processing in evolving populations

Olivier Rivoire

I will present some simple models of evolutionary dynamics in fluctuating environments for which the adaptive value of different modalities of acquisition and transmission of information can be compared. The models lead to generalizations of well-known quantities of information theory and provide a bridge between population genetics and stochastic control.

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James L. Rosindell

Imperial College London (UK)

Unifying Ecology and Macroevolution with Individual-Based Theory

James L. Rosindell

A contemporary goal in both ecology and evolutionary biology is to develop theory that transcends the boundary between the two disciplines, in order to understand phenomena that cannot be explained by either field in isolation. This is challenging because macroevolution typically uses lineage-based models whilst ecology often focuses on individual organisms. Here we develop a new parsimonious individual-based theory by adding mild selection to the neutral theory of biodiversity. We show that this model generates realistic phylogenies showing a slowdown in diversification and also improves on the ecological predictions of neutral theory by explaining the occurrence of very common species. Moreover, we find the distribution of individual fitness changes over time, with average fitness increasing at a pace that depends positively on community size. Consequently large communities tend to produce fitter species than smaller communities. These findings have broad implications beyond biodiversity theory, potentially impacting, for example, invasion biology and paleontology.

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Denis Roze

CNRS Station biologique de Roscoff (France)

Effects of interference between selected loci in partially inbred populations

Denis Roze

Most of population genetics theory on the effects of interference between selected loci (or on the effects of selected loci on linked neutral sites) considers randomly mating populations. However, many (if not most) natural populations do not mate at random: in some cases, hermaphroditic individuals may self-fertilize at a given rate, while in other cases limited dispersal causes mating to occur among related individuals. During this talk, I will present results from models of partially selfing populations, showing that inbreeding may strongly affect selective interference between loci. In particular, intermediate selfing rates deterministically generate positive associations between beneficial alleles at different loci (while negative associations are generated in the absence of inbreeding, through the Hill-Robertson effect), which select against recombination. I also develop new approximations for the effect of recurrent deleterious mutations on neutral diversity at linked sites (background selection), showing that previous approximations may strongly underestimate the strength of background selection when inbreeding is high.

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Claus Rueffler

University of Vienna (Austria)

Does Organismal Complexity Favor the Evolution of Diversity?

Claus Rueffler

It has recently been proposed that, on theoretical grounds, one should expect a positive correlation between organismal complexity and diversity. This conclusion is based on the finding that in a Lotka-Volterra competition model, so-called evolutionary branching points are more likely to exist the more quantitative traits determine the carrying capacity function and the competition coefficient. We present two results elaborating on this finding. First, the prediction can also be derived in a model independent manner based on general considerations about the fitness landscape in a multidimensional trait space. Second, in order to get a more mechanistic understanding of this finding we analyze an explicit Lotka-Volterra consumer-resource model in which consumers and resources are both characterized by several quantitative traits and in which the fitness landscape emerges from the interaction between consumer and resource traits. This analysis supports the proposition that complexity favors the evolution of diversity. An additional insight is that not only increasing complexity in the evolving population (the consumer) but also increasing complexity in its environment (the resource distribution) facilitates evolutionary branching.

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Mohammadkarim Saeedghalati

University of Duisburg-Essen (Germany)

Age as the main factor in shaping the rank abundance distribution of human gut microbiome.

Mohammadkarim Saeedghalati, Farnoush Farahpour, Daniel Hoffmann

By introducing a novel method for normalizing rank-abundance distributions (RADs) which makes them comparable and using clustering methods, we study the data of Gut microbial communities of ~ 500 individuals from the US metropolitan areas, rural Malawi and Amazonas of Venezuela with different ages, ranging from a few weeks to ~ 80 years. We show that although the microbial contents of populations in different countries are different, the shape of rank-abundance distributions (RADs) are highly correlated with age, not the diet or country. This finding can imply the effect of a changing environment caused by dietary diversity on RADs and so on microbial diversity. We have tested this idea by developing a simple stochastic model. This one-parameter model, not even create a Zipf's like behavior in the tale of distribution (i.e., rare species) but also create reasonable shape in the head part (i.e., abundant species). The only parameter of this model is the rate of change of environment. Studying the shape of RADs in a changing environment, not even helps us to understand ecology and evolution more deeply but also can be a good indicator to test models in these areas.

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Sumithra Sankaran

Indian Institute of Science (Bangalore, India)

Characterising patchiness and scale of interactions in semi-arid vegetation patterns

S. Sankaran, S. Majumder, A. Viswanathan, V. Guttal

Semi-arid ecosystems can exhibit striking vegetation patterns, which may have no characteristic size of patchiness. Elucidating local scale processes that generate these macroscopic patterns is of fundamental ecological importance. In addition, they may provide insights and tools to forecast the future dynamics of these highly vulnerable ecosystems. Recent studies have shown that, spatial patterns of semi-arid systems with no characteristic length scales can be explained by local facilitative interactions with global competition for resources (Kefi et al, Nature, 2007). Such power-law patch size distributions, further, have been proposed as representative of the eco-system's resilience. However, no alternative models that could potentially explain similar patterns, have been investigated. Here, our aim is to study whether such patterns could emerge from only local facilitative and local competitive processes and if so, whether it is consistently representative of resilience in the system. We analyse a model from the literature of nonequilibrium statistical physics (Lübeck S, (2006). Journal of Statistical Physics 123:193) in which facilitation occurs at local scales. We incorporate a competition constraint in this model, the scale of which is then varied (between only-local and global). We characterize the resulting spatial patterns by using previously used spatial metrics such as the distribution of patch sizes, as well as analyses of the power spectra, correlation functions and fractal geometries. We find that scale-free patch size distributions can emerge even in the absence of global competitive constraints. However in the context of regime shifts, the efficacy of this measure as symptomatic of the system's resilience is questionable. We find that, the probability that the system is approaching a regime shift when such patch size distributions are observed, is highly dependent on the strength and scale of interactions. We show that the power spectrum could serve as a more reliable measure of resilience.

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Arnaud Sentis

University of Toulouse III Paul Sabatier (France)

Ecological consequences of temperature-induced change in body size: species survival and population dynamics under global change.

Arnaud Sentis, Amrei Binzer and David S. Boukal

Body-size reduction is emerging as a third universal response to global warming, beside changes in the phenology and distributions of species. However, the ecological consequences of size reduction for the dynamics and persistence of ecological communities facing environmental change remains unexplored. Here, we developed a nonlinear bioenergetic population dynamic model parametrized with empirical data for the temperature dependencies of body-size and biological rates. We next analyzed the individual and interactive effects of increasing temperature, nutrient enrichment, and strength of the temperature size response (TSR) on the dynamics of a three-species food chain. We found that warming counteracts the destabilizing effects of enrichment a low temperature but increases the risk of starvation of consumers at high temperature. Interestingly, TSR influences both system stability at low temperature and starvation risk at high temperature. However, the magnitude and sign of these effects depends on the relative change in species body-size with temperature: the persistence of the food-chain increases only if the strength of TSR is similar for the three species or stronger for the top or intermediate species than for the basal species. We next show that these results can be explained by the effects of changing species body-size and food-chain size structure on species interaction strength and consumer energetic efficiency. Our model contributes to identifying the mechanisms that explain how environmental effects cascade through the food-chain and influence its persistence. We conclude that considering the links between environmental factors, species interactions, and phenotypic plasticity is crucial to improve our ability to predict the impacts of global changes on ecosystem diversity and stability.

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Eunha Shim

Soongsil University (South Korea)

Differential impact of sickle cell trait on symptomatic and asymptomatic malaria

Eunha Shim, Zhilan Feng, and Carlos Castillo-Chavez

Individuals who carry the sickle cell trait (S-gene) have a greatly reduced risk of experiencing symptomatic malaria infections. However, previous studies suggest that the sickle cell trait does not protect against acquiring asymptomatic malaria infections, although the proportion of symptomatic infections is up to 50% in areas where malaria is endemic. To examine the differential impact of the sickle cell trait on symptomatic and asymptomatic malaria, we developed a mathematical model of malaria transmission that incorporates the evolutionary dynamics of S-gene frequency. Our model indicates that the fitness of sickle cell trait is likely to increase with the proportion of symptomatic malaria infections. Our model also shows that control efforts aimed at diminishing the burden of symptomatic malaria are not likely to eradicate malaria in endemic areas, due to the increase in the relative prevalence of asymptomatic infection, the reservoir of malaria. Furthermore, when the prevalence of symptomatic malaria is reduced, both the fitness and frequency of the S-gene may decrease. In turn, a decreased frequency of the S-gene may eventually increase the overall prevalence of both symptomatic and asymptomatic malaria. Therefore, the control of symptomatic malaria might result in evolutionary repercussions, despite short-term epidemiological benefits.

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Rahul Siddharthan

The Institute of Mathematical Sciences (Chennai, India)

Inferring TFBS evolution: position-specific evolution in transcription factor binding sites

Rahul Siddharthan

Examining the question of how transcription factor binding sites (TFBS) evolve across species, we present a methodology that consists of identifying large numbers of individual binding sites for a factor in one “anchor” species (from publicly available data) together with orthologous sites in closely related species, training a model of nucleotide evolution on them fitting parameters to maximise the likelihood of the observed data, and comparing the position-specific stationary distribution of the model (the long-term equilibrium distribution of nucleotides at that position under the model, reflective of selective pressures) with observed nucleotide frequencies. We show that the standard “general time-reversible” (GTR) model is incapable of generating all possible distributions, and, in particular, fails when the stationary distribution is highly skewed, as in most TFBS loci. We argue that in a scenario where individual mutations in a population can be subjected to rapid selection and fixation, the Felsenstein 1981 model is an acceptable choice. In most cases we find that the position-specific stationary vectors inferred in this way are in excellent agreement with the position weight matrices (PWMs) obtained from the anchor species alone, which in turn are similar to literature PWMs. Additionally, we infer probability distributions for ancestral nucleotides and look at conditional stationary vectors, demonstrating that there are significant positional dependencies, probably arising from compensatory mutations, that are often ignored in computational approaches to TFBS prediction. We argue that this approach is a powerful and flexible way to explore evolutionary questions in transcriptional regulation within closely-related species. (Submitted)

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Arno Siri-Jégousse

Universidad de Guanajuato (Mexico)

The Bolthausen-Sznitman coalescent and its applications in genetics

Fabian Freund, Götz Kersting, Juan Carlos Pardo, Arno Siri-Jégousse

In recent years, the Bolthausen-Sznitman coalescent has been used to model genealogies of populations under strong selection. As a consequence it is of certain interest to study functionals permitting to develop classical methods of estimation of the rate of mutation or neutrality tests of mutations (as for example the sites-frequency spectrum or the total length) in the special case of the Bolthausen-Sznitman coalescent. An overview of these results, developed by the authors and many others, will be given in this talk.

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Etienne Sirot

Université de Bretagne Sud (Vannes, France)

Competition and negotiation over antipredatory vigilance in groups of prey.

Etienne Sirot

Animals living under the threat of predation often have to interrupt their activities to scan for predators. When they live in groups, however, they may also rely on the vigilance of their companions to be warned whenever an attack occurs. We must then expect mutual influences between the vigilance behaviour of flock members, and competition over the task of collective vigilance. To study such interactions between individuals and their effects on collective patterns of vigilance, I built a game-theoretical model of vigilance for a pair of animals foraging under predation risk. In this model, the strategy of each individual is described by the instantaneous probability of becoming vigilant, as a function of the other's attitude. Each individual then responds to the attitude of its companion, and influences this companion through its own behaviour. The ultimate pattern of vigilance for the pair is then the outcome of a negotiation process, whereby each individual constantly tries to influence the behaviour of its companion to selfish ends. The game played by the animals and the resulting strategies take radically different forms, depending on the predators' targeting strategy. If predators choose their target at random, the prey respond by displaying moderate vigilance and taking turns scanning. Competition over vigilance takes then the shape of a war of attrition, each individual waiting for the other to be the sentinel. By contrast, if predators tend to preferentially target individuals that do not react instantaneously, vigilance increases and there is always at least one individual scanning. Lastly, when predators' preference for stragglers becomes extreme, vigilance decreases again and the pair scan simultaneously. In this situation, the evolutionarily stable responses correspond to the behaviour expected under a cooperative scenario.

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Mircea T. Sofonea

Université de Montpellier (France)

From within-host interactions to epidemiological competition and back again

Mircea T. SOFONEA, Samuel ALIZON, Yannis MICHALAKIS

Multiple infections are a major concern in public health, human and veterinary medicine and phytopathology but they are also an interesting subject for ecology and evolution. In a coinfecting host, the different parasite genotypes can interact in various ways. The growth rate of each parasite genotype can be affected by the parasite load of the other genotypes, either positively by means of public goods (e.g., siderophores), either negatively in case of spite (e.g., bacteriocins), along other parasite load dependent interactions. Within-host interactions thus create diverse parasite load dynamics that makes it difficult to predict the epidemiology at the between-host level. In particular, the best genotype at one level may not be the best at the other level. The unpredictable outcome of the within-host interactions between parasites and the combinatorial complexity of the cotransmissions are probably the two main reasons why the vast majority of epidemiological models still leans on classical SIR models which consider only one parasite genotype infecting a population of hosts while models allowing for several genotypes are often restricted to two strains, or arbitrarily choose between a superinfection pattern and a coinfection pattern. We present here a deterministic nested model with explicit within-host interactions that allows for partial cotransmission with an arbitrary number of parasite genotypes. We use both analytical and numerical methods to show that our model goes over the co/super-infection dichotomy and that it can generate counter-intuitive epidemiological feedbacks due to parasite diversity. We finally study the effect of between-host dynamics on the evolution of the within-host parasite traits.

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Max Souza

Universidade Federal Fluminense (Brazil)

Fixation in large populations: a continuous view of a discrete problem

Fabio A. C. C. Chalub & Max O. Souza

We study fixation in large, but finite, populations of two types, with dynamics governed by birth-death processes. For a restricted class of such processes, that includes most of the evolutionary processes usually discussed in the literature, we derive a continuous approximation for the probability of fixation that is valid beyond the weak-selection (WS) limit. Indeed, in the derivation three regimes naturally appear: selection-driven, balanced, and quasi-neutral — the latter two require WS, while the former can appear with or without WS. We then obtain asymptotic approximations for evolutionary dynamics with at most one equilibrium, in the selection-driven regime, that does not preclude a weak-selection regime. As an application, we study the fixation pattern when the infinite population limit has an interior Evolutionary Stable Strategy (ESS): (i) we show that the fixation pattern for the Hawk and Dove game satisfies what we term the one-half law: if the Evolutionary Stable Strategy (ESS) is outside a small interval around $1/2$, the fixation is of dominance type; (ii) we also show that, outside of the weak-selection regime, the long-term dynamics of large populations can have very little resemblance to the infinite population case; in addition, we also present results for the case of two equilibria, and show that even when there is weak-selection, the long-term dynamics can be dramatically different from the one predicted by the Replicator Dynamics. Finally, we present continuous restatements for large populations of two classical concepts naturally defined in the discrete case: (i) the definition of an ESS_N strategy; (ii) the definition of a risk-dominant strategy. We then present three applications of these restatements: (i) we obtain a generalised one-third law, valid in the quasi-neutral regime, that includes, as special cases, both the one-third law under linear fitness and the generalised one-third law for d -player games; (ii) we extend the ideas behind the (generalised) one-third law outside the quasi-neutral regime and, as a generalisation, we introduce the concept of critical-frequency; (iii) we recover the classification of risk-dominant strategies for d -player games.

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Mike Steel

University of Canterbury (Christchurch, New Zealand)

When good models go bad: provable properties of phylogenetic tree methods, under model mis-specification

Mike Steel

In this talk, I describe some mathematical results that impact on the accuracy of methods for inferring evolutionary ('phylogenetic') trees from character and distance data when simple models of character evolution no longer apply.

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Cristian Tomasetti

Johns Hopkins University (Baltimore, USA)

Stem cell divisions, number of drivers and tumor evolution.

Cristian Tomasetti, Bert Vogelstein

Cancer arises through the sequential accumulation of (epi)mutations in oncogenes and tumor suppressor genes. We show that cancer incidence in many tissues is strongly correlated with the total number of divisions of the normal self-renewing cells maintaining that tissue's homeostasis. The slope for the correlation we found indicates that the number of required drivers to develop cancer must be smaller than what was previously thought. We describe a novel approach to derive this estimate that combines conventional epidemiologic studies with genome-wide sequencing data. In two well-documented cancer types (lung and colon adenocarcinomas), we find that no more than three sequential mutations are needed. Finally, we explore the timing of drivers in tumor evolution.

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Jaspreet Toor

University of Sheffield (UK)

The evolution of host resistance to disease in the presence of predators

Jaspreet Toor; Dr. Alex Best

Although host-parasite models have been widely studied, the inclusion of predators has often been overlooked until recently. In this study, we examine a host-parasite model with a predator and show that the predator changes the evolutionary behaviour of the host. We find that the hosts maximize their levels of resistance at intermediate predation rates, where the risk and cost of infection are both high due to the presence of infected hosts and predators. We show that the branching possibilities increase with the predation rate for regions where the susceptible and infected hosts coexist with the predator. Hence, the results reveal that the addition of a predator has a considerable impact on host-parasite populations.

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Pete Trimmer

University of Bristol (UK)

Predicting behavioural responses to rapidly-altered environments: state-dependent detection theory.

Pete C. Trimmer*, Sean M. Ehlman, Andy Sih

The rapid expansion of the human population in recent years has resulted in the natural habitats of many animals being altered substantially. This has occurred without sufficient time for natural selection to have yet had a significant effect on adjusting the behaviour of many animals, for instance in response to newly introduced species. We make use of signal detection theory, within a wider theoretical framework of state-dependent modelling, to consider the effect of rapid changes. We allow thresholds for action to be a function of an animal's reserves, and show how those optimal thresholds can be calculated. We term this framework, 'state-dependent detection theory'. By altering the environment, we show various effects of animals using those formerly adaptive traits (the previously evolved thresholds). Introducing novel animals which appear dangerous – but are actually safe – can have catastrophic consequences for a species. We show that following some forms of HIREC, even though individuals may have a similar (or even increased) expected lifespan, they may reproduce far less often, leading to a collapse in the population. Although the effect of HIREC is often difficult to predict, we suggest that state-dependent detection theory is a useful route ahead.

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Maggie Triska

University of Western Australia (Perth, Australia)

The effectiveness of surveillance strategies to detect new biological invasions depends on the organism's dispersal characteristics

Maggie Triska, Michael Renton

Biological invasions are often associated with negative impacts such as reductions in biodiversity, economic loss due to trade restrictions and high management or eradication costs. It is essential to detect biological invasions early to reduce these potential impacts. The early detection of invasions relies on optimal surveillance methods. The spread of most organisms includes long distance dispersal events, which can be represented by leptokurtic dispersal kernels or 'fat-tailed' distributions. However, modelling of surveillance strategies for biological invasion often ignore leptokurtic dispersal, by using constant dispersal or even ignoring the dynamics of spread. The consequences of neglecting leptokurtic dispersal when determining optimal surveillance methods are unknown. The aim of this study was to investigate whether the efficacy of different surveillance strategies to detect new biological invasions depends on the organism's dispersal characteristics, particularly the degree to which its dispersal is leptokurtic. We considered multiple surveillance strategies, including different sampling densities and arrangements. We used simulation modelling to represent the biological invasion and surveillance strategy, and for simplicity focussed on passive dispersal. We assessed dispersal characteristics using two dispersal kernels (Weibull and exponential) with varying degrees of leptokurtic dispersal within Weibull distributions. We determined that the time to detection decreased as the degree of leptokurtic dispersal increased, however, the extent of the invasion was greater at the time of detection than in non-leptokurtic models. Sampling arrangement did not make a difference for any dispersal type, but all dispersal types had reduced time to detection as the sampling density increased. Overall, the relationship between the sampling density and expected surveillance outcome (i.e., the efficacy of different surveillance strategies) relied on dispersal type. Therefore, it is important to consider dispersal characteristics when seeking and defining optimal surveillance strategies for biological invasions. Lastly, we apply our approach to specific case studies, such as grape phylloxera.

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Mélissa Verin

TU Munich (Germany)

The neutral evolution of iteroparity

Mélissa Verin, Frédéric Menu and Etienne Rajon

Iteroparous individuals reproduce several times instead of just once, as semelparous do. Many species are iteroparous at various degrees (i.e., they differ by the mean number of reproductive events), despite a well-known advantage to semelparity: semelparous genotypes grow more rapidly in stable environments where resources are in excess. Existing theory might still explain the evolutionary success of iteroparity, either by a direct advantage (it can provide higher lifetime fecundity) or by its buffering effect in varying environments. Here we confront this Malthusian view of the evolution of iteroparity by considering that resources are limiting, such that a population can only grow in size up to a point where it stabilizes. Using an adaptive dynamics approach, we show that semelparity loses its selective advantage in this context, and that all reproduction strategies (i.e., semelparous and iteroparous at any degree) are strictly neutral when they bear equal lifetime fecundity. Then we develop a neutral model for the evolution of these strategies, showing that the most probable outcome is the highest degree of iteroparity. In light of these results, the observation that many species are semelparous becomes puzzling. We argue that some ecological contexts may favor semelparity, either directly (e.g., when survival until the next reproductive season is unlikely) or by yielding population dynamics that scarcely limit growth.

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Helene Weigang

University of Helsinki (Finland)

On the evolution of patch-quality dependent immigration

Helene Weigang, Eva Kisdi, Mats Gyllenberg

Immigration decisions during dispersal often depend on habitat quality. To analyse the evolution of immigration we present an eco-evolutionary model: a population inhabits a heterogeneous landscape which consists of an infinite number of patches. Individuals are characterised by their immigration behaviour, i.e., their habitat choice/preference or acceptance probability. With the methods of adaptive dynamics, we derive both analytical and numerical results for the evolution of patch-quality dependent immigration when also seasonal survival, survival until maturation and dispersal (emigration) are patch-quality dependent. We study the effects of death rates, dispersal season length, emigration probabilities and local catastrophes on the evolution of immigration. We illustrate that the immigration probability decreases with increasing encounter rate, death rate, dispersal season length, if patches of other quality become more safe and if individuals are more likely to emigrate from other patches. Furthermore habitat preference can increase if patches become less frequent. The acceptance probability into a patch of certain quality increases with increasing dispersal death rate and when emigration and survival until reproduction increases in patches of same quality. In addition we highlight an example of the emergence and coexistence of a generalist and specialist strategy.

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David Welch

University of Auckland (New Zealand)

Inference under the coalescent in a continuous landscape

Stéphane Guindon, Hongbin Guo, David Welch

Phylogeographic inference is increasingly widely practiced by biologists and ecologists who have collected spatially located genomic data. The promise of phylogeography is that it enables accurate estimates of past and present population sizes and migration and dispersal patterns. But this promise rests on being able to fit complex data sets to complex models, which requires complex statistical software. The dominant models currently used by practitioners consider the genealogical process as being independent of the spatial process which is known to be inaccurate but greatly simplifies inference. The structured coalescent models the dependence of the genealogical and spatial process but considers the population as structured into discrete demes, so is not applicable to a populations inhabiting a continuous landscape. Further, inference under the structured coalescent is typically limited to 2-3 demes. In a recent series of articles, Barton, Etheridge, Veber and colleagues proposed a model that extends the coalescent to a population living on a continuous landscape — the spatial Λ -Fleming-Viot process or the continuous landscape coalescent (CLC) — that has attracted much interest from mathematical modelers. We have developed a Markov chain Monte Carlo sampler to infer the parameters of the CLC from spatially tagged sequence data. Using simulations, we demonstrate that accurate estimates of neighborhood size and dispersal distance can be recovered under realistic experimental conditions, suggesting that the model can be of practical use for the analysis of samples taken from a population in a continuous landscape.

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Thorsten Wiegand

UFZ (Leipzig, Germany)

Understanding the assembly and dynamics of species-rich communities using spatially-explicit and stochastic community models

Thorsten Wiegand, Felix May and Andreas Huth

Assessing the relative importance of processes that determine the spatial distribution of species and the assembly and dynamics of species rich plant communities is one of the major challenges in ecology. I argue that we can advance in this question by adopting a spatially explicit perspective that allows using the incredible information that is buried in fully mapped mega plot data of forest communities. This can be done by taking advantage of recent advances in three fields: spatial point pattern analysis, inference for stochastic simulation models, and individual-based and spatially continuous community models that produce output that can be directly compared with the census data. Fitting the model outputs to observed patterns that capture different aspect of community dynamics and spatial structures (including annual mortality rate, species richness, species abundance distribution, beta-diversity, and the species-area relationship) simultaneously allows for identifying minimum sets of processes required to describe the community with a given level of detail. In the first part of my talk I show that a spatially explicit extension of the classical Hubbell model can quantitatively predict the above patterns independently, but it is unable to quantitatively match the species-area relationship and beta-diversity simultaneously. In a second part I show how this pattern-oriented approach allows assessing the relative importance of species differences in e.g., dispersal, negative density dependence and habitat associations for the emergence of the observed structural patterns. This spatially-explicit approach moves previous theory towards a dynamic spatial theory of biodiversity and demonstrates the value of spatial data to identify ecological processes. This opens up new avenues to evaluate the consequences of additional process for community assembly and dynamics.

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C. Scott Wylie

Brown University (Providence, USA)

Entropic tradeoffs in antibiotic resistance evolution

C. Scott Wylie, Eugene Raynes, Paul Sniegowski, and Dan Weinreich

Biological systems are often subject to mechanistic tradeoffs, such that a change in one trait constrains a second, incompatible, trait to change in the opposite direction. One way to detect mechanistic tradeoff is a comparative approach: isolate many naturally occurring variants and look for negative correlations between their traits. However, the comparative approach is confounded by the fact that natural selection presents us with only a biased subset of all possible variation. Here, we comprehensively study tradeoffs in the ability of an antibiotic resistance enzyme, TEM β -lactamase, to protect *E. coli* from two different drugs: ampicillin (amp) and cefotaxime (ctx). Among clinical isolates of β -lactamase alleles, we find that mutations typically decrease fitness toward amp while simultaneously increasing fitness toward ctx— observations consistent with a mechanistic tradeoff and the fact that ctx was introduced into clinical use at a later date than amp. However, when we examined a collection of all single point mutations, we found no correlation between fitness effects against amp and those against cef, indicating no mechanistic tradeoff. To reconcile our seemingly contradictory observations, we propose that the evolutionary process induces an illusory, entropic tradeoff: When a selective pressure is added to a population's environment, the population typically evolves toward a compromise between the best solution and the most mutationally accessible one (with highest entropy), which typically entails a fitness penalty in the ancestral environment. We formalize our hypothesis in a generic mathematical model that describes conditions under which entropic tradeoffs are predicted to exist. Our results shed light on a strikingly wide array of biological questions, ranging from disease mapping, the evolution of sex, and designing drug treatment regimens.

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Tatiana Yakushkina

National Research University (Moscow, Russian Federation)

Evolutionary games with randomly changing payoff matrices

Tatiana Yakushkina, David B. Saakian, Alexander Bratus, Chin-Kun Hu

Evolutionary games commonly consider a constant payoff matrix, however it is reasonable to investigate models with dynamic payoff matrices. In this work, we assume a possibility of switching the system between two regimes with different sets of payoffs. Potentially, such a model can qualitatively describe the development of bacterial or cancer cells with a mutator gene present. A finite population evolutionary game is studied. The model represents the simplest version of annealed disorder in the payoff matrix and is exactly solvable. The state of the underlying game is defined by probability distribution of total number of players adopting every particular strategy. Time evolution of the state is governed by chemical master equation with transition rates dependent on any smooth payoff function. We analyze the dynamics of the model, and derive the equations for both the maximum and the variance of the distribution by applying the Hamilton-Jacobi formalism. As an example, we use Moran process and local update mechanism methods for process simulation. Numerical simulation results confirm the accuracy of our analytical solution. For two-strategy games, which could be classified according to phase portrait type (so-called Prisoner's dilemma, Coordination, and Hawk-Dove classes), we study all possible combinations of payoff matrices. Suggested approach is applicable to any finite number of payoff matrices.

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Masato Yamamichi

Kyoto University (Japan)

Effects of genetic architectures on polymorphism dynamics under negative frequency-dependent selection

Masato Yamamichi, Masaki Hosoi

Negative frequency-dependent selection (NFDS), where scarce phenotypes have a fitness advantage over abundant phenotypes, is a pervasive mechanism for maintaining intraspecific variation that occasionally causes temporal oscillations of phenotype frequencies. However, allelic variation can be stochastically eliminated when oscillatory dynamics amplitude is enhanced. Natural selection works at the phenotypic level, whereas loss of genetic variation occurs at the allelic level; therefore, a better understanding of allele extinction under NFDS requires consideration of the genetic architectures linking these two levels. Herein, we show that genetic architectures underlying phenotypic polymorphisms can dramatically alter evolutionary dynamics under NFDS in single-locus diallelic models. Identical phenotypic polymorphisms arise from various genetic architectures, including haploid, diploid, and diploid inheritance with maternal effects (e.g., genomic imprinting in mammals or delayed inheritance in snails). We demonstrate that maternal inheritance buffers the influence of selection on allele dynamics, resulting in two different consequences of allele persistence. Maternal effects stabilize fluctuation and prevent allele extinction under highly nonlinear NFDS; under weak NFDS, they promote stochastic extinction of alleles. Our findings suggest that understanding both the nature of NFDS and the genetic architectures underlying polymorphisms is important to predict contemporary evolution, thereby providing an insight into chiral polymorphism maintenance in snails.

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Posters

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Vitalii Akimenko

Taras Shevchenko National University of Kyiv (Ukraine)

Evolutionary Dynamics of Age-Structured Polycyclic One-Sex Population

Vitalii Akimenko, Roumen Anguelov

We consider the age-structured model of population dynamics based on the system of initial-boundary value problems for the non-linear transport equations with integral boundary condition. This model describes the evolutionary dynamics of polycyclic population with proliferating and quiescent individuals. Obtained for this system explicit solution in the form of travelling waves allows us to develop an accurate numerical algorithm and carry out the numerical simulation of different scenarios of polycyclic population dynamics. We study the asymptotically stable states of dynamical system, quasi-periodical behavior - harmonic oscillations and pulse sequences for the densities of proliferating and quiescent individuals. The results obtained in this work provide insight into the temporal evolution of polycyclic population with non-linear effect of feedback of individual's density growth on the mortality process.

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Farah Al-Shorbaji

Bournemouth University (Bournemouth, United Kingdom)

Managing the spread of emerging infectious diseases in freshwater wildlife

Al-Shorbaji F, Roche B, Gozlan R, Britton R, and Andreou D.

Increased trade has contributed to a significant increase in the translocation of pathogens across the globe, with a knock-on effect on the emergence of infectious diseases. Many of these emerging pathogens have severe consequences for a wide range of plant and animal species, often leading to a decrease in community biodiversity. The chytrid fungus in amphibians and White Nose Syndrome in bats highlight the magnitude of damage that these infections can cause. One growing concern for freshwater ecosystems stems from the introduction of *Sphaerothecum destruens* along the invasion path of a healthy host from China, topmouth gudgeon *Pseudorasbora parva*, which acts as a super-spreader of the disease. This intracellular pathogen has caused chronic declines of sunbleak *Leucaspis delineatus* populations in Europe, leading to the species' extinction in many European countries. The pathogen is also the agent of disease outbreaks in farmed Atlantic salmon *Salmo salar* and Chinook salmon *Oncorhynchus tshawytscha* populations in the US. Understanding such generalist parasites is particularly complex, as the structure of the local community assemblage plays a significant role in disease dynamics. In addition, pathogens in aquatic environments are particularly difficult to monitor and detect and chronic population decline is very difficult to observe closely in the wild. Here, we combine ecological and epidemiological modelling techniques to explore how the host assemblage of communities impacts disease dynamics and vice versa. We examined how resource competition and predation between native and invasive species influences the spread of infection within a host community. Eradication protocols of invasive species are frequently used but can be ineffective in eradicating the associated generalist pathogens from the environment and result in long term damage to the community. Therefore, we aimed to determine the optimal community management approach to limit this pathogen's impact on local biodiversity and ecosystem services (e.g., farms, sport fishing).

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Hélène Arduin

Institut Pasteur (Paris, France)

Detecting and quantifying between-pathogens interactions in humans: an agent based model simulation study

Arduin Hélène, Watier Laurence, Guillemot Didier, Opatowski Lulla

In infectious diseases epidemiology, studies and models of pathogen transmission within populations generally focus on a single pathogen. However, it is more and more suggested that pathogens can interact within the host, for colonisation or infection. Strong associations between influenza viruses and infections by *Streptococcus pneumoniae* (pneumococcus) have been documented in humans for example. When they exist, such interactions may strongly impact the global dynamics of a pathogen, and lead a single-pathogen-study to erroneous conclusions. Furthermore, better knowledge and consideration of existing interactions is of major importance as they could offer new possibilities for treatment and control strategies against infections caused by interacting pathogens. Detection and analysis of interactions is commonly performed through disease incidence data, by using classic regression methods. However it is not clear whether these methods are appropriate. Here we present a simulation study in which we assess the ability of different statistical methods to analyse pathogens interactions from incidence data. We used an agent based model (ABM) to simulate the co-circulation of influenza viruses and pneumococcus in a virtual population of humans. Population size, density and model parameters were calibrated in order to obtain realistic dynamics. To explore a range of hypotheses three different interaction parameters were defined, based on a literature review of influenza and pneumococcus studies. They include synergy in transmission, synergy in infection and synergy in acquisition. By varying these parameters, 54 scenarios of interactions between the two pathogens were simulated and weekly influenza- and pneumococcal infection-incidence curves were extrapolated. Usual statistical methods found in literature include multiple linear regression, Poisson regression, negative binomial regression and dynamic model fitting. These methods are applied on the ABM-simulated incidence datasets, and their ability at detecting and quantifying the force of interaction is compared.

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Guillaume Baudoin

Institut de Recherche sur la Biologie de l'Insecte (Tours, France)

Invasion dynamic of an urban termite pest in Paris

Baudouin G, Suppo C, Dupont S, Dedeine F, Bagnères A-G

The termite *Reticulitermes flavipes* is a great invader in France. It was certainly first introduced from Louisiana during the 18th century. Since then, it spread through the west of France and reached Paris, where it was recorded for the first time in 1945. Contrary to its native range (the east coast of USA), in France, *R. flavipes* is mostly found in cities (Bordeaux, Poitiers, Tours, Marseille, Paris, Rouen. . .) where it can find all needs (cellulosic matters, warm and humidity). This subterranean pest can cause important damages to buildings and is very difficult to detect. The aim of my PhD project is to 1) identifying dispersion and introduction factors in an urban area using spatial and genetic structure analysis of the Parisian termite population and 2) using existing models, understanding the dynamic of infestation in urban landscape which seems to be favorable to this species in France.

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Koen van Benthem

University of Zurich (Switzerland)

Disentangling evolutionary and plastic processes underlying trait dynamics.

Koen van Benthem, Marjolein Bruijning, Timothée Bonnet, Eelke Jongejans, Erik Postma and Arpat Ozgul

Recently it has become apparent that evolution can take place on ecological time-scales. To generate a better understanding of trait dynamics, multiple frameworks have been developed to disentangle their underlying evolutionary and ecological processes. Due to applications of these frameworks being rare, it is still unclear how they compare to each other. Here we evaluate four main frameworks: the quantitative genetic animal model, the genotype-phenotype-environment equation, the age-structured Price equation and the application of the age-structured Price equation to integral projection models. By applying each of these four frameworks to an individual-based (genetically explicit) simulated dataset, we show that estimated contributions from different processes differ strongly among the frameworks. This is due not only to the estimation procedure of the frameworks, but also due to the way the different processes are defined in each framework. Furthermore we investigate the theoretical limits of the frameworks. On the whole, our findings provide a basis for choosing which framework suits different biological questions and analyses best.

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Kazuhiro Bessho

The University of British Columbia (Vancouver, Canada)

The evolution of ploidy level in macroalgal life cycles and the effect of spatial structure

Kazuhiro Bessho, Sarah P. Otto

Sexual eukaryotic organisms alternate between haploid and diploid phases in their life cycles. While the haploid phase is reduced in many animals and plants, other organisms, including macroalgae, exhibit a variety of life cycles with both free-living haploid and diploid generations and morphological diversity among the stages. In species with diploid-dominant heteromorphic life cycles, the diploid phase is substantially larger than the haploid phase, whereas in others the opposite is observed. By contrast, species with isomorphic life cycles exhibit similar haploid and diploid phases. To clarify the conditions under which each life cycle is evolutionally stable, we analyze genetic models for life cycle evolution in macroalgae. We derive the fixation probabilities of mutant alleles introduced into a resident population, allowing for different viabilities and fecundities in the haploid and diploid stages. We next incorporate ploidy-specific differences in dispersal within an individual-based model. We find that species with isomorphic life cycles tend to evolve when the advantages of a large size from greater fecundity exceed the advantages that smaller individuals gain from releasing gametes into the boundary layer. Alternatively, when fertilization success is highest from small individuals, a heteromorphic life cycle can be favored with small gamete-producing haploids. We discuss the parameter values that distinguish regimes in which different life cycles are favored.

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Robert Beyer

CentraleSupélec (Paris, France)

Tree Growth Modelling via Spatial Leaf Density

Robert Beyer, Véronique Letort, Dominik Bayer, Hans Pretzsch, Paul-Henry Cournede

Modern mathematical ecology could not be imagined without the concept of the spatial density of a biological population. We apply this concept to the spatial description of leaves in a tree crown. This surprisingly unstudied characterization of foliage does not face the difficulties commonly associated with topological descriptions of crown structure in which leaves are considered individually, namely computational heaviness when the number of leaves and other elementary units becomes large. Spatial leaf density does not face this problem, while at the same time being much more flexible a description of crown shape than rigid empirical parameterizations of crown envelopes frequently used in large scale models. We model spatial tree growth in terms of leaf density dynamics. Beer-Lambert's law allows a generic determination of local light conditions in the crown, from which light-dependent local biomass production via photosynthesis follows straightforwardly. The latter quantity is subsequently transported in the direction of the local light gradient, representing unconstrained phototropism, and eventually allocated to new foliage and wood according to the pipe model theory. We compare our model to long-term experimental data of European beech as well as spatial Lidar data, and obtain good results as well as model-based evidence for morphological hypotheses regarding plastic tree species.

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Julien Clavel

Ecole Normale Supérieure (Paris, France)

A major role of climatic changes on evolutionary rates in birds and mammals

Julien Clavel; Gilles Escarguel; Gildas Merceron

Distinct evolutionary theories of how species diversify predict distinct temporal trends in the pace of phenotypic evolution. One of the leading theory, based on the concept of adaptive radiation, predicts that phenotypic evolution should slowdown in the course of a clade's history as species fill ecological space. Empirical evidence for this theory has often been sought by testing statistical support for an "early-burst" model of phenotypic evolution in phylogenies of extant taxa. Models of trait evolution have thus focused on testing the role of biotic interactions on evolutionary rates, leaving the role of abiotic drivers mostly untested. Here, we show that models accounting for the role of abiotic drivers in fact receive much more support than models accounting for the role of biotic ones. We begin by developing a phylogenetic comparative approach that allows explicitly testing if and how rates of phenotypic evolution depend on measured abiotic variable. We apply this approach to comprehensive bird and mammal phylogenies in association with datasets of body sizes of 9343 extant species and global temperature trends since the mid-Cretaceous. We find strong support for a model in which temperature has had a major effect on rates of body-size evolution in both mammals and birds. Specifically, increased rates are associated with global climatic cooling that most likely represents adaptive responses to changing selective pressures. Our results suggest that the effect of climate on evolutionary rates is a general feature of endotherms evolution in spite of differences in ecology and evolutionary history across taxonomic groups. These results suggest that climatic changes have had a major role in shaping species evolution in the past, and could also have a major role in shaping their future evolution.

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Dorian Collot

UMR Génétique Quantitative et Evolution (Le Moulon, France)

Modelling respiro-fermentative dynamics of *Saccharomyces cerevisiae* batch culture to understand the evolution of life-history strategies.

Dorian Collot, Thibault Nidelet, Christine Dillmann, Delphine Sicard, Judith Legrand

Adaptation of organisms to their environment relies on many phenotypic traits called life-history traits. Due to physical and biological constraints, selection cannot maximize all those traits together, and better understanding of adaptation requires multi-trait analysis. We are interested in the adaptation of the yeast *Saccharomyces cerevisiae* via several traits related to fermentation and respiration such as resource consumption rate, biomass yield or mortality. Two extreme life-history strategies have been identified from experimental data: on the one hand big cells which have a high consumption rate and a low reproductive rate, on the other hand smaller cells which have a high biomass yield and a higher reproductive rate. In addition, an experimental evolution of six strains in four different environments has demonstrated that high-content sugar environment select for big cells life-history strategy while lower sugar environment select for small cells strategy (Spor, Evolution, 2014). In order to understand the evolutionary dynamics of those strains during the experimental evolution, an ODE model was built. This model includes both fermentation and respiration phases and accounts for cell's mortality. Ancestral and evolved strains from experimental evolution were characterized by fitting model's parameters using an ABC algorithm. Once calibrated, the model can be used to simulate competition between strains with different life-history strategies, and help to predict the outcome of competition depending on strains' traits and on the environment. In the future, we will explore how trade-off between traits shapes the evolutionary dynamics of yeast in a changing environment.

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Paul Darmé

Ecole Normale Supérieure (Paris, France)

Genome-wide patterns of evolution in experimental populations of *Caenorhabditis elegans* with low standing genetic diversity

Paul Darmé, Thiago Guzella, Henrique Teotónio

The genetic changes that accompany adaptation to a new environment are a topic of general interest in evolutionary biology. Only recently it has become possible to study the dynamics of evolution at the genome-wide. Most studies tend to focus on asexual organisms starting from an isogenic population, with adaptation depending entirely on new mutations, or on sexual organisms with abundant standing genetic variation, with minor or no impact from de novo mutations. To combine the two perspectives, the nematode *C. elegans* provides an interesting system. In the wild, it consists mostly of hermaphrodites, reproducing by selfing, with relatively rare outcrossing with males, with works showing low diversity in populations worldwide. Therefore, adaptation is likely to be conditioned on relatively low levels of diversity. In this work, we use experimental populations of *C. elegans* adapting to a new environment to study the genome-wide evolutionary dynamics. Starting from a founder population obtained by intercrossing 16 wild-isolates, rounds of inbreeding were performed to produce six different replicate populations having initially low levels of standing genetic variation. This setting closely resembles what is currently thought of about the ecology of *C. elegans*. The six populations were then subjected to experimental evolution for 100 generations under a new laboratory environment. Previously published results show that these populations have adapted to this new environment. Therefore, here we characterize genomic patterns in the beginning and in the end of the experiment, by sequencing a pool of individuals from each of these populations in these two time-points. An initial analysis of the data reveals fixation of some of the sites that were segregating in the starting populations, and also points to putative new mutations that would have arisen during the experiment. Finally, using computer simulations, we obtain likely estimates of parameters describing the underlying population genetics processes.

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E. Yagmur Erten

IRD (Montpellier, France)

Parasite evolution on heterogeneous contact networks

E. Yagmur Erten, Samuel Alizon, Sebastien Lion

Contact patterns between individuals have many implications on ecological and evolutionary dynamics, and are known to strongly affect the evolution of infectious diseases. Host contact networks have often been shown to be heterogeneous. The heterogeneity in terms of the number of contacts can have major consequences, resulting in “superspreading events”, where most of the secondary cases are caused by a small fraction of the population. In this project we investigate virulence evolution on heterogeneous contact networks, under several biological scenarios, and using an agent-based simulation model. We consider an SIS model of infection dynamics, and assume virulence is linked to transmission. We model heterogeneity by simulating a gamma- distributed-network population, where individuals differ in terms of number of contacts they have. We let virulence evolve through mutations and track the level of virulence throughout the simulation. We compare results obtained on gamma-distributed-network model with that obtained on more regular networks, in order to capture the effect of host contact structures on parasite evolution.

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Eugene Geidelberg

Station Biologique de Roscoff (Roscoff, France)

Facing widespread, single combination anti-retroviral treatment, will HIV vanish?

Eugene Geidelberg and Samuel Alizon

To date, the best way of combating HIV is with highly active anti-retroviral therapy (HAART), a combination of drugs which tamper with the viral life cycle, sending the concentration of viruses in the blood to near zero. By 2015, the WHO hopes to have 15 million people on HAART, mainly in Sub-Saharan Africa, where HIV prevalence is at its highest. Epidemiological studies that predict treatment success ignore drug resistant viruses, resistance seems to incur a strong fitness cost, limiting the transmission of drug resistance (TDR). These costs have mostly been observed where patients are closely monitored and where second-line treatments are available. This is unlikely in resource-limited countries where all infections will be treated with the same drug, regardless of whether their infection is resistant. We hypothesise that the epidemiological role of drug resistance could be non negligible in this setting. Our model predicts that very high patient adherence to the treatment is required to successfully eliminate the virus. Second, the evolution of drug resistance can maintain the epidemic despite treatment, even if the cost of resistance is high. Finally, the virus may also evolve a higher viral load after treatment, bringing with it higher virulence: following an eradication failure we might face not only drug-resistant, but also more virulent strains. Models including more realistic details (contact network, within-host dynamics) are surely needed but our first approach clearly confirms that one should be careful about resistance evolution when giving millions of people the same combination of drugs.

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Wesley A C Godoy

Universidade de Sao Paulo (Brasil)

Competitive interactions and local neighbourhood density dependence in natural enemies of pests

Godoy, W. A. C.

Predators or parasitoids frequently attack the same prey or host. The persistence of competing species in time and space depends essentially on the fecundity and survival of each competitor, but also on the ability of the more-efficient competitor to self-regulate its density, allowing its opponent to exploit part of the available resource. Measuring the effects of coexistence between natural enemies competing for the same pest species, in the same patch, is essential for the implementation of integrated pest-management programs in agricultural systems that use different species of natural enemies. In this study, the coexistence between parasitoids exploiting the same patch was simulated with a spatially explicit model incorporating the local neighbourhood density-dependence concept to avoid competitive exclusion, allowing long-term coexistence between species. The model employed in this study initially assumes a square grid containing a central patch surrounded by neighbours in a universe of 100 x 100 patches, and includes a function to count the number of individuals of the more-efficient competitor. Reproductive rates for the better and the worse competitor, as well as the death rate of adults, were experimentally obtained and used in the model. A sensitivity analysis for reproductive rates, death rate of adults, and threshold number of the better competitor above which recruitment cannot occur was employed to determine the limits for coexistence. The initial conditions assume that each competitor occupies one-half of the grid. The most influential parameter for determining the limit for coexistence between species was the threshold number of the better-competitor, which shows the required conditions for the two competitor species to coexist.

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Quentin Griette

Université de Montpellier (Montpellier, FRANCE)

Virulence evolution at the front line of spreading epidemics

Quentin Griette, Gael Raoul, Sylvain Gandon

Understanding and predicting the spatial spread of emerging pathogens is a major challenge for the public health management of infectious diseases. Theoretical epidemiology shows that the speed of an epidemic is governed by the life history characteristics of the pathogen and its ability to disperse. Rapid evolution of these traits during the invasion may thus affect the speed of epidemics. Here we present the influence of virulence evolution on the spatial spread of an epidemic. At the edge of the invasion front, more virulent and transmissible genotypes are expected to win the competition with other pathogens. Behind the front line, however, more prudent exploitation strategies outcompete virulent pathogens. Crucially, even when the presence of the virulent mutant is limited to the edge of the front, the invasion speed can be dramatically altered by pathogen evolution. Our analysis is based on a system of reaction-diffusion equations, that we extend with individual-based simulations in order to discuss the additional effects of demographic stochasticity taking place at the front line on virulence evolution. We carefully show the existence of travelling wave solutions to this system and get some qualitative properties of the fronts. We then get empirical results on the associated stochastic process using our simulations.

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Ghjuvan Grimaud

INRIA (Villefranche-sur-mer, France)

How will marine phytoplankton face global warming? An Adaptive Dynamics global scale study.

Ghjuvan Grimaud, Francis Mairet, Olivier Bernard

Marine phytoplankton can't regulate their inner temperature, which makes them particularly sensitive regarding temperature fluctuations and global warming (Chen et al, journal? 2015). The in situ temperature temporal variations therefore act as a selection pressure. Using the Adaptive Dynamics theory and an optimization method, we study phytoplankton adaptation at global ocean scale. Based on 200 laboratory experimental data sets of phytoplankton growth rate versus temperature, we assume that the adaptive traits (i.e., the phenotypic traits which are likely to evolve) are the minimal, optimal, maximal temperatures for growth and the maximal growth rate, T_{min} , T_{opt} , T_{max} and μ_{max} respectively. We show that the cardinal temperatures are correlated but a possible relationship between the cardinal temperature and the maximal growth rate is more controversial. We study the evolution of an ubiquitous phytoplankton species at global ocean scale using in situ sea surface temperature data on 3 years at 1° latitude/longitude resolution. We compare the evolutionary equilibrium of two thermal growth models with different assumptions made on adaptive traits correlations. We validate our approach and the optimal adaptive trait correlation by comparing model predictions with the experimental data sets. We show that temperature actually drives evolution in oceans and that the optimum temperature for phytoplankton growth is strongly linked to thermal amplitude variations. Moreover, T_{opt} at evolutionary equilibrium is always equal or higher than the annual average temperature experienced by phytoplankton. Finally, we investigate the difference δT_m between T_{max} at evolutionary equilibrium and the maximal temperature experienced annually $\max(T)$. Some regions have a δT_m close to zero, and could thus undergo ecological shift in phytoplankton community structure.

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Thiago Guzella

Ecole Normale Supérieure (Paris, France)

Linkage and genome dynamics under different rates of environmental change

Thiago Guzella, Ivo Chelo, Henrique Teotónio

Genetic linkage is a key parameter determining evolutionary dynamics. One way in which it can influence the dynamics is via interference between competing lineages, an effect often discussed in the context of the evolution of sex and recombination rates. However, despite many theoretical works studying the impact of linkage, experimental data is scarce. In this work, we manipulate the mating system in the nematode *Caenorhabditis elegans*, producing populations that differ in effective rates of recombination: a hermaphroditic monoecious population, with obligatory selfing, and a male-female dioecious population, with obligatory outcrossing. Starting from ancestral populations from these two mating systems, having similar initial levels of genetic diversity, we performed experimental evolution under which the worms faced a new environment, being faced with osmotic stress. This new environment constitutes an additional parameter that is expected to impinge on the evolutionary dynamics: in one treatment, the concentration of salt increased in a sudden manner, while in the concentration increased gradually. At three time points, individuals sampled from the various populations, besides the ancestral populations for each mating system, were genotyped for almost 800 single-nucleotide polymorphisms spanning all six chromosomes. Preliminary analysis of the dynamics of haplotype blocks reveals widespread changes in the monoecious populations, with large regions sweeping through during the experiment, while a much lower number of regions in the dioecious population undergo frequency changes, with the latter populations having essentially constant levels of genetic diversity throughout time. Using simulations and applying recent theoretical analyses to integrate the impact of linkage and the rate of environmental change, we obtain estimates for the population genetics parameters that explain the dynamics that have been observed.

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Benoit Henry

IECL (Nancy, France)

Moments and CLT for the frequency spectrum of a splitting tree with neutral Poissonian mutations.

Nicolas Champagnat, Benoit Henry

In this talk, we consider a branching population where individuals live and reproduce independently. Their lifetimes are i.i.d. and they give birth at a constant rate b . This model is called a splitting tree, and the population counting process $(N_t, t \in \mathbb{R}_+)$ is a homogeneous, binary Crump-Mode-Jagers process. We suppose that mutations affect individuals independently at a constant rate θ during their lifetimes, under the infinite-alleles assumption: each new mutation gives a new type, called allele, to his carrier. We study the allele frequency spectrum which is the numbers $A(k, t)$ of types represented by k alive individuals in the population at time t . It is known that $e^{-\alpha t N_t}$ and $e^{-\alpha t A(k, t)}$ converge almost surely to some exponential random variable on the non-extinction event. We then show a CLT for this convergence using a new method to compute the moments of the frequency spectrum. The purpose of this talk is to present a new method for the computation of the moments of the frequency spectrum together with CLTs for the convergence of $e^{-\alpha t N_t}$ and $(e^{-\alpha t A(k, t)})_{k \geq 1}$ using renewal methods.

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Gereon A. Kaiping

University of Southampton (Southampton, United Kingdom)

Economics and Genetics: How market-structured migration modifies domestic animal evolution

Gereon A. Kaiping, Guy S. Jacobs and Timothy J. Sluckin

Human decisions carry significant influence on the evolutionary trajectories of many non-human species. This influence is particularly strong in the case of domestic animals and cultivated plants. Here humans control directly both breeding opportunities and the environment to which individuals are exposed. More significant in an evolutionary context may be the fact that, through trade-related changes in ownership of domestic species, humans also influence their migration patterns. Here we present the results of an initial pilot study of the impact of market-mediated gene flow in the genetic evolution of connected animal herds. Our study extends a model introduced by Bolnick and Otto (*Ecology and Evolution*, 2013) which focussed on gene- and patch-dependent migration. We calculate the evolutionary equilibria of two competing animal breeds with different reproductive rates. The economics enters because one human group richer than the other, and the utility values between for the breeds differ. Under a simple representation of the trading process, this model is sufficient to derive asymmetric, non-constant migration rates. A symmetric model would, of course, predict that the less fit breed would die out. But constant asymmetric migration rates can allow the less fit breed to locally dominate. Indeed, when migration rates are derived from a more realistic market model, the influence of the trade-induced migration even permits the less fit breed to fixate in the poorer patch, and prevail in the richer patch. Our findings may have relevance in a variety of contexts. One example involves development interventions, in which imported domestic animals or their germplasm are introduced to indigenous populations. A second concerns the evolution of breed distributions and the adoption of different domesticate species by agriculturalists during the Neolithic Transition.

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Tsukushi Kamiya

University of Groningen (Groningen, The Netherlands)

Optimal defence deployment tactics: insights from coevolutionary interactions

Tsukushi Kamiya, Leonardo Ona, Sander van Doorn

For protection against natural enemies, organisms deploy a variety of defence mechanisms, which are typically at the expense of other life history components. Facing this trade-off, organisms are expected to optimally balance the cost and benefit of defence deployment. Because the process of detecting and mounting a response may involve several physiological cascades, induced responses can be time-consuming. Thus, timely protection would benefit from having an existing arsenal, which requires a constitutive investment into costly defence against likely future risks. Existing theoretical models address this question in terms of the optimal combination of constitutive and inducible defence. However, theory so far leaves out the evolution of enemies and the fact that the efficiency of protection depends on genotype specific species interactions. All organisms deploy generalist defence strategies that grant broad protection. In addition, specialist adaptations may recognise specific threats and combat a narrower range of insults, but with higher efficacy. Given that natural enemies are evolving and hence able to evade specialist defence, coevolutionary arms-races should emerge between specialist defence systems and their antagonistic counterparts. Thus, the degree of specificity and the defence deployment tactics comprise two important dimensions in determining the success of a defence response. Using a simple network model incorporating host-parasite coevolution, we explore the influence of specific species interactions on the optimal defence deployment tactics. We discuss the results in light of insect immunity, which is increasingly used as a model system for aiding the fundamental understanding of innate immune systems displayed among all taxa.

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Marguerite Lapierre

Collège de France (Paris, France)

Reference Models in Molecular Evolution

Marguerite Lapierre, Cécile Delaporte, Amaury Lambert, Guillaume Achaz

The current model of reference in Molecular evolution is the Neutral Theory introduced by M Kimura, which states that the vast majority of mutations that segregate through generations are neutral. This theory and the mathematical model it relies on have four major hypotheses: neutrality, panmixia, constant population size and a low variance of offspring number. In practice, to account for real situations, the two first hypotheses are often amended with demography and sub-populations, but the two other hypotheses are almost never reconsidered. Alternative models have been theoretically described: the birth-death model (branching process) and the coalescent with multiple mergers. These models allow to take into account variation in the population size, a foundation event, selection or variability in the number of descendants. I will present these alternative models and how they fit the data of large population sequencing projects, such as the 1000 Human Genomes project. Moreover, we study how these different models can converge to similar ones in a certain range of parameter.

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Marc Manceau

Collège de France (Paris, France)

The species problem from a modeler's point of view

Marc Manceau, Amaury Lambert, H el ene Morlon

The species problem is the coined term designating the lack of consensus around the species definition in biology. In spite of that, the concept is still widely used by systematists and modelers and is now being increasingly used in conservation policies. For bio-statisticians, the species problem consists in clustering individuals on a phenotypic base. The phenotype of interest could be morphologic, genetic, geographic, or whatever trait that could be considered a clue to distinguish separately evolving metapopulation lineage, the general definition of species from De Queiroz. The modeler's point of view studied here is related to the same problem, but the way to express it is more theoretical. Given a genealogy of individuals and a process of differentiation applied on the genealogy, how can we build a phylogeny? In particular, we would like the species clustering rules to be as biologically informative as possible. In this paper, we highlight in particular three desirable properties. We then give an insight into two already defined and one new species clustering. Each species clustering satisfies a precise set of these properties. We compare them on a simulation basis with some statistics of the shape of real phylogenies. We hope that giving explicit and well-defined ways to cluster individuals into species based on a genealogy and on phenotypic differences will make a step forward towards a better integration of the individual level into models of diversification.

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Sebastian Matuszewski

EPFL (Lausanne, Switzerland)

Catch me if you can: Adaptation from standing genetic variation to a moving phenotypic optimum

Sebastian Matuszewski, Joachim Hermisson, Michael Kopp

Numerous studies have tried to provide a formal framework for the description of the adaptive process. Out of these, two complementary modelling approaches have emerged: While so-called adaptive-walk models consider adaptation from the successive fixation of de-novo mutations only, quantitative genetic models assume that adaptation proceeds exclusively from pre-existing standing genetic variation. The latter approach, however, has focused on short-term evolution of population means and variances rather than on the statistical properties of adaptive substitutions. Our aim is to combine these two approaches by describing the ecological and genetic factors that determine the genetic basis of adaptation from standing genetic variation in terms of the effect-size distribution of individual alleles. Specifically, we consider the evolution of a quantitative trait to a gradually changing environment. By means of analytical approximations, we derive the distribution of adaptive substitutions from standing genetic variation, that is, the distribution of the phenotypic effects of those alleles from the standing variation that become fixed during adaptation. We find that, compared to adaptation from de-novo mutations, (i) adaptation from standing variation proceeds by the fixation of more alleles of small effect; (ii) populations that adapt from standing genetic variation remain better adapted and can traverse larger distances in phenotype space if the rate of environmental change is fast rather than slow.

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Andreas Mayer

LPTENS (Paris, France)

Evolution of immune mechanisms

Andreas Mayer, Thierry Mora, Aleksandra Walczak, Olivier Rivoire

Biological organisms have evolved a wide range of strategies to defend themselves against pathogens. From an evolutionary standpoint these strategies differ substantially in how they process and pass on information about the environment. Here we develop a common mathematical framework to assess the capacity of different strategies to cope with random environmental changes. To maximize the long term growth rate the population needs to balance the beneficial effect of being protected if the pathogen is present against the cost of protection. We find that optimal strategies often involve bet-hedging and identify the conditions under which this is the most advantageous strategy. We describe the conditions in which learning about the environment during the lifetime of an organism is beneficial.

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Etsuko Nonaka

University of Helsinki (Helsinki, Finland)

Spatial distributions of genetic diversity and local adaptation in metapopulations on heterogeneous landscapes

Etsuko Nonaka

Existing theories of population genetics for spatially subdivided populations often assume a constant genetic variance across local populations for mathematical tractability. Genetic diversity is a key ingredient determining evolutionary potential of populations, especially under changing environments. It can be temporally and spatially variable and influenced by selection, gene flow, and genetic drift. In heterogeneous landscapes, spatial habitat structure influences such evolutionary as well as demographic processes and determines gene flow and the prevalence of genetic drift, resulting in heterogeneous spatial distributions of genetic diversity. We developed an eco-evolutionary model of a metapopulation living in a heterogeneous landscape to investigate 1) the effects of dynamic vs. constant genetic diversity on local adaptation, and 2) how landscape structure may affect the spatial distributions of genetic diversity. The results suggest that dynamic genetic diversity can produce different patterns of local adaptation than when it is kept constant at the mean value. Long-term averages of genetic diversity and the degree of local adaptation can be well predicted by population size and types of immigrants, which are in turn predicted largely by patch area and connectivity. Frequent extinction and colonization events can obscure this relationship.

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Andrej Novak

Faculty of Electrical Engineering and Computing (Zagreb, Croatia)

Continuum model of gene expression by small non-coding RNAs and protein Argonaute.

Andrej Novak, Gabriela C. Racz

In this poster we present mathematical model of gene expression based on coupled system of partial differential equations that describes complex evolution of mRNA and sRNA concentrations in a small part of tissue. Model of the interaction between one mRNA and different types of non-coding sRNAs in biological cells have been recently described by system the of coupled reaction-diffusion equations. In order to model interaction between mRNAs and sRNAs more accurately, it is not sufficient to only focus on their concentrations in the cell or tissue. Studies have shown that members of the Argonaute (Ago) protein family have essential role in RNA silencing process, as one of the key components of RNA-induced silencing complex (RISC). sRNA alone is not enough to suppress the expression of specific genes. In order for suppression to occur, it is necessary that sRNA interacts with multiprotein complex RISC, more specifically with its essential component - Ago protein. We propose mathematical model that takes in to account the importance of Ago protein, allowing us to model evolution of mRNA, sRNA concentrations on the tissue level. We also present computational results.

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Leonardo Oña

Centre for Ecological and Evolutionary Studies (Groningen, The Netherlands)

Evolution of sexual and clonal populations on complex adaptive landscapes.

Oña, Leonardo; van Doorn, Sander

In the present work, we studied how clonal and sexual populations realise complex innovations depending on specific properties of the genotype-phenotype map. In clonal populations evolving on complex adaptive landscapes, such innovations appear as large fitness jumps that are alternated by periods of neutral evolution. Sexual populations may have an advantage relative to clonal populations during the initial phase of nearly neutral evolution, because they can more rapidly explore large regions of genotype space by recombining alleles in novel combinations. However, once a favourable combination of alleles has been found, clonal populations will be able to transmit this genotype faithfully, whereas it will be broken up by recombination in sexual populations. The strength of genetical associations and, as a consequence, the effect of gene interactions on evolutionary trajectories is affected by the rate of recombination. This implies that complex traits might evolve differently in sexual and asexual populations, which may be reflected in the organisation of their biochemical networks. In order to test this hypothesis, we examined mechanistic models of network evolution, and analysed evolutionary simulations of simple biochemical network models as well as more complex pathways and larger network modules. Comparisons between these scenarios can reveal whether there are systematic differences in the structure of the biochemical networks between clonal and sexual populations.

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Swati Patel

University of California Davis (Davis, USA)

Eco-evolutionary dynamics of an intraguild predation module

Swati Patel

Feedbacks between ecological and evolutionary processes can have important impacts on complex communities, with direct and indirect species interactions. In this talk, I will discuss specifically the relationship between these feedbacks, the types of interactions in a community and community stability. I will start by presenting a result on how to determine the effects of eco-evolutionary feedbacks on stability for rapid and slow evolution. Then, I will discuss examples in tightly-coupled ecological modules and the insights these provide into when and how feedbacks stabilize or destabilize a community.

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Yuriy Pichugin

New Zealand Institute for Advanced Study (Auckland, NZ)

The evolution of cooperation in group structured populations with migration: implications for the evolution of multicellularity.

Yuriy Pichugin, Chaitanya S. Gokhale, Julian Garcia, Arne Traulsen, Paul B. Rainey

The evolution of cooperation in group-structured populations has received much attention, but little is known about the effects of particle migration between groups. Here we incorporated four different modes of migration that differed in the degree of coordination among the particles. For each mode of migration, we identify the set of multiplayer games, in which the cooperative strategy has higher fixation probability than defection. The comparison shows that the set of games under which cooperation may evolve expands depending upon the degree of coordination among the migrating particles. We also show that weak altruism can evolve under all mode of particle migration provided that the benefit to cost ratio is high enough. Strong altruism evolves only if the mode of migration involves coordination of particle actions. The findings have implications for understanding the evolution of multicellularity where in the earliest capacity for autonomous replication was absent. Migration of particles between collectives, while typically thought of in terms of dispersal, also acts to establish genealogical connections between recurrences of collectives. In so doing migration – depending upon its frequency and degree of coordination among particles – establishes conditions that allow selection to work at the level of collectives.

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Verónica Miró Pina

Collège de France

Spatial patterns of speciation

Verónica Miró Pina, Emmanuel Schertzer

The speciation process can be influenced by many genetic and ecological factors and give rise to complex spatial patterns. One particularly intriguing example is the case of ring species, in which two geographically segregated subpopulations can exchange genes by reproducing with one or several intermediate subpopulations. The geographic constraints that may have shaped those species complexes and the evolutionary forces maintaining them are still unclear. Using a population based model we study how genetical dynamics (mutation, migration, recombination) can contribute to the emergence and the stability of these patterns and we show that complex patterns of speciation can emerge, even in the absence of geographical barriers, between subpopulations initially connected by a certain gene flow.

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Arunas L. Radzvilavicius

University College London (UK)

Modelling the role of mitochondria in the evolution of germline and two sexes

Arunas L. Radzvilavicius

The origin of the germline-soma distinction in metazoans is a fundamental unsolved question. Somatic gametogenesis in sessile sponges and corals is in stark contrast to early germline sequestration in bilaterians with higher energy requirements, fast evolution of small mitochondrial genomes and elaborate body plans. We have developed a sophisticated evolutionary model to investigate whether selection for mitochondrial quality can drive germline evolution. In basal metazoans with low mutation rates, somatic gametogenesis optimizes gamete quality through segregation of mitochondrial mutations in multiple cell divisions. Selection for mitochondrial quality in somatic tissues explains the evolution of anisogamy and male–female dimorphism. Increasing mitochondrial mutation rate in motile bilaterians drives the early sequestration of a dedicated germline, permitting the evolution of complex developmental processes linked to the Cambrian explosion.

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Sébastien Raguideau

INRA (Jouy-en-Josas, France)

Modeling Fiber Degradation by Human Gut Microbiome

Sébastien Raguideau, Sandra Plancade, Béatrice Laroche, Marion Leclerc.

The human intestinal microbiota is a complex microbial ecosystem that plays a crucial role in several aspects of human health. It is particularly involved in the metabolism of residual fibers, through anaerobic digestion, thus providing significant energy (Short Chain Fatty Acids, simple sugars) and vitamins to the host. Its description is therefore a critical question. So far, a standard approach has been to characterize the taxonomic range and diversity of the main species sampled from feces. Paradoxically, while a very large taxonomic diversity has been observed between individuals, the gut microbiome harbors the same metabolic functions across individuals. From the ecological point of view, the gut bacteria undergo a strong environmental selection pressure in the human gut, leading to a limited number of viable functional traits. Deciphering these traits from microbiome samples of a variety of individuals might be the best way to characterize gut microbiota micro-organisms. In this work, we aim at characterizing the main fiber degradation traits using recently available metagenomic data. Whole Genome Sequencing (WGS) data from metagenomic analyses give an insight of the content in terms of genes of an entire microbial community, even if the organisms that compose it cannot be cultivated, as in the gut microbiome. In addition to the potential of conventional molecular inventory techniques (such as targeting ADNr16s), which allows an analysis of diversity, WGS approaches provide an access to the functions. We show how these data can be used to elucidate the functional structuration of carbohydrates degradation among 1267 samples. In order to do so, we developed a Non-Negative Matrix Factorization (NMF) approach with biologically informative regularization and constraints. We obtain a limited number of interpretable functional profiles (about 20) allowing us to reconstruct up to 80 % of the signal.

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Mahdi Saber Raza

City University London (UK)

Using Survival Analysis to Investigate Breast Cancer in the Kurdistan Region of Iraq

Mark Broom and Martin Newby

The incidence of breast cancer varies greatly around the world. Breast cancer is the most common type of cancer in women in both the developed and developing countries (WHO, 2008). The incidence of breast cancer is increasing in developing countries due to increased life expectancy, increased urbanization and wider adoption of western lifestyles. In Kurdistan, in the north of Iraq, breast cancer is mainly a disease of pre-menopausal women with several pregnancies according to Majid, et al., (2009). Incidence rates for younger patients are comparable to Western countries; however they are higher than most Middle-Eastern countries which noticeably decline with age unlike in the West. Also, delays in diagnosis can lead to clinical stages being more advanced. In order to measure the survival of women with breast cancer in the Kurdistan Region, secondary data have been used based on laboratory investigations. These data are supplied by two main hospitals in the Kurdistan Region, which are: Hewa and Nanakali Hospitals (from 1991 until 1, June, 2014), and were collected from existing databases. Classical survival analysis is applied to this data, which includes Cox regression to determine the significant risk factors, the Kaplan-Meier method to find the survival curve for the chosen significant variable and log-rank tests to compare within each specific variable. The type of data supplied by each hospital has meant that to properly carry out the above analysis, and in particular to find the survival function, we have needed to develop a new Markov chain based model. We shall discuss the data, the new model, as well as preliminary analytical results. REFERENCES WHO (2008). The global burden of disease: 2004 update. Majid RA, Mohammed HA, Saeed HM, Safar BM, Rashid RM, Hughson MD(2009). Breast cancer in Kurdish women of northern Iraq: incidence, clinical stage, and case control analysis of parity and family risk. BMC Women's Health, Vol. 9, No. 33.

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Martin Andrade Restrepo

Institut Jacques Monod (Paris, France)

On the Emergence of Clustering along Space-Trait Gradients

Martin Andrade, Regis Ferriere, Nicolas Champagnat, Feng Gao

We present an analysis of the emergence of clustering in a stochastic model introduced in [1] representing the interaction between spatial competition and local selection in terms of a trait and a gradually varying environment. We study both numerically and analytically the emergence and characteristics of clustering in terms of the system's parameters and initial conditions. Our main contributions are the derivation of approximate formulas relating the population's distribution and the model's parameters, an analysis of the characteristics of these distributions, and the discovery of different cluster-inducing mechanisms as a function of the system's initial conditions. Bibliography [1] Champagnat, N., Méléard, S. (2007). Invasion and adaptive evolution for individual-based spatially structured populations. *Journal of Mathematical Biology* 55(2), 147–188.

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Tomas A. Revilla

Biology Centre Czech Academy of Sciences (Czech Republic)

Pollinator foraging flexibility and the coexistence of competing plants

Tomas A. Revilla and Vlastimil Krivan

Models of plant-animal mutualism rely increasingly on concepts derived from consumer-resource theory (e.g., saturating functional responses). We applied a consumer-resource approach to study the coexistence between two plants and a common pollinator. Our model considers two important details: an explicit distinction between plants and plant resources, and pollinator foraging flexibility. In the presence of a non-flexible pollinator, plant coexistence typically requires that the strength of intra-specific competition be greater than inter-specific competition (for factors not related to the pollinator). In contrast, when the pollinator diet responds to differences between energy gains from both plants, plant coexistence becomes more difficult to attain, even if inter-specific competition is absent. This runs opposite to the well known result that flexible consumers maintain diversity by reducing consumption pressure on rare resources, but it is easy to explain as the consequences positive feedbacks that characterize mutualisms.

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Tom Rosenström

University of Bristol and University of Helsinki (Finland)

Depressive symptoms as adaptive management of divorce threat: a model of optimal

Tom Rosenström, Tim W Fawcett, Andy D Higginson, Niina Metsä-Simola, Alasdair I Houston, Pekka Martikainen

The bargaining model of depression views depression as an adaptive response that trades some obviously fitness-reducing factors (e.g., heightened mortality risk) for other factors that increase expected fitness (e.g., future reproductive benefits from resolving marital conflict). Analogous trade-offs are assumed by related evolutionary explanations such as the “social navigation” and “adaptive rumination” hypotheses. We use an evolutionary approach to assess whether such a fundamental trade-off can explain the incidence of depression around the time of relationship breakdown. We identify the times and situations in which a ‘depressed’ behavioral mode is optimal, assuming that it alters the trade-off between current survival probability and future reproductive possibilities. The model predicts that depression should peak at the time of divorce. This prediction is supported by data on the purchases of antidepressants recorded in a national register of Finns ($n = 304\ 112$): the model explains ~94% of the change in prevalence of antidepressant purchases for the 10-year period around the time of divorce. However, our model cannot explain the novel observation that the peak in antidepressant purchases around the time of divorce is more pronounced in older people. Evolutionary models of depression that only consider offspring production cannot account for this age-related pattern, because reproductive potential declines with old age. We discuss the potential for inclusive fitness and/or parental care theory to increase our understanding of the evolution of depression.

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Mattias Siljestam

Uppsala University (Sweden)

MHC polymorphism as a result of evolutionary branching

Mattias Siljestam and Claus R uffler

MHC-genes are highly polymorphic loci where alternative alleles are maintained by heterozygote advantage. The MHC class II genes are responsible for inducing immune defence against diseases by antigen presentation. We present a model showing that polymorphism at a MHC class II locus can evolve through evolutionary branching. In our model, alleles at the MHC locus code for gene products that are responsible for inducing the immune defence for two diseases with defence against both being vital to complete the life cycle. Additionally, we assume a trade-off in the sense that MHC alleles that induce an effective defence against one disease are less effective in inducing a defence against the other disease, and vice versa. We find evolutionary branching in MHC alleles if the trade-off in performance is sufficiently strong, i.e., if the performance of a genotype homozygous for a generalist MHC allele is sufficiently poor. In this case, the heterozygous genotype carrying both specialist alleles has high fitness. Given the condition for branching is fulfilled, two different outcomes are possible. First, a single branching event leads to the evolution of an allelic dimorphism of two specialist alleles. Second, two consecutive branching events lead to the evolution of an allelic trimorphism consisting of two specialist and a generalist allele.

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Gayle J. Somerville

University of Western Australia (Perth, Australia)

Herbicide resistance

Gayle J. Somerville, Stephen B. Powles, Michael Renton

Does adding a spatial component to a herbicide resistance population model improve understanding and predictions of the buildup of herbicide resistance over time? Weeds are patchy, and these patches can be dynamic. A model of weed population dynamics and herbicide resistance evolution that includes a spatial component can allow for more realistic modelling of important spatial heterogeneity in genetic mutations and frequencies and density/yield interactions, and the stochastic nature of genetic drift and migration. This can lead to new insights and understanding and an increase in grower and researcher confidence in these predictions. One useful tool to increase the transparency, accuracy and usefulness of a herbicide resistance model is through increasing the realism whereby biological processes are represented in the model. To model plant interactions occurring uniformly across a whole field of weeds is unrealistic; biological interactions and dispersal are typically local scale, likely causing the patches of weeds that occur in fields. The aim here was therefore to include a spatial component in an existing model by dividing a single homogeneous population into many individual sub-populations in areas defined as ‘quadrats’. This allowed us to incorporate both natural and anthropogenic pollen and seed spread within and between quadrats into the new SOMER (Spatial Options in Modelling Evolutionary Resistance) model. The spatial model has already provided new insights. For example, earlier non-spatial models predict that the number of resistant weeds in a field typically increases by a constant factor each year, at least until densities become high. However preliminary results from this spatial model indicate that resistance builds up more slowly when spatial factors are accounted for, due the need for the resistance genes to spread through the population. Additional studies evaluating the importance of pollen dispersal and the movement of seed by machinery are currently being examined.

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Sabrina Heike Streipert

Missouri University of Science and Technology (Rolla, United States)

The Beverton-Holt difference equation with periodic growth rate

Sabrina Streipert, Martin Bohner

We study the periodically forced Beverton-Holt difference equation with periodic carrying capacity and periodic inherent growth rate. For this equation, we present a proof of the first Cushing-Henson conjecture, the existence of a unique periodic and globally attractive solution. The classical second Cushing-Henson conjecture that has the biological interpretation that a periodic environment is deleterious for the population is violated as an example shows. We present two alternative formulations of the second Cushing-Henson conjecture, relating the average of the periodic solution to the average of the carrying capacity.

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