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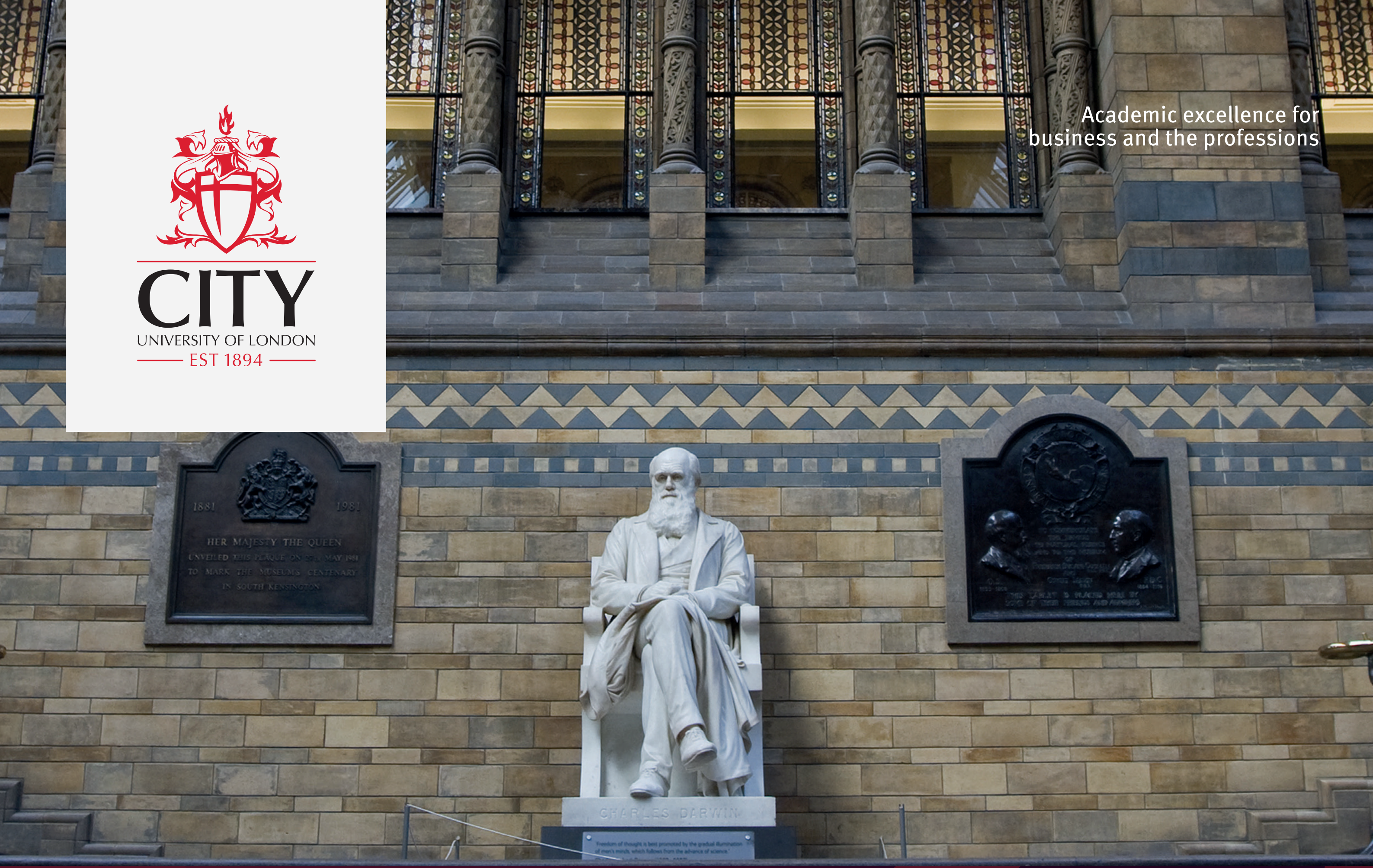

Mathematical Models in Ecology and Evolution

Book of abstracts

10th – 12th July 2017
City, University of London

Sponsored by:
LONDON MATHEMATICAL SOCIETY
ESMTB

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Contents

Welcome to Mathematical Models in Ecology and Evolution 2017

Mathematical Modelling plays a central and increasingly important role in ecology and evolution. The object of the meeting is to show the latest development of mathematical models in ecology and evolution and to demonstrate the important role of such modelling to a new generation of researchers. This conference is the sixth in an ongoing bi-annual series of events, the first of which was held at the University of Sussex (2007). Subsequent events have been held at the University of Bristol (2009), University of Groningen (2011), University of York (2013) and College de France, Paris (2015).

At this year's meeting there will be six plenary talks, over 160 shorter talks organised into 32 sessions (organised minisymposia or comprising submitted talks) and over 20 posters. Thus there should be plenty to grab your attention, and indeed the biggest problem should be deciding what you have to miss!

We hope that you enjoy MMEE2017,

Mark Broom (on behalf of the Local Organising Committee and Scientific Committee)

Programme Overview

Monday 10th July

Time	Presentation	Room
08:30	Registration and pre-conference coffee	OTLT Foyer
09:00	Welcome: David Bolton (Deputy President, City, University of London) & Mark Broom (City, University of London)	OTLT
09:30	Plenary: Hanna Kokko (University of Zurich)	OTLT
10:30	Coffee Break	Great Hall
11:00	Minisymposium 1A: Collective behaviour and decision-making	A130
11:00	Minisymposium 1B: Complex ecological communities I	A109
11:00	Minisymposium 1C: Evolutionary games I	A110
11:00	Minisymposium 1D: Fitness landscapes	AG03
11:00	Minisymposium 1E: Stochastic spreading processes on networks	AG07b
13:00	Lunch Break	Great Hall
14:15	Submitted talks 2A: Mathematical genetics I	A130
14:15	Submitted talks 2B: Metapopulation models	A109
14:15	Submitted talks 2C: Evolutionary game theory I	A110
14:15	Submitted talks 2D: Life history models	AG03
14:15	Submitted talks 2E: Complex populations and networks	AG07b
16:15	Coffee Break	OTLT Foyer
16:45	Plenary: Ross Cressman (Wilfrid Laurier University)	OTLT
17:45	End of day	

Tuesday 11th July

Time	Presentation	Room
08:30	Registration and pre-conference coffee	OTLT Foyer
09:00	Plenary: Nuala Sheehan (University of Leicester)	OTLT
10:00	Coffee Break	Great Hall
10:30	Minisymposium 3A: Evolution of collective identity	A130
10:30	Minisymposium 3B: Complex ecological communities II	A109
10:30	Minisymposium 3C: Social evolution in subdivided populations	A110
10:30	Minisymposium 3D: Modelling plankton ecosystems	A111
10:30	Minisymposium 3E: Forecasting cancer evolution I	AG03
10:30	Minisymposium: 3F Evolutionary games II	AG07b

12:30	Posters and Lunch Break	Great Hall
14:30	Submitted talks 4A: Mathematical genetics II	A130
14:30	Submitted talks 4B: Spatial populations and animal movement I	A109
14:30	Submitted talks 4C: Medical and epidemic models I	A110
14:30	Submitted talks 4D: Population dynamics I	A111
14:30	Submitted talks 4E: Ecosystems	AG03
14:30	Submitted talks 4F: Evolutionary game theory II	AG07b
16:30	Coffee Break	Great Hall
17:00	Posters Continued	Great Hall
18:00	Public Lecture: Iain Couzin (University of Konstanz)	OTLT
19:00	Conference Reception	OTLT Foyer
20:30	End of day	

Wednesday 12th July

Time	**Presentation**	**Room**
08:30	Registration and pre-conference coffee	OTLT Foyer
09:00	Plenary: Nick Chater (University of Warwick)	OTLT
10:00	Coffee Break	Great Hall
10:30	Minisymposium 5A: Adaptive strategies in ecological networks	A130
10:30	Minisymposium 5B: Forecasting cancer evolution	A109
10:30	Minisymposium 5C: Game theory and the evolution of cooperation	A110
10:30	Minisymposium 5D: Mathematical genetics III	AG03
10:30	Minisymposium 5E: Hosts, parasites and pests	AG07b
12:30	Lunch Break	Great Hall
13:45	Submitted talks 6A: Evolutionary game theory III	A130
13:45	Submitted talks 6B: Spatial populations and animal movement II	A109
13:45	Submitted talks 6C: Branching processes and inference frameworks	A110
13:45	Submitted talks 6D: Medical and epidemic models II	AG03
13:45	Submitted talks 6E: Population dynamics II	AG07b
15:45	Coffee Break	OTLT Foyer
16:15	Plenary: Caroline Colijn (Imperial College London)	OTLT
17:15	End of day	

Poster Presentation

P1: Diepreye Ayabina - Detecting disruptive sites in the tuberculosis genome

P2: Katarina Bodova - Unraveling the F-box - The evolution of F-boxes in non-self-recognition self-incompatibility systems

P3: Atheeta Ching - Diagonal Stability in Lotka-Volterra Systems

P4: Jacob Dinner O’Sullivan - Spatially explicit theoretical community assembly

P5: Abeer Elbahrawy - Bitcoin ecology: Quantifying and modelling the long- term dynamics of the cryptocurrency market

P6: E. Yagmur Erten - Cell-level life history trade-offs under cancer risk

P7: Lynn Govaert - Partitioning community trait variation into ecological and evolutionary contributions

P8: Carolina Grejo - Evolution of species: the mutation as a strategy of survival

P9: Orestes Gutierrez - To what degree are attack rates constrained by eco- logical and biological factors?

P10: Jitesh Jhawar - Role of stochasticity in the dynamics of fish schools

P11: Vincent Keenan - Anomalous invasion speeds in highly polymorphic populations Invasion ecology

P12: Yoram Louzoun – Commensal pathogens as a source of a coexistence mechanism

P13: Sebastian Matuszewski - On the (un)predictibality of a large intragenic fitness landscape

P14: Jorge Pena - The economics of egg trading revisited

P15: Aakanksha Rathore - Spatial dynamics of Blackbuck herds

P16: Tom Ratz - Adaptive dynamics as a tool to predict when flexible parenting evolves

P17: Jessie Renton - Evolution in dynamic population structures

P18: Andrew Rowntree - Stability analysis of Discrete mutualism models with delay

P19: Zhijun Wu - Equilibrium Distribution of Populations of Biological Species on Networks of Social Sites

P20: Mark Zimmerman - When to expect predator-prey coevolutionary arms races

Monday 11:00 Sessions

Minisymposium 1A: Collective Behaviour and Decision-Making

Room A130

Andrea Baronchelli	The Spontaneous Emergence of Conventions	11:00
Andreagiovanni Reina	A model of the best-of-N nest-site selection process in honeybees	11:24
Arianna Bottinelli	The breakdown of coordination and the emergence of dangerous collective motions in high-density crowds	11:48
Colin Torney	Cues and collective decision-making in migrating ungulates	12:12
Renaud Bastien	A Simple Model of Collective Behaviour Driven by the Visual Field	12:36

Minisymposium 1B: Coexistence in complex ecological communities I

Room A109

Geza Meszena	Mathematical niche theory	11:00
Namiko Mitarai	Assembly rules and a minimal theory for invasion and extinction in food webs	11:30
Francesco Carrara	The structure of interactions in microbial microcosms	12:00
Annette Ostling	Emergent structure and dynamics in stochastic, open, competitive communities	12:30

Minisymposium 1C: Evolutionary games I

Room A110

Mark Broom	Modelling evolution in structured populations using multiplayer games	11:00
Karen Pattni	Evolving multiplayer networks: Modelling the evolution of cooperation in a mobile population	11:24
Rosalyn Rael	Species trait distributions in evolutionarily assembled model food webs	11:48
Li You	Game theory for modeling cancer and its treatment	12:12
Yannick Viossat	Strong forms of non-convergence to evolutionary stable states for all reasonable evolutionary dynamics	12:36

Minisymposium 1D: Fitness landscapes 2.0: Big data and the predictability of evolution

Room AG03

Thomas Bataillon	Properties of beneficial mutations: fitness landscape models and inference from population genomics data	11:00
Guillaume Achaz	Epistatic constraints in fitness landscapes, theory and practice	11:24
Kristina Crona	Higher Order Epistasis and Evolutionary Dynamics	11:48
Ines Fragata	Sounds of silence: The fitness landscape of synonymous mutations	12:12
Richard Watson	Evolving fitness landscapes: How evolution learns to improve evolvability on rugged fitness landscapes	12:36

Minisymposium 1E: Stochastic spreading processes on networks

Room AG07b

Chris Overton	Deterministic approximations of stochastic dynamics in evolutionary graph theory	11:00
Joel Miller	Spread of infection in random spatial networks	11:24
Robert Wilkinson	The impact of the infectious period on epidemics	11:48
Luc Berthouze	Impact of higher-order structure on critical behavior in a complex contagion model	12:12
David Sirl	On a network epidemic model with preventative rewiring	12:36

Monday 14:15 Sessions

Submitted Talks 2A: Mathematical genetics I

Room A130

Kevin Gomez	Modeling how selection in one trait interferes with adaption in another	14:15
Salome Bourg	How evolution draws trade-offs: an evolutionary physiology model	14:35
Yoav Soen	Darwinian Selection Induces Transient Lamarckian Adaption in a Holobiont Model	14:55
Diogo Santos	From phenotypes to fitness time is relative in evolution	15:15
Belgin Seymenoglu	Invariant manifolds of a model from population genetics	15:35
Matthew Edgington	Engineered underdominance gene drive as a tool for public health and ecology	15:55

Submitted Talks 2B: Metapopulation models

Room A109

Stephen Cornell	Optimal connectivity measures for dynamic landscape metapopulations	14:15
Philip Pollett	Metapopulations in evolving landscapes	14:35
Meike Wittmann	Eco-evolutionary buffering: rapid evolution facilities regional species coexistence despite local priority effects	14:55
Tommi Mononen	Less severe patch-wise epidemics in dense patch clusters in comparison to sparse areas	15:15
Andrea Baronchelli	Emergence of metapopulations and echo chanbers in mobile agents	15:35

Submitted Talks 2C: Evolutionary game theory I

Room A110

Matthijs van Veelen	How to test Hamiltons rule empirically	14:15
Ben Allen	Evolutionary Games on Any Graphs	14:35
Shmuel Gal	Using Stochastic Games to model Predator-Prey Search Pursuit behaviour	14:55
Krzysztof Argasinski	Dynamical approach to the game theoretic selection models based on state	15:15
Coralie Fritsch	A numerical approach to determine mutant invasion fitness and evolutionary singular strategies	15:35
Vladimir Svigler	On Arbitrarily Long Periodic Orbits of Evolutionary Games on Graphs	15:55

Submitted Talks 2D: Life history models

Room AG03

Danya Rose	Ecological and social changes affecting human evolution: or grandmothers and long childhood dependency make the human life history	14:15
Ricardo Martinez-Garcia	Lack of ecological and life-history context can create the illusion of microbial social interactions	14:35
Dmitrii Logofet	Polyvariant Ontogeny in Plants: A Primary Role of the Second Positive Eigenvalue	14:55
Yuriy Pichugin	Fragmentation models and the evolution of life cycles	15:15
Simran Sandhu	Using variational principles for modelling self-replicating systems	15:35

Submitted Talks 2E: Complex populations and networks

Room AG07b

Ghjuvan Grimaud	Evolution of metabolic networks under non-balanced growth conditions	14:15
Guy Cooper	The Evolution of the Germ-Soma Divide	14:35
Jessica Baker	Context-dependent communication: costly signaling in a social network can lead to a “poverty trap”	14:55
Arnaud Dragicevic	Spacetime Discounted Value of Network Connectivity	15:15
Hiroshi Toyoizumi	The Relatedness in the Field Observations and Computer Simulations: The Bias of the Observation	15:35
Elske van der Vaart	Taking Error Into Account When Fitting Models Using Approximate Bayesian Computation	15:55

Tuesday 10:30 Sessions

Minisymposium 3A: Evolution of collective identity

Room A130

Joshua Plotkin	New perspectives on cooperation in iterated games	10:30
Sergey Gavrilets	Closer than brothers: The evolutionary roots of identity fusion	10:54
Nichola Raihani	Signaling in the evolution of costly social behavior	11:18
Vincent Jansen	Groups, words and the words that groups use	11:42
Alex Stewart	Group thinking and generosity in the evolution of cooperation	12:06

Minisymposium 3B: Coexistence in complex ecological communities II

Room A109

Jon Pitchford	The ecological complexity of global macro-economics	10:30
Samraat Pawaar	Metabolic constraints on complex ecosystems	11:00
Gyuri Barabas	The effect of intra-interspecific competition on coexistence in multispecies communities	11:30
Axel Rossberg	How structural instability of ecological communities manifests in nature	12:00

Minisymposium 3C: Social evolution in subdivided populations: Beyond the usual assumptions

Room A110

Florence Debarre	Fidelity of parent-offspring transmission and the evolution of social behaviour in structured populations	10:30
Charles Mullon	A kin selection perspective on multi-dimensional adaptive dynamics in subdivided populations	10:54
Hye Jin Park	Ecological feedback on evolutionary spatial dynamics with social dilemmas	11:18
Jorge Pena	Invasion and fixation of nonlinear cooperation in subdivided populations	11:42
Antonio M Rodrigues	Social evolution in a demographic context	12:06

Minisymposium 3D: Recent advances in modelling plankton ecosystems
Room A111

Aditee Mitra	The New Mixotrophic-Paradigm in Marine Ecology	10:30
Ben Ward	An Efficient Instant Acclimation Approximation of Dynamic Phytoplankton Stoichiometry	11:00
Andrew Morozov	Imperfect prey selectivity of generalist predators promotes biodiversity and irregularity in food webs	11:30
Ivan Sudakov	Large ecosystems in a changing environment: interactions and feedbacks	12:00

Minisymposium 3E: Forecasting cancer evolution: combining mathematical modelling and experimental/clinical data I
Room AG03

Fabian Theis	Reconstructing branching lineages in single cell genomics	10:30
Sandy Anderson	The Evolution of Colorectal Cancer Under Immune Predation	11:00
Simon Tavare	Inference from cancer sequencing data	11:30
Benjamin Werner	Forecasting resistance evolution in cancer from liquid biopsies	12:00

Minisymposium 3F: Evolutionary games II
Room AG07b

Ross Cressman	Interaction times change evolutionary outcomes	10:30
Vlastimil Krivan	A game-theoretic approach to modeling foraging dynamics	10:54
Boyu Zhang	Extortion and contribution game: rationality versus fairness	11:18
Fei Xu	Optimal Forager against Ideal Free Distributed Prey	11:42
Jozsef Garay	Sib cannibalism as a mutualism	12:06

Tuesday 14:30 Sessions

Submitted Talks 4A: Mathematical genetics II

Room A130

Reinhard Burger	Two-locus clines on the real line with a step environment	14:30
Swati Patel	Recombination rates affect eco-evolutionary feedbacks	14:50
Sviatoslav Rybnikov	Recombination rate coevolution in a quantitative trait model with diploid antagonists	15:10
Alexandre Blanckaert	The resolution of genetic incompatibility in a hybrid-population	15:30
Martin Pontz	Evolutionary dynamics in the two-locus two-allele model with weak selection	15:50
Katarina Bodova	A simple approximation for the complex dynamics of quantitative traits	16:10

Submitted Talks 4B: Spatial populations and animal movement I

Room A109

Tahani Al-Karkhi	Pattern formation in a PMZC plankton model	14:30
Linke Potgieter	The development of a spatio-temporal model for investigating biological control release strategies in water hyacinth	14:50
Marie-Carolina Prima	Combining network theory and reaction-advection-diffusion modelling: a mechanistic approach for predicting animal distribution in dynamic environments	15:10
Petr Stehlik	Exponential number of stationary solutions for reaction-diffusion equations on graphs	15:30
Laura Alessandretti	Multi-scale spatio-temporal analysis of Human Mobility	15:50

Submitted Talks 4C: Medical and epidemic models I
Room A110

Christoforos Hadichrysanthou	Within-host of influenza A: Can simples mathematical models help?	14:30
Rebecca Chisholm	Infectious diseases dynamics in the presence of asymptomatic infections	14:50
Istvan Kiss	Mean-field Models for non Markovian Epidemics on Networks	15:10
Ruairi Donnelly	Feedbacks between disease progress and vector aggregation, lessons from plant viruses	15:30
Robin Thompson	Accounting for donor viral diversity gives high estimates of the number of HIV founder virions in recipients	15:50
Shaher Momani	Applications of Fractional Calculus in Biological Systems: Theory and Numerics	16:10

Submitted Talks 4D: Population dynamics I
Room A111

Igor Ervenko	Dynamical Facilitation of the Ideal Free Distribution in Non-Ideal Populations	14:30
Stephen Baigent	The Ideal Free Distribution for Multiple Species	14:50
Halil Egilmez	Modelling seasonal dynamics of bacteria-phage interactions with a temperature-dependent lysogeny	15:10
Caz Taylor	A spatial network model for population dynamics of migratory species	15:30
Yoram Iouzoun	Fluctuations-induced coexistence in public goods dynamics	15:50
Krishna Dasu	Rich dynamics exhibited by predator-prey systems with mutual interference in the presence of inhibitory effect: A detailed theoretical investigation	16:10

Submitted Talks 4E: Ecosystems

Room AG03

Aisling Daly	The impact of resource dependence on the spatial population dynamics of an in silico microbial community	14:30
Thomas Bury	Regime shifts in socio-ecological systems: Silent early warning signals in the natural subsystem	14:50
Faranoush Farahpour	Eco-evolutionary dynamics in interaction space of competitive communities: How diversity emerges and persists	15:10
Surnithra Sankaran	Demographic noise promotes bistability in ecosystems	15:30
Thomas Koffel	A theoretical study of facilitative succession and ecosystem development by nitrogen fixers	15:50

Submitted Talks 4F: Evolutionary game theory II

Room AG07b

Robert Spencer	Modelling kleptoparasitism in an urban gull (Laridae) population	14:30
Esteban Vargas Bernal	Modelling sexual selection in Tungara frog and rationality of mate choice	14:50
Chakib Jerry	Commercial fishing model: Application of differential game theory	15:10
Zhijun Wu	Evolution of Cooperation Between Two Yeast Strains	15:30
Slimane BenMiled	HermaDEB: a model for the energy allocation in Hermaphrodite	15:50
Amira Kebir	When presentism and externalism meet sex changing cost to explain multiple sex change hermaphrodite	16:10

Wednesday 10:30 Sessions

Minisymposium 5A: Adaptive strategies in ecological networks – drivers, dynamic constraints, and the link with data

Room A130

Nicolas Loeuille	Effects of local negative feedbacks on the evolution of species within metacommunities	10:30
Korinna Allhoff	Selective effects of temperature on body size depend on trophic	11:00
Eric Tromeur	Eco-evolutionary consequences of harvesting complex food webs	11:30
Anje-Margriet Neutel	Quantitative feedback analysis as a way to study adaptive strategies in food webs	12:00

Minisymposium 5B: Forecasting cancer evolution: combining mathematical modelling and experimental/clinical data II

Room A109

Vito Latora	The growth of spatial networks	10:30
Jacob Scott	The game's the thing: how we'll learn the evolution of the king (of maladies)	11:00
Ingmar Glauche	Lessons form clonal dynamics in diseased and non-diseased hematopoiesis	11:30
Marc Williams	Measuring and predicting clonal evolution in human cancers with genomics	12:00

Minisymposium 5C: The second workshop on new trends in game-theoretical studies on the evolution of cooperation

Room A110

Isamu Okada	Costly reputation systems and the evolution of indirect reciprocity in the donation game	10:30
Hitoshi Yamamoto	Development of a norm ecosystem to understand different roles of social norms in indirect reciprocity	11:00
Christian Hilbe	Why we obscure positive traits and good deeds	11:30
Satosi Uchida	Games with prospect: a simple solution mechanism to social dilemma	12:00

Minisymposium 5D: Mathematical genetics III

Room AG03

Fabio Chalub	Regularity and time-inhomogeneity in the Wright-Fisher dynamics	10:30
Max Souza	Fixation: The Fingerprint of Evolutionary Processes	10:50
Tadeas Prikopil	When does an invasion of a novel trait imply substitution?	11:10
Daniel Crouch	Statistical aspects of natural selection in relation to the evolution of sexual reproduction	11:30
Yevhen Suprunenko	A new model of isolation-by-distance that overcomes longstanding technical limitations	11:50
Veronica Miro Pina	How does geographic distance translate into genetic distance?	12:10

Minisymposium 5E: Hosts, parasites and pests

Room AG07b

Fabio Lopes	A stochastic model for immune response with mutations and evolution	10:30
Hanna Schenk	Extinction times in host-parasite dynamics	10:50
Charlotte Ferris	Evolution of host defence in fluctuating environments	11:10
Frithjof Lutscher	Behavioural responses to resource heterogeneity can accelerate biological invasions	11:30
Ross Booton	Modelling immune function, pesticide exposure and infection in honey bee individuals	11:50
Cameline Orlendo	The evolution of sheep immunity in response to nematode infection	12:10

Wednesday 13:45 Sessions

Submitted Talks 6A: Evolutionary game theory III

Room A130

Caitlin Stern	The dynamics of cooperation when interactions change the rules of the game	13:45
Julian Garcia	Large-scale cooperation and antisocial punishment	14:05
Peter Czuppon	A spatial model for selection and cooperation	14:25
Rebecca Hoyle	Modelling social influence on cooperation: the public goods game on a multiplex network	14:45
Samuel Levin	The evolution of cooperation in simple molecular replicators	15:05
Jadeep Joshi	Demographic noise and the evolution of tag based cooperation	15:25

Submitted Talks 6B: Spatial populations an animal movement II

Room A109

Jane Shaw MacDonald	Approximating Dispersal Outcomes Using Weighted Mean First Passage Times	13:45
Nurdan Cabukoglu	Animal Diffusion Model Depending on Well-Being	14:05
Yi-Shan Wang	Partial differential equation techniques for analyzing animal movement: A comparison of three methods	14:25
Jitesh Jhawar	Role of stochasticity in the dynamics of fish schools	14:45
Jonathan Potts	How movement responses can shape demographic dynamics in strongly competing populations	15:05

Submitted Talks 6C: Branching processes and inference frameworks

Room A110

Francisco Richter	Generalizing species diversification models	13:45
Sophie Penisson	A genealogical model for the ancestor paradox	14:05
Anne Kandler	The crucial role of rare variants for inferring transmission processes	14:25
Krzysztof Bartoszek	The Ornstein-Uhlenbeck process modelling evolution of interacting populations	14:45
Cornelia Metzig	Phylogenetic Branching of Pathogens from Dynamic Host Contact Networks	15:05
Nicola De Maio	The Bacterial Sequential Markov Coalescent	15:25

Submitted Talks 6D: Medical and epidemic models II

Room AG03

Cristian Tomasetti	On the proportion of mutations in cancer due to normal cell division	13:45
Mark Robertson-Tessi	Tumor phenotypic plasticity, natural selection, and the microenvironment: An integrated, multiscale approach to designing better therapies	14:05
Faina Berezovskaya	Predator Prey Shared Resource Model in Cancer immunoediting	14:25
Daniel Nichol	Collateral Sensitivity is Contingent on the Repeatability of Evolution	14:45
Weni Huang	Revealing mutant fitness and timing by spatial mixing of sub-clones in tumour	15:05

Submitted Talks 6E: Population Dynamics II

AG07b

John Donohue	The population –level consequence of protective parenting	13:45
Vincent Keenan	Anomalous invasion speeds in highly polymorphic populations. Invasion ecology	14:05
Laurens Kilsdonk	The alternative states of monopolization	14:25
Kalle Parvinen	Environmental dimensionality	14:45
Georgy Karev	From experiment to theory: what can we learn from growth curves?	15:05

Plenary Speakers

Iain Couzin
Collective Sensing and Decision-Making in Animal Groups: From Fish Schools to Primate Societies

The extraordinary synchrony of motion exhibited as a flock of birds arcs overhead, or a school of fish turns, as a ripple of light, is captivating. Like some animate fluid the individual organisms appear to move as one, their minds seemingly connected by an invisible network. Professor Couzin's lecture will provide a visual guide to collective animal behavior, using the latest imaging technologies to reveal how and why animals exhibit collective motion, the huge impact swarms have on human life, and the remarkable collective sensing and decision-making capabilities that have arisen in animal groups.

Nick Chater
The biological and social worlds: Compare and contrast

Over many centuries, parallels have been drawn between social and biological phenomena, with insights propagating in both directions. This talk highlights considers some of those parallels: e.g., biological and cultural evolution; and between the emergence of complex coordinated behaviour among biological and social agents. While the parallels are striking, there are also some sharp contrasts between explanation in the biological and social science.

Caroline Colijn
Bacterial Olympics: modelling and detecting competition to control resistance

The rise and spread of antimicrobial resistance (AMR) is one of the most pressing examples of evolution today, as we are threatened with a ”post- antibiotic” era of untreatable infectious diseases. Resistance arises following selective pressure from the use of antibiotics. But once resistant strains have emerged, they can circulate alongside their drug-sensitive counterparts. It is not clear whether resistance is best controlled by reducing the selective pressure of antibiotics, or by treating aggressively to reduce opportunities for resistance to emerge.

Modelling must play a central role in answering these questions: the dynamics occur at the scale of whole populations and the time scales are too long for direct experiments. I will argue that the effectiveness of competition amongst the circulating pathogen strains is key to understanding how to control resistance, and I will describe why the whole-population scale is essential to understanding the future of resistance. I will then move to the challenges of measuring competition. The rise of sequencing technologies present an exciting opportunity to examine the ancestry and evolution of pathogen populations in the recent past and watch as resistance evolves and spreads. I will propose ways to use this rich genomic information to under- stand and model competition and the future of resistance.

Ross Cressman

The evolution of cooperation: Theory and experiment

The evolution of cooperation is still a fundamental puzzle in evolutionary biology and social science. Theory developed for the two-player Prisoners Dilemma (PD) game and Ultimatum Game (UG) or for the multi- player Public Goods Game (PGG) predicts cooperation should not evolve unless there are extending circumstances that favour cooperation such as kin selection, reciprocity (direct or indirect), graph selection, reward and/or punishment, etc. On the other hand, experiments based on these games (with either humans as participants or other species) consistently show some level of cooperation no matter what the circumstances. The theory has been developed and the experiments have been conducted by researchers in many different disciplines over many decades.

The presentation will give an overview of some recent experiments and their related theory. It will also consider in more depth progress in several directions; including the role of peer punishment in the PD game, of institutional reward and punishment in PGG, of the emergence of cooperative communities in UG, and of player control over the number of rounds that they interact with the same individual in repeated two-player games.

Hanna Kokko

Bet-hedging in evolutionary theory

Bet-hedging in biology has been called a seductive explanation, meaning that it is often applied whenever organisms appear to benefit by diversifying their portfolio of actions or traits. The real definition of bet-hedging is more stringent: a bet-hedger enjoys an evolutionary long-term advantage because its traits predict that variance in fitness is reduced (a benefit) while arithmetic fitness falls below that of a baseline (a cost) - where the baseline is a non- bet-hedger. The baseline non-bet-hedger may or may not exist in reality; bet-hedging occurs is a statement that can only be made in a comparative sense (i.e. relative to another strategy). We discuss a few examples: (1) sexual reproduction can be thought of as bet-hedging, but this may apply more strongly against certain types of asexual reproduction than others. In simple models at least, it is difficult to explain sex purely based on bet-hedging benefits, simply because the expected cost of sex is too large. (2) Dispersal, which is costly (risky) but diversifies the fates of offspring, can be thought of as a bet-hedging strategy. Bet-hedging theory predicts that reducing variance through one route (e.g. dispersal in space, or dispersal in time i.e. dormancy) should reduce selection to reduce it through another alternative (here sex can be thought to be dispersal in identity as an allele ends up in new genetic backgrounds). Against this expectation it is curious to note a pattern in nature: facultatively sexual organisms often undergo sexual life cycles in conditions that also promote dispersal in time or space. I will ask whether we really can explain such positive correlations based on theory.

Nuala Sheehan

Reconstructing Pedigrees from Genetic Marker Data

In theory, estimating the pedigree for a given set of individuals from genetic marker data simply requires consideration of all possible relationships amongst them and then computing the likelihood for each. Due to the large number of possible pedigrees, brute force enumeration rapidly becomes impractical. Existing likelihood-based approaches to pedigree structure estimation are either restricted to small numbers of individuals or else deliver a reconstruction that will probably have high likelihood but is not guaranteed to be optimal. By encoding the pedigree learning problem as an integer linear program, we can efficiently construct large pedigrees with guaranteed maxi- mal likelihood for the standard situation where all individuals are observed at unlinked marker loci, founder genotypes are in Hardy-Weinberg equilibrium and segregation of genes from parents to offspring is Mendelian. Since the simple factorisation of the likelihood in this setting defines a Bayesian network (BN), the reconstruction problem is equivalent to searching for an optimal BN where the search is constrained to BNs that are valid pedigrees.

The more realistic situation, where observed individuals are typically connected by (possibly many) missing individuals poses a far harder problem, however. Such applications will require efficient formulations of general purpose and graph learning algorithms. In particular, a Bayesian approach enabling the incorporation of additional prior information in a principled way would seem appropriate. Some of the issues involved and some proposed approaches to the problem will be discussed.

Abstracts

Epistatic constraints in fitness landscapes, theory and practice

Guillaume Achaz, Museum National d'Histoire Naturelle, France and Collège de France

Co-authors:
Luca Ferretti, Sophie Brouillet, Sebastian Matuszewski, Dan Weinreich, Fumio Tajima

How constrained is life evolution? How free are mutations along evolutionary paths? What are the fundamental processes that constraint evolution? What types of interactions matter for the evolution of life molecules? What are the minimal set of rules that one has to incorporate into the models to explain the constraint as we see them in biological systems. In the last decade, several experimental fitness landscapes were published. Their analysis, although only starting, show clearly that models of fitness landscapes proposed so far (e.g. Kaufman NK, Rough Mount Fuji, Fisher Geometric Landscape, etc.) cannot explain their structures. Using previous and newly developed summary statistics that describe fitness landscapes, we measure the fit between model and experimental fitness landscapes. While increasing the convergence between model prediction and biological observations, we should take a step further to understand how and why biological interactions matter in evolution.

Multi-scale spatio-temporal analysis of Human Mobility

Laura Alessandretti, City, University of London, United Kingdom

Co-authors: Piotr Sapiezynskib, Sune Lehmann, Andrea Baronchelli

The understanding of human mobility has advanced in recent years due to the availability of digital traces. There is consensus that distances and waiting times between consecutive locations in an individual`s trajectory are heavy tailed distributed. Mechanisms explaining the emergence of these statistical properties include individuals adopting Levyflight strategies. The debate is, however, still open also because limited data resolution has hindered the understanding of human motion at all spatial and temporal scales. Here, we characterise mobility behaviour across an unprecedented range of scales, analysing 850 individuals traces sampled every 16 seconds for 25 months with 10 meters spatial resolution. We show that the distributions of distances between consecutive locations and discoveries are best approximated by log-normal distributions across several orders of magnitude and that natural time-scales result from the deep-routed regularity of human mobility. Our findings provide key elements to explain and model the fundamental mechanisms governing mobility behaviour.

Pattern formation in a PMZC plankton model

Tahani A. S. Al-karkhi, University of Essex, United Kingdom

Co-authors: Edward Codling, Hadi Susanto

We focus on the phenomena of pattern formation in a reaction–diffusion model of plankton dynamics that includes info-chemical mediated trophic interactions. We consider both a simplified two species and extended four species model. Where the grazing pressure of microzooplankton (M) on phytoplankton (P) is controlled through external info-chemical (C) mediated predation by copepods (Z). We undertake a stability analysis of both the two species and four species models and compare the system dynamics. We also explore spatial pattern formation in both models and consider under what conditions a Turing pattern is exhibited or when spatiotemporal chaos is observed.

Evolutionary Games on Any Graph

Benjamin Allen, Emmanuel College, Boston, United States

Co-authors: Gabor Lippner, Yu-Ting Chen, Babak Fotouhi, Naghmeh Momeni, Shing-Tung Yau

Evolutionary games on graphs are a model for the evolution of social behavior in structured populations. Conditions for the success of a game strategy are known for regular graphs, in which all individuals have the same number of neighbors. The general case, in which the number of neighbors can vary, has remained open. We derive a condition for the success, under weak selection, of any pairwise game strategy on any graph or network. Our method relies on calculating the coalescence times of random walks. We evaluate large numbers of diverse population structures for their propensity to favor cooperation. We study how small changes in population structure -graph surgery- affect evolutionary outcomes. We find that cooperation flourishes most in societies that are based on strong pairwise ties.
[Note: the manuscript corresponding to this talk has been accepted for publication in *Nature*. A preprint is available at http://arxiv.org/abs/1605.06530]

Selective effects of temperature on body size depend on trophic interactions and network position

Korinna T. Allhoff, UPMC / IEES Paris, France

Co-authors: Avril Weinbach, Elisa Thébault, Francois Massol and Nicolas Loeuille

Individual body size is a key trait constraining interspecific interactions within food webs. It is particularly linked to individual metabolic rate. Because climate warming affects metabolic rates, it creates direct selective effects on body size. Most experimental studies and empirical observations suggest that body size decreases under warming, though important exceptions have been noticed. Using a consumer resource model that is structured through the evolution of the consumer body size, we analyse the conditions under which body size increases or decreases may be expected. We focus here on how variations in attack rates and position within the trophic network may affect the evolution of body size under warming. We observe that no change or increases in body sizes are possible when attack rates are constant or increasing with temperature, while body size reductions are only expected when attack rates have a thermal optimum and are initially locally adapted. As for the impact of trophic position, we found that body size at lower levels vary less under warming than body sizes at higher trophic levels, which may be explained by increased levels of stabilizing selection.

The Evolution of Colorectal Cancer Under Immune Predation

A.R.A Anderson, Moffitt Cancer Center, United States

Co-authors: T.A. Graham, C.D. Gatenbee, A.M. Baker, R. Schenck, M.R Tessi

Tumor cells carry antigens that make them susceptible to elimination by the immune system. This imposes a strong selection pressure that favors clones which can evade immune predation. Here, we use multi-region whole exome sequencing and immunohistiochemistry (IHC) to explore how the relationship between tumor immune ecology and antigenic heterogeneity changes throughout the progression of colorectal cancer. A multi-predator (immune) multi-prey (tumor clones) cellular automata (CA) is developed to examine which tumor-immune interactions could be responsible for the observed clinical patterns of immune composition and antigenic burden.

Genomic analysis reveals that antigenic heterogeneity and immune composition are significantly different when comparing adenomas (A) to either adenomas that have emerging carcinomas (AC) or carcinomas (C). IHC indicates that PDL1 expression is higher in A than in AC or C ($p < 0.01$). PDL1 and epithelial cells also have a positive spatial correlation in A ($p <0.05$), but no such relationship in tissues with any carcinoma (AC and C). IHC also reveals that macrophages tend to increase throughout progression ($p < 0.05$), but CD8 T-cells do not vary significantly across stages. Simulations show that tumors lacking an active immune escape mechanism are well controlled by predation, with selection removing antigenic clones, keeping diversity low. Only clones that evolve an immune escape mechanism exhibit elevated antigenic diversity, a phenomenon that occurs because there is no longer selection to remove highly antigenic clones.

The low/moderate antigen load in A suggests that the immune system is successfully containing the neoplasm. The high levels of PDL-1 are likely preventing complete elimination, but may not provide enough protection for total escape. However, the high antigen load in tissues with carcinomas indicates that the tumor has evolved a more potent immune escape strategy, possibly via macrophage recruitment.

Our results suggest that antigenic load, when coupled with IHC, can be used to gauge the degree to which the immune system is able to control tumor growth. This, in turn, has treatment implications for immunotherapy, as tumors that have evolved an immune escape strategy may respond differently to those that have not.

Dynamical approach to the game theoretic selection models based on state

Krzysztof Argasinski, Institute of Mathematics of Polish Academy of Sciences, Warszawa Poland

Co-authors: Ryszard Rudnicki, John McNamara

The attempt to integration of the classical evolutionary game theory based on replicator dynamics and the state based approach. In the new approach, individuals have different heritable strategies, however the individuals carrying the same strategy can differ on the state or situation in which they act. Thus, the classical replicator dynamics is completed by the additional subsystem of differential equations describing the process of state changes. In effect the interactions described by game structure, in addition to the demographic payoffs (births and deaths) can lead to the change of state of the competing individuals. The new framework is illustrated by following examples of owner-intruder game with explicit dynamics of role changes and inclusive fitness model with the explicit distinction between donors and recipients.

Detecting disruptive sites in the tuberculosis genome

Diepreye Ayabina, Imperial College London, United Kingdom

Co-authors: Louis Grandjean, Caroline Colijn

Evolutionary tools, especially phylogenetic trees, are increasingly being used to study short-term variation in infectious pathogens. The Mycobacterium tuberculosis genome consists of about ~ 4000 genes and approximately a tenth of these are in two families of genes that constitute a highly repetitive class of antigenic genes which are poorly characterized. These repetitive regions are highly variable, thus are a potential source of useful phylogenetic information, but they are prone to considerable sequencing/alignment error, and so are often removed before reconstruction of a phylogenetic tree (and onward analysis). Furthermore, sites known to be under selection, such as sites where mutations confer antibiotic resistance, are often removed prior to tree inference, because their evolution is likely not to be consistent with a tree model due to convergent evolution (homoplasy). However, there is no consensus in the literature as to what sites or regions of a multiple sequence alignment should be included and which should be excluded before a phylogenetic analysis, with some researchers excluding repetitive regions and resistance sites and others not. Here we present a phylogeny-based method to detect phylogenetically disruptive sites: sites which, when removed, result in a substantially altered phylogeny. The method associates each site with a tree distance. We take a classification approach to the question of which sites should be removed prior to phylogenetic analysis, using the tree distances as an input and testing whether we can automatically identify disruptive sites. We test our method on simulated data in which the disruptive sites are known, and on a tuberculosis dataset that is enriched for resistance. In both cases, our method can identify sites that are phylogenetically disruptive. We illustrate the effect excluding these sites has on onward inference of the phylogeny and the homoplasy.

The Ideal Free Distribution for Multiple Species

Steve Baigent, University College London, United Kingdom

I will discuss the ideal free distribution (IFD) for the optimal spatial allocation of multiple species in multiple habitats (e.g. [1]). Recently IFD have been studied as Cournot-Nash equilibria by Blanchet and Carlier using Monge-Kantorovich mass transport theory [2]. I will review this approach, and discuss an alternative approach
from which it is easily established when equilibria are also Evolutionarily Stable Strategies.
[1] Cressman, R., & Křivan, V. (2006). Migration dynamics for the ideal free distribution. *The American Naturalist*, *168*(3), 384–397.
[2] Blanchet A, Carlier G. 2014 From Nash to Cournot–Nash equilibria via the Monge–Kantorovich problem. *Phil. Trans. R. Soc. A* **372**: 20130398

The effect of intra- and interspecific competition on coexistence in multispecies communities

György Barabas, Linköping University, Sweden

Co-authors: Matthew J. Michalska-Smith, Stefano Allesina

The familiar textbook statement, concerning competition between two species, is that intraspecific competition must exceed interspecific competition for coexistence. What is rarely mentioned is that this intuitive, compelling rule works exclusively in the case of two competitors. In multispecies competitive communities, such simple rules are not available. The main reason is that two-species communities have a very simple structure, while for multiple species, the exact same set of competition coefficients arranged in different ways will lead to communities with vastly different properties. Here we ask whether the two-species coexistence rule can be generalized to multispecies competitive communities, and how community structure affects coexistence. We derive a multispecies generalization of the two-species rule in the context of symmetric Lotka-Volterra competition, and present explicit stability conditions for random competitive communities. We then explore the influence of community structure on coexistence by finding the arrangements of competition coefficients that are the most/least conducive to stability. Results show that both the most and least stabilized cases have striking, biologically interpretable global structures. The distribution of intraspecific coefficients leading to the most and least stabilized communities also follows a predictable pattern that can be justified analytically. In addition, the size of the parameter space allowing for feasible communities always increases with the strength of intraspecific effects in a characteristic way that is independent of the interspecific interaction structure. We conclude by presenting some extensions of our results to nonsymmetric competition.

Context-dependent communication: costly signaling in a social network can lead to a “poverty trap”

Jessica Barker, Aarhus University, Denmark

Co-authors: Marion Dumas, Eleanor Power

The “handicap principle” is an influential model in behavioral ecology showing how honest signals can be maintained via costs. In this model there is a fixed relationship between signal strength, the signaler’s underlying quality, and the audience’s perception of quality, but in many social systems there is evidence that the same signal can be interpreted differently in different contexts, such as the signaler’s position in a social network. First, we consider how network position can affect the benefits and costs of signaling; second, we allow the audience to use network position as a cue of quality. The latter model explains empirical results that a more centrally-positioned signaler enjoys a greater increase in perceived quality from a given signal. This could yield a “poverty trap”, where individuals with low centrality cannot afford to signal, and the audience’s perception of quality and the network position become decoupled from the signaler’s underlying quality.

The Spontaneous Emergence of Conventions

Andrea Baronchelli, City, University of London, United Kingdom

How do shared conventions emerge in complex decentralised social systems? This question engages fields as diverse as linguistics, sociology, and cognitive science. Previous empirical attempts to solve this puzzle all presuppose that formal or informal institutions, such as incentives for global agreement, coordinated leadership, or aggregated information about the population, are needed to facilitate a solution. Evolutionary theories of social conventions, by contrast, hypothesise that such institutions are not necessary in order for social conventions to form. However, empirical tests of this hypothesis have been hindered by the difficulties of evaluating the real-time creation of new collective behaviours in large decentralised populations. Here, I will present experimental results - replicated at several scales - that demonstrate the spontaneous creation of universally adopted social conventions and show how simple changes in a population’s network structure can direct the dynamics of norm formation, driving human populations with no ambition for large scale coordination to rapidly evolve shared social conventions. I will also show that a simple model describes well the experimental results on different classes of social networks.

Key references:
D. Centola and A. Baronchelli "The spontaneous emergence of conventions: An experimental study of cultural evolution ", PNAS 112, 1989 (2015)
A. Baronchelli et al "Sharp transition towards shared vocabularies in multi-agent systems", J. Stat. Mech. P06014 (2006)
(more info here: http://bit.ly/1U3L7YF)

Emergence of metapopulations and echo chambers in mobile agents

Andrea Baronchelli, City, University of London, United Kingdom

Co-authors: Michele Starnini, Mattia Frasca

Multi-agent models often describe populations segregated either in the physical space, i.e. subdivided in metapopulations, or in the ecology of opinions, i.e. partitioned in echo chambers. Here I will show how both kinds of segregation can emerge from the interplay between homophily and social influence in a simple model of mobile agents endowed with a continuous opinion variable. In the model, physical proximity determines a progressive convergence of opinions but differing opinions result in agents moving away from each others. This feedback between mobility and social dynamics determines the onset of a stable dynamical metapopulation scenario where physically separated groups of like-minded individuals interact with each other through the exchange of agents. The further introduction of confirmation bias in social interactions, defined as the tendency of an individual to favour opinions that match his own, leads to the emergence of echo chambers where different opinions coexist also within the same group. Thanks to its flexibility and rich phenomenology, the model may be of interest to researchers investigating the origin of segregation in the offline and online world.

Reference:
Michele Starnini, Mattia Frasca and Andrea Baronchelli "*Emergence of metapopulations and echo chambers in mobile agents*" Scientific Reports 6, 31834 (2016).

The Ornstein-Uhlenbeck process modelling evolution of interacting populations

Krzysztof Bartoszek, Uppsala University, Sweden

Co-authors: Sylvain Glemin, Ingemar Kaj, Martin Lascoux

In this talk we present our recent work where we consider an Ornstein-Uhlenbeck (OU) process that evolves on a phylogeny with migration between branches. The standard OU process includes random perturbations and stabilizing selection and assumes that species evolve independently. However, evolving species may interact through various ecological process and also exchange genes, especially in plants. This is particularly true if we want to study phenotypic evolution among diverging populations within species. We will discuss a straightforward statistical approach (with analytical solutions) that allows for the inclusion of adaptation and migration in a common phylogenetic framework. Currently, the OU process is the model of choice when one wants to study adaptation, especially with different regimes for different clades. A major point is that migration effects, if ignored, can be misinterpreted as strong convergent evolution. We illustrate the model and finding with detailed simulations for a variety of evolutionary setups.

A Simple Model of Collective Behaviour Driven by the Visual Field

Renaud Bastien, University of Konstanz, Germany

Co-authors: Iain Couzin, Pawel Romanczuk

In recent years our understanding of collective behavior have been greatly enhanced by the development of simple model of behaviour. Classical examples are given by the Viscek model, where animals align with each other, or the Couzin model, that proposes the existence of different zones of interaction. Despite their explanatory power, those models often rely often on information that are not directly available to an individual. Those information should be integrated through their perception. Here I will show how a simple model can be constructed that relate directly the visual field of each individual and the dynamic observed at the scale of group. This framework allow to understand how visual features can be combined to create basic interaction between individual. I will then discuss the limits and possibilities offered by this approach.

Properties of beneficial mutations: fitness landscape models and inference from population genomics data

Thomas Bataillon, AArhus University, Denmark.

Many instances of genomic regions exhibiting footprint of natural selection favouring new variants have been discovered and we can provide ample proof that adaptation happens. But we know still very little about beneficial mutations– the raw stuff enabling adaptation. We know even less about what factors limit rates of adaptation. Population genetic theory makes predictions and allows in principle to make demographic and selective inference from the patterns of polymorphism within species and divergence between species. Yet models specifying the fitness effects of mutations are often missing. I will show how fitness landscape models can be mobilized to develop methods for inferring the distribution of fitness effects and, a glimpse on what factors are governing rates of adaptation. Properties of beneficial mutations can be inferred from experimental evolution and population genomics data. The applicability of insights gained from experimental evolution to comprehend adaptation in nature will be discussed.

HermaDEB: a model for the energy allocation in Hermaphrodite

Slimane BenMiled, Universite de Tunis El Manar, Tunisia

Co-authors: Dorra Louatia, Narjes Bellamine Ben Saoud

Size-advantage hypothesis models (SAH) allow to understand which sex to be first and when to change sex in hermaphrodite species through optimal allocation of energy to male versus female roles. While sex allocation depends directly on how an organism allocates energy throughout its lifetime, the standard dynamic energy budget (DEB) model captures this by simply supplementing the rates of acquisition and utilization of energy by individuals.

In this paper we build DEB model to study the most important physiological factors influencing the size at sex change, L_{change} and size at sex change/maximum size, L_{ratio}. We prove that the fraction which determines how much to invest in somatic maintenance and growth, κ, the cost of the structure relative to the energy allocated to the soma and the somatic maintenance rate coefficient are the most influential factors. We also show that the ratio between male and female gamete costs has a small influence on L_{change} and L_{ratio}.

Keywords: Individual based model, dynamic energy budget theory, sex allocation theory, metabolism, evolution, hermaphrodite

Predator–Prey–shared Resource Model in Cancer immunoediting

Faina Berezovskaya, Howard University, United States

Co-author: Irina Kareva

Types of interactions intrinsic to ecology (predator - prey, competition for recourse) are used in the proposed model of tumor - immune - glucose interactions, formulated here as a non-standard predator - prey - common resource system. The outcome of these interactions ranges from tumor elimination, to tumor dormancy, to unrestrained tumor growth. A detailed bifurcation analysis of three subsystems of the model suggests that oscillatory regimes are a result of competition for shared resource (glucose) between the predator (immune cells) and the prey (cancer cells). Increased immune stimulation might be sufficient to control tumor growth but not to eliminate the tumor. Existence of competition for nutrients between cancer and immune cells may provide additional mechanistic insight as to why the efficacy of many immunotherapies may be limited.

Impact of higher-order structure on critical behaviour in a complex contagion model

Luc Berthouze, University of Sussex, United Kingdom

Network structure is known to be a key determinant of criticality in many complex systems. In this work, we construct networks with identical degree distribution and global clustering value but different subgraph decomposition and study the critical behaviour of a complex contagion model (a process in which individuals may require multiple infectious transmissions before changing state) operating on them. Using maximal variability in both the time needed to reach final size and final size as markers of the critical transition, we show how diversity in higher-order structure results in transitions occurring at different levels of initial conditions. These results suggest that (1) degree distribution and clustering are not necessarily good predictors of the location of the critical transition and (2) there may be more subtle ways by which to steer networks toward or away from the critical regime, e.g., through controlling the prevalence of higher-order subgraphs.

Keywords: network; higher-order structure; contagion; criticality

The resolution of genetic incompatibility in a hybrid population

Alexandre Blanckaert, Instituto Gulbenkian de Ciencia, Portugal

Co-author: Claudia Bank

Hybridization has recently gained increasing and controversial interest as a potential engine of speciation. It has been hypothesized that the differential sorting of genetic incompatibilities from parental species could result in hybrid speciation, where the hybrid population maintains some mixed combination of the parental incompatibilities. We here investigate the allele-frequency dynamics of an isolated hybrid population. Using models of 2 or 4 loci, we investigate the fate of one or two genetic incompatibilities of the Dobzhansky-Muller type. We study the influence of the dominance of the epistatic effect and of the initial contribution of genomes from each source population. We find that hybrid speciation remains a rare event even under the most favorable conditions of symmetric contribution of the parental populations, selection for the incompatible alleles, free recombination, and codominance of the incompatibilities. Moreover, we demonstrate that codominant incompatibilities tend to be resolved much faster than recessive ones, making the former less likely to be observed.

A simple approximation for the complex dynamics of quantitative traits

Katarina Bodova, IST, Austria

Co-authors: Gasper Tkacik, Nick Barton

Selection, mutation and random drift affect the dynamics of allele frequencies and consequently of quantitative traits. While the macroscopic dynamics of quantitative traits can be measured, the underlying allele frequencies are typically unobserved. Can we understand how the macroscopic observables evolve without following these microscopic processes? I will show how the complex dynamics of quantitative traits can be approximated by a simple system by combining a static maximum entropy principle in statistical physics with quasi-stationarity assumption. This results in a method applicable to a wide range of biological systems.

Unraveling the F-box - The evolution of F-boxes in non-self recognition self-incompatibility systems

Katarina Bodova, IST, Austria

Co-authors: Gasper Tkacik, Nick Barton

Understanding the origin and maintenance of the extraordinary diversity observed at loci involved in genetically based recognition systems such as self-incompatibility (SI) in plants has long fascinated evolutionary biologists. Self-incompatibility is widespread in flowering plants and functions to prevent self-fertilization and the deleterious effects of inbreeding depression. The incredible diversity observed in natural populations is maintained by negative frequency dependent selection, a form of balancing selection where a rare allele has a selective advantage. Yet one of the biggest and most intriguing questions in the evolution of SI is how new alleles (S haplotypes) evolve. This evolutionary puzzle originates from the complexities involved in the coevolution of the male and female determining components of the incompatibility reaction. Here we investigate the pathways and conditions associated with novel S haplotype evolution in a non-self recognition self incompatibility system. To do this we use a deterministic population genetic model and stochastic simulations of finite population size. These results provide new insights into the evolutionary dynamics of non-self recognition SI systems in plants. This is a joint work with Tadeas Priklopil, Melinda Pickup and David Field.

Modelling immune function, pesticide exposure and infection in honey bee individuals

Ross Booton, University of Sheffield, United Kingdom

Co-authors: Ryo Yamaguchi, James A. R. Marshall, Dylan Z. Childs, Yoh Iwasa

Global honey bee populations continue to fail due to a range of multi-causal factors, but the mechanism by which these stressors interact is currently poorly understood. Here we studied the effects of two such interacting stressors; infection and pesticide exposure in the context of the honey bee immune system. We model the dynamics of a within-host infection and the associated immune response of the honey bee. We consider both the indirect effects on immunosuppression and the direct effects on development and mortality of honey bees exposed to pesticides. We demonstrate that sub-lethal exposure to pesticides can promote infection through the suppression of the immune system. This happens through the depletion of the immune response which causes rapid proliferation in infection load. Our model provides the first assessment of how pesticide stress, infection load and the immune system interact to cause the breakdown of the within-host cellular dynamics of individual honey bees.

The breakdown of coordination and the emergence of dangerous collective motions in high-density crowds.

Arianna Bottinelli, Uppsala University, Sweden

Co-authors: David T.J. Sumpter, Jesse L. Silverberg

Communication and information transfer between human subjects gives rise to social conventions, shared norms, and efficient self-organized phenomena such as collective decision making. However, when people gather at high density, coordination breaks down, social norms do not apply anymore to individual people and dangerous collective movements can emerge, causing injuries and death.Taking inspiration from mode analysis and from the physics of jammed granular materials, we were able to identify Goldstone modes and stochastic resonance as candidate mechanisms for emergent injurious collective motions. However, what is the relationship between collective motion at high density and the breakdown of communication and of coordination is still an open question. Understanding the coupling between information transfer and movement in the extreme case presented by high-density crowds is likely to be a fundamental step in understanding the dangers arising at mass gatherings.

How evolution draws trade-offs: an evolutionary physiology model

Salome Bourg, University Lyon, France

Co-authors: E.Rajon, F.Menu

Variation in phenotypic traits is constrained by negative relationships known as tradeoffs. Evolution in multitrait spaces depends on trade-off shapes, i.e. the combinations of traits readily accessible by mutations. Many trade-offs find their origin in the differential allocation of resources to traits, controlled by a physiological mechanism that involves DNA-encoded proteins like hormones. Therefore, contrary to the common view that trade-offs result from fixed constraints, their shape could change by mutation and evolve. The present study addresses this hypothesis theoretically. In our model, hormones and receptors with mutable conformations and expressions regulate the allocation of an energetic resource to traits. We

consider the fixation of such mutants through selection acting on the traits and genetic drift. We show that the physiological mechanism hence modeled can evolve, such that the evolutionarily expected trade-off shape depends on previously unanticipated parameters such as the energetic loss associated with storage.

Modelling evolution in structured populations using multiplayer games

Mark Broom, City, University of London, United Kingdom

Co-authors: Karan Pattni, Jan Rychtar

Within the last ten years, models of evolution have begun to incorporate structured populations, including spatial structure, through the modelling of evolutionary processes on graphs (evolutionary graph theory). One limitation of this otherwise quite general framework is that interactions are restricted to pairwise ones, through the edges connecting pairs of individuals. Yet many animal interactions can involve many individuals, and theoretical models also describe such multi-player interactions. We shall discuss a more general modelling framework of interactions of structured populations, including the example of competition between territorial animals. Depending upon the behaviour concerned, we can embed the results of different evolutionary games within our structure, as occurs for pairwise games such as the Prisoner's Dilemma or the Hawk-Dove game on graphs. For a population to evolve we also need an evolutionary dynamics, and we demonstrate a birth-death dynamics for our framework. Finally we discuss some examples together with some important differences between this approach and evolutionary graph theory.

Two-locus clines on the real line with a step environment

Reinhard Bürger, University of Vienna, Austria

We investigate a cline model with two diallelic, recombining loci under selection caused by an abrupt environmental change. The habitat is linear and unbounded; dispersal occurs by diffusion. Selection is modeled by step functions such that in one region one allele at each locus is advantageous and in the other deleterious. We admit environmentally independent, intermediate dominance at both loci. First, an explicit expression for the single-locus cline with dominance is derived, thus generalizing classical results. The slope of the cline in the center is independent of dominance. Second, under the assumption of strong recombination, the first-order approximation of the allele-frequency cline at each of the loci is derived, as is the linkage disequilibrium. Therefore, we obtain the quasi-linkage-equilibrium approximation of the two-locus cline. Its asymptotic properties are characterized explicitly. The consequences of dominance and linkage for the shape of the two-locus cline are explored for arbitrary recombination rates.

Regime shifts in socio-ecological systems : Silent early warning signals in the natural subsystem

Thomas Bury, University of Waterloo, Canada

Co-author: Chris T. Bauch

Abrupt and often irreversible transitions can be observed in a wide variety of systems including ecological communities, complex disease and social networks. Despite their seemingly unpredictable nature, generic early warning signals have been proposed which,

once verified for a particular system, could provide the means for preventing unwanted transitions. However, not all state variables in complex systems guarantee early warning signals, even if strongly influenced by the critical transition. We explain this “silence” using theory surrounding multi-dimensional stochastic processes, and show how one can infer which variables will exhibit traits of an upcoming transition.

In applying this to generic socio-ecological systems, we demonstrate that signals in the ecological subsystem are often silent. Given the potential for drastic, long-lasting regime shifts in these systems, prediction of upcoming tipping points is of significant importance. Our work sheds light on the mechanisms that suppress / exemplify the proposed early warning signals, and suggests that monitoring shifts in human behaviour is vital for the sustainability of ecological systems.

Animal Diffusion Model Depending on Well-being

Nurdan Cabukoglu, University of Leicester, United Kingdom

Co-author: Alexander Gorban

Migration behaviour of animals has evolved under control of natural selection. Therefore, migration should increase the average reproduction coefficient (Darwinian fitness) [1]. Despite of that, the models of animal space distribution have followed the assumption of the random walk from the very beginning [2]. We assume that animal migration differs from the wanderings of a “drunk sailor” [3] and increases Darwinian fitness as far as it is possible. Description of the space of available migration strategies requires evaluation of information about the future living conditions, which can be used by a migrating animal [4,5]. For example, we have to decide how big the area is, where the information is collected before migration decision. In this work we study new kinesis models of the form:

$$\frac{\partial u_i}{\partial t} = r_i(u_1, \dots, u_k, s)u_i + d_i \nabla (e^{-a_i r_i} \nabla u_i)$$

(1)

where u_i is the population density of *i*th animal, *s* represents the abiotic characteristics of the living conditions, r_i is the reproduction coefficient, $d_i > 0$ is the equilibrium diffusion coefficient (defined for $r_i = 0$), and the coefficient $a_i > 0$ characterises dependence of the diffusion coefficient on the reproduction coefficient.

The space distribution strategy is summarised in the “diffusion coefficient” $d_i e^{-a_i r_i}$, which depends only on the local in space and time value of the reproduction coefficient. Diffusion depends on well-being measured by this coefficient. For good conditions (high r_i) diffusion is slow and for worse conditions (lower $_i$) it is fast.

We analyse how this dependence of diffusion on well-being effects patch dynamics and waves in population dynamics.

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The structure of interactions in microbial microcosms

Francesco Carrara, ETH Zurich, Switzerland

Co-authors: Andrea Giometto, Mathew Seymour, Andrea Rinaldo, Florian Altermatt

Here, we investigate how functional diversity affects the stability of species coexistence and productivity in multispecies communities by characterizing experimentally all pairwise species interactions in a pool of 11 species of eukaryotes (10 protists and one rotifer) belonging to three different functional groups. Species within the same functional group showed stronger competitive interactions compared to among-functional group interactions. This often led to competitive exclusion between species that had higher functional relatedness, but only at low levels of species richness. Communities with higher functional diversity resulted in increased species coexistence and community biomass production. We show how simulations of a stochastic community model, derived from the empirical interaction matrix, predict multispecies community dynamics across multiple functional groups. By combining theoretical analysis with experiments we disentangled the relationship between species richness and functional diversity, showing that functional diversity per se is a crucial driver of productivity and stability in multispecies community.

Regularity and time-inhomogeneity in the Wright-Fisher dynamics

Fabio Chalub, Universidade Nova de Lisboa, Portugal

Co-author: Max Souza

We will introduce the Wright-Fisher model with a very general function describing naturalselection. We will study the dependence between the fixation probability and the initial condition. In particular, we will show that if natural selection is described by an affine function (as in 2-player evolutionary game theory), the fixation probability is an increasing function in the initial presence. However, if fitnesses functions are more general, this dependence may be very general. In particular, any fixation probability can be described by a Wright-Fisher process: there are situations in which an increase in the initial presence of a type can lead to a decrease in the fixation probability. This phenomena is not possible in Birth-Death processes. We will also discuss time-dependent processes and show that evolutionary equivalents of the Parrondo paradox happen in the Moran process, but not in the Wright-Fisher process.

Diagonal Stability in Lotka-Volterra Systems

Atheeta Ching, University College London, United Kingdom

Co-author: Stephen Baigent

Long term dynamics are a crucial part of population ecology. The interactions between different species in a Lotka-Volterra model can be represented by a matrix. If this matrix is diagonally stable, there is a known Lyapunov function showing that any existing interior steady state will be globally stable, i.e. we have the co-existence of all species as time goes to infinity. Our work provides insight by exploring the geometric interpretation behind diagonally stable matrices in dimensions 3x3 and 4x4, allowing us to find other equivalent conditions. Zeeman and Zeeman introduced split-Lyapunov stability (originally in competitive systems) which also implies global stability of the interior steady state and is much easier to compute in higher dimensions. Numerical work was carried out to compare this class of matrices to diagonally stable matrices, examining whether it can be a viable alternative.

Infectious diseases dynamics in the presence of asymptomatic infections

Rebecca Chisolm, The University of Melbourne, Australia

Pathogens that cause symptomatic disease infrequently in their hosts raise a number of interesting ecological and evolutionary questions. In this presentation I will discuss how we have used mathematical models to address two such questions.

First, if asymptomatically-infected hosts are less contagious than symptomatically-infected hosts, how do mostly commensal organisms that cause symptomatic disease infrequently, such as *Streptococcus pyogenes* and *Staphlococcus aureus,* have sustained and sometimes complex patterns of transmission? Results suggest that asymptomatic infection can act to either increase or decrease pathogen persistence in the host population depending on the relative infectiousness of asymptomatic versus symptomatic infectives, and the relative durations of asymptomatic versus symptomatic infection.

The second question concerns the causative agent of human tuberculosis – *Mycobacterium tuberculosis* – whose host population is dominated by asymptomatic latent infections which are noninfectious but have a small chance of activating to the active disease state during a host’s lifetime. If *M. tuberculosis* began interactions with humans as an active disease without latency, how could it begin to evolve latency properties without putting itself at an immediate reproductive disadvantage? Results suggest that the emergence of tuberculosis latency may have been enabled by a mechanism akin to cryptic genetic variation in that detrimental latency properties were hidden from natural selection until their expression became evolutionarily favoured.

The Evolution of the Germ-Soma Divide

Guy Alexander Cooper, University of Oxford, United Kingdom

Co-author: Stuart Andrew West

The somatic cells of multicellular organisms have sacrificed their personal reproduction and focused on cooperative behaviours that help the germline cells reproduce. In contrast, many clonally-grouped microbial species have not adopted this arrangement. Why did the strategy of germ-soma division evolve in some populations but not others? We develop and analyse a kin selection model that is applicable to a wide range of social microbe species. Within structured populations of cells, we find that a germ-soma divide is favoured by natural selection if: 1) cells depend significantly on social interactions for growth or survival; 2) social group relatedness is high; 3) the efficiency benefits to specialisation are high and 4) the cooperative actions of cells provide little direct benefit to self. Our work provides a general framework for understanding why some microbial populations in the deep past may have undergone an evolutionary transition to complex multicellularity whereas others did not.

Optimal connectivity measures for dynamic landscape metapopulations

Stephen Cornell, University of Liverpool, United Kingdom

Co-authors: Yevhen Suprunenko, Otso Ovaskainen

Landscape connectivity is frequently used to estimate the conservation value of a habitat patch. It is calculated as the sum of contributions from other patches weighted by a decaying function of spatial separation - the “connectivity kernel”. Taking inspiration from metapopulation models, the connectivity kernel is typically chosen to be the same as the focal organism's dispersal kernel, but in fact there is no theory that underpins this choice. I use analytical calculations (exact in a known, biologically relevant limit) for a dynamic landscape stochastic patch occupancy metapopulation to explore the correlation between occupancy and connectivity for general kernels. The optimal connectivity kernel, which maximises this correlation, does not have the same shape as the dispersal kernel, and has a length scale that is several times larger than that for dispersal. These results suggest simple improvements to connectivity measures that would predict patch occupancy better, and hence aid reserve network design.

Interaction times change evolutionary outcomes

Ross Cressman, Wilfrid Laurier University, Canada

Co-author: Vlastimil Krivan

Evolutionary game theory was developed under a number of simplifying assumptions. One that is not often explicitly stated is that each interaction among individuals takes the same amount of time no matter what strategies these individuals use. When interaction time is strategy-dependent, it is more realistic to take individual fitness as the payoff received per unit time. For instance, two Hawks interacting in the standard two-player Hawk-Dove game are assumed to engage in a fight, implying that they may be involved in fewer interactions than Doves who avoid such contests.

The talk will characterize how interaction times affect the evolutionary outcome (e.g. the evolutionarily stable strategy (ESS) and Nash equilibrium (NE)) in general two-strategy symmetric games (i.e. matrix games) and apply the results to the Hawk-Dove game. I will also show that cooperation can evolve in the repeated Prisoner’s Dilemma game when the number of rounds is under the players’ control. If time permits, this outcome will be related to the results from game experiments based on the corresponding opting out game.

Higher Order Epistasis and Evolutionary Dynamics

Kristina Crona, American University, United States

Higher order epistasis is of practical importance for antibiotic and HIV drug resistance. For instance, a triple mutant may lead to treatment failure, whereas the corresponding single and double mutant are harmless. Recent studies indicate that higher order epistasis is prevalent in nature. However, the full impact on evolutionary dynamics is not well understood. Peaks and mutational trajectories depend on gene interactions, with implications for predictability, recombination and other aspects of adaptation. We show that a maximal number of peaks for a fitness landscape requires the highest possible order of interactions, and that exponential growth of the number of peaks is possible in the absence of higher order epistasis. Both interactions and dimensionality shape fitness landscapes. High dimensionality eliminates the problem with many inaccessible peaks for some landscapes. However, we show that the problem remains regardless of dimension for a class of landscapes associated with stabilizing selection. Our work horse for relating higher order interactions and evolutionary dynamics is a recently developed rank order based approach to higher order epistasis (joint with Greene, Gavryushkin and Beerenwinkel). We take advantage of a complete characterization of rank orders of genotypes that imply higher order epistasis, along with similar results for fitness graphs. Rank orders determine mutational trajectories, which explains how rank order induced interactions can relate global and local properties of fitness landscapes.

Statistical aspects of natural selection in relation to the evolution of sexual reproduction

Daniel Crouch, University of Oxford, United Kingdom

The prevalence of sexual reproduction remains mysterious, as it poses clear evolutionary drawbacks compared to reproducing asexually. Several possible explanations exist, with one of the most likely being that finite population size causes linkage disequilibria to randomly generate and impede the progress of natural selection, and that these are eroded by recombination via sexual reproduction. Previous investigations have either analysed this phenomenon in detail for small numbers of loci, or performed population simulations for many loci. Here we present a quantitative genetic model for fitness, based on the Price Equation, in order to examine the theoretical consequences of randomly generated linkage disequilibria when there are many loci. In addition, most previous work has been concerned with the long term consequences of deleterious linkage disequilibria for population fitness. The expected change in mean fitness between consecutive generations, a measure of short term evolutionary success, is shown under random environmental influences to be related to the autocovariance in mean fitness between the generations, capturing the effects of stochastic forces such as genetic drift. Interaction between genetic drift and natural selection, due to randomly generated linkage disequilibria, is demonstrated to be one possible source of mean fitness autocovariance. This suggests a possible role for sexual reproduction in reducing the negative effects of genetic drift, thereby improving the short term efficacy of natural selection.

A spatial model for selection and cooperation

Peter Czuppon, MPI for Evolutionary Biology, Germany

Co-author: Peter Pfaffelhuber

We study the evolution of cooperation in an interacting particle system with two types (called co-operators and defectors). The model we investigate is motivated by the public goods dilemma and implemented by an extension of a two-type biased voter model. Co-operators produce a public good and thus help neighbours (of either type) to reproduce at rate γ. However, defectors have a (positive) bias α with respect to co-operators due to not producing the public good. In the talk we will investigate the asymptotical behaviour of this model in several dimensions and present a sharp result for the survival (and in fact fixation) of co-operators in one dimension.

The impact of resource dependence on the spatial population dynamics of an *in silico* microbial community

Presenting author: Aisling J. Daly, Ghent University, Belgium

Co-authors: Jan M. Baetens, Bernard De Baets

Theoretical models have identified two key mechanisms sustaining biodiversity, often critically important to ecosystem viability: the localisation of competition and mobility, and cyclic competition. These models typically neglect two important factors: evenness, and the resource-dependence of demographic processes. The latter implies that the resource-dependence of demographic processes in nature is ignored. Evenness has been shown to be a key factor in preserving the functionality and stability of an ecosystem, but is often overlooked in modelling studies.

We extend existing individual-based models by incorporating these factors to align them more closely with real-world microbial ecosystems, and to investigate how this affects community biodiversity and productivity. We thereby demonstrate the existence of a trade-off between maintaining biodiversity and increasing biomass production, supporting experimental observations. We additionally address the effects of using a lattice-based or lattice-free model, in particular on the model community's spatial population dynamics.

Rich dynamics exhibited by predator-prey systems with mutual interference in the presence of inhibitory effect: A detailed theoretical investigation

Krishna Kiran Varnsi Dasu, Sri Sathya Sai Institute of Higher Learning, India

Off late mathematicians and field scientists working in the area of agricultural entomology have been conducting experiments on biological control of pests, by studying the interactions of the eco-system as predator-prey models. In these models, the pest is assumed to be as prey and natural enemy is viewed to be as predator. One of the approaches for achieving the biological conservation of ecosystems (in this case biological control), is to provide the predators with additional food supplements in order to enhance their longevity and fecundity, so as to effectively control the prey(pest). A detailed study for additional food provided predator-prey model involving type IV functional response has been done by the author and his team. It is concluded that by providing the predators with additional food of high quality (with quantity belongs to a specified range) one can, not only limit but also eradicate the prey from the ecosystem and that high quality food favors biological control. One of the major limitations of the above study is that the proposed model predicts an unbounded growth for predators after prey gets eradicated from the ecosystem. In this work, a detailed theoretical investigation of predator-prey systems with mutual interference of the predators and in the presence of inhibitory effect of the prey is done. The limitations in the earlier works have been overcome in the present study.

Fidelity of parent-offspring transmission and the evolution of social behavior in structured populations

Florence Débarre, CNRS, France

The theoretical investigation of how spatial structure affects the evolution of social behavior has mostly been done under the assumption that parent-offspring strategy transmission is perfect, i.e., for genetically transmitted traits, that mutation is very weak or absent. In this talk, we investigate the evolution of social behavior in structured populations under arbitrary mutation probabilities. We consider spatially structured populations of fixed size N, in which two types of individuals, A and B, corresponding to two types of social behavior, are competing. Under the assumption of small phenotypic differences (weak selection), we provide a formula for the expected frequency of type A individuals in the population, and deduce conditions for the long-term success of one strategy against another. We then illustrate this result with three common life-cycles (Wright-Fisher, Moran Birth-Death and Moran Death-Birth), and specific population structures. Qualitatively, we find that some life-cycles (Moran Birth-Death, Wright-Fisher -- when social interactions affect fecundities) prevent the evolution of altruistic behavior, confirming previous results obtained with perfect strategy transmission. Imperfect strategy transmission also alters the balance between the benefits and costs of staying next to one's kin, leading to surprising results in subdivided populations, in that higher emigration probabilities can be favourable to the evolution of altruistic strategies.

The Bacterial Sequential Markov Coalescent

Nicola De Maio, University of Oxford, United Kingdom

Co-author: Daniel J Wilson

Recombination is fundamental in microbial evolution, leading to the spread of antibiotic resistance and the avoidance of clonal interference. Bacterial recombination is usually modelled similarly to homologous gene conversion in eukaryotes, using the coalescent with gene conversion (CGC). However, this is computationally demanding. We present a new approximation to the CGC: the bacterial sequential Markov coalescent (BSMC) which allows the efficient modelling of bacterial genomes. We imitate the Sequential Markov Coalescent, but accounting for strong correlations and linkage disequilibrium across distant loci due to the clonal frame. We use Approximate Bayesian Computation inference and correctly recover parameters simulated under the exact CGC. We also infer recombination and mutation rate from a whole genome alignment of Bacillus cereus. We implemented our model within the new bacterial evolution simulation software FastSimBac, providing reduced computational demand and more general simulation scenarios than previous methods. FastSimBac is available from https://bitbucket.org/nicofmay/fastsimbac .

Spatially explicit theoretical community assembly

Jacob Dinner O’Sullivan, Queen Mary, University of London, United Kingdom

Co-author: Axel Rossberg

Spatial patterns in the biodiversity of meta-communities are the result of multiple interacting ecological processes including the dispersal of biomass between patches, biotic interactions, and the effect of spatio-temporal environmental heterogeneity on habitat suitability. The relative importance of ecological niches in determining meta-community composition has been challenged by the development of neutral ecological theories which assume that the specific ecological traits of an assemblage of species do not significantly impact upon regional-scale distributions of biodiversity. Using numerical simulations we examine the impact of dispersal rate and biological interaction strengths on regional scale biodiversity patterns emerging from a non-neutral model of coupled local and regional dynamics. We ask how dispersal regimes impact upon the central mechanisms of modern coexistence theory, which emphasizes stabilizing niche differences and relative fitness differences as key to species coexistence within a landscape. Finally we analyse how spatial extension affect the structural stability of theoretical communities.

Feedbacks between disease progress and vector aggregation, lessons from plant viruses.

Ruairi Donnelly, University of Cambridge, United Kingdom

We introduce a novel model for analysing the spread of plant viruses with a focus on vector behaviour and aggregation. For viruses acquired and inoculated through epidermal cells by aphids (described as non-persistent due to brief retention in the vector), transmission is associated with transient probing stages of plant selection making vector behaviour key to virus transmission. Moreover, aphid offspring may develop to be winged or wingless and therefore transmission can occur globally or locally. In this talk we will characterise patterns of disease spread for such viruses, analyse strategies for manipulating vector behaviour, and contrast results for local and global vector movement.

The population-level consequences of protective parenting

John G. Donohue, University of Limerick, Ireland

Co-author: Petri T. Piiroinen

In many animal species, recruitment is facilitated by adults' efforts to protect offspring from predation. Theoretical studies of this phenomenon have usually focused on resolving the conflict between an individual's self-preservation and its attempts to successfully reproduce. While the decision to protect is made at the level of a single individual, the aggregation of these decisions may affect population density and structure. This idea motivates the development of a functional response for predators that is compatible with the protective behaviour of prey. Using this functional response, we study the long-term behaviour of a protective prey population under different levels of predation. We find that the effects of protection vary significantly depending on the riskiness associated with interference. Moreover, protection-driven Allee effects can allow large populations to survive in environments characterised by intense predation.

Spacetime Discounted Value of Network Connectivity

Arnaud Z. Dragicevic, Istanbul Technical University, Turkey

In order to unveil the value of network connectivity, discounted both in space and time, we formalize the construction of networks as an optimal control dynamic graph-theoretic problem. The network is based on a set of leaders and followers linked through edges. The node dynamics, built upon the consensus protocol, form a time evolutive Mahalanobis distance weighted by the opportunity costs. The results show that the network equilibrium depends on the influence of leader nodes, while the network connectivity depends on the cohesiveness among followers. Through numerical simulations, we find that – past a threshold level of opportunity costs – the values of shadow prices become stationary. Likewise, the model outputs show that, at a fixed level of foregone gains, agents value the safeguard of connections less in time than in space.

Keywords: Bioeconomics, Graph Theory, Optimal Control, Connectivity Value, Spacetime discounting

Engineered underdominance gene drive as a tool for public health and ecology

Matthew Edgington, The Pirbright Institute, United Kingdom

Co-author: Luke Alphey

Mosquito-borne diseases pose serious threats to public health and ecosystems. For example, ca390 million dengue virus infections occur annually and avian malaria has caused the reduction/extinction of many native Hawaiian birds. Gene drives are theoretically able to spread desirable traits (e.g. reduced vector competence) into populations since they pass between generations at super-Mendelian rates. Thus, they are a potential solution to such issues.

Here we use population genetics models to explore a class of gene drive called engineered underdominance. Such systems have attracted attention since they should replace, not eliminate, target populations and not spread to untargeted areas (both key regulatory features). In particular, we consider a range of potential genetic components and release

strategies, investigating conditions for successful population replacement and, in theory, disease reduction/elimination. For each case considered we discuss the time taken to approach equilibrium as a key factor in comparing different classes of gene drive.

Modelling seasonal dynamics of bacteria-phage interactions with a temperature-dependent lysogeny.

Halil Ibrahim Egilmez, University of Leicester, United Kingdom

Co-author: Andrew Morozov, Martha R. J. Clokie, Edouard Galyov

Melioidosis is a serious illness caused by the pathogen Burkholderia pseudomallei living in water and soil. It results in around 40% fatality of those who become infected, and it disproportionately affects low paid agricultural workers in Southeast Asia. Currently the seasonal population dynamics of the pathogen is poorly understood which hinders efficient control and prevention of the disease. Recent empirical findings demonstrate that the population number of bacteria can be regulated by their specific phages abundantly found in soil and water and that these phages differentially infect bacteria according to temperature conditions. Phages are predominantly lytic at a higher temperature of 37^oC and are mainly lysogenic lower temperatures. Typical seasonal and daily variations in the environmental temperature therefore result in a frequently occurring switches between the types of phage-bacteria interactions. In this work, we developed a set of mathematical models to analyse the impact of such phages and to predict dynamics of the B. pseudomallei populations in the surface water and soil under seasonally changing environmental conditions. The model parameters were taken from either our research, or other scientific publications. The modelling outcomes appear to correlate with the apparent higher risk of melioidosis acquisition during the “warm and wet” season. We have identified the main dynamical regimes in the system and their dependence on the key model parameters. These findings may have an impact on the improvement of disease management policy in Southeast Asia.

Bitcoin ecology: Quantifying and modelling the long-term dynamics of the cryptocurrency market

Abeer Elbahrawya, City, University of London, United Kingdom

Co-authors: Laura Alessandretti, Anne Kandler, Romualdo Pastor-Satorras, and Andrea Baronchelli

The cryptocurrency market has reached a record of $91 billion market capitalization in May 2017, after months of steady growth. Despite its increasing relevance in the financial world, however, a comprehensive analysis of the whole system is still lacking, as most studies have focused exclusively on the behaviour of one (Bitcoin) or few cryptocurrencies. Here, we consider the history of the entire market and analyse the behaviour of 1; 469 cryptocurrencies introduced since April 2013. We reveal that, while new cryptocurrencies appear and disappear continuously and their market capitalization is increasing exponentially, several statistical properties of the market have been stable for years. These include the number of active cryptocurrencies, the market share distribution and the turnover of cryptocurrencies. Adopting an ecological perspective, we show that the so-called neutral model of evolution is able to reproduce a number of key empirical observations, despite its simplicity and the assumption of no selective advantage of one cryptocurrency over another. Our results shed light on the properties of the cryptocurrency market and establish a first formal link between ecological modelling and the study of this growing system. We anticipate they will spark further research in this direction.

Dynamical Facilitation of the Ideal Free Distribution in Non-Ideal Populations

Igor Erovenko, University of North Carolina at Greensboro, United States

Co-authors: Garrett Street, Jonathan Rowell

The Ideal Free Distribution (IFD) requires that individuals can accurately perceive density dependent habitat quality. Failure to detect quality below a given perception threshold results in distributions approaching spatial uniformity, yet the true quality of occupied habitat will produce variation in fitness contributing to population growth. A population may thus approach the IFD despite being unable to detect habitat quality. We extend a simple model of discrete patch choice under perception limits to include movement driven by perceived patch quality, and population dynamics driven by true quality, to investigate the influence of population growth on achieving an IFD. Growing populations were able to overcome the perception threshold and approach, but never fully achieve, an IFD due to random redistribution between patches of perceived equal quality occurring between reproductive bouts. This produced oscillations in the population distribution, with peaks most closely approximating the IFD occurring immediately after reproductive events, and higher reproductive rates producing distributions closer to the IFD. We conclude that a population of non-ideally behaving individuals could achieve an IFD given only resource-dependent population growth, mitigated by dispersal and the frequency of reproductive events, and suggest approaches to further investigate this phenomenon in both theoretical and empirical studies.

Cell-level life history trade-offs under cancer risk

E. Yagmur Erten, University of Zurich, Switzerland

Co-authors: Athena Aktipis, Carlo Maley, Hanna Kokko

Multi-cellular organisms are characterized by a division of labour between the cells. As part of their role in the tissue maintenance, stem cells go through a large number of divisions throughout the lifetime of an organism. More divisions mean an increased mutational load and consequently a higher probability of cancer. How do multi-cellular organisms make sure to rid themselves of the `bad' cells that can cheat and start to proliferate at their own interest, without depleting their stem cell pool too fast? We present a new model of cellular differentiation where we combine past insights from models of the differentiation process with an investigation of optimal apoptosis rules, based on either direct damage measurements or limits of the number of `permitted' cell divisions. Our ultimate aim is to relate the insights from our cell-level model to the level of the organism, creating predictions for species differing greatly in body size.

Eco-evolutionary dynamics in interaction space of competitive communities: How diversity emerges and persists

Farnoush Farahpour, University of Duisburg-Essen, Germany

Co-authors: Mohammadkarim Saeedghalati, Daniel Hoffmann

In recent years, biologists have increasingly recognized that evolution and species interactions are inseparably linked. Eco-evolutionary studies, which are attempting to incorporate the reciprocal influence of ecological interactions and evolutionary dynamics, are usually done in 3 different levels: molecular level, genetic level and phenotypic level. In one step further, interaction network of species could be considered as the subject of eco-evolutionary dynamics. This approach, despite its ability to shed light on very fundamental ambiguities in the field, has not gained enough attention in literature. In this study we introduced a stochastic ecoevolutionary model in interaction space in which species are competing for common resources and are subject to a life-history trade-off. With this simple intuitive model we showed that trade-off is a determinant factor in diversity and also evolutionary process in interaction space of competing species has a tendency for enhancing intransitive relations.

Evolution of host defence in fluctuating environments

Charlotte Ferris, University of Sheffield, United Kingdom

Co-author: Alex Best

Given rapidly changing environments, it is important for us to understand how the evolution of host defence and parasite infectivity respond to fluctuating environments. I will present results from a study of evolution of host resistance to parasitism when the host birth rate is time-dependent. I will show how the amplitude and period of seasonality affect the evolution of the host population, as well as other life-history traits, notably the recovery rate. I will discuss a special case where evolution can drive the population dynamics through a period-doubling bifurcation.

Sounds of silence: The fitness landscape of synonymous mutations

Inês Fragata, Instituto Gulbenkian de Ciência (IGC), Portugal

Co-authors: Sebastian Matuszewski, Mark Schmitz, Claudia Bank

The assumption that silent/synonymous mutations do not produce changes in organismal fitness is fundamental to many population-genetic studies. However, there is increasing evidence that synonymous mutations produce effects, yet, it is largely unknown how pervasive these are. Furthermore, silent mutations change the topology and the topography of the genotype-fitness landscape and may thus affect adaptation by changing the accessibility of evolutionary paths. Here, we investigate the effects of synonymous mutations by exploring the fitness landscapes created by all possible single-codon mutations in a 9-amino-acid region of yeast Hsp90 across six different environments. We observe that the fitness effects of synonymous mutations are affected by amino-acid positions and environment. The arising "codon-fitness landscape" is more rugged in buried than in exposed positions and in stressful environments. We test the accessibility of the landscape with and without synonymous mutations, and discuss the potential impact of silent mutations on adaptation.

A numerical approach to determine mutant invasion fitness and evolutionary singular strategies

Coralie Fritsch, IECL and CMAP, France

Co-authors: Fabien Campillo, Otso Ovaskainen

We propose a general numerical approach that can be used to study the invasion fitness of a mutant in evolutionary models and to determine evolutionary singular strategies when the competitive exclusion principle holds. We illustrate this method with a mass-structured individual-based chemostat model. We assume that the mutations are rare and that the resident population is large, in which case the mutant population can be viewed, on a short time scale, as evolving in a constant environment. Both deterministic and stochastic models can be proposed to describe such a problem. We exploit a previously derived mathematical relationship between these models to derive a general method for analyzing the invasion fitness of stochastic models. Our method is based on a deterministic reduced model for which it is straightforward to determine the feasibility of invasion and the convergence-stable evolutionary singular strategy. This approach is based on mathematical results which have been proved by Fabien Campillo, Nicolas Champagnat and Coralie Fritsch in previous works.

Using Stochastic Games to model Predator-Prey Search-Pursuit behavior

Shmuel Gal, University of Haifa, Israel

Co-authors: Jerome Casas, Steve Alpern

In previous works we modeled predator-prey behavior as a repeated search-pursuit game which takes place in a patch consisting of discrete locations with specific probabilities of capture for each. We now present two stochastic games that take into account the risk of the prey while changing locations and the decrease in motivation of the predator during unsuccessful attempts. The first model is the stochastic game Delta with the state variable i - the location of the present encounter. At this moment the prey has to choose a new location j with risk of moving there depending on i and j: This game continues until either "capture" or "ultimate escape" has been reached. We present an algorithm for solving Delta which converges at a geometric rate to the optimal solution. The second model is the stochastic game Gamma with the state variable k - the number of remaining inspections for the searcher. This number is reduced by one after each inspection. We present the optimal solution by a recursive formula involving solutions of Gamma with smaller k.

Sib cannibalism as a mutualism

József Garay, Eötvös Loránd University, Hungary

The general kin demographic selection model is presented. We point out that sib cannibalism is adaptive if the sib cannibal can decrease its developmental time, and the shorter development time can increase the rate of survival from sib cannibal juvenile to adult, and also when sib cannibalism increases fecundity in the adult stage. Cannibalism between the closest relatives can be considered as a mutualistic kin strategy when the benefit of cannibalism is greater than the cost of it.

Large-scale cooperation and antisocial Punishment

Julian Garcia, Monash University, Australia

Co-author: Arne Traulsen

Large scale cooperation remains an evolutionary puzzle. Experimental and theoretical research highlights the importance of punishment. In large scale societies, punishment is often delegated to institutions, such that resources must be committed to punish free riders before the social dilemma. So far, most models of punishment have restricted the set of possible behaviors, which biases conclusions. Seemingly paradoxical antisocial behaviors are excluded, despite their empirical relevance. We show that antisocial sanctions can undermine cooperation if individuals are unable to condition their behavior on the existence of sanctioning institutions. However, if we allow for conditional behaviors, anti-social sanctioning institutions provide no threat to cooperation. This is due to an evolutionarily stable mixture of a minority supporting pro-social institutions and those who only cooperate if such institutions are in place. A minority of sanction supporters is enough to guarantee substantial cooperation. Our finding resonates with the empirical observation that even in societies with pro-social institutions, some individuals seek to cheat the system if they see a chance to do so. The explanatory power of this model arises from letting evolution, and not the modeller, decide which strategies are relevant - an approach that could be leveraged across a broad range of evolutionary models.

Closer than brothers: The evolutionary roots of identity fusion

Sergey Gavrilets, University of Tennessee, United States

Co-authors: Harvey Whitehouse, Jonathan Jong, Michael D. Buhrmester, Angel Gomez, Brock Bastian, Christopher M. Kavanagh, Martha Newson, Miriam Matthews, Jonathan A. Lanman, Ryan McKay

Across the historical and ethnographic records, from warriors and soldiers to suicide bombers and religious martyrs, humans have proven capable of not just cooperating within groups, but of making extremely costly personal sacrifices for them. Willingness to lay down one's life for non-kin represents an evolutionary puzzle. Recent research in social psychology shows that some type of shared experience can produce a visceral sense of oneness with the group - "identity fusion" - which in turn can motivate extreme pro-social behaviour (e.g., willingness to risk or even give up one's life for the group). Building on this research we develop a mathematical model that shows how conditioning cooperation on previous shared experience or present threat can allow self-sacrifice to evolve. The model leads to a number of predictions which we then test empirically in a range of special sample populations (including military veterans, college fraternity/sorority members, football fans, martial arts practitioners, and twins).

Lessons from clonal dynamics in diseased and non-diseased hematopoiesis

Ingmar Glauche, Technische Universität Dresden, Germany

Continuously regenerating tissues, such as blood, skin or colon, require a constant supply of newly generated, functional cells. These cells derive from a pool of tissue-specific, somatic stem cells that retain the ability to maintain their own population while at the same time contributing to differentiated progeny. The availability of several methods to unambiguously mark individual cells enabled access to ancestral relationships between stem and differentiated cells, generally referred to as clonality, and has contributed significantly to the understanding of the mechanisms that govern both tissue maintenance and regeneration. For several regenerative systems it could be shown that clonal competition is a selection mechanism that strongly influences the temporal clonal dynamics. Along these lines, cancer development is a process of accelerated heterogeneity generation with continuous clonal selection. The selection process is substantially altered in the context of an anti-cancer therapy.

The standardized assessment of the BCRABL fusion gene in chronic myeloid leukemia makes this disease a primary example to study cancer treatment and potential relapse as a clonal competition process between normal and malignant cells in a closely monitored setting. I will illustrate how the application of a mechanistic model of hematopoietic stem cell organization represents a strategy to derive predictions about experimentally inaccessible quantities that can be used for predicting treatment outcome.

I will furthermore present a range of studies that access different aspects of clonality in non-diseased hematopoiesis. I will illustrate that clonal dynamics are instructive to infer differentiation sequences during hematopoietic maturation and outline the experimental limitations of relevant experimental approaches. I will also show how monitoring the dynamics of individual clones over time can be used to predict rapid clonal conversion in clinically relevant settings, e.g. by monitoring patients that underwent gene therapy.

Modeling how selection in one trait interferes with adaptation in another

Kevin Gomez, University of Arizona, United States

Co-authors: Dr. Joanna Masel, Dr. Jason Bertram

When beneficial mutations appear rapidly, distinct beneficial mutations often compete rather than combine, because they are linked to different genetic backgrounds. Without recombination, only beneficial mutations occurring on the fittest (relatively low frequency) genetic backgrounds contribute. Traveling waves have been used to quantify the resulting rate of adaptation under asexual reproduction (Desai & Fisher 2007), with all beneficial mutations interchangeable (evolution in one trait dimension of "relative fitness"). We developed a two-dimensional traveling wave model, and used it to quantify the negative genetic correlations arising between fitness-related traits as a consequence of linkage disequilibria, determining the extent to which adaptation in one trait is slowed by adaptation in the other. The genotype-fitness landscape not only affects the speed of adaptive evolution directly through mutation rates and selection coefficients, but also indirectly by shaping linkage disequilibria between loci encoding different adaptive traits. Simulations are used to confirm our analytical results.

Partitioning community trait variation into ecological and evolutionary contributions

Lynn Govaert, University of Leuven, Belgium

Co-authors: Jelena H. Pantel, Luc De Meester

During the last decade there has been an upsurge in interest to quantify the relative contribution of ecological and evolutionary processes to observed trait change. Partitioning these contributions is a cornerstone of the field of eco-evolutionary dynamics. We compare metrics to partition ecological and evolutionary processes to trait change that are based on the Price equation and on reaction norms, and extend them for the analysis of community data and of trait variation in space. We highlight advantages and limitations of the different partitioning metrics giving different results, with the Price equation based partitioning metrics not being able to differentiate between genetic and non-genetic trait changes within genetic lineages. For data sets that are both amenable to the reaction norm and Price equation based partitioning metrics, we advocate the use of an extended metric that combines the strengths of both approaches. Applied at the community level, this metric can partition trait change in components due to phenotypic plasticity within genetic lineages, genetic changes within lineages, genetic changes due to changes in frequencies of genetic lineages, evolution of plasticity, and components due to changes in frequencies of species and the gain and loss of species in the community. We make a plea for a careful choice of the partitioning metrics to be used and take its limitations into account.

Evolution of species: the mutation as a strategy of survival

Carolina Grejo, Universidade de São Paulo, Brasil

Co-author: Fabio Machado

We propose a model for an evolution of pathogens having a mutation as a survival strategy. The process evolves on the oriented binary tree with root, where each level of the tree represents a type of pathogen. More precisely, each level represents the fitness of that pathogen, and pathogens in the same level have the same fitness. We also consider that pathogens in a higher level have a higher fitness. The immune system takes an exponential time to recognize and produce antibodies capable of eliminating pathogens. In each mark of this Poisson point process all the pathogens with lower fitness in the system is eliminated. We prove the existence of phase transitions on the model and we also prove that exists an interval where all branches at the process will be extinct with probability one, but the process survive with positive probability.

Evolution of metabolic networks under non-balanced growth conditions

Ghjuvan Grimaud, Michigan State University, United States

Co-authors: Elena Litchman, Thomas Koffel, Christopher Klausmeier

Mathematical frameworks such as the Adaptive Dynamics theory1,2 (AD) have been developed to describe evolution of phenotypic traits in a specific eco-evolutionary context but cannot account for trait innovations. Contrarily, Systems Biology genome-scale metabolic modeling allows a mechanistic derivation of phenotypic traits. The Dynamic Reduction of Unbalanced Metabolism (DRUM)3 is a new and promising metabolic modeling method for non-balanced growth conditions; metabolic networks are divided into sub-networks connected by accumulating metabolites, drastically reducing the size of the system while keeping the core information. Here, we propose evoDRUM, a new Evolutionary Systems Biology mathematical framework combining the novel metabolic modeling under dynamic conditions (DRUM) with the eco-evolutionary modeling of trait evolution (AD). Metabolic networks evolution proceeds through a universal mutation space4, driven by a step by step mutant/resident invasion dynamics. First applied to simple metabolic networks with several resources and temporally fluctuating conditions, we then use it for genome-scale metabolic networks.

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To what degree are attack rates constrained by ecological and biological factors?

Orestes Gutierrez, Queen Mary, University of London, United Kingdom

Co-authors: Axel Rossberg, Pavel Katrina

Ecological and biomechanical characteristics can be fixed to calculate the range of attack rates that ensures that a species will avoid starvation and overexploitation. At the individual level, evolution implies larger attack rates are more likely to be selected, but what are the mechanisms that constrain the evolution of attack rates, so that they lie in the dynamic range that allows species persistence? Our project attempts to find which characteristics of ecological and evolutionary models are most significant at constraining attack rates by comparing two hypotheses. (1) The biological constraints hypothesis claims that there are biomechanical costs associated with higher attack rates that force an upper bound on a consumer's ability to gather resources. (2) The ecological constraints hypothesis suggests that the theory of group selection can significantly explain how groups whose traits lead to the over-exploitation of resources become extinct, and that only those with sustainable attack rates remain.

Within-host models of influenza A: Can simple mathematical models help?

Christoforos Hadjichrysanthou, Imperial College London, United Kingdom

Co-authors: Frank de Wolf, Roy M. Anderson

Influenza is a significant cause of morbidity and mortality worldwide. I will show how the development of simple mathematical models of within host dynamics of influenza A viral infection can facilitate a deeper quantitative understanding of viral kinetics and of key attributes of immunotherapeutic drugs for the treatment of infection. Although the viral dynamics is highly nonlinear, closed-form solutions for various quantities that reflect the severity of the infection at different times post acquisition can be derived through analytical approaches. Such quantities include the area under the viral load curve, peak viral load and time to peak viral load. These tools can play an integral role in the interpretation of the viral load data and provide a template for the investigation of the efficacy of potential drug or immune system based therapies.

Why we obscure positive traits and good deeds

Christian Hilbe, IST, Austria

People sometimes make their admirable deeds and accomplishments hard to spot, such as they give anonymously or avoid bragging. Such “buried” signals are hard to reconcile with standard models of signaling or reciprocity, which motivate pro-social and costly behavior by reputational gains. To explain these phenomena, we design a simple game theory model, which we call the signal-burying game. The signal-burying game has the novel feature that senders can bury their signal by deliberately reducing the probability of the signal being observed. If the signal is observed, however, it is identified as having been buried. We show that buried signals can be maintained in equilibrium, even if conventional costly signals cannot, provided higher quality senders have a higher probability of their buried signals being observed, or higher quality senders care less about lower quality receivers. We show that this equilibrium is robust to stricter requirements and to alternative model specifications, and that it emerges in evolutionary simulations. We conclude that burying has evolved because it is able to convey information that other well-known signaling mechanisms cannot convey. We apply our analysis to shed light on a number of otherwise puzzling social phenomena, including modesty, anonymous donations, subtlety in art and fashion, and over-eagerness.

Modelling social influence on cooperation: the public goods game on a multiplex network

Rebecca B. Hoyle, University of Southampton, United Kingdom

Co-author: James M. Allen

We consider economic and social influences on the evolution of cooperative behaviour using a modified public goods game on a multiplex network as a model. We find that social influence leads to the persistence of initial cooperation strategies and so can promote the survival of highly cooperative strategies even when the economic reward for cooperation is relatively modest. This result holds for a range of social norms and for differing economic and social group structures.

Revealing mutant fitness and timing by spatial mixing of sub-clones in tumour

Weini Huang, Queen Mary, University of London, United Kingdom

Heterogeneity is a natural product of evolution in cancer progress and often leads to therapy resistance. While it is hard to have *in vivo* time dynamics of tumor growth in patients, it is more likely to obtain spatial information for example in solid tumor samples. Here, we build a stochastic spatial model of a mutant arising in a wild-type population to access sub-clonal mixing patterns and show how this spatial information can reveal the underlying evolutionary dynamics. We monitor the mutant frequency and the mixing score (Shannon's entropy) over time. Our definition of mixing score consists with the visual observations of spatial patterns of driver genes in archival colorectal cancer samples. We further show that intermediate selection advantage for the mutant type will lead to the highest mixing among the wild type and the mutant. A hump-shaped curve of mixing score is observed over time after the mutant arises. The higher the fitness advantage of the mutant has, the higher the peak is.

Groups, words and the words that groups use

Vincent Jansen, Royal Holloway, University of London, United Kingdom

Co-authors: John Bryden, Shaun Wright

Within a community, individuals tend to group together with those with which they share characteristics. At the same time, much of our characteristics and preferences are influenced by those that we interact with. These two processes create dynamics which give rise to clusters of individuals which share certain characteristics [1]. In human networks we have found evidence of such processes in the language that we use [2,3]. We have shown that on Twitter tribes of users tend to form, and the network emerging from user communication can be structured into a hierarchy of communities, and that the members of such tribes have similar word usage, and use specific words [2]. Consequently, communities can be characterised by their words. We can also show that word usage is passed on from speaker to speaker, demonstrating that language use spreads among those engaged in conversation. This suggests that characteristic language can evolve within a group as their collective identity.

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Commercial fishing model: Application of differential game theory

Chakib Jerry, University of Moulay Ismail, Morocco

Co-author : Mounir Jerry

The purpose of this work is to study the competition of two companies (with two different capitals) exploiting the same resource among which each wants to maximize her profit generated by the exploitation. In this work the considered companies are two fishing fleets considered as two players where each one is looking to maximize the income generated by the exploitation. For that purpose, the theory of the differential games is used which could allow us to guarantee a sustainability of the exploitation for both fleets.
We suppose that the players (fleets) do not cooperate and we determine the strategy which leads to the Nash equilibrium. Trajectories which lead to equilibrium guarantee the viability of the stock and could be suggested to the decision-makers worried about the durability of their activity.
Keywords: Fishing effort, capital evolution, income maximisation, differential game, Nash equilibrium.

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Role of stochasticity in the dynamics of fish schools

Jitesh Jhawar, Indian Institute of Science

Co-authors: Amith Kumar, Hari Krishnan, Vishwesha Guttal

In animal groups, stochasticity plays an important role at the level of both individual and collective movement dynamics. However, investigations of the role of stochasticity in collective behaviour are limited. Here, we use an experimental setup of schooling fish and quantify group polarisation, defined as alignment of direction of group members, at different group sizes. We find that group polarisation is highest for small group sizes and reduces as a function of increasing group size. Using techniques of stochastic calculus, we argue that stochasticity can shift the group between high and low ordered states, resulting in bistability.

We developed a simple individual based mathematical model of schooling behaviour and derived analytical expressions that translates individual scale behavior to group scale behaviour. Our model suggests links between individual level and group level stochasticity and captures the empirically observed dynamics of stochastically induced stable states.

Demographic noise and the evolution of tag based cooperation

Jaideep Joshi, Indian Institute of Science

Co-author: Vishwesha Guttal

Cooperation among organisms, where the cooperator suffers a personal cost to benefit others, is ubiquitous in nature. In well mixed populations, cooperators can be easily invaded by defectors. Cooperators can sustain if they interact preferentially with other cooperators. Preferential interactions can occur if they are mediated by a phenotypic trait carried only by cooperators,also called `tag' or `greenbeard'. However, such tag-based cooperation can collapse if defectors also evolve the tag. We develop an analytical modelthat combines selection, mutation and genetic drift, and show that demographic noise can facilitate the evolution of tag-based cooperation. We find a cyclical dynamics where the population switches between tag-carrying and tagless states. We show that with a broad definition of the tag as allowed in our model, several questions, such as the evolution of quorum sensing and multicellularity, can be conceptualized and solved as problems of tag-based cooperation.

The crucial role of rare variants for inferring transmission processes

Anne Kandler, Max Planck Institute, Germany

The concept of neutral evolution has been used fields as diverse as population genetics, ecology or cultural evolution. We apply an overlapping generation neutral model which originated in the ecological literature to cultural data. In particular, we focus on the progeny distribution and derive the first analytical representation under the hypothesis of neutrality. We show that it consists of two phases: a power law phase with an universally-applicable exponent of -3/2, followed by an exponential cut-off for variants with very large numbers of progeny. Maximum likelihood estimations of the parameters of the neutral model then provide a direct way of evaluating the consistency between theory and observed data. We apply our approach to a data set of baby names from Australia. We find that while neutrality provides a plausible description of the progeny distribution of abundant variant types, rare variant types deviate from neutrality. This indicates that analyses based on only the most popular variants, as is often the case in studies of cultural evolution, can provide misleading evidence for the neutral hypothesis. We further show that a kind of anti-novelty bias is able to replicate more closely the complete progeny distribution of this data set.

From experiment to theory: what can we learn from growth curves?

Georgy Karev, National Institutes of Health, United States

Co-author: Irina Kareva

Finding an appropriate functional form to describe population growth based on key properties of the described system allows making justified predictions about population development. Here we pose an alternative question: what can we infer about population properties based on which growth function fits its growth dynamics best? We investigate Gomeprtzian, inhomogeneous Malthusian and logistic, two-stages hyperbolic-exponential and linear-exponential, and three-stage models and identify whether the population that fits best is homogeneous, heterogeneous, grows in a density-dependent or frequency-dependent manner, and whether it depends on external resources during any or all stages of its development.

Most of the models are constructed within the frameworks of inhomogeneous frequency-dependent models. If, for example, the logistic curve fits the data better than Gompertz curve, the population is more likely polymorphic than monomorphic, and in the former case the population growth may depend on an external (possibly dynamic) resource at all stages of population development, not only when the population size becomes large. Exponential-linear dynamics may be the evidence that the population (i.e., tumor) is inhomogeneous, and the distribution of the clones' growth rates is close to truncated Malthusian distribution. Adding a saturation stage to the exponential-linear dynamics allows reproducing three-stage dynamics, including linear, exponential and saturation stages, which was observed in viral RNA replication models. A key difference of the proposed model from the previously proposed models is that it allows replicating all three dynamical regimes with just one model.

We apply these and other models and predictions to tumor growth and demographic data obtained from the literature.

When presentism and externalism meet sex changing cost to explain multiple sex change hermaphrodite

Amira Kebir, Universite de Tunis el Manar, Tunisia

Co-authors: Nina Fefferman, Slimane Ben Miled

Sex allocation theory succeeds to understand when sequential hermaphrodites change sex. However, almost all models suppose that sex change occurs only once. This strong hypothesis is challenged by the large number of multiple sex change species. Few have answered the question of when and why some species have multiple sex change and others change sex only once. A possible explanation lies in the way in which these species maximize their fitness: Is individual hermaphrodite splits its time between maximizing its reproductive fitness as a female and maximizing its reproductive fitness as a male, or is evolutionary fitness as a hermaphrodite optimized by longer-term strategy? Here we compare these two points of view and extend a new formalism to sex allocation model that underlines all sex allocation models as the result of a dynamical game whose payoff depend on sex changing costs. With this formalism we prove that for a long term strategy, female-to-male sex changing cost appears not to have an impact on sex type. However, lower male-to-female sex changing cost favors multiple sex change hermaphrodite only; otherwise it favors one-sex change sequential hermaphrodite together with female-to-male sex change. This result demonstrates that asymmetry of the cost of sex change causes an asymmetry in the transition from one to multiple sex changes.

Anomalous invasion speeds in highly polymorphic populations – Invasion ecology

Vincent Keenan, University of Liverpool, United Kingdom

Co-author: Stephen Cornell

Environmental and climate change pose new challenges to the natural world, and many species are adapting to this change by shifting their ranges. Dispersal and population growth rate have been identified as key among the many contributing factors to this complicated process. Previous work has shown that a population with two phenotypes (with the possibility of mutation at birth between them), differing in both their dispersal and reproductive abilities, exhibits “anomalous” invasion speeds - i.e., can invade at a faster rate than a monomorphic population containing either phenotype alone. However in nature there are often a range of dispersal and reproductive abilities within a population. In this talk I will examine the case for a population with a general number of phenotypes. We have used a mathematical modelling approach using a system of generalised Lotka-Volterra partial differential equations and numerical calculations to confirm our findings. The results showed that faster invasion speeds were still possible but were dependent on the parameters of only two particular phenotypes - all other phenotypes did not contribute. Surprisingly, we found that this invasion speed need not be determined by the most dispersive nor the most fecund phenotypes. These results have important repercussions for predicting the rate of invasion, and evolution of dispersal during range expansions.

The alternative states of monopolization

Laurens Jean Kilsdonk, Universiteit Leuven, Belgium

Co-author: Luc De Meester

Monopolization is the process whereby early arriving lineages to a new patch through local adaptation obtain an advantage over later arriving lineages and therefore are able to outcompete these later arriving lineages. We use simple dynamic models to study this eco-evolutionary priority effect. Under certain conditions (e.g. high immigration rate) a population cannot locally adapt and therefore there is no monopolization. We found that changing conditions, e.g. decreasing the immigration rate, could lead to a regime shift from a suboptimally adapted regime with high gene flow to an optimally adapted regime with low gene flow. Moreover, we found that to shift back to the suboptimally adapted regime conditions have to be changed beyond the point at which the shift to the optimally adapted (monopolized) regime occurred. Our models show monopolization as an alternative state in even the simplest systems, thus they could be very common.

Mean-field Models for non-Markovian Epidemics on Networks

Istvan Z. Kiss, University of Sussex, United Kingdom

Co-authors: Neil Sherborne, Konstantin Blyuss, Gergely Rost, Zsolt Vizi, Joel C. Miller

In this work, a number of generalisations of mean-field models to non-Markovian epidemics on networks is presented. These include pairwise models with multiple stages of infectionand infectious periods of fixed length, as well as an extension of the edge-based compartmental model to general but independent infection and recovery processes. Some of the resulting models are a system of delay and/or integro-differential equations, and in general these show excellent agreement with results based on stochastic simulation. In many cases we compute R_0 or an R_0-like threshold quantity and the analytical relation between these and the final epidemic size. It is also possible to develop a model hierarchy and show that we are able to recover earlier models directly form the more complex ones by making extra assumptions about the network (e.g. fully connected, regular) or the infection (e.g. Markovian) or recovery (e.g. Markovian, fixed infectious period) processes. By showing the rigorous link between non- Markovian dynamics and various mean-field models, we provide the framework for a more systematic understanding of non-Markovian dynamics which may find further applications or use models inspired by evolutionary or ecological dynamics.

A theoretical study of facilitative succession and ecosystem development by nitrogen fixers

Thomas Koffel, UMR Eco&Sols, France

Co-authors: Simon Boudsocq, Nicolas Loeuille, Tanguy Daufresne

Symbiotic nitrogen (N)-fixing organisms such as actinorhizal plants and legumes tend to thrive during primary succession, as typical bedrocks lack available N. In turn, fixed N accumulates in soils through biomass turnover and recycling, benefiting the whole community. Yet, it is unclear how this facilitation mechanism interacts with competition for other nutrients, e.g. phosphorus (P), and when this leads to succession mostly driven by facilitation. Here, we introduce a resource-explicit, community assembly model of N-fixing species competing for N and P and analyze successional trajectories along resource availability gradients using a recently developed extension of graphical resource competition theory. We show that facilitative succession only occurs under low N availability, and presents three characteristics: autogenic ecosystem development, relatively ordered trajectories and late succession bistability. Put together, these results lead to an enriched version of Tilman’s resource-ratio theory of succession.

A game-theoretic approach to modeling foraging dynamics

Vlastimil Krivan, Biology Centre AS CR and Faculty of Science USB, Czech Republic

Co-authors: Theodore Galanthay, Ross Cressman

This talk is motivated by the Hawk-Dove model, where two opponents contest some unspecified resource of value 2V, and, provided, they both decide to fight, there is an associated cost C. This textbook example nicely illustrates evolution of aggressiveness, but it is difficult to apply to real data. First, it is often not clear what the two parameters are, especially as they need to be expressed in a single currency. Second, the resource value should depend on the amount of the resource. In this talk we construct population dynamic models motivated by the Hawk-Dove game and we study dependence of the aggressiveness in the population on resource availability.

The growth of spatial networks

Vito Latora, Queen Mary, University of London, United Kingdom

Spatially embedded complex networks, such as nervous systems, the Internet, and transportation networks, generally have nontrivial topological patterns of connections combined with nearly minimal wiring costs. We report here the empirical analysis of a database describing the growth of the nervous system of the C. elegant from the moment of fertilization to adulthood. We discuss the basic mechanisms that drive the evolution of such spatial network and we propose how to model its growth.

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The evolution of cooperation in simple molecular replicators

Samuel R. Levin, University of Oxford, United Kingdom

Co-author: Stuart A. West

In order for the first genomes to evolve, independent replicators had to act cooperatively, with some reducing their own replication rate to help copy others. It has been argued that limited diffusion explains this early cooperation. However, social evolution models have shown that limited diffusion on its own often does not favour cooperation. Here we model early replicators using social evolution tools. We show that: (1) replicators can be considered to be cooperating as a result of kin selection; (2) limited diffusion on its own does not favour cooperation; (3) the addition of overlapping generations, likely a general trait of molecular replicators, promotes cooperation. These results suggest key life history features in the evolution of the genome, and that the same factors can favour cooperation across the entire tree of life.

Effects of local negative feedbacks on the evolution of species within metacommunities

Nicolas Loeuille, UPMC, France

Co-author: Mathew Leibold

Local negative feedbacks occur when the occupation of a site by a species decreases the subsequent fitness of related individuals compared to potential competitors. Such negative feedbacks can enhance diversity by changing the spatial structure of the environment. The conditions, however, involve dispersive, environmental and evolutionary processes in complex interactive ways. We introduce a model that accounts for four mechanisms: colonisation-competition-extinction ecological dynamics, evolutionary dynamics, local negative feedbacks and environmental averaging. Three qualitatively distinct dynamics are possible, one dominated by specialists, another dominated by generalists and an intermediate situation exhibiting taxon cycles. We discuss how metacommunity diversity, macro-ecological patterns and environmental patterning are linked to the three qualitative dynamics. The model provides classical shapes for morph-abundance distributions, or diversity-area relationships. Diversity can be high when specialists dominate or when taxon cycles happen. Finally, local negative feedbacks often yield fine-grain environments for taxon cycle dynamics and coarse-grain environments when generalists dominate.

Polyvariant Ontogeny in Plants: A Primary Role of the Second Positive Eigenvalue

Dmitrii O. Logofet, Institute of Atmospheric Physics, Russia

Matrix population models describe the time dynamics of a single-species population that is structured (into a finite number of individual groups) by an observable attribute of individuals: age, size, ontogenetic stage, or so. The basic equation is $\boldsymbol{x}(t+1)=\boldsymbol{L}\boldsymbol{x}(t)$, where nonnegative matrix $\boldsymbol{L}$ "projects" the population structure vector $\boldsymbol{x}(t)$ for one time step further. The matrix pattern is associated with the *life cycle graph*, a digraph that follows from the species biology and prescribes transitions among status groups of individuals and the population recruitment for one step. *Polyvariant ontogeny*, as the diversity of pathways in the digraph, is commonly considered the adaptation mechanism, while the dominant eigenvalue $\lambda_1(\boldsymbol{L})$ the quantitative measure of adaptation.
I demonstrate the crucial role the second eigenvalue $\lambda_2(\boldsymbol{L})>0$ plays in proving the function $R_1(\boldsymbol{L})=1–\det(\boldsymbol{I}–\boldsymbol{L})$ to possess the *indicator property*, namely, to locate at the same side of 1 as $\lambda_1(\boldsymbol{L})$ does. The proof ensues from a recent theory of rank-1 corrections of nonnegative matrices, expanding the classical Perron–Frobenius theory.

Keywords: Dominant eigenvalue, Rank-one corrections, Spectral radius, Potential-growth indicator

A stochastic model for immune response with mutations and evolution

Fabio Lopes, University of Chile

Co-authors: Carolina Grejo, Fabio Machado

We propose a stochastic model for pathogen dynamics with mutations and evolution in the presence of immune response. In our model, pathogens reproduce but mutations introducing new pathogen types may occur. Beneficial mutations lead to pathogen types that have better fitness than their ancestor types and can be transmitted to all descendant types. The immune system can only eliminate a pathogen type after it has already managed to eliminate all its ancestor types with lower fitnesses. That is, it spends a random time to eliminate a pathogen type (all pathogens at once) after its ancestor types are eliminated. We show that pathogens may evade the immune system due to their mutation rate. This contrasts with the results of Schinazi and Schweinsberg for a similar non-spatial dynamics in which each pathogen type is independently eliminated after a random time.

Fluctuations-induced coexistence in public goods dynamics

Presenting author: Yoram Louzoun, Bar Ilan University, Israel

Co-authors: H Behar, N Brenner, G Ariel

Cooperative interactions between individuals in a population and their stability properties are central to population dynamics and evolution. We introduce a generic class of nonlinear dynamical systems describing such interactions between producers and non-producers of a rapidly equilibrating common resource extracted from a finite environment. In the deterministic mean field approximation, fast-growing non-producers drive the entire population to extinction.

However, the presence of arbitrarily small perturbations destabilizes this fixed point into a stochastic attractor where both phenotypes can survive. Phase space arguments and moment closure are used to characterize the attractor and show that its properties are not determined by the noise amplitude, but rather it is stabilized by the stochastic nonlinear dynamics. Spatial Monte Carlo simulations with demographic fluctuations and diffusion illustrate a similar effect, establishing the validity of the two dimensional stochastic differential equation as an approximation.

The functional distribution of the noise emerges as the main factor determining the dynamical outcome. Noise resulting from diffusion between different regions, or additive noise, induce coexistence while multiplicative or local demographic noise do not alter the outcome of deterministic dynamics. The results are discussed in a general context of the effect of noise on phase space structure.

Commensal pathogens as a source of a coexistence mechanism

Yoram Louzoun, Bar Ilan University, Israel

Co-author: Hilla Behar

Most known organisms carry commensal viruses or bacteria. These parasites are often treated as an inevitable nuisance. We here show that they may be essential for the survival of the host specie, and may actually be the force driving speciation.

Viruses that do not hurt their natural host but are deadly for other species have been argued to facilitate invasion. We show using a generic SIR model that the opposite may be the general case. Such viruses may be the force sustaining multiple distinct populations through spatial segregation, in the absence of physical barriers. This segregation protects the hosts against invasion by neighboring, possibly more fit, populations. The virus induced segregation can eventually lead to allopatric speciation, with no animal dispersal, geographical changes or human activities.

We further propose a mechanism, where the introduction of a new virus to a population with a heterogeneous response (based for example on the MHC polymorphism) can lead to the segregation of distinct sub-populations reacting to different strains of the virus. The existence of such a mechanism may require further experimental validation.

Keywords: allopatric speciation, spatial segregation, host virus interaction, stochastic process, co-existence.

Behavioural responses to resource heterogeneity can accelerate biological invasions

Frithjof Lutscher, University of Ottawa, Canada

Co-author: Jeffrey Musgrave

The abundance and spatial distribution of resources and the movement behaviour of individuals determines how fast an invasive species spreads. Whether landscape manipulations can be used to slow invasive species is of great interest in forest ecosystems, where tree removal, thinning, and increasing tree diversity are discussed as management options. Classically, the focus is on availability and accessibility of resources; more recent considerations include individual-level behavioural movement responses to a spatially heterogeneous resource distribution. We derive a novel model for insect-host dynamics that includes three common behavioural aspects of foraging: lower movement rate and higher ovipositioning rate in, and movement bias towards resource-rich areas. We show that each mechanism can increase the speed of invasion in a source-sink landscape above that in a homogeneous landscape with larger resource availability. We parameterize our model and illustrate our results with data for Emerald ash borer, a recent forest pest in North America.

Approximating Dispersal Outcomes Using Weighted Mean First Passage Times

Jane Shaw MacDonald, University of Ottawa, Canada

Co-author: Frithjof Lutscher

Models for growth and spatial movement of individuals in ecology often take the form of reaction diffusion equations or other spatially explicit equations. These types of equations can be quite difficult to parametrize and analyze. One way forward is to derive simpler, spatially implicit models from spatially explicit models through appropriate approximations, for example via the mean first passage time. This method works well for symmetric dispersal processes but fails in the presence of asymmetry. In this work, we present a novel method that uses an appropriately weighted passage time to capture the asymmetry of the process. The weight function is derived from the underlying random walk process. We apply our method to a moving habitat model that has been proposed to study the effects of climate change on population dynamics. We show that the method gives excellent approximations to the minimal patch size required for population persistence.

Lack of ecological and life-history context can create the illusion of microbial social interactions.

Ricardo Martinez-Garcia, Princeton University, United States

Co-author: Corina E. Tarnita

Upon starvation, *Dictyostelium discoideum* free-living amoebae aggregate to form multicellular fruiting bodies, possibly made of more than one genotype, in which cells differentiate between dead stalk cells and reproductive spores. Lab-measured spore contributions indicate a strong skew in the fraction of spores that belong to each genotype, which, inconsistently with nature observations, should result in low genotypic diversity. Recent work suggests that this inconsistency stems from the one-dimensional assessment of fitness (spore production) and that the solution lies in tradeoffs between multiple life-history traits, e.g: spore number versus viability. I will present an experimentally-grounded socially-neutral model (no social genotype interactions) for the life cycle of social amoebae and show how it qualitatively recapitulates all existing findings regarding strain mixes. This allow for potential simple resolutions to long-standing paradoxical results, but does not resolve strain coexistence. I will finalize by discussing the ecological scenarios that could promote diversity in *D. discoideum.*

On the (un)predictibality of a large intragenic fitness landscape

Sebastian Matuszewski, EPFL Lausanne, Switzerland

Co-authors: Claudia Bank, Ryan T. Hietpas, Jeffrey D. Jensen

Central for studying the predictability of evolution is the fitness landscape (FL) concept. Novel experimental approaches enable accurate and extensive studies of mutational fitness effects, allowing us to test theoretical predictions and improve our understanding of the shape of the true underlying FL and its implications for the predictability of evolution. Here, we present a uniquely large complete multi-allelic FL of 640 systematically engineered mutants in the heat-shock protein Hsp90 in yeast. Despite a prevalent pattern of negative epistasis, we find that the global fitness peak is reached via four positively epistatic mutations. Extending recently proposed theoretical and statistical approaches, we quantify features of the global multi-allelic FL. Using subsets of the data, we demonstrate that extrapolation beyond a known part of the landscape is difficult owing to both local ruggedness and mutation-specific epistatic hotspots and that inference is additionally confounded by the nonrandom choice of mutations for experimental FL.

Mathematical niche theory

Géza Meszéna, Eötvös University, Hungary

Intuitively it is widely accepted that different species are adapted to different niches. We provided the exact and general mathematical theory behind this intuition. It is a first principles, bottom up description of population interactions, which identifies the niche of a species by its way of regulation within the ecosystem. The interaction matrix has a central role in the theory, which is therefore amenable for unification with other such approaches. The lecture describes applicability of this concept for complex trophic networks. High diversity must be niche-based; its neutral interpretation cannot be true. It is therefore a central issue, whether a new species occupies a part of the pre-existing niche-space, or the niche space is enlarged by each new species. High diversity is impossible without high primary productivity, but productivity does not lead to high diversity without the possibility of emergence of niche diversity.

Phylogenetic Branching of Pathogens from Dynamic Host Contact Networks

Cornelia Metzig, Imperial College London, United Kingdom

Co-author: Caroline Colijn

Understanding the effect of transmission patterns on branching patterns in phylogenetic trees for pathogens remains a challenging research question. We address this by simulating pathogen transmission (and resulting pathogen phylogenetic trees) on a novel dynamic contact network model. It exhibits realistic features of social networks (short average pathlength, skewed degree distribution, clustering and positive assortiveness). The network's skewed degree distribution can be derived theoretically. The network has stationary size, as it includes entry and exit of people (and contacts). We study different contact network hypotheses and the role of ``population turnover'', i.e. the rate at which people enter and exit. This is important in human populations, but is lacking in commonly used static models. We study its effect with a variety of tree statistics which are all informative, and where possible we compare simulated and real phylogenetic trees.

Spread of infection in random spatial networks

Joel Miller, Institute for Disease Modeling, United States

Co-authors: John Lang, Jamie Kaiser, Hans De Sterck

Random network models play a prominent role in the study of complex phenomena on real-life networks. Many real-world networks exhibit spatial structure, but this has been difficult to study with random networks. We develop a class of random spatial networks (RSNs) which generalizes many existing random network models but adds spatial structure in a way that allows for analytical investigations. We use RSNs to propose a new generalization of small-world networks, where the average shortest path lengths in the graph are small but with close spatial proximity of neighboring nodes playing the role of large clustering. Small-world effects are demonstrated on these unclustered spatial small-world networks. We analytically study susceptible-infectious-recovered disease spreading through RSNs and demonstrate the existence of traveling wave solutions. Under particular conditions, the population-scale dynamics are dominated by long-range hops followed by local spread of traveling waves.

How does geographic distance translate into genetic distance?

Veronica Miro Pina, College de France

Geographic structure can affect patterns of genetic differentiation and speciation rates. We investigate the dynamics of genetic distances in a geographically structured metapopulation, which is modelled as a graph, with N vertices corresponding the subpopulations. The dynamics of the genetic distances is controlled by mutation and migration events. Under a large population-long chromosome limit, we show that the genetic distance between two subpopulations can be expressed in terms of the hitting time between two random walks in the metapopulation graph. Our result shows that the genetic distance between two subpopulations does not only depend on the migration rate between them, but on the whole metapopulation structure. In particular, colonising new demes can modify the whole genetic structure of the population. We apply this result to analyse the stability of different speciation patterns such as ring species and to study how the genetic distances evolve after colonisation of new demes.

Assembly rules and a minimal theory for invasion and extinction in food webs.

Namiko Mitarai, University of Copenhagen, Denmark

Co-authors: Jan O. Haerter, Kim Sneppen

We propose a minimal theory of the evolution of a food web by invasion of new species. Our theory is based on the standard generalized Lotka-Volterra equations, where basal species compete through resource depletion. The theory is “minimal”, as each species only feeds on a single resource, leading to a hierarchical, tree-like food web.

We prove that at each invasion step there is one uniquely determined outcome: either the invader peacefully coexists with the residents and resources are re-distributed; the invader is eliminated; or one or several of the resident species are removed in a uniquely defined extinction cascade. At the end of either of these processes the resulting food web relaxes to a globally stable (and feasible) steady state.

We break down the essence of our theory in the conceptual “invasion extinction model” (IEM), which allows us to analytically compute the persistence time and the extinction size distribution.

The New Mixotrophic-Paradigm in Marine Ecology

Aditee Mitra, Swansea University, United Kingdom

Co-author: Kevin J Flynn

The classic view of marine plankton ecology sees single-celled plankton divided between “plant-like” phytoplankton (primary producers) and “animal-like” microzooplankton (primary consumers). Decades of theoretical, conceptual and biogeochemical models have also been based on this plant-animal phytoplankton-zooplankton dichotomy. Recently, though, we have realised that actually most phytoplankton, and ca. 1/3rd microzooplankton are mixotrophs, using a mixture of strategies for growth. These microscopic "triffids" - photosynthesizing and eating within the single organism cell - are the norm rather than the exception. Accordingly, models based upon "plant-like" phytoplankton and "animal-like" microzooplankton are no longer tenable. Revised models, operating with new functional classifications of planktonic protists, reveal the importance of the mixotrophic-paradigm to marine trophic dynamics and biogeochemical cycling. In light of these, one may question the applicability and usefulness of results from modelling efforts based on the traditional paradigm. Applications of Fractional Calculus in Epidemic Models: Theory and Numerics

Applications of Fractional Calculus in Biological Systems: Theory and Numerics

Shaher Momani, The University of Jordan, Jordan

Co-author: Omar Abu Arqub

Fractional calculus has been used successfully and efficiently to descripe the behavior of many biological systems, such as dynamics of tumor-immune system, dynamics of HIV infection of CD4+ T cells, Population dynamics and SEIR epidemic systems. In this talk we deal with recent applications of fractional calculus to complex epidemic systems and an effective numerical method for their numerical solutions. We present a new version of the reproducing kernel Hilbert space method (RKHSM) for the solution of differential equations of integer and fractional order with Caputo derivatives of α order, where $\alpha \in (1,2]$. Some numerical examples are provided to demonstrate the efficiency and accuracy of the present method by comparing the results of this method with exact solutions.

This talk also includes a quick review of the origins and evolution of the basic concepts of some complex epidemic models, fractional calculus and reproducing Hilbert space theory.

Keywords: Epidemic models; Fractional differential equations; Caputo derivatives; RKHSM; Numerical solution.

Less severe patch-wise epidemics in dense patch clusters in comparison to sparse areas

Tommi Mononen, University of Helsinki, Finland

Co-author: Lasse Ruokolainen

We are modelling evolutionary host-pathogen dynamics of free-living pathogens in a spatio-temporal landscape using a metacommunity perspective. Each community in a habitat patch network consists of host, pathogen and pathogen consuming predator populations. The communities are connected by host dispersal, and infected hosts work as a vector species for pathogens. We assume that pathogens can gain resistance against the consumption of pathogen predators. Moreover, we assume that there is a trade-off between resistance and reproduction in pathogens. The system shows two situations, where epidemics are more severe in sparse areas than in patch-dense areas. In the first case, the permanent lack of resistance can make some patches disease-free resulting a lower number of infected hosts per patch in dense areas. In the second case, patches in dense areas have lower disease outbreak sizes although pathogen resistance against consumption becomes elevated.

Imperfect prey selectivity of generalist predators promotes biodiversity and irregularity in food webs

Andrew Morozov, University of Leicester, United Kingdom

Ecological communities are often characterised by many species occupying the same trophic level and competing over a small number of vital resources, and planktonic ecosystems including hundreds of coexisting phytoplankton and zooplankton species provides a particularly important study case. The mechanisms maintaining high biodiversity in such systems are still poorly understood. For example, a good understanding of the ‘paradox of plankton’ - the coexistence of many phytoplankton species competing over a few vital nutrient resources in an apparently homogeneous environment- is still lacking. In this talk, I revisit the role of prey selectivity by generalist predators in promoting biodiversity in food webs. Mathematically, I consider a generic tri-trophic food web, consisting of a single limiting nutrient resource, a large number of primary producers (phytoplankton) and a generalist predator (mesozooplankton). Firstly, I suggest a novel framework to describe the predator functional response, combining food selectivity for distinctly different functional prey groups with proportion-based consumption of similar prey species. Model simulation reveals that intermediate levels of prey selectivity can explain high species richness, functional biodiversity, and variability among prey species observed in plankton communities. In contrast, perfect food selectivity or purely proportion-based food consumption (largely implemented in the current literature) would lead to a collapse of prey functional biodiversity. The model results are in agreement with empirical phytoplankton rank-abundance curves.

A kin selection perspective on multi-dimensional adaptive dynamics in subdivided Populations

Charles Mullon, University of Lausanne, Switzerland

Co-authors: Laurent Keller and Laurent Lehmann

Spatial limitations entail that individuals that interact with one another tend to be more related than random individuals, which in turn entails kin selection effects. These effects on singular strategies and their convergence stability are well understood, but less so on uninvadability. We derived an invasion fitness measure that reveals the effects of kin selection through relatedness, and used this measure to derive the conditions when a multidimensional strategy is uninvadable. This showed that kin selection can hinder uninvadability when the effect of one trait on relatedness is correlated to the indirect fitness effects of another trait. We illustrate our result by studying the co-evolution of a social behaviour underpinned by a Matrix game and dispersal. In contrast to previous findings, we find that selection is disruptive under a significant range of model parameters and leads to a social polymorphism, highlighting the importance of kin selection effects in subdivided populations.

Quantitative feedback analysis as a way to study adaptive strategies in food webs

Anje-Margriet Neutel, British Antarctic Survey

In 1981, Peter Yodzis performed a model disturbance experiment where he randomly permuted pairs of interaction strengths in his theoretically parameterised community networks. Disruption of the biologically "plausible" equilibrium structures led to a dramatic decrease in model stability. More than anything, his results made clear that we have to go beyond connectedness, beyond the pair-wise interactions, to the feedbacks in the systems, to understand the stability of communities. But how far do we have to go to explain the stability of complex natural community networks? How many levels of feedback do we need to consider, to capture the stability of a complex *n*-level system? And does this understanding of the feedbacks tell us anything about key biological properties, about the relation between stability and the functioning of ecosystems, or even about adaptation and development? Here we use observations on the material flow in a range of terrestrial food webs. With the empirical material-flow structure, translated into traditional community matrices of the type that Yodzis used, we analyse the multitude of feedbacks in the systems. We find that 3-link feedback loops are key in understanding stability, sustainability and the adaptive strategy of competition.

Collateral Sensitivity is Contingent on the Repeatability of Evolution

Daniel Nichol, University of Oxford and Institute of Cancer Research, United Kingdom

Co-authors: Joseph Rutter, Peter Jeavons, Alexander Anderson, Robert Bonomo, Jacob Scott

Background
Treatments accounting for evolutionary principles are needed to maintain the efficacy of antibiotics or to overcome resistance to cancer therapies. One treatment strategy is the identification of drug sequences wherein the evolution of resistance to each drug sensitises the population to the next; a phenomenon known as *collateral sensitivity.* We introduce a mathematical model to explore the potential for sequential drug therapies to prevent drug resistance, and test the robustness of sequences designed through experimental evolution.

Methods
A mathematical model of evolution over a fitness landscape is introduced and parameterised by empirically derived landscapes. Using model derived likelihoods for evolutionary trajectories, an exhaustive analysis of all short drug sequences is performed to identify optimal sequences and test the efficacy of random sequences. Experimental evolution is simulated to determine the robustness of sequences derived from experimental evolution.

Results

From an exhaustive analysis of drug sequences, we demonstrate that the majority (~70%) of short drug sequences promote resistance to the final antibiotic, indicating that the rational design of sequential therapies is essential. Derivation of the optimal drug sequences reveals that, for 7/15 drugs, the evolutionary trajectory to the most resistant genotype can be rendered in accessible through evolutionary steering. This suggests that evolutionarily-informed therapies could minimise drug resistance. Through *in silico* simulations we find that a drug pair that exhibits a collaterally sensitive response in a single replicate of experimental evolution will exhibit cross-resistance in a second replicate with likelihood greater than 50%. The existence of such between-replicate differential response is confirmed through experimental evolution.

Conclusions

We conclude that both arbitrary drug sequences, and those derived from the present methodology of low replicate number experimental evolution, are dependent on the repeatability of evolution and can inadvertently promote drug resistance in rugged landscapes.

Costly reputation systems and the evolution of indirect reciprocity in the donation game

Isamu Okada, Soka University, Japan

Co-authors: Tatsuya Sasaki, Yutaka Nakai

Building reliable reputation systems is key to improving trust between unrelated people. For instance, a rule of thumb for online shopping is to trust those who have a good reputation and avoid those who have a bad reputation. However, making trustful assessments of good or bad requires time and effort and leads to a temptation to free ride on others' efforts in making assessments. What can motivate people to contribute to a voluntary moral assessment? This is the moral free-rider problem. To address this problem, we take a different approach from the traditional approach of voluntary policing. We consider pre-commitment to costly moral assessment. In the model the participants who do not commit are assigned a bad reputation and will be refused help in the following interactions. We in terms of evolutionary game theory analyze the model for different moral assessment rules that include the Staying norm.

The evolution of sheep immunity in response to nematode infection

Cameline Orlendo, University of Glasgow, United Kingdom

Co-authors: Daniel Balaz, Christian Cobbold, Louise Mathews, Michael Stear

There is considerable variation in the distribution of parasite numbers amongst lambs infected with gastrointestinal nematodes. One hypothesis that could explain the observed heterogeneity is that, hosts mount varying strengths of immune responses when infected. The immunity mounted by lambs against nematode infections is composed of two components; the IgE immunity which lowers worm numbers within a host, and the IgA immunity which lowers the number of parasites released by the host back into the communal pastural area. In this work, we use adaptive dynamics to study the evolution of the strength of immune responses mounted by hosts following nematode infections. We use the lamb's rate or weight gain as a measure of host fitness, and assume that weight gain is determined by the hosts use of protein nutrients for growth versus immune response to infection. We observe that branching occurs when the protein cost of mounting the IgA immunity, which controls the fecundity of adult nematodes, is expensive, and the protein cost of mounting the IgE immunity, which controls worms numbers within a host, is inexpensive. We conclude that, varying protein costs of the two distinct immune components could lead to evolution of varying immune strengths mounted by infected lambs.

Emergent structure and dynamics in stochastic, open, competitive communities

Annette Ostling, University of Michigan, United States

Co-author: Rafael D'Andrea

Niche differentiation could explain biodiversity maintenance, but remains difficult to demonstrate. Inference based on trait patterns could point to mechanisms worthy of more intensive study. However, classical trait pattern predictions of evenness were derived assuming equilibrium, deterministic, closed communities, making application to nature tenuous. Recent literature suggests niche differentiation may drive the spontaneous formation of species clusters, but it is not known whether the phenomenon occurs across different niche mechanisms and how other conditions affect its appearance. We propose a metric to quantify clustering, and show with simulations of stochastic niche models that clustering occurs across different niche mechanisms, and is more likely to appear regional diversity is high and immigration is low. We also highlight the complex effect of niche differentiation on species dynamics in stochastic open communities and show that the strength of clustering pattern is related to the strength of effect of niche differentiation on species' dynamics.

Deterministic approximations of stochastic dynamics in evolutionary graph theory

Christopher Overton, University of Liverpool, United Kingdom

Co-authors: Mark Broom, Christoforos Hadjichrysanthou, Kieran Sharkey

Evolutionary graph theory aims to investigate the dynamics of evolution in a context where there is spatial population structure which is represented by a graph. Previous studies in this area have mainly focused on the outcome of evolutionary processes on highly idealised graphs. On such structures, quantities of interest, such as the fixation probability of an invading mutant, can be calculated analytically.

Investigations of the evolution of populations represented by complex heterogeneous graphs require computationally intensive methods. In this presentation we discuss methods of obtaining approximate descriptions of the underlying stochastic dynamics within a deterministic framework. In particular, we derive approximations directly from the master equation. Although these approximations are commonly used in the modelling of epidemics on networks, their application in evolutionary dynamics is particularly challenging. The purpose of this work is to develop deterministic approximation methods with low computational complexity to describe stochastic evolutionary dynamics on arbitrary graphs.

Ecological feedback on evolutionary spatial dynamics with social dilemmas

Hye Jin Park, Max Planck Institute for Evolutionary Biology, Germany

Co-author: Chaitanya S. Gokhale

Cooperators raise the group benefit but individually perform worse than defectors causing social dilemmas. Due to the lower benefit of cooperators, they eventually die out without any mechanisms to enhance cooperation. More recently, combined with constant diffusion of individuals on twodimensional space, eco-evolutionary dynamics has shown to sustain a mixture of cooperators and defectors in a population. Ecology, in this case, is determined by the changes in population densities over time. However not just the interactions but the phenotypic properties of individuals can also be affected by ecology. For example, an individuals' mobility is not constant but varies with circumstance. While a work in progress, preliminary results already indicate that the inclusion of such frequency-dependent diffusion dynamics can help an otherwise doomed population to survive on the edge of heterogeneous coexistence.

Environmental dimensionality

Kalle Parvinen, University of Turku, Finland

Mechanistic population models can always be decomposed into two parts: an impact map that describes how the present community affects the environment characterized by regulating variables, and a sensitivity map that describes how population growth depends on the regulating variables. According to the competitive exclusion principle the number of coexisting species in a system is less than or equal to the number of regulating variables. Since the decomposition is not unique, a given decomposition may or may not contain a minimal representation of the regulating variables. Here we show how the dimension of population regulation can be determined by analyzing the impact and sensitivity maps. The impact dimension is reduced if not all environments can be reached, and the sensitivity dimension is reduced when not all environmental variables affect population growth independently. These dimensions give valuable information about the potential coexistence of species.

Recombination rates affect eco-evolutionary feedbacks

Swati Patel, University of Vienna, Austria

Co-author: Reinhard Burger

Much theoretical work has been done to understand how eco-evolutionary feedbacks qualitatively alter the dynamics of ecological and evolutionary processes. However, there has been relatively little work done on how underlying genetic processes impact the effects of eco-evolutionary feedbacks. Here, we investigate an eco-evolutionary model of a predator evolving in a trait controlled by two potentially linked loci, which determine its interactions with two prey species. We show that recombination between the two loci can alter the effects of eco-evolutionary feedbacks. In particular, we find that eco-evolutionary feedbacks may drive cycling of population densities, allele frequencies, and linkage disequilibrium for an intermediate range of recombination rates. Importantly, this cycling enables the maintenance of genetic variation for higher recombination rates than predicted in a purely evolutionary model. Our work highlights that the aspects of the genetics of evolving traits play an important role in the overall effects of eco-evolutionary feedbacks.

Evolving multiplayer networks: Modelling the evolution of cooperation in a mobile population

Karan Pattni, City, University of London, United Kingdom

Co-authors: Mark Broom, Jan Rychtar

A population of finite individuals is considered that can move through a structured environment using the flexible evolutionary framework of Broom-Rychtar (2012). The behaviour of the individuals follows a Markov movement model where decisions about whether they should stay or leave depends upon the group of individuals they are with at present. The interaction between individuals is modelled using a multiplayer public goods game. This talk demonstrates that cooperation can evolve when there is a cost associated with movement. Combining the movement cost with a larger population size has a positive effect on the evolution of cooperation. Moreover, increasing the exploration time, which is the amount of time an individual is allowed to explore its environment, also has a positive effect.

Metabolic constraints on complex ecosystems

Samraat Pawaar, Imperial College London, United Kingdom

The rate of energy use (metabolic rate) of individual organisms sets the rate of interactions between organisms. I will present ongoing work on how metabolic constraints on interactions within (intraspecific interference) and between species (search and consumption rate) constrain three key rates of complex communities: assembly, functioning (productivity and carbon fixation), and recovery from external perturbations.

Invasion and fixation of nonlinear cooperation in subdivided populations

Jorge Pena, GEOMAR Helmholtz Centre for Ocean Research, Germany

Co-authors: Georg Noldeke, Laurent Lehmann

Most models of social evolution in subdivided populations assume either phenotypically close strategies or additive interactions, with the resulting conditions for the evolution of cooperation consisting of simple expressions depending on costs, benefits, and a single relatedness coefficient. Here, we go beyond this usual assumption and explore the invasion and fixation of mutants playing multiplayer cooperation games in an infinite island model under either a Moran or a Wright-Fisher demography. When selection is weak, we derive a number of interesting results, including a generalization of Taylor's famous cancellation result and instances of collective action dilemmas for which higher (rather than lower) dispersal rates promote the evolution of cooperation. Overall, our work shows how accounting for nonlinear social interactions in subdivided populations can lead to a richer set of evolutionary outcomes and to comparative static results that are in stark contrast to the predictions of standard additive models.

Keywords: invasion fitness, subdivided populations, multiplayer games, dispersal

The economics of egg trading revisited

Jorge Pena, GEOMAR Helmholtz Centre for Ocean Research, Germany

Co-authors: Georg Noldeke, Oscar Puebla

Egg trading (the exchange of eggs during mating by simultaneous hermaphrodites) is a classic example of cooperation between unrelated individuals. Recently, Henshaw et al. (2014) showed that the evolutionary dynamics of traders and non-traders is under positive frequency dependence, so that egg trading can go to fixation once the frequency of traders is above a certain threshold. Here we revisit and extend this model to account for: i) senescence of eggs, ii) costs of egg production, and iii) a third cheater strategy that never releases eggs and only reproduces through the male function. We find that the presence of cheaters can destabilize the trading equilibrium, leaving either the non-trader monomorphic state or a polymorphism where traders and cheaters co-exist as the only stable equilibrium. Our results suggest that the evolution of egg trading is less likely in the presence of cheaters and costly egg production.

Keywords: egg trading, simultaneous hermaphrodites, replicator dynamics

A genealogical model for the ancestor paradox

Sophie Penisson, Universite Paris Est Creteil, France

Thinking naively, the structure of a person's ancestor tree is a binary tree, implying that this person has 2n ancestors n generations back. Such an exponential growth conflicts however with the steadily decreasing size of the worldwide population back in time. This apparent paradox is explained by shared ancestors, referred to as pedigree collapse. Indeed, when family members such as cousins marry, lines of ancestors merge and the number of individuals on their ancestral tree decreases compared to the binary tree of reference. We propose a stochastic model of the pedigree collapse, in the form of a random directed acyclic graph. We study the probabilities for couples to be cousins of a given degree (with the possibility of being related at multiple degrees) and the probability for a graph of having the desired diamond shape of a collapsed pedigree.

Fragmentation models and the evolution of life cycles

Yuriy Pichugin, Max Planck Institute for Evolutionary Biology, Germany

Co-authors: Jorge Pena, Paul B. Rainey, Arne Traulsen

Reproduction is an essential feature of living organisms. Reproduction modes exhibit a great variety: from binary splitting in bacteria to complex collective-level reproduction in multicellular organisms. However, what drives the evolution of reproduction modes is still unclear. We developed a model of population, where new groups are produced by fragmentation of existing groups. Fitness of the population depends on reproduction mode: at which size(s) group fragments and offspring of what sizes are produced. Reproduction modes, which maximize the population fitness are evolutionary optimal. Model allows reproduction modes where groups may fragment at various sizes. We found that in evolutionary optimal mode, all groups divide upon reaching the same size and produce the same pattern of offspring groups. If all cells survive the fragmentation, the optimal mode involves production of exactly two offspring groups. If a cell is lost upon reproduction, fragmentation into multiple groups may be optimal.

The ecological complexity of global macro-economics

Jon Pitchford, University of York, United Kingdom

Co-authors: Simon Croft, Alex James, Mike Plank

For decades researchers have recognised similarities between ecosystems and economic supply chains: both involve complex interactions between entities which interact, and which may be aggregated, at various scales. Here we will outline the well-established economic theory of the Leontief inverse and its associated matrices, and ask how more recent developments in the theory of ecological networks might influence their implications. Using increasingly available large data sets from economics, we will show how matrix structure and the level of aggregation impacts upon important system-scale properties. This has direct relevance to economic stability and efficiency under organisational perturbations. Moreover, there is potential for useful insights into the management of ecological resources at the ecosystem scale.

New perspectives on cooperation in iterated games

Joshua B. Plotkin, University of Pennsylvania, United States

Co-author: Alexander Stewart

I will discuss recent developments in the theory of iterated games, and their implications for the evolution of cooperation in populations. We introduce a coordinate system for describing memory-k strategies in iterated games, based on results of Press, Dyson, and Akin. This coordinate system allows us to determine all evolutionary robust strategies in very general settings. We find evolutionary dynamics characterized by periods of behavioral stasis punctuated by stochastic shifts between different basins of robust strategies, caused by neutral drift. We describe how the volume of robust cooperative strategies depends on a players' memory capacity, the size of groups in which games are played, the space of available strategy mutations, and the possibility of heritable mutations to payoffs.

Metapopulations in evolving landscapes

Phil. Pollett, The University of Queensland, Australia

Co-authors: Ross McVinish, Jessica (Yui Sze) Chan

I will describe a model for populations that occupy several geographically separated patches of habitat, one which accounts for the evolution over time of landscape characteristics that affect the persistence of local populations. In particular, the probability of local extinction is allowed to evolve according to a Markov chain. This covers the widely studied case where patches are classified as being either suitable or unsuitable for occupancy. I will explain why, for large population networks, the persistence and equilibrium levels of the population are determined by the distribution of the life span of local populations, and not by the specific landscape dynamics.

Evolutionary dynamics in the two-locus two-allele model with weak selection

Martin Pontz, University of Vienna, Austria

Co-authors: Josef Hofbauer, Reinhard Bürger

Two-locus two-allele models are the simplest models to explore the role of epistasis for a variety of important evolutionary problems, including the maintenance of polymorphism. However, due to the mathematical complexity arising from the fact that epistasis generates linkage disequilibrium, few general insights have emerged. Here, we study a simpler problem by assuming that linkage disequilibrium can be ignored. This is a valid approximation if selection is sufficiently weak relative to recombination. The central point in our analysis is the inference of the number and stability of fully polymorphic equilibria from the boundary flow, i.e., from the dynamics at the four marginal single-locus subsystems. For general fitness matrices, this is rather difficult, however, for many specific classes of fitness schemes, including purely additive-by-additive epistasis, multilinear epistasis, and the symmetric viability model, we obtain complete characterizations of the possible equilibrium structures.

The development of a spatio-temporal model for investigating biological control release strategies in water hyacinth

Linke Potgieter, Stellenbosch University, South Africa

Co-authors: Helene van Schalkwyk, Cang Hui

A reaction-diffusion model, consisting of a system of delayed partial differential equations, for a temporally variable and spatially heterogeneous environment, is developed to mathematically describe the spatial dynamics of water hyacinth and the interacting populations of the various life stages of the *Neochetina eichhorniae* weevil as a biological control agent on a bounded two-dimensional spatial domain. Preliminary validation tests indicate that the model may succeed in realistically representing the spatio-temporal dynamics. A modelling framework is thereby provided that may be used to evaluate the effectiveness of different biological control release strategies, providing guidance towards the optimal magnitude, timing, frequency and distribution of agent releases. Numerical solutions emphasise the benefit of frequent releases of *N. eichhorniae*, as well as the advantage of more distributed releases along the edges of an infested water body. Furthermore, releases commencing in summer are shown to be significantly more efficient and cost-effective than releases commencing in winter.

How movement responses can shape demographic dynamics in strongly competing populations

Jonathan R. Potts, University of Sheffield, United Kingdom

Co-author: Sergei V. Petrovskii

Animal movement is a key mechanism for shaping population dynamics. However, the processes by which movement can affect the survival and co-existence of interacting populations are not well understood. Here, we examine the effect of movement responses to foreign populations on demographic dynamics. We look at a simple model of two competing populations, where inter-specific competition is greater than intra-specific competition. Without space, this is a bistable system. When space is incorporated as diffusive movement, a travelling wave moves from the stronger population to the weaker. However, by incorporating behaviourally-induced directed movement towards the stronger population, the weaker one can slow the travelling wave down, even reversing its direction. Hence movement responses can switch the predictions of traditional mechanistic models. Finally, incorporating dynamic movement responses can also enable stable co-existence in an homogeneous environment, overturning long-held assumptions about the Competitive Exclusion Principle.

When does an invasion of a novel trait imply substitution?

T. Priklopil, University of Lausanne, Switzerland

Co-author: L. Lehmann

The focus of much of evolutionary biology is to identify the direction and strength of selection. In order to determine whether selection is directional or not, one essentially needs to calculate whether an invasion of a novel phenotype/allele implies a substitution of its ancestor. Unfortunately, for arbitrary strength of selection the full consideration of an evolutionary trajectory (usually non-linear) renders the problem too difficult. However, when the phenotypic difference of the invader and its ancestor is small, meaning that the selection is effectively weak, such calculations can often be made exact. In this case, it has been shown by numerous authors over more than four decades, that a successful invasion generically implies substitution and the direction of selection can be expressed by a quantity that is proportional to a frequency-independent selection gradient. Surprisingly, to date, the existing literature is scattered across various denominations of theoretical biology thus validating the “invasion implies substitution” only under some particular assumptions about the population. Consequently, several biologically important cases do not have a rigorous proof. Here, we review the existing literature and outline the conditions on the genetic, spatial and demographic structure for which the outcome of invasion can be calculated.

Combining network theory and reaction-advection-diffusion modelling: a mechanistic approach for predicting animal distribution in dynamic environments

Marie-Caroline Prima, Laval University, Canada

Co-authors: Thierry Duchesne, André Fortin, Daniel Fortin

Landscape connectivity is a key determinant of animal distribution. Changes in landscape properties generally alter landscape connectivity, resulting in a different movement flow of individuals within patch networks, and, therefore, in their distribution. We developed a reaction-advection-diffusion model to predict animal distribution based on residency time in resource patches and on functional connectivity among those patches. We parameterized the model using telemetry data of free-ranging bison travelling among meadows found in a forested landscape. We found that the graph most relevant to this system, among a set of simple and complex graphs, was an ultra-small world scale-free network, a complex graph. Simple graphs provided less accurate predictions of bison distribution. The analysis illustrates the risk of only considering simple graphs when inferring animal distribution in dynamic landscapes. Our modeling approach provides a powerful tool to predict animal spatial distribution when environmental conditions change following, for example, habitat management.

Species trait distributions in evolutionarily assembled model food webs

Rosalyn Rael, Tulane University, United States

Food webs, or ecological networks representing consumer-resource relationships, are widely used tools for studying ecosystem stability, resilience, and diversity. Combined with dynamic models, food webs have been used to understand how ecological interactions play a role in shaping ecosystem structure. However, the strengths and nature of the interactions can change over longer time scales as ecosystems evolve and undergo natural changes in composition with species adapting, going extinct, and new species emerging. In this talk I will present an evolutionary game theory model that combines deterministic ecological dynamics with a stochastic speciation process and discuss patterns in trait distributions, abundance, extinction, and structural changes that emerge as food webs evolve. This work demonstrates how a few relatively simple evolutionary and ecological assumptions can be integrated to model ecological change and produce complex ecosystem structures that can be used to study vulnerability and stability of natural systems.

Signalling in the evolution of costly social behaviour

Nichola Raihani, UCL, United Kingdom

This talk will explore the extent to which costly social behaviours – including cooperation and punishment - can be understood as having a signalling function. I will first explain the evolutionary logic of costly signalling, before presenting behavioural experiments (using lab and real-world data) that support the costly signalling function of both helpful and harmful behaviour.

Spatial dynamics of Blackbuck herds

Aakanksha Rathore, Indian Institute of Science

Co-authors: Vishwesha Guttal, Kavita Isvaran

Animal groups show striking patterns in their structure and movement. Sometimes, these patterns also have functional consequences (Gueron et. al.,1996) .Mathematical models can help us understand the interaction rules which individuals follow. However, very few emprical studies have recorded such fine scale interactions in the natural systems (Farine et. al., 2016; Strandburg-Peshkin et. al, 2017). One reason for this dearth of studies from the wild might be difficulty in capturing multiple spatial interactions at single time instant.

Advancement in aerial imagery techniques allows us to observe and record such interactions. I am studying spatial dynamics of Blackbuck (Antilope cervivapra) herds using aerial imagery techniques. I am looking at fine-scale interactions to know how information spreads within a herd and how habitat affects the decisions of the individuals. The data collection for the study was done at Blackbuck National Park,Gujarat. I will be presenting some preleminary results from my study.

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Adaptive dynamics as a tool to predict when flexible parenting evolves

Tom Ratz, University of Edinburgh, United Kingdom

Co-authors: Hope Klug, Michael B. Bonsall

Parental care is a major component of an individual’s investment into reproduction and affects both parent and offspring fitness. Moreover, parenting behaviors and the level of care provided are known to be highly responsive to environmental conditions (e.g. climatic, ecological and social factors). Phenotypic plasticity is expected to be a key mechanism in response to short-term environmental variation and should play an important role in the evolution of parental care. However, no theoretical work has addressed these assumptions and the environmental and life-history conditions allowing plasticity in parental care to evolve remain to be clarified. Here we fill this gap by incorporating phenotypic plasticity into a model of the ecological dynamics of a species with parental care. Using the adaptive dynamics approach, we investigated the effect of environmental and life-history parameters on the success of plastic mutants invading a resident population displaying fixed levels of parental care.

Keywords: Invasion analysis, life-history, parental care, phenotypic plasticity, stochastic environment*.*

A model of the best-of-N nest-site selection process in honeybees

Andreagiovanni Reina, University of Sheffield, United Kingdom

Co-authors: James A. R. Marshall, Vito Trianni, Thomas Bose

The ability of a honeybee swarm to select the best nest site plays a fundamental role in determining the future colony's fitness. To date, the nest-site selection process has mostly been modelled and theoretically analysed for the case of binary decisions. However, when the number of alternative nests is larger than two, the decision process dynamics qualitatively change. In this work, we extend previous analyses of a value-sensitive decision-making mechanism to a decision process among N nests. First, we present the decision-making dynamics in the symmetric case of N equal-quality nests. Then, we generalise our findings to a best-of-N decision scenario with one superior nest and N-1 inferior nests, previously studied empirically in bees and ants. Whereas previous binary models highlighted the crucial role of inhibitory stop-signalling, the key parameter in our new analysis is the relative time invested by swarm members in individual discovery and in signalling behaviours.

Evolution in dynamic population structures

Jessie Renton, UCL, United Kingdom

Co-author: Karen Page

Evolutionary processes occur in structured populations of individuals be they cells arranged in a tissue or humans in our social networks, however traditional models of evolutionary dynamics have tended to assume homogenous populations. Developments in evolutionary graph theory have demonstrated that the introduction of explicit structure by placing individuals on the nodes of a graph can have substantial effects on the dynamics. However the majority of results apply to special cases of graphs. Further, the extended versions of adaptive dynamics and the replicator equation assume that graphs are static, while population structures in reality are changing. We explore the effects of a dynamic population structure on evolution, considering the organisation of epithelial cells as an example of a population where individual cells undergo neighbour exchange.

Generalizing species diversification models

Francisco Richter, University of Groningen, The Netherlands

Co-authors: Ernst Wit, Rampal Etienne

The mechanisms controlling species diversification are poorly understood. Sophisticated diversification models have been developed, but they focused on specific cases and no general method to study the combined effect of ecological factors exists. No general method has been developed for several reasons. Firstly, evolutionary processes have extremely complex dynamics. Secondly, decay and fossilization degrade crucial evidence useful for phylogenetic analyses. Thirdly, diversification processes have many potential explanatory variables, which increases the dimensionality of the models enormously. To overcome these issues, we propose a general diversification model expressing the evolutionary species diversification dynamics as a combination of two generalized linear models. The fact that we typically only have data on extant species can be described as a missing data problem for which we developed an MCEM-type algorithm. We show that our method performs well for cases where an exact solution is available, and discuss potential future usage of our approach.

Keywords: Diversification models, GLM, MCEM

Tumor phenotypic plasticity, natural selection, and the microenvironment: An integrated, multiscale approach to designing better therapies

Mark Robertson-Tessi, Moffitt Cancer Center & Research Institute, United States

Co-authors: Casey Adam, Dan Nichol, Robert Gillies, Robert Gatenby, Alexander Anderson

Heterogeneity is widely observed between and within tumors and the potential clinical significance of these variations is increasingly being recognized. The tumor microenvironment selects for phenotypes that are best adapted to survive and grow. However, this environment is temporally and spatially heterogeneous largely due to variations in blood flow, which results in local fluctuations of nutrients, growth factors and cellular populations. Tumor cells adapt to changing conditions through a variety of mechanisms with different timescales, which has significant implications for the application

of therapies. Using a hybrid multiscale mathematical model of tumor growth in vascularized tissue, we investigate the selection pressures exerted by variations in the tumor microenvironment. Key components of the model include: normal and tumor metabolism; an adaptive immune system; and a dynamic vasculature. Tumor cells are given several phenotypic axes that can change with time, each of which has associated cost-benefit functions. The model was parameterized and calibrated based on *in vitro* and murine experiments. Under various conditions of vascularity and immune response, tumors develop heterogeneous spatiotemporal structures that we call “metaphenotypes”, and which collectively have an evolutionary advantage in that region of the tumor. The emergent metaphenotypes are dependent on timescales of microenvironmental change; for instance, intermittent hypoxia due to blood vessel leakiness selects for plastic, rapidly responding tumor strategies; while prolonged nutrient deprivation selects for aggressive, hard-wired, glycolytic cells. Treatment success is highly dependent on understanding these metaphenotypes. Using the model in combination with *in vivo* experiments in a spontaneous prostate tumor mouse model, we show how therapy timing and dose can change the evolutionary course of the tumor and affect outcomes. We categorize the signature of each therapy response as a function of initial tumor heterogeneity and implement drug sequences that promote a synergistic response for a given tumor metaphenotype.

Social evolution in a demographic context

Antonio M. M. Rodrigues, University of Cambridge, United Kingdom

Recent years have witnessed a growing interest in understanding how demography shapes social interactions. Demography influences social transactions beyond their immediate consequences as well as the genetic background upon which games are played. Researchers have relied on alternative frameworks to develop demographic models, which have been used to study the effect of multiple demographic factors on the outcome of social interactions. However, how the structural and implicit assumptions of the models impact the conclusions of these studies has been relatively neglected. Here, I present a general analysis of this problem. Moreover, I provide a concrete example of how unstated assumptions may lead to misunderstandings regarding the effect of demography on social evolution, and how this prevents the empirical testing of model predictions.

Ecological and social changes affecting human evolution: or grandmothers and long childhood dependency make the human life history

Danya Rose, University of Sydney, Australia

Co-authors: Peter Kim, Kristen Hawkes, John McQueen

Pliocene climate change resulted in a choice for our last common ancestor with chimpanzees: to remain in the forests, where many food sources were easy for young to obtain; or to eke out a living in the spreading savannas, where food was no longer as easy for young to reach on their own, but novel strategies could be explored to keep populations viable.

One such strategy is the adoption of grandmothering. The grandmother hypothesis is proposed to explain the unique (among primates) human life history: by contributing to the upbringing of their grandchildren, hale post-reproductive females free their daughters to have more offspring sooner. This provides an incentive for average life expectancy at birth to increase, while age of menopause remains at or near the ancestral level.

Using an agent-based model to explore some dimensions of a large parameter space, we show how with an increasing age of independence (corresponding to the difficulty of young obtaining food on their own), grandmothering allows the evolution of a human-like life history and reproduction rate.

Keywords: Human evolution, Ecology, Grandmother hypothesis

How structural instability of ecological communities manifests in nature

Axel G. Rossberg, Queen Mary, University of London, United Kingdom

Ecological communities are called structurally unstable if small external pressures or changes in ecological parameters can have large effects on species abundances. In a variable environment, this might lead to extinctions and so constrain coexistence. Mathematical theories have been developed to quantify structural instability, to predict its strength depending on community properties, and to explain how it arises in complex communities. But how does this affect communities in nature? Does Nature employ some devious strategies to avoid the phenomenon altogether? Is the onset of structural instability shadowed by other, stronger limitations to coexistence? Or is it omnipresent but complex communities to persist despite it? A number of patterns in community structure and dynamics all lead to the same conclusions: none of this is the case. Natural communities adjust species richness exactly to the point where structural instability sets in, which leads to a rich, predictable phenomenology at community level.

Stability analysis of Discrete mutualism models with delay

Andrew Rowntree, University of Chester, United Kingdom

Co-authors: Jason Roberts, Nikos Kavallaris

In this poster we present a delayed two-species mutualism model that has been discretised by a piecewise constant arguments approach. We display necessary and sufficient conditions for the asymptotic stability of the system’s nontrivial equilibrium at certain values of the delay, we then ascertain that the value of the delay determines the order of the system’s characteristic polynomial and thus has an influence on the conditions for its stability. To illustrate this, we have developed multiple images of the system’s stability region in a chosen parameter plane demonstrating the change of the region’s size and shape corresponding to the increasing value of delay within the system. Moreover, we introduce another known delay model for mutualism that exists within ecology literature and we discretise it in the same fashion, we then perform the same analysis and computational work as a means for a direct comparison with the first model.

Recombination rate coevolution in a quantitative trait model with diploid antagonists

Sviatoslav R. Rybnikov, University of Haifa, Israel

Co-author: Zeev M. Frenkel, Abraham B. Korol

Antagonistic interactions, known to cause oscillations in the participants' genetic structure, are believed to be a plausible explanation for the evolution of sex/recombination (the Red Queen hypothesis). Yet, analysis of numerous theoretical models (usually with haploid antagonists) reveals that such interactions may and may not favor sex/recombination, depending on fitness matrix and selection intensity. Using numerical analysis of a quantitative trait model (QTM) with frequency-dependent selection, we examine recombination rate coevolution in diploid antagonists. Both host and parasite have three selected loci and selectively neutral recombination modifier. Unlike an earlier haploid QTM, where recombination was favored in parasite but not in host, in our diploid QTM all four possible outcomes were observed: modifier allele for non-zero recombination spread in the parasite population, in the host population, in both of them, and in none of them. The proportion of different outcomes depended on the modifier linkage to the selected system.

Using variational principles for modelling self-replicating systems

Simran Sanhu, University of Leicester, United Kingdom

Co-author: A Morozov

A fundamental modelling approach to revealing evolutionary optimal genotypes, traits or behavioural patterns is maximising the long term average per capita population growth rate which can be defined as the generalized fitness function. This idea uses variational principles of modelling natural selection in self-replicating systems. However, finding such a generalised fitness function is usually a challenging mathematical task and can be easily done only for relatively simple models. Here we develop a new generic method of finding the maximum of the fitness function and thus obtaining the evolutionary and invasive stable strategy. The essence of the method is considering long term dynamics of the underlying population equations and then approximating the fitness function based on the information about the per capita growth rates for competing strategies. As a meaningful illustrative example, we explore optimal strategies of Diel Vertical Migration (DVM) of zooplankton which is a widespread phenomenon in both oceans and lakes, and is generally considered to be the largest synchronized movement of biomass on Earth. We consider models of with several developmental stages of zooplankton and compare the optimal migration strategies between younger and older stages. Unlike previous studies, we explore not only the case of fixed density of zooplankton predators (fish) but also a more realistic case, where the amount of predators is a dynamical variable. We investigate the dependence of strategies for different development stages on key parameters such as the amount of food, predation level, cost of migration, etc. The results obtained through modelling are in general in good agreement with the empirical data from the ocean and lakes.

Demographic noise promotes bistability in ecosystems

Suminthra Sankaran, Indian Institute of Science, India

Co-authors: S. Majumder, A. Kushal, V. Guttal

Ecosystem regime shifts can often be abrupt, occurring in response to small changes in environmental conditions. Several simulation and analytical models capture these discontinuous changes for a variety of ecosystems, ranging from inter-tidal mussel beds to semi-arid vegetation. Typically, strong positive feedbacks between organisms are considered a necessary condition for the occurrence of discontinuous state transitions. However, these models are complex, consisting of numerous parameters and detailed biotic and abiotic interactions, making it difficult to disentangle processes that cause abrupt transitions. In our study, we analyse a simple spatial model from non-equilibrium statistical physics consisting of only two parameters - one that controls environmental conditions affecting birth-death processes in the system and another that controls facilitation strength. By constructing and expanding the Master-Equation of this model and analysing the resultant Fokker-Plank equation, we demonstrate that demographic noise can promote bistability even in systems with weak positive interactions.

From phenotypes to fitness – time is relative in evolution

Diogo Santos, Instituto Gulbenkian Ciencia, Portugal

Co-author: Lilia Perfeito

Fitness measures how quickly alleles change in frequency under natural selection. Time is always implicit in evolutionary models but its units are rarely made explicit. When measuring phenotypes such as absolute growth rate, the units of measurement need to be made explicit. By doing so, we uncovered a curious effect, by which evolutionary time runs at different speeds depending on how restricted population growth is. In other words, when the generation time of a population is externally imposed, relative fitness is no longer an accurate measure of natural selection. We explore this effect and describe how it affects selective sweeps, probability of fixation of beneficial mutations and adaptation dynamics. Moreover, we show how different populations cannot be compared unless they share a common reference and how our inference of epistasis can be biased by this temporal effect. Finally we suggest less biased ways to measure selection in experimental evolution.

Extinction times in host-parasite dynamics

Hanna Schenk, MPI for Evolutionary Biology, Germany

Co-author: Arne Traulsen

Host-parasite dynamics are believed to follow Red Queen oscillations: regular fluctuations in genotype frequencies that do not allow for an overall winner. When several genotypes are present a specific host is not resistant to all parasites, neither can a parasite type infect all hosts. But regular oscillations are restricted to deterministic models. In stochastic models extinction of a genotype becomes more probable when its frequency is low. It is of value to know when a type dies out depending on population size, intensity of selection, etc. But the extinction (or fixation) time is not calculated easily. We work towards a simple rule of thumb to estimate the time to extinction when numerical calculations fail or simulations become too costly.

The game's the thing: how we'll learn the evolution of the king [of maladies]

Jacob Scott, Cleveland Clinic, United States

Tumors are heterogeneous evolving ecosystems composed of sub-populations of neoplastic cells that follow distinct strategies for survival and propagation. The evolutionary fitness of these neoplastic sub-populations depends not only on the genotype of the cells, but also on the context which includes: the composition and properties of the tumor microenvironment (TME), including extracellular matrix and gradients of chemical species; and non-neoplastic cellular components of TME, such as cancer-associated fibroblasts (CAFs), endothelia and immune cells. Evolutionary game theory (EGT) provides a framework to analyze the outcomes of interactions of competing strategies which is gaining momentum in mathematical oncology, but which has only recently begun to be grounded in experimental reality. Here, we develop a method to measure the games played between two cancer cell lines: a parental non-small cell lung cancers (NSCLC) line sensitive to targeted therapy (ALK TKI); and a line derived from the same parental cells but resistant to this therapy. Using a combination of time lapse microscopy and computer vision, we are able to measure the game played by these two cell types, and provide the first empirical confirmation for the theoretical postulate of EGT in mathematical oncology that we can treat not just the player (cells), but that we can change the game. Confirmation that we can perturb the evolutionary game cancer cells are playing therapeutically opens the possibility for clinical translation of theoretical insights gleaned from EGT.

Invariant manifolds of a model from population genetics

Belgin Seymenoglu, UCL, United Kingdom

Co-author: Stephen Baigent

In 1976, Nagylaki and Crow proposed a continuous-time model for the population frequencies, which focuses on one gene with two variants (or alleles). Much of my time has been spent plotting phase plane diagrams for this model, but whatever values I put in for the parameters, I always find a stubborn special curve in my diagram - an invariant manifold. I have proved that the manifold does indeed exist for a certain case of the Nagylaki-Crow model. Remarkably, there is no need to assume additivity of the parameters or competitiveness of the system.

If time permits, I will also display a gallery of colourful phase plots showing that the invariant manifold need not be unique, smooth or convex.

On a network epidemic model with preventative rewiring

David Sirl, University of Nottingham, United Kingdom

Co-authors: Frank Ball, Tom Britton, KaYin Leung

In this work we consider a stochastic SIR (Susceptible-Infectious-Removed) epidemic evolving upon a network described by a Configuration Model random graph, which draws graph uniformly from all graphs with a specified degree distribution. (We call this the CM-SIR epidemic model.) We consider the Markovian case where the infectious period distribution is exponential and infection processes are Poisson.

A recent paper [Britton, Juher, Saldaña (2016), Bull. Math. Biol. 78:2427-2454] studied (amongst other things) a variation of this CM-SIR model in which individuals `drop' edges which connect to infectious neighbours, in order to try to avoid infection. Britton et al. used two approaches (branching process approximations and pair approximations) to study the early behaviour of this epidemic process. We take a third approach, deriving deterministic and Gaussian approximations to the stochastic model. We find that the final outcome of the epidemic (the mean proportion infected during a large outbreak) can be formulated in terms of that of a related standard CM-SIR model (without dropping of edges). Our work also provides an alternative justification/derivation of the Volz/Miller approximation of CM-SIR epidemics by a deterministic system which is driven by a single ODE [Miller, Slim, Volz (2012), J. R. Soc. Interface 9:890-906].

Darwinian Selection Induces Transient Lamarckian Adaptation in a Holobiont Model

Yoav Soen, Weizmann Institute of Science, Israel

Co-authors: Osmanovic D, Kessler DA, Rabin Y.

It is becoming increasingly clear that any individual animal (and plant) is actually a holobiont partnership between a host and many microbes undergoing selection at a much faster rate. How this holobiont structure influence the modes and kinetics of adaptation is, however, largely unclear. To address this question, we introduce a Population (Symbio-) Genetics model of holobiont adaptation under toxic stress and show that the structure of holobionts

supports adaptations that are traditionally considered impossible for hosts and bacteria alone. These adaptations are due to emergent holobiont properties arising from interactions between two levels of selection; rapid selection of symbiotic microorganisms within their host and slower selection of the entire holobiont unit. We show that rapid changes in the bacterial population within a holobiont increase the toxin tolerance of its offspring. Formulating this in quantitative terms reveals distinct modes of transient Lamarckian adaptation, corresponding to alleviations of toxic and physiologic stress, respectively. On longer timescales, the toxic stress promotes 'group selection' of bacterial communities with higher average detoxification per bacterium (in contrast to the usual selection of better fit individual bacteria). Analysis of host-intrinsic phenotypes further uncovers a bacterial-mediated mode of assimilation, analogous to Genetic Assimilation by host-intrinsic alleles.
The fundamental insights and infrastructure offered by this model open new directions of experimental and theoretical research.

Fixation: The Fingerprint of Evolutionary Processes

Max Souza, Universidade Federal Fluminense, Brazil

Co-author: Fabio A. C. C. Chalub

Starting from the classical Moran and Wright-Fisher processes we will show how a class of discrete processes can be completely determined by prescribing their fixation probability, and also that will be interesting processes for which such determination does not hold. We will also show that for large populations, and fixation given by smooth function, the corresponding processes will be in the weak-selection regime. Finally, we will show how fixation in large population of d-player games can produce very complex fixation patterns.

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Modelling kleptoparasitism in an urban gull (*Laridae*) population

Robert Spencer, Middlesex University, United Kingdom

Co-author: Mark Broom

Kleptoparasitism has been modelled extensively using evolutionary game theory. This has provided theoretical insights into the behaviours that should be successful when individuals search for food in groups. We used the compartmental approach to modelling kleptoparasitism developed by Broom and colleagues (Broom & Ruxton, 1998; Broom, Luther & Ruxton, 2004) to investigate behaviour in a real foraging population of gulls at an urban site. Kleptoparasitism was modelled to assess whether the density of different behaviours in the gull population was at an equilibrium and whether individual foragers were making effective use of kleptoparasitism. We found plausible values of handling and fight duration at which the density of behaviours may be at an equilibrium but only 23% of individuals were using evolutionarily stable strategies. Competitive differences between the 3 species making up the population influenced the behavioural decisions individuals made, the results of the model were limited because it did not account for these differences.

Exponential number of stationary solutions for reaction-diffusion equations on graphs

Petr Stehlik, University of West Bohemia, Czech Republic

We study the Nagumo reaction-diffusion equation on graphs and its dependence on the underlying graph structure and reaction-diffusion parameters. We provide necessary and sufficient conditions for the existence and nonexistence of spatially heterogeneous stationary solutions. Furthermore, we observe that for sufficiently strong reactions (or sufficiently weak diffusion) there are 3^n stationary solutions out of which 2^n are asymptotically stable. Our analysis reveals interesting relationship between the analytic properties (diffusion and reaction parameters) and various graph characteristics (degree distribution, graph diameter, eigenvalues). We illustrate our results by a detailed analysis of the Nagumo equation on a simple graph and conclude with a list of open questions.

The dynamics of cooperation when interactions change the rules of the game

Authors and affiliations:

Caitlin A. Stern, Santa Fe Institute, United States and Aarhus University, Denmark

Co-author: Andreas Roepstorff

Models of the evolution of cooperative behaviour often analyse iterated games to determine which strategies are favoured when individuals interact repeatedly. Here, we relax the common assumption that payoffs for a given behaviour are constant across interactions by allowing past behaviour to influence future payoffs. We seek a general understanding of when interactions that change the rules of the game promote versus inhibit cooperation. Using game theoretic models, we study two sets of ways in which past interactions can influence future payoffs: changes in the impact of group contributions and in group composition. Depending upon the factor, cooperation becomes more or less likely compared to the constant payoffs model. Our results suggest that, when past interactions can change the rules of the game, the conditions under which cooperation can emerge change in complex ways. Taking into account changing payoffs is crucial for understanding the emergence of cooperation in real-world contexts.

Group thinking and generosity in the evolution of cooperation

Alexander Stewart, University College London

The emergence of group-level social behaviors - from the sharing of a resource to quorum sensing to eusociality - is a fundamental evolutionary phenomenon. In humans such behaviors are complex and various, rich in reciprocity and prosociality as well as inter-group conflict and antisocial “defecting’’ behaviors. What is more, groups of humans can take things a step further and develop a sense of “collective identity’’ that both emerges from and reinforces underlying group behaviors.

Can we use evolutionary thinking to understand the emergence of group behaviors and collective identity in humans? I will discuss applications of evolutionary game theory to make predictions about the types of group behaviors that can emerge in repeated games, and discuss how those behaviors can be linked to explicit measures of collective identity. In particular I will focus on when cooperative social norms will emerge at the group level, and the stability of cooperation once it becomes established. I will present predictions for the likelihood of cooperation emerging and persisting in a population as a function of the external environment and the cognitive abilities of individual players, and the kinds of experiments we can run to test these predictions.

Large ecosystems in a changing environment: interactions and feedbacks

Ivan Sudakov, University of Dayton, United States

A multispecies population model surviving on distributed resources is considered. The basic model is demanded as Lotka-Volterra type and modeling the large ecosystem and the effect of climate is incorporated into the model by considering the effect of environmental temperature on the system dynamics. In particular, a feedback between species abundances and resources via environmental temperature factor is introduced. This model is apparently the first of its kind to include a feedback mechanism coupling climate and population dynamics. In case of a positive climate feedback loop we observe catastrophic bifurcations related to the extinction of all species.

A new model of isolation-by-distance that overcomes longstanding technical limitations

Yevhen F. Suprunenko, University of Liverpool, United Kingdom

Co-authors: Dmitri Finkelshtein, Panu Somervuo, Otso Ovaskainen, Stephen J. Cornell

In population genetics, models of isolation-by-distance (IBD) are crucial for understanding the role of evolutionary processes in the generation and maintenance of population genetic structure. However, despite the great importance and ubiquity of IBD in nature, a realistic mathematically tractable model is still missing due to the formidable technical difficulty of modelling nonlinear stochastic population dynamics. Instead, existing models of IBD use oversimplified/unrealistic approximations, or only a limited number of evolutionary processes can be considered, e.g. selection and local density-dependent population regulation pose long-standing problems. Here, we present a model of IBD which overcomes these technical limitations. The model takes into account explicit continuous spatial stochastic dynamics, selection, local density-dependent population regulation, limited spatial dispersal, genetic drift, mutation. We present approximate analytical solutions, asymptotically exact in a biologically relevant limit, for IBD patterns for neutral and non-neutral markers using arbitrary interaction kernels. Simulations show good agreement with our analytical predictions.

On Arbitrarily Long Periodic Orbits of Evolutionary Games on Graphs

Vladimír Švígler, University of West Bohemia, Czech Republic

Co-author: Jeremias Epperlein

A periodic behavior is a well observed phenomena in biological and economical systems. We show that evolutionary games on graphs with imitation dynamics can display periodic behavior for an arbitrary choice of game theoretical parameters describing social-dilemma games. We construct graphs and corresponding initial conditions whose trajectories are periodic with an arbitrary minimal period length. We also examine a periodic behavior of evolutionary games on graphs with the underlying graph being an acyclic (tree) graph. Astonishingly, even this acyclic structure allows for arbitrary long periodic behavior.

Inference from cancer sequencing data

Simon Tavaré, University of Cambridge, United Kingdom

I will describe some theoretical aspects of modelling cancer evolution, in particular what seems to be easy to infer and what seems to be hard. The methodology comes from the ABC and coalescent part of the subject, with due allowance for the cancer setting. Time permitting, I will also describe our part of the CRUK Grand Challenge competition, which will provide novel in-situ data on a vast scale.

A spatial network model for population dynamics of migratory species.

Caz Taylor, Tulane University, United States

Population Ecology lacks mathematical tools to model the population dynamics of species that migrate seasonally, especially those that travel long distances between breeding regions and over-wintering regions. Hence the dynamics of such species are not well understood and when they are observed to be in decline, it is difficult to pinpoint the causes of those declines. Support for different hypotheses of causes of declines in real species is often provided in the form of correlations between patterns of local declines and habitat loss or weather patterns, assessment of occupancy patterns, or changes in vital rates. Here I present a spatial network model of migratory species with three types of “nodes” representing breeding regions, stationary non-breeding regions, and migration pathways. I use the model to explore how patterns of occupancy, correlations between habitat loss and declines, and changes in vital rates can be used as indicators of drivers of population trends.

Reconstructing branching lineages in single cell genomics

Fabian J. Theis, Helmholtz Center Munich, Germany

Single-cell technologies have gained popularity in developmental biology because they allow resolving potential heterogeneities due to asynchronicity of differentiating cells. Common data analysis encompasses normalization, followed by dimension reduction and clustering to identify subgroups. However, in the case of cellular differentiation, we may not expect clear clusters to be present - instead cells tend to follow continuous branching lineages.

We show that modeling the high-dimensional state space as a diffusion process, where cells move to close-by cells with a distance-dependent probability well reflects the differentiating characteristics. Based on the underlying diffusion map transition kernel, we then order cells according to a diffusion pseudotime (DPT), which allows for a robust identification of branching decisions and corresponding trajectories of single cells. We demonstrate the method on scRNA-seq data of myeloid differentiation. DPT identifies a dominant branching into different myeloid lineages and a minor subpopulation of lymphoid outliers. Moreover, a graded transition reflecting erythroid differentiation is identified that dissent from previously stated cluster sequences. We identify driver genes and propose how to include additional data sets for integrative analysis across multiple downstream lineages.

As outlook I will discuss algorithmic and computational challenges we are facing with future studies with even larger numbers of single cells and with multiple time points, conditions and replicates.

Accounting for donor viral diversity gives high estimates of the number of HIV founder virions in recipients

Robin Thompson, University of Oxford, United Kingdom

Co-authors: C. Wymant, J. Raghwani, C. Fraser, K.A. Lythgoe

Following observations that most sexually transmitted HIV infections are initiated by single strains, it was hoped that signatures of transmission would be identified and used as targets for vaccines. Selection at transmission can solve the paradox of a very low transmission probability per contact but multiple transmitted/founder strains when successful transmission does occur in 20-40% of cases. However, genotypic and phenotypic signatures of transmission have proved elusive.

Using a probabilistic modeling approach, we show that selection need not be invoked to explain this paradox. If transmission is only possible for a minority of contacts and changing viral diversity in donors throughout their courses of infection is accounted for, it is possible to resolve the low transmission probability but relatively frequent multi-strain transmission. We apply our mathematical framework to published whole-genome deep sequencing data, and infer distributions of the numbers of virions and distinct strains establishing infections in a population.

On the proportion of mutations in cancer due to normal cell division

Cristian Tomasetti, Johns Hopkins University, United States

Co-authors: K. Lahouel, L. Younes, D. Geman, L. Li, B. Vogelstein

Cancers are caused by mutations that may be inherited, induced by environmental factors, or the result of random mistakes made during normal DNA replication. A fundamental problem in cancer etiology is the estimation of the proportion of mutations attributable to each one of these three factors. Unlike environmentally-induced (E) mutations, replicative (R) mutations are expected to have approximately the same distribution in all humans, regardless of their environment. To test the implications of this expectation, we use a new mathematical model of cancer initiation and progression, with parameters for R estimated from biological experiments, and show via simulations that the model is able to approximate observed cancer incidence curves. These result suggest that R mutations play a major role in cancer causation. Using a completely orthogonal method, based solely on cancer genome sequencing, epidemiologic data, and a statistical model (1), we show that R mutations can be estimated to be responsible for 2/3 of the mutations that occur in human cancers.

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Cues and collective decision-making in migrating ungulates

Colin Torney, University of Glasgow, United Kingdom

Co-authors: Andrew Berdahl, Grant Hopcraft, Lacey Hughey, Leon Debell, Doug McCauley

In this talk I will discuss methods to collect data relating to collective movement decisions of migrating animal groups. I will present an analysis of the social interactions that occur between individuals undertaking a large scale migration in two distinct systems, caribou on Victoria Island, Canada and wildebeest in the Serengeti National Park, Tanzania. Scaling from these rules to group level properties, such as collective accuracy in route choice, requires a multiscale approach. I will discuss methods that allow us to investigate how individual use of social cues produces emergent behaviour at the group level.

The Relatedness in the Field Observations and Computer Simulations: The Bias of the Observation

Hiroshi Toyoizumi, Waseda University, Japan

Co-authors: Sho Shinbaba, Jeremy Field

We discuss how to adjust the simulation to the field observation data, such as the average relatedness in a cooperative group. The cooperation is said to be advantageous when the group is formed by related individuals. In real world, the relatedness in the group is not static but dynamically fluctuating as the structural change of the group. In addition to the field observation, the complex group dynamics may be analyzed by computer simulations. By picking up a group at random in the field, we can observe the relatedness inside the group directly. However, longer and stable groups are picked up more likely, so the observed group is biased, and the simulation result cannot be directly compared with the field observation. Here, by using the point process theory and the relation between time-average and event-average, we show how we can adjust the bias of observations.

Eco-evolutionary consequences of harvesting complex food webs

Eric Tromeur, UPMC, France

Co-author: Nicolas Loeuille

Overfishing is endangering the structure and the resilience of marine food webs. As a consequence, many scientists are calling for an ecosystem-based fisheries management, able to integrate the complexity of marine ecosystems, as well as the multiple ecosystem services they provide. Changing fishing patterns is key to achieve this objective. In particular, it has been shown that shifting from a fishing pattern based on the selective harvest on certain species, to a pattern of balanced harvest, where species are harvested in proportion to their productivity, could promote both yield and resilience, and limit the impact on food web structure. However, changing fishing patterns also modifies selective pressures, with potential unforeseen consequences. To assess these adaptive effects, we use the model developed by Loeuille & Loreau (2005), that generates realistic size-structured food web with an eco-evolutionary algorithm. This allows us to comparatively investigate the ecological as well as the evolutionary consequences of various fishing patterns, including a balanced harvest.

Games with prospect: a simple solution mechanism to social dilemma

Satosi Uchida, RINRI Institute, Japan

Co-author; Hitoshi Yamamoto

Social dilemma is one of the most puzzling issues in social sciences. Massive theoretical efforts from various disciplines such as economics, biology, mathematics or even physics have been put to figure out solution mechanisms to the dilemma for the last decades. Punishment is thought to be a key mechanism, but from game theoretical perspectives, peer-punishments themselves encompass higher order dilemmas. Therefore, punishment models with additional (mostly complex) mechanisms have been proposed to prevent higher order dilemmas. So far, a game theoretical model only with peer-punishments to solve the dilemma does not exist. Here we propose a simple peer-punishment model in which cognitive distortions of human beings described by prospect theory are taken into account and which solves the social dilemma. Going beyond the expected utility theory, we show that the cooperative social state can be not only evolutionarily stable but globally stable in a wide range of parameter values.

Taking Error Into Account When Fitting Models Using Approximate Bayesian Computation

Elske van der Vaart, Tilburg University, The Netherlands

Co-authors: Dennis Prangle, Richard Sibly

Approximate Bayesian Computation (ABC) is an increasingly popular technique for calibrating and evaluating complex ecological models. However, ensuring the accuracy of its estimates remains difficult. In this talk, we introduce an improved approach to evaluation for cases where the empirical data consist of repeated measures of the same quantity – such as a time series. We do this by estimating combined model and / or measurement error from the discrepancy between the observations and the model at its best-fitting parameter values. We incorporate this error into a probabilistic ABC algorithm and apply it to a toy example and a realistic 14-parameter simulation model of earthworms that is used in ecotoxicology. A comparison with exact methods and a diagnostic 'coverage test' show that our approach improves estimation of parameter values and their credible intervals for both models. We hope our approach will help promote the use of realistic computer models in ecology.

How to test Hamilton’s rule empirically

Matthijs van Veelen, University of Amsterdam, The Netherlands

Co-authors: Benjamin Allen, Moshe Hoffman, Burton Simon, Carl Velle

The discussion about the validity of Hamilton’s rule mostly takes place in the theory domain. Some papers, on the other hand, try to test empirically whether or not Hamilton’s rule holds (see Bourke, 2014, for an overview). We try to bridge the gap between theory and empirics by describing what violations would look like.

A first complication is that there are different ways to define costs and benefits; there is the “counterfactual method” (Karlin and Matessi, 1983) and the “regression method” (Gardner et al., 2011).

With costs and benefits according to the regression method, Hamilton's rule holds by construction. Therefore there is no need to go out and gather data, if the aim is to empirically test whether or not Hamilton's rule holds.

With costs and benefits according to the counterfactual method, violations of Hamilton's rule are possible, but being able to observe them requires looking in the right place. Violations can be observed as selection happens (that is: out of equilibrium), but if the system is in equilibrium, violations can only be observed if cooperators and defectors coexist.

Since none of the explicit tests of Hamilton's rule, as surveyed in Bourke (2014), look at polymorphisms, or at out-of-equilibrium dynamics, it is surprising that a relatively large share of the studies surveyed do find negative values for inclusive fitness. We discuss possible explanations for those "false negatives".

Modeling sexual selection in Tungara frog and rationality of mate choice

Esteban Vargas Bernal, Universidad de los Andes, Colombia

Co-author: Camilo Sanabria Malagon

The males of the species of frogs Engystomops pustulosus produce simple and complex calls to lure females. Complex calls lead males to a greater reproductive success than what simple calls do. However, the complex calls are also more attractive to their main predator, the bat Trachops cirrhosus. Therefore, the complexity of the calls lets the frogs keep a trade off between reproductive success and predation. In this work, we verify this trade off from the perspective of game theory. We first model the proportion of simple calls as a symmetric game of two strategies. We also model the effect of adding a third strategy, males that keep quiet and intercept females. Our model reproduces the observed behavior reported in the literature. From the model with three strategies, we verify that the quiet strategy could only coexists with the simple and complex strategies if it has a high rate.

Strong forms of non-convergence to evolutionary stable states for all reasonable evolutionary dynamics.

Yannick Viossat, Universite Paris-Dauphine, France

It is well known that evolutionary dynamics, such as the replicator dynamics need not converge to an ESState, but may converge instead to an equilibrium which is not an ESState or cycle indefinitely. We provide more extreme examples of non-convergence to an ESState : for any myopic adaptive dynamics that depend continuously on the payoffs of the game, there is an open set of games with a unique ESS (a strict Nash equilibrium) and no other equilibria such that, for many initial conditions, the pure strategy corresponding to the ESS gets essentially eliminated. The proof combines variants of universally cycling games due to Hofbauer and Swinkels with a trick from [Viossat, Y., 2007, The Replicator Dynamics Does not Lead to Correlated Equilibria, Games and Econ. Behav. 59, 397-407].

Partial differential equation techniques for analysing animal movement: A comparison of three methods

Yi-Shan Wang, University of Sheffield, United Kingdom

Partial differential equation (PDE) techniques provide efficient methods for deriving space use patterns arising from individual movement mechanisms. However, these methods depend on simplifying assumptions, so it is necessary to be cautious when deriving quantitative conclusions. Here, I show that a popular method, initiated by Patlak in 1953, can give inaccurate descriptions of space-use even for very simple movement models. However, two more recent methods, based on transport equation formalisms, lead to more accurate descriptions of space-use. I will discuss the relative merits of these three PDE methods by focussing on various analytically-tractable movement models, including biased random walks and central-place foraging models.

An Efficient ‘Instant Acclimation’ Approximation of Dynamic Phytoplankton Stoichiometry

Ben A. Ward, University of Bristol, United Kingdom

The elemental ratios of carbon to limiting and non-limiting nutrients in marine organic matter are variable. This affects the coupling of global carbon and nutrient cycles, modifying both the productivity of marine foodwebs, and the sequestration of carbon in the deep ocean. It is important that models of these systems are able to correctly reproduce the observed variability in phytoplankton carbon-to- nutrient ratios. ‘Dynamic Quota’ models have achieved some success in this regard by representing each phytoplankton population with explicit state-variables for the biomass of carbon and each limiting nutrient (such as nitrogen and phosphorus). However, the computational expense associated with transporting each state variable in 3D ocean models has prevented many large-scale models from moving beyond a much simpler ‘Fixed Stoichiometry’ (Monod) formulation. Although less physiologically realistic, the Fixed Stoichiometry approach is computationally much more efficient, because it represents each phytoplankton population in terms of just one state variable. Here we compare the Dynamic Quota and Fixed Stoichiometry models to a third ‘Instant Acclimation’ model, which combines the stoichiometric flexibility of the Dynamic Quota model with the computational efficiency of the Fixed Stoichiometry model. The Instant Acclimation model is mathematically equivalent to the Dynamic Quota model at equilibrium, and we will show that it also provides a very accurate approximation under a wide range of dynamic conditions. The accuracy, simplicity and computational efficiency of the Instant Acclimation model recommends it as a candidate for incorporating flexible stoichiometry into marine ecosystem models, especially in situations where the number of model state-variables is very tightly constrained.

Evolving fitness landscapes: How evolution learns to improve evolvability on rugged fitness landscapes

Richard A. Watson, University of Southampton, United Kingdom

Co-authors: Loizos Kounios, Jeff Clune, Kostas Kouvaris, Günter P. Wagner, Mihaela Pavlicev, Daniel M. Weinreich

The mapping from genotype to phenotype determines the characteristics of the fitness landscape experienced by selection. When this mapping evolves, e.g. via changes in the strength of gene-regulatory interactions, the fitness landscape changes. Here we show that the conditions where this facilitates evolvability can be predicted using the theory of learning. The conditions that enable simple learning systems to generalize, i.e., to recognise novel patterns that have structural regularities in common with past observations, correspond to conditions where natural selection can systematically favours mappings that benefit future evolvability, i.e. by modifying the fitness landscape in a way that favours novel phenotypes that have structural regularities in common with previously selected phenotypes. Using numerical simulations of evolution on highly epistatic fitness landscapes we illustrate how an evolving gene-regulation network reduces local fitness peaks and facilitates access to higher fitness phenotypes.

Forecasting resistance evolution in cancer from liquid biopsies

Benjamin Werner, Institute of Cancer Research, United Kingdom

Identifying and exploiting tumour specific futures as therapeutic targets are the aim of modern cancer treatment strategies. Specifically designed molecules that target cancer genomic pathways are now available for many known driver mutations. Unfortunately, even if patients have an initial strong response, a later relapse of the disease is common. Here, I will discuss some of the potential reasons for treatment failure and resistance evolution and how a theoretical evolutionary perspective might help in understanding and quantifying these mechanisms. One of the most important and clinically challenging reasons for resistance is intra-tumour heterogeneity. I briefly discuss some approaches how this heterogeneity might be better classified from multi-region sequencing data and how this might improve the selection for potential targets of treatment. I then will discuss how sequential sampling of circulating tumour DNA (ctDNA) in patients during treatment can be used to forecast the evolution of treatment resistance. Interestingly, a combination of sequential sampling and evolutionary modeling does not only detect resistance but also allows quantifying some properties of the evolutionary process.

The impact of the infectious period on epidemics

Robert R Wilkinson, University of Liverpool, United Kingdom

Co-author: Kieran J Sharkey

We discuss some new theorems describing the impact of the infectious period distribution on the severity of an epidemic. This is done in the context of a general, fully non-Markovian, Susceptible-Exposed-Infectious-Recovered (SEIR) epidemic taking place on an arbitrary static network. The main theorems are stated in terms of *m*-convex ordering of random variables. Corollaries include showing that increasing the infectious period in the usual stochastic order serves to increase the expected impact of an epidemic, and for an infectious period with fixed mean, the expected impact is maximised when it is non-random. For gamma and Weibull distributions, decreasing the variance while keeping the mean constant increases the expected impact.

Measuring and predicting clonal evolution in human cancers with genomics

Marc Williams, Barts Cancer Institute, United Kingdom

High throughput genomics has shown that tumours across all cancer types are highly heterogeneous, to the point that each cell may potentially be genetically unique. In single samples of cancers that have been subjected to high depth sequencing this heterogeneity

manifests itself as mutations at different variant allele frequencies (VAF), that is some mutations are present in a high proportion of cells in the tumour, others in lower proportions.

Using a mathematical model of tumour evolution together with Bayesian statistical inference we show how these VAF distributions encode the underlying evolutionary processes in tumour growth. This allows us to measure the mutation rate, the fitness advantage and the time of emergence of sub-populations which are selected for during tumour growth. We observed that such sub populations had strikingly high fitness advantages (>20%) and emerged early (within the first 15 tumour doublings). Taken together, these measurements allow for predicting how the cancer genome is expected to change over time with potential important applications in rationalizing sampling and treatment strategies.

Eco-evolutionary buffering: rapid evolution facilitates regional species coexistence despite local priority effects

Meike Wittmann, University of Vienna, Austria

Co-authors: Tadashi Fukami

In patchy landscapes, early-arriving species often exclude competing species from local communities. Observations of such "priority effects" are puzzling because theory suggests that priority effects hinder regional species coexistence. Here we develop an eco-evolutionary hypothesis to solve this conundrum. We build a metacommunity model in which priority effects occur via interspecific interference. Within each species, one genotype is sensitive to interspecific interference and one genotype is, at least partially, resistant. Because resistance is costly, species evolve to become less resistant as they become regionally more common. Rare species can then invade local patches and consequently recover in regional frequency. This "eco-evolutionary buffering" can jointly maintain genetic variation within species as well as regional species diversity. Because this mechanism is based on stochastic patch dynamics, it works best when many small communities are connected by infrequent dispersal. Intriguingly, rare species recovery is possible even while local priority effects remain strong.

Evolution of Cooperation Between Two Yeast Strains

Zhijun Wu, Iowa State University, United States

Co-authors: Min Wang, Yuanyuan Huang

Evolution of cooperation of biological species is an active research subject in evolutionary biology and ecology. Evolutionary game theory is a powerful modeling and simulation tool for the study of ecology and evolution. Here, we use a lab-developed population of two yeast strains, called the cooperator and cheater strains, to demonstrate the nature of the game that can be played by the yeast strains and how cooperation can be maintained in such a population. We review the lab experiments as well as previous computer simulations. We present our recent simulation results on spatial effects on cooperation between the yeast strains when the interactions among the yeast cells are restricted to their small neighborhood. Our results show that cooperation is increased when the interactions are spatially restricted whether the game is of a prisoner’s dilemma, snow drifting, or mutual benefit type. We also show when spatially restricted, groups of cooperators are able to sustain and expand as group sizes become large, while groups of cheaters fail to expand and tend to collapse.

Equilibrium Distribution of Populations of Biological Species on Networks of Social Sites

Zhijun Wu, Iowa State University, United States

Co-authors: Min Wang, Wen Zhou

We discuss how a population of biological species evolves or spreads over a network of social sites to achieve the greatest possible social payoff – a problem that may have potential applications in biology, medicine, or social sciences. This problem can be formulated as an evolutionary game called the network population game, with the ultimate distribution of the population on the network sites as an equilibrium state of the game. It is then important to understand the nature of the equilibrium states and their stabilities. We show that the equilibrium states and their stability conditions of a network population game can be obtained through the solution of a corresponding optimization problem called the payoff maximization problem. We can then apply the general optimization theory to the solution of the payoff maximization problem and justify a set of of optimality and stability conditions for the equilibrium states of the network population game.

Optimal Forager against Ideal Free Distributed Prey

Fei Xu, Wilfrid Laurier University, Canada

The introduced dispersal-foraging game is a combination of prey habitat selection between two patch types and optimal-foraging approaches. Prey’s patch preference and forager behavior determine the prey’s survival rate. The forager’s energy gain depends on local prey density in both types of exhaustible patches and on leaving time. We introduce two game-solution concepts. The static solution combines the ideal free distribution of the prey with optimal-foraging theory. The dynamical solution is given by a game dynamics describing the behavioral changes of prey and forager. We show (1) that each stable equilibrium dynamical solution is always a static solution, but not conversely; (2) that at an equilibrium dynamical solution, the forager can stabilize prey mixed patch use strategy in cases where ideal free distribution theory predicts that prey will use only one patch type; and (3) that when the equilibrium dynamical solution is unstable at fixed prey density, stable behavior cycles occur where neither forager nor prey keep a fixed behavior.

Development of a norm ecosystem to understand different roles of social norms in indirect reciprocity

Hitoshi Yamamoto, Rissho University, Japan

Co-authors: Isamu Okada, Satoshi Uchida, Tatsuya Sasaki

People sometimes cooperate with others at their own expense without the expectation of a direct return. This altruistic behavior is able to be explained as indirect reciprocity. Although previous works on indirect reciprocity have considered some action rules and assessment rules, all possible norms in indirect reciprocity have not been studied all-together. How cooperation evolves cannot be fully understood unless the evolution of norms is also considered. Here we have developed a "norm ecosystem" in which various norms coexist and constructed a social model using evolutionary game theory. We have clarified that different norms have roles in the emergence and maintenance of cooperation in the process of evolving altruistic behavior.

Game theory for modeling cancer and its treatment

Li You, Maastricht University, The Netherlands

Co-authors: Frank Thuijsman, Joel Brown, Jessica Cunningham, Katerina Stankova

Cancer can be viewed as an evolutionary process and as such can be modeled and explained using evolutionary game theory. The cancer treatment can then be viewed as a Stackelberg game between the oncologist as a leader and the cancer as a follower. The current standard care for cancer therapy is to kill the largest possible number of tumor cells by applying the maximum tolerated dose. While this approach is often initially successful at reducing tumor burden, it inevitably fails due to evolution and proliferation of resistant cancer phenotypes. Moreover, this highest tolerable dose regime is typically very aggressive to the patient and very expensive. Shifting the goal of therapy from complete elimination of tumor burden to instead controlling the tumor burden (with much lower treatment doses) for a maximum period of time – the so-called adaptive therapy – can change the approach to therapy dramatically. In this talk we will model such an adaptive treatment and compare its outcomes with the highest tolerable dose regimen.

Extortion and contribution game: rationality versus fairness

Boyu Zhang, Beijing Normal University, China

Classical studies have suggested that humans should learn to adopt reciprocal strategies to establish mutual cooperation in repeated interactions. On the other hand, the recently discovered theory of ZD strategies has found that subjects who use extortionate strategies are able to exploit and subdue cooperators. Although such extortioners have been predicted to defeat any opponent, theoretical studies questioned whether extortion can evolve in reality. Here we introduce an extortion and contribution game, which describes the competition between extortioners and cooperators. We show with an economic experiment and an evolutionary game model that randomly matching leads to extortion and direct reciprocity together with reputation promotes fairness.

When to expect predator-prey coevolutionary arms races

Mark Zimmerman, North Carolina State University, United States

Co-author: Brian Langerhans

Much of evolution is coevolution: reciprocal evolutionary change between interacting species driven by natural selection. However, classic examples of “coevolutionary arms races,” such as tight predator-prey coevolution may be rare. Prey-switching behavior of a predator between its focal prey and alternative prey which can impact the dynamics of coevolution between the focal prey and the predator. Simulations of a population of prey and predators through multiple generations and tracking the prey escape trait and the predator capture trait of the individuals we can see how changes in the parameters of prey-switching and quality of alternative prey have on the coevolution of traits. By including trade-offs of escape/capture ability with reproductive ability there are more dynamics to explore and a range in parameter space that prevents arms races.