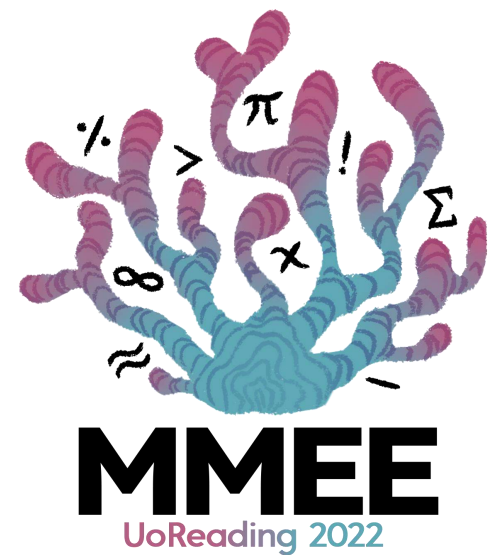


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UoReading 2022

List of Abstracts

Plenary Lectures



Spatial ecological dynamics: insights from statistical physics

Alan Hastings ^{a 1}, Jon Machta, Andrew Noble, Karen Abbott, Shadi Esmaeili and Vahini Reddy Nareddy

¹ Department of Environmental Science and Policy, University of California, Davis, US

^a – Presenting author

An appealing aspect of statistical physics models is the concept of universality, where classes of models have similar behavior. Spurred in part by an intriguing data set on individual yield of over 4000 trees in a pistachio orchard over 6 years where trees tend to mast and alternate high and low years, we have been applying ideas from statistical physics toward investigating spatial synchrony in cycling ecological systems. I will cover the specific system we have been looking at, present the necessary background about the statistical physics ideas, and discuss ongoing work and questions we are considering now.

Models of nested populations and the eco-evolution of collective functions

Silvia De Monte^{1, 2}

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² Research Group Dynamics of Microbial
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Directed evolution experiments have demonstrated the possibility to artificially select genes or cellular lineages with specific traits or functions. Recently, increasing effort is devoted to applying the same principles to microbial communities, e.g. selecting for the production or uptake of specific compounds. This program applies selection on populations of collectives (communities), each of which encompasses heterogeneous populations of self-replicating units (cells).

In this talk I will discuss two models implementing such nested structure, and address the interplay of the eco-evolutionary dynamics at the two different scales of description.

The first model considers a simple community composed of two species, which are both essential to achieve collectively the community function. I will show that collective-level selection drives the evolution of interspecific interactions, so that the target function becomes heritable. This happens via the emergence of a 'development' that corrects for the possible stochastic variation in community composition.

The second model considers communities made up of a large number of species. Species interactions are in this case assumed to be initially random, and selection is applied to a collective trait - the total population size. I will present a model for the evolution of the interaction matrix under unbiased community-level mutations. Analytical approximations of the evolution process recapitulate numerical simulations and represent the interplay of directional and stochastic variation in shaping the selected communities. In particular, they show that, generically, selection for higher biomass enhances mutualism and diversity of the community.

How to make a better (time-calibrated) phylogenetic tree

Mark Pagel¹

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of Reading, Reading, UK

Time-calibrated phylogenetic trees are the Holy Grail of tree building, providing not just a statement of relatedness and descent, but the timings of historical events of speciation. I selectively review the history of using DNA or protein sequence data to produce time-calibrated trees based on the so-called molecular clock hypothesis, that rates of sequence evolution are constant through time, and review several models that have been developed to manage deviations from clock-like behaviour. I show how the best known of these – the relaxed clock method – has justifiably revolutionised the inference and use of time-trees, but at a cost of having wide uncertainty in its estimates of timings. I introduce a new Poisson-mediated clock that modifies the basic relaxed clock approach and typically yields 25-40% reductions in the uncertainty of inferred timings, with little change to the goodness of fit of the model to the sequence data. I briefly discuss the philosophical issue this raises of balancing goodness of fit against uncertainty in the inference of trees.

Predicting the effects of climate warming: from chemistry to evolution

Priyanga Amarasekare¹

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I want to make the argument that understanding life on earth requires developing theory that integrates across levels of information, from chemistry to evolution. I am going to focus on temperature variation and phenotypic plasticity, not least because temperature is integral to all life processes, and climate warming poses one of the greatest threats to life on earth. Predicting the effects of warming requires knowing whether organisms have sufficient plasticity to respond to current levels of warming, and whether plasticity can evolve fast enough to keep pace with warming. But, existing plasticity is the result of past evolution, while future plasticity is the result future evolution. My thesis is that chemistry is integral to both understanding past evolution and predicting future evolution. I will present theory and data to support this idea and discuss future research directions.

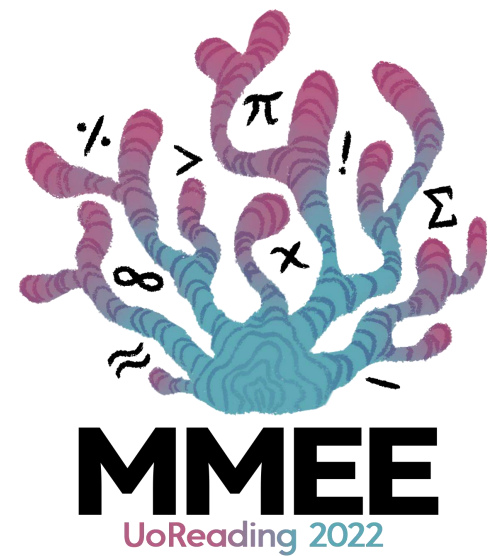
Prediction of climate change impacts on marine ecosystems: from knowledge to understanding

Julia Blanchard¹

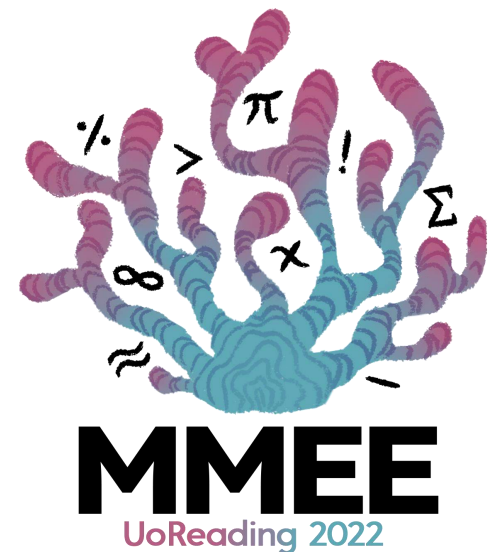
¹ Institute of Marine and Antarctic Research, University of Tasmania, Tasmania, Australia

Predicting future climate change impacts on ecosystems requires models that i) can accurately capture past changes in ecosystem states and ii) an understanding of what and how these changes occur. We have solid empirical knowledge of some of the changes happening to marine ecosystems. However, there are large uncertainties in our understanding of the mechanisms driving change. Multi-model ensembles of marine ecosystem models synthesise what we think we understand about how ecological systems respond to changes in the environment, by capturing a range of perspectives about plausible mechanisms and processes. The Fisheries and Marine Ecosystem Model Intercomparison Project (FishMIP) is one such initiative that aims to help better understand and project the long-term impacts of climate change on fisheries and marine ecosystems and to help inform policy. FishMIP currently comprises 9 global and 20 regional models that capture the biomass flow through ecosystems in different ways. I will discuss how the diversity of models has helped us build a knowledge base of potential impacts of global marine ecosystem responses. I will then outline the key hurdles that we need to overcome to advance our understanding and prediction of past and future marine ecosystems, and the fisheries they support.

Day 1



Mini-symposium 1 - Dynamics and structure of large ecological networks



Surviving species in large systems of Lotka-Volterra differential equations

Mr Maxime Clenet ^{a 1}, François Massol²
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¹ CNRS, Gustave Eiffel University –
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Institut Pasteur Lille – France

^a – Presenting author

The understanding of large ecosystems represents an important challenge in theoretical ecology, as does the understanding of large systems of interacting individuals in the life sciences. The complexity of these systems makes it necessary to use mathematical modeling. The Lotka-Volterra model represents a simple, robust and versatile model used to describe large interacting systems such as food webs, microbiome. This model consists of N coupled differential equations linking the abundances of the different species present in the system. We study theoretically the system after "randomizing" the interactions between the different species present, on the grounds that the true value of each interaction is difficult to observe or estimate. When the number of species becomes very large, many theoretical questions emerge about the quantity of species that can coexist with each other. In this presentation, we describe precisely the feasibility properties (i.e every species persists in the ecosystem) and the existence of an attrition phenomenon depending on the characteristics of the interactions. In both cases, we provide information about these equilibria and resistance to small perturbations (stability). In a more general setting, we describe mathematically the properties of a multi-community model.

Keywords: Ecosystems dynamics

How local network dynamics explain spatial and temporal biodiversity patterns in large metacommunities

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^a – Presenting author

A key phenomenon determining structure and dynamics of ecological communities is ecological structural instability, a high sensitivity of ecological communities to press perturbations that arises with increasing species richness. At local scale, ecological structural instability explains amongst other the regulation of alpha diversity seen in empirical data and the structure of trophic pyramids of species richness. Here we show that ecological structural instability arises not only locally but across scales in large, spatially extended ecological communities (metacommunities), and demonstrate how the interplay of local and regional biodiversity limits generates well-known spatio-temporal biodiversity patterns. Interestingly, this includes a phase transition to intrinsically driven local species turnover at high regional species richness, explaining corresponding observations of slow local turnover at approximately constant species richness.

Keywords: Population dynamics, Biodiversity, Ecological structural instability

Coupling disturbances and ecosystem service provisioning in complex ecological networks

Dr Anna Eklöf ***a*** ¹

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a – Presenting author

Ecosystem services are important for the well-being of human societies. At the same time, the ecosystems providing the services are under constant pressure from various anthropogenic activities, causing loss of biodiversity. The loss of one species can trigger secondary extinctions of additional species, since all species are connected to each other via interaction networks. The consequences of these secondary extinctions for services are not well-known. Here we address this question by developing a framework for coupling of threats affecting species to ecosystem service provisioning via the species interaction network. We use a novel, highly resolved data set of the Baltic Sea and simulate secondary extinctions using a Bayesian network approach. We simulate different response functions for how loss of services providing species are affecting ecosystem service provisioning. We find that indirect effects from threats cause secondary extinction of service providing species which negatively effect ecosystem services and that the magnitude of these effects are highly dependent on the response function used. We also show that the effects depend on which combination of threat and services that are considered, and that services provided by few species and species at high trophic levels are more vulnerable. Understanding linkages between ecological threats, species interactions in ecological networks and ecosystem service provisioning will help reveal important knowledge gaps for linking biodiversity loss with strategies for effective ecosystem service management.

Keywords: Ecosystems dynamics

Weighted empirical food webs: mass cycling and visualisations

Dr Mateusz Iskrzyński ^{a12}, Łukasz Pawluczuk¹, Franco Ruzzenenti²³, Brian Fath ²⁴

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³ Integrated Research on Energy, Environment and Society, Faculty of Science and Engineering, University of Groningen, Groningen, The Netherlands

⁴ Biology Department, Towson University, Towson, Maryland, USA

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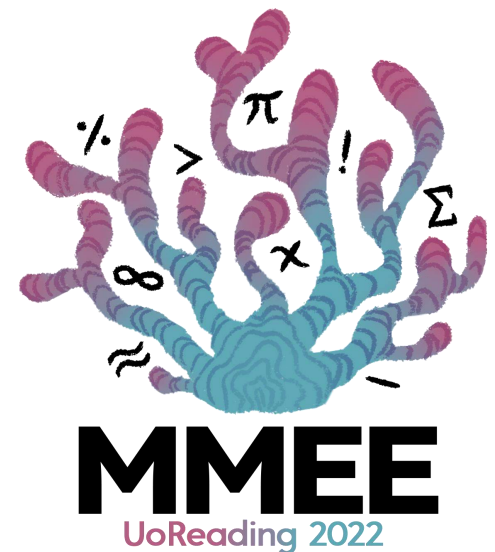
We studied mass cycling in 169 mostly aquatic weighted real-world food webs [i]. We found no correlation between the portion of all flows that is due to cycles (Finn Cycling Index) and the largest eigenvalues of unweighted adjacency matrices used as a cycling proxy in the past. Our analysis of nodes' contributions to cycling quantified the roles of detritivores and reciprocal flows. We created [ii] an ensemble of mutually complementary visualisation methods for weighted food webs: <https://github.com/ibs-pan/foodwebviz>. A heat map of food web flows or diet proportions shows their general pattern at a glance while retaining their precise identification. An interactive graph allows tracing the flow of matter over subsequent links. The user can select nodes, zoom, adjust layout parameters and manually drag-and-drop nodes. An intuitive animation of particles moving between the nodes uses colours and time dimension to trace connections better.

[i] <https://doi.org/10.1111/jiec.13217>

[ii] <https://doi.org/10.1111/2041-210X.13839>

Keywords: Ecological networks, Food web structure

Mini-symposium 2 - Vegetation modelling- nonlinear PDE approach



Linking spatial self-organization to community assembly and biodiversity

Professor Ehud Meron^{a 1}

¹ Ben Gurion University of the Negev,
Israel

^a – Presenting author

Temporal shifts to drier climates impose environmental stresses on plant communities that may result in community reassembly and threatened ecosystem services, but also may trigger self-organization in spatial patterns of biota and resources [1], which act to relax these stresses. The complex relationships between these counteracting processes – community reassembly and spatial self-organization – have hardly been studied. Using a spatio-temporal nonlinear PDE model of dryland plant communities and a trait-based approach, we study the response of such communities to increasing water-deficit stress [2]. We first show that spatial patterning acts to reverse shifts from fast-growing species to stress-tolerant species, as well as to reverse functional-diversity loss. We then show that spatial self-organization buffers the impact of further stress on community structure. Finally, we identify multistability ranges of uniform and patterned community states and use them to propose forms of non-uniform ecosystem management that integrate the need for provisioning ecosystem services with the need to preserve community structure.

Keywords: Spatial Ecology

Multiscale modelling of plant biomechanics and growth

Dr Mariya Ptashnyk^{a 1}

¹ Heriot-Watt University, Edinburgh

^a – Presenting author

Plant roots are essential for the proper growth of plants and the quality of crop by being responsible for nutrients and water uptake. A challenging and exciting question is to identify the main mechanisms regulating plant root growth and development. In this talk we will consider mathematical modelling and analysis of mechanical properties of plant tissues and plant root growth. In the multiscale modelling of the interplay between the mechanics, microstructure and chemistry we shall assume that elastic properties of plant tissues depend on the chemical processes and tissue microstructure, whereas chemical reactions depend on mechanical stresses within plant cell walls and tissues. To model plant root growth we will consider both the macroscopic density-based approach and the microscopic description of growth processes on the plant cell level. Experimental data on mechanical properties and growth of plant roots are used to parametrise and validate the mathematical models.

Keywords: Vegetation modelling

Dynamics of savanna-forest ecosystems with resource limitations and heterogeneity

Dr Denis Patterson^{a 1}

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^a – Presenting author

We consider a spatially extended version of a classic forest-savanna model with non-local seed dispersal and fire spread dynamics. We investigate the emergence of non-homogeneous solutions in the presence of resource limitation on the forest tree growth rate. Analytic and computational tools reveal a myriad of patterned steady-state and spatially oscillating solutions; we track these solutions as a function of system parameters, such as dispersal scales and growth rates. Large savanna-forest ecosystems are also subject to multifarious heterogeneity due to altitude, soil quality, rainfall, and other exogenous gradients. Existing modeling with two vegetation species has shown how such gradients can determine savanna-forest boundaries via the so-called Maxwell point theory. We build on this work by analyzing our more realistic four species model with a rainfall gradient accounting for environmental heterogeneity. We track the emergence (and disappearance) of “front-pinned” solutions as a function of system parameters, such as dispersal range, and illustrate a rich phenomenology of other complex solutions which can emerge due to heterogeneity.

Keywords: Ecosystems dynamics

Characterizing ecosystem changes associated with desertification transitions

Dr Juan A. Bonachela **a**¹

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a – Presenting author

Models that describe vegetation in semi-arid ecosystems have been the focus of intense research due to the rich phenomenology of their described dynamics. Depending on the specific ways key ingredients such as plant facilitation and resource competition are implemented, models can show from scale-free to regular spatial distribution of plants, either forming stable or transitory patterns, and either abrupt or smooth desertification transitions occurring as water availability decreases. Importantly, which theoretical tools are available to study the system and (hopefully) anticipate such transitions is intrinsically linked to the dynamics and emergent spatial distribution of vegetation. In this talk, we will review some of these models, with an emphasis on the desertification transition. We will discuss both generic and mechanistic models that aim to describe the transition in different systems, whether the associated transition is smooth or catastrophic, and the use of concepts from physics and mathematics to characterize such shifts and the phenomenology around them (for example, changes in resilience). We will explore the effect that the underlying vegetation pattern and transition can have in higher trophic levels, and discuss how additional interactions with e.g. fauna or human-driven ecosystem engineering can alter the transitions and thus offer management opportunities that may increase the robustness and resilience of the ecosystem.

The role of nonlocal competition in vegetation pattern formation: is it an alternative to scale-dependent feedback?

Dr Ricardo Martinez-Garcia ***a*** ¹

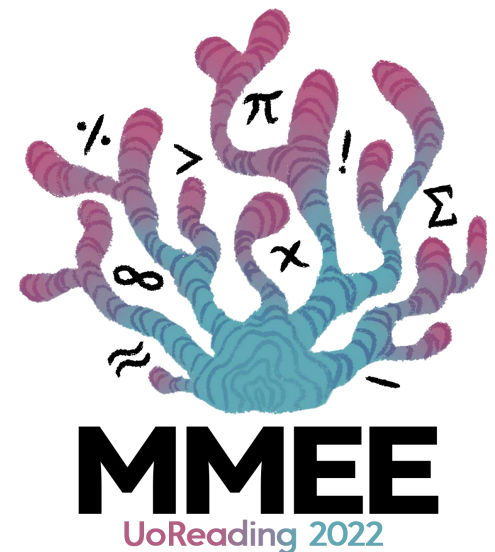
¹ ICTP-South American Institute of Fundamental Research & Institute for Theoretical Physics of the State University of São Paulo

a – Presenting author

Self-organized spatial patterns of vegetation are frequent in drylands and, because pattern shape correlates with water availability, they have been suggested as important indicators of ecosystem health. However, the mechanisms underlying their emergence remain unclear. Several models, accounting for different mechanisms, have been proposed to explain the emergence of these patterns. Some theories hypothesize that patterns could result from a water-mediated scale-dependent feedback (SDF), whereby interactions favoring plant growth dominate at short distances and growth-inhibitory interactions dominate in the long-range. However, we know little about how the sign of net plant-to-plant interactions changes with inter-individual distance, which challenges the relevance of this SDF for vegetation pattern formation. Assuming that net plant interactions are always inhibitory, alternative theories also recover pattern shapes observed in nature. These alternative hypotheses leading to visually indistinguishable patterns predict disagreeing desertification dynamics following the spotted pattern, limiting its potential use as ecosystem-state indicator. In this presentation, I will focus on this latter hypothesis. I will first present in which conditions long-range competition alone can generate regular patterns of population density in systems with one and two species. Then, I will discuss the ecological implications of those patterns both for population persistence and species coexistence.

Keywords: Spatial ecology

Mini-symposium 3 - Cancer vs microbial community modelling: divides and bridges



A quantitative description of phenotypic plasticity and its consequences

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^a – Presenting author

Tumour cells and infectious microbes face changing environments frequently. These fluctuations can arise due to changes in nutrient availability, the host's immune response, or drug treatments. How cells respond to modified environmental conditions is crucial to their persistence. Tumours and microbes have evolved several strategies to cope with such fluctuating environments. While the molecular basis of the process may differ, they can be abstracted by similar mathematical models. One such mechanism is phenotypic plasticity: the ability of one genotype to express varying phenotypes when exposed to different environmental conditions. We investigate how phenotypically plastic cell populations grow and persist within their environment. Additionally, we explore how phenotypic plasticity affects drug treatments. We find that phenotypically-plastic cell populations generate and maintain phenotype heterogeneity, and the proportion of each phenotype always approaches a stable distribution. The propensity of transitions determines the stable phenotype distribution and how fast it is approached. Trait heterogeneity is recognized as a recurrent problem for cancer and antimicrobial treatments. By showing that targeting phenotype transitions can improve the effectiveness of primary therapy, we suggest that adaptive mechanisms are a viable target for adjuvant therapy.

Keywords: Population dynamics

A modified fluctuation-test framework characterizes population dynamics and mutation rate of cancer persister cells

Dr Simone Pompei **a** ¹

¹ IFOM Foundation, Milan, Italy

a – Presenting author

Recent work suggests that, during certain treatments, cultured cancer cells exhibit complex survival strategies that are similar to those observed in bacteria. We set up an interdisciplinary collaboration with the aim of gauging these claims with quantitative standards. By a combination of mathematical modelling and quantitative experiments, we characterised the dynamics of cloned colorectal cancer cell lines under treatment with clinically approved targeted therapies. We found evidence for two phenotypic switches in response to the drug treatment: persistence and stress induced mutagenesis. Using a custom-developed two-step fluctuation test, we could quantify the transition to persistence, and the mutation rates of cells before and after treatment. We found that persisters are largely induced by drug treatment and show a 7- to 50-fold increase of their mutation rate under treatment. If they can be translated to patients, these findings may have important implications for the planning of cancer drug treatment.

Keywords: Evolutionary models

Influence of mutations in phenotypically structured populations in a time periodic environment

Dr Cecile Carrere ^{*a*} ¹ and G.Nadin²

¹ Université d'Orleans – France

² CNRS Sorbonne Université – France

a – Presenting author

Solid tumours often present large internal heterogeneity, with several phenotypes coexisting in a single location. To better understand this phenomenon, we propose with G.Nadin a model of trait-structured populations to describe the cancerous cells population, with periodic in time fluctuations of the environment. These fluctuations might be due in particular to regular treatment administration. We consider two main classes of treatment protocol: either a low dose, constant treatment (called metronomic), or strong doses of treatment with long pauses between injections (called MTD for Maximal Tolerated Dose). In our framework, we can express the mean total cancerous cells population as the eigenvalue of a parabolic periodic operator. This allows us to explore the influence of different parameters on the global population. In particular, we show that the metronomic protocol will always favor a homogeneous population.

Keywords: Population dynamics

Timescale of evolution in growing populations with rare mutations

Dr Michael Nicholson^{*a*1}

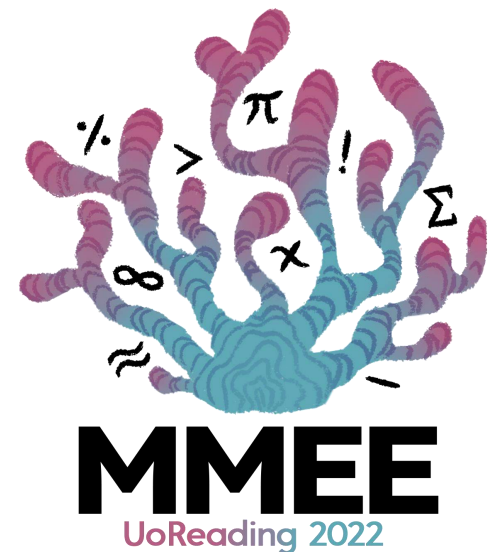
¹ CRUK Scotland Centre, Institute of Genetics and Cancer, University of Edinburgh

a – Presenting author

The number of cells of a given type, and how long we wait until this type exists, are common questions when considering exponentially growing populations such as bacteria or cancer. Here, I will present recent progress on a general framework to answer these questions, aiming to provide a toolkit for modellers in this area. As an application, I will discuss when we expect altered mutational processes to lead to the detection of distinct driver mutations in colorectal cancer.

Keywords: Evolutionary models

General Session 1 – Phylogenies and evolutionary genetics



Chaotic evolutionary dynamics by selfish genetic elements

Prof. Vincent AA Jansen ^{a1}, Dr Timothy W Russell², and Dr Matthew J Russell³

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³ School of Mathematical Sciences, University of Nottingham, Nottingham, NG7 2RD, UK

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Selfish genetic elements (SGEs) are genes that seek to enhance their own frequency, at no benefit or even a cost to the individual that carries them. Theoretical models of evolutionary dynamics tend to focus on populations near, or at, equilibrium gene frequencies. Analysis of these models is often limited to linear stability and there is therefore a tendency to limit attention to models that lend themselves to this procedure, i.e. focusing on models which do not exhibit complex dynamics to warrant a different approach. Given the evolutionarily complex behaviour of SGEs, for example selective sweeps followed by stasis (see e.g. Ubeda et al. 2019 Russell et al. 2019), we ask whether the interaction between selfish driver and target loci, interacting with specificity, can lead to complex behaviour. We show that genetic systems, with sufficiently high diversity, can have chaotic dynamics arising from the linking of many heteroclinic cycles into a heteroclinic network. We show, using symbolic dynamics, that this leads to a horseshoe map and positive Lyapunov exponents, one of the hallmarks of chaos. The positive Lyapunov exponents and accompanying dependence on initial conditions means that gene frequencies in nearby populations are driven apart. Populations diverge quickly, showcasing how chaotic dynamics can isolate populations. We believe this provides a possible explanation for some observed, but hitherto not convincingly explained chaotic genetic patterns, for example chaotic genetic patchiness.

TW Russell, MJ Russell, F Úbeda, VAA Jansen (2019) Stable cycling in quasi-linkage equilibrium: fluctuating dynamics under gene conversion and selection. (2019) *Journal of Theoretical Biology* 477, 84-95, <https://doi.org/10.1016/j.jtbi.2019.06.010>

F Úbeda, TW Russell, VAA Jansen (2019) PRDM9 and the evolution of recombination hotspots. *Theoretical Population Biology* 126, 19-32, <https://doi.org/10.1016/j.tpb.2018.12.005>

Stochastic physics of species extinctions in a large population

Dr Ivan Sudakow^{a1,2}

¹ The Open University, UK

² The University of Dayton, Ohio, USA

^a – Presenting author

We develop a stochastic physics-inspired approach to analyze how environmental forcing influences the severity of species extinctions. This approach is based on the large deviations theory of stochastic processes (the Freidlin-Wentzell theory). We show that there are three possible fundamentally different scenarios of extinctions, which we call catastrophic extinctions, asymmetric ones, and extinctions with exponentially small probabilities. The realization of those scenarios depends on environmental noise properties and the boundaries of niches, which define the domain, where species survive. Furthermore, we describe a hysteresis effect in species extinction showing that fluctuations can lead to dramatic consequences even if an averaged resource supply is sufficient to support population survival.

Keywords: Niche Theory

Quantifying dynamics of normal haematopoiesis from somatic evolution

Dr Nathaniel Mon Pere^{a 1}

¹ Institution

^a – Presenting author

The production of blood cells is known to be driven by a relatively small group of hematopoietic stem cells (HSC) which both self-renew and provide lineage progenitors throughout the entirety of an individual's lifetime. However, many properties of these dynamics are still debated or unknown, in part due to the difficulty of studying HSC behaviour in vivo. Because the stem cell pool self-renews it acquires somatic mutations which are subject to evolutionary pressures and stochastic drift. We show that information on the underlying dynamics is encoded in observations of this mutational landscape, which in turn can be obtained by modern sequencing methods. In particular, we develop predictions for the distribution of single cell mutational burdens and the site frequency spectrum based on a model of stem cell dynamics which spans both the ontogenic growth of the system as well as its balanced turnover during adulthood. Using publicly available data containing variant information on HSCs, we apply our predictions to estimate fundamental quantities such as the per-division mutation rate, the size of the HSC pool, the HSC division rate, and the proportion of asymmetric divisions.

Statistical tools for seedbank detection

Jere Koskela ^{a1}, Prof Jochen Blath², Dr
Eugenio Buzzoni and Dr Maite Wilke
Berenguer³

¹ University of Warwick, Warwick, UK

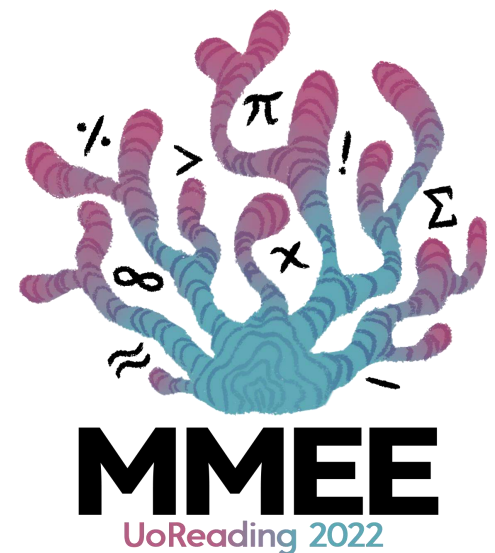
² Goethe-Universität Frankfurt, Frankfurt,
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Germany

a – Presenting author

There is a growing awareness in the importance of reversible dormancy as a bet-hedging strategy in quantitative modelling of evolution, particularly among microbial organisms and plants. There are (at least) two modelling regimes for dormancy in coalescent models: the so-called weak seed bank which arises from short periods of dormancy (measured in numbers of generations), and the strong seed bank which arises from periods of dormancy on the order of the effective population size. The weak seed bank is equivalent to the Kingman coalescent with an altered effective population size, while the strong seed bank resembles the structured coalescent, albeit with an infinite effective population size in the dormant subpopulation. I will review all four models, and demonstrate that a modest amount of DNA sequence data distinguishes between them with high confidence, at least in the idealised setting of simulated data.

General Session 2 – Spatial Ecology I



Searching for an Antagonistic Hider on a Tree, with Some Indication of its Location

Prof Steve Alpern^{a 1}

¹ Institution

^a – Presenting author

A Hider locates anywhere on a rooted binary tree (Q,O) , optimally at a leaf node. The Searcher performs a unit speed depth-first search of the tree, starting at the root O . The payoff to the Hider in this zero sum game is the search time T taken for the Searcher to reach the stationary Hider. When reaching a branch node, the Searcher is given a hint as to which branch the Hider is on. The hint is correct with known probability $p > 1/2$ unless the Hider is on neither branch, in which case the hint is random. This problem reduces to the original problem of Isaacs (1965), as solved by Gal(1979), when p is $1/2$. At each branch node, one of the branches is 'preferred', which means it should always be searched first when the hint says so. This problem models the predator-prey search problem when the prey has an odor which mixes with ambient odors, but which is still useful to the predator. Other situations have sound or radiation emitted by the Hider which aids detection.

New generation geostationary satellite observations reveal the impact of heat waves on the diurnal dynamics of ecosystem productivity

Dr Xing Li ^{a1}, Youngryel Ryu^{1,2}, Jingfeng Xiao³, Bolun Li¹, Jiangong Liu¹, Benjamin Dechant⁴ and Sungchan Jeong²

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² Department of Landscape Architecture and Rural Systems Engineering, College of Agriculture and Life Sciences, Seoul National University, South Korea

³ Earth Systems Research Center, Institute for the Study of Earth, Oceans, and Space, University of New Hampshire, Durham, NH, USA

⁴ German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

Emerging new generation satellites including geostationary satellites (e.g., GOES-R, GK2A), ECOSTRESS and OCO-3 have opened up new opportunities to investigate the diurnal cycles of ecosystem processes and enable the exploration of the interactions between ecosystem processes and environmental conditions at the sub-daily scale. Here we used observations from the GOES-R along with MODIS and ERA-5 reanalysis data to examine the effect of severe heat waves on the diurnal variations of ecosystem productivity in 2020 across the United States. The hourly gross primary production (GPP) was estimated using a regression tree model based on land surface temperature and shortwave incoming radiation from GOES-R, vegetation indices and land cover from MODIS, and vapor pressure deficit derived from ERA-5. Our model estimated the hourly GPP fairly well ($R^2 = 0.88$, $RMSE = 2.55 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), and the predicted GPP overall captured the diurnal patterns of tower-based GPP for different ecosystems. The diurnal dynamics of GPP during the heat wave differed considerably between dryland ecosystems on the one hand and well-watered forests and croplands on the other hand. For dryland ecosystems located in Southwest U.S., GPP peaked in the morning. During the heat wave, the peak hour and diurnal centroid of GPP were further shifted towards earlier morning compared to unstressed conditions. This enhanced asymmetry in the diurnal cycle of GPP resulted from considerable increase of water and heat stress at noon and in the afternoon. For the forest and cropland, in contrast, the peak hour and diurnal centroid of GPP did not show significant shifts towards morning during the heat. Our results demonstrate that with temporally dense observations, geostationary satellites offer a unique opportunity to monitor the diurnal variations in ecosystem productivity, and will profoundly improve our understanding of climate-ecosystem interactions at the sub-daily scale from regional to global scales.

^a – Presenting author

Keywords: Remote-sensing-based models

Complex Spatio-Temporal Dynamics in a Model of Social Protests

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

Emergence of the wrapped Cauchy distribution in mixed directional data¹

Dr Joseph Bailey^{a 1}

¹ Institution

^a – Presenting author

Inferring the most appropriate distribution (or distributions) to describe observed directional data is important in many applications of circular statistics. In particular, animal movement paths are typically analysed and modelled by considering the distribution of step lengths and turning (or absolute) angles. Characteristics of circular distributions, such as kurtosis, have significant effects on the qualitative and quantitative results of descriptive and predictive models². Here we demonstrate that a single heavy-tailed wrapped Cauchy distribution can appear to fit directional data mixed from two different underlying wrapped normal distributions. We derive mathematical expressions to calculate the parameter space for which this occurs and illustrate the result by analysing an example data set of the movements of African bull elephants (*Loxodonta Africana*)³. We conclude that the presence of a heavy-tailed wrapped Cauchy distribution in observed directional data can, in certain cases, be explained by data coming from two distinct underlying distributions. We discuss how this may relate to the presence of multiple movement modes within an observed path when analysing animal movement data and potential applications to improve current HMM methods used for discerning multiple movement behaviours.

¹ Bailey, J.D., Codling, E.A. Emergence of the wrapped Cauchy distribution in mixed directional data. *AStA Adv Stat Anal* 105, 229–246 (2021). <https://doi.org/10.1007/s10182-020-00380-7>

² E.A. Codling, R.N. Beaton, G.J. Thorn. Diffusion about the mean drift location in a biased random walk. *Ecology* 91(10):3106–3113. 2010 \newline

³ J. Wall, G. Wittemyer, V. LeMay, I. Douglas-Hamilton, B. Klinkenberg. Elliptical time-density model to estimate wildlife utilization distributions. *Methods in Ecology and Evolution* 5(8):780–790, 2014.

Schrödinger's range-shifting cat: Analytic results for the impact of asymmetric environmental dependence on species responses to climate change

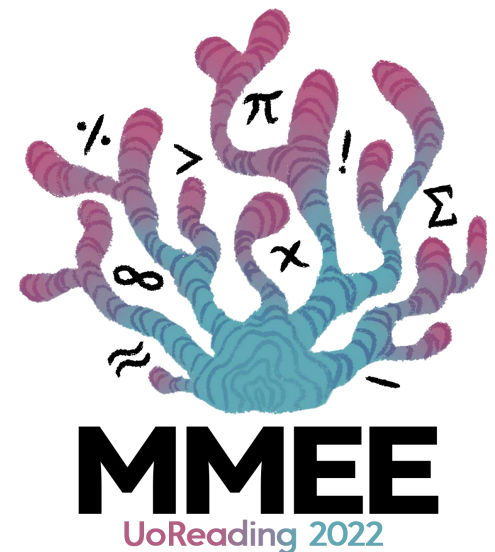
Dr Chris Terry ^{a1} and Axel Rossberg¹

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Analytic models for how species will respond to climate change can highlight key parameter dependencies. By mapping equations for population dynamics onto corresponding problems from quantum mechanics with known solutions we derive analytical results that significantly extend previously known results within the reaction-diffusion equation framework. In particular, we are able to derive specific results for the frequently observed case of asymmetric environmental response curve. We use these to find expressions for three key responses to climate change: 1) population persistence, 2) lag between range displacement and climate displacement, 3) location of maximum population sensitivity, in terms of parameters representing climate velocity, dispersal rate, maximum growth rate, niche width, high-frequency climate variability and environmental performance curve skew. Surprisingly, under our model assumptions, the direction of performance curve asymmetry does not strongly contribute to either persistence or lags. A simple metapopulation simulation corroborated this result. Measures to support range-shifting populations may have most benefit where the environmental dependence is shallow, irrespective of whether this is the 'leading' or 'trailing' edge. Our results introduce new tools to ecology and illustrate the continued role of analytic theory.

Mini-symposium 4 - The role of competition in shaping ecological networks



Interference competition – the hidden force behind food web structure and stability

Dr Korinna Allhoff^{a1}

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^a – Presenting author

Dynamic-systems theory has greatly improved our understanding of the forces that shape ecological networks, where nodes represent species and links represent species interactions. This knowledge provides valuable insights into the functioning of complex ecosystems and into their responses to various drivers of global change. In this context, the role of interference competition in shaping ecological networks has received surprisingly little attention, despite the fact that competitive interactions occur at all trophic levels. During my talk, I will review several food web models from recent literature. Each of these models considers interference competition in one way or another, usually following a set of oversimplified rules. The description of these rules often lacks clarity, meaning that underlying model assumptions are neither defined explicitly nor corroborated with empirical evidence. I will demonstrate that simulation results obtained from these models, such as stability or coexistence patterns, are often highly sensitive to modifications in the exact shape of the competition term. The same is true concerning the specific parameter choice describing the overall strength of interference competition in the system. Based on these insights, I argue that network scientists should aim at developing a dynamic-systems theory of competition networks, based on empirical observation, and at incorporating such theory into existing models of ecological networks.

Keywords: Interaction networks

Hierarchy reduces instability of competition networks by causing asymmetries in energy loss

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² University of Hohenheim, Germany

³ British Antarctic Survey, UK

^a – Presenting author

Explaining the coexistence of many competing species is a fundamental challenge for ecological theory. We analyzed the dynamics of interference competition in 30 multispecies bryozoan assemblages from high latitudes. We translated the outcomes of observed competition battles into “energy loss webs” and calculated the inter- and intraspecific interaction strengths from these (negative) flux rates and the observed population densities. All observed networks turned out to be unstable. However, the instability was mitigated considerably by the asymmetric patterning of strong and weak competitive strengths, which resulted from highly transitive community structures. Natural organisation reduced instability by keeping both short and longer feedback loops weak. Our results support the idea that competition leads to competitive exclusion, not because of their transitivity and hierarchy, but despite it.

Competition across scales: Insights into the organization of (benthic) competition networks from an individual-based model

Mr Sebastian Lorenz Krüger ^{a1}, Franziska Koch¹, Anje-Margriet Neutel², David K. A. Barnes², and Korinna T. Allhoff³

¹ University of Tübingen, Germany

² British Antarctic Survey, UK

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^a – Presenting author

Unravelling the relationship between structure and stability of ecosystems has been one of the most pervasive topics in ecological research. Current insights, however, are mostly limited to systems dominated by antagonistic or mutualistic interactions. In particular the role of competition in shaping ecological networks has been largely ignored. To help fill this gap, we implemented an individual-based model based on empirical observation of Bryozoan species fighting for space on the seabed. We use this model as a starting point to construct what we call “energy-loss webs”. These networks capture how fiercely the model species compete with each other at a given time. Their structure emerges in a self-organized manner from simple rules describing colonization, colony growth and local confrontations between individual colonies. The individual-based approach allows us to study how the choice of specific rules describing local interactions affects the organisation of the whole assemblage. In particular, we derive testable predictions on how network structure and stability (measured via dominant eigenvalues) change over time, for example during community assembly or in response to altered disturbance regimes. Preliminary results show a clear correlation between system (in-)stability and the weight of the strongest 2-link feedback loop, which is qualitatively in line with a recent analysis of empirical data. Different model modifications furthermore allow us to assess if the observed relation between structure and stability depends on specific model assumptions reflecting Bryozoan competition or whether it holds for competitive systems in general, possibly even beyond ecology.

Keywords: Interaction networks

Resource partitioning among different-sized savanna herbivores

Ms Yuhong Li ^{a 1} and Dr Han Olff¹

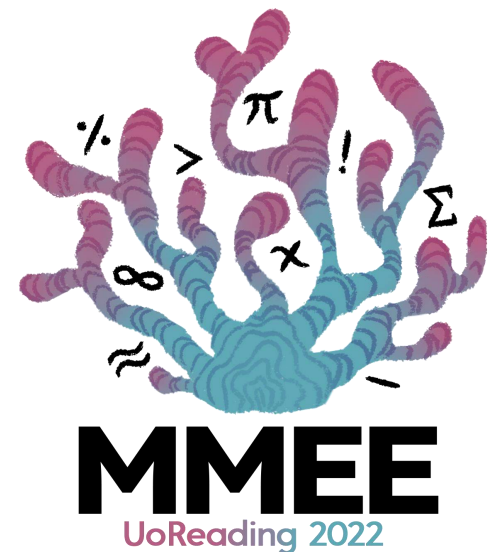
¹ University of Groningen, The Netherlands

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Dietary niche partitioning is seen as an important mechanism for coexistence of ecologically similar consumers, and a leading explanation for the high diversity of co-occurring mammalian herbivores in African savannas landscape. Ultimately, individuals of two different herbivore species will never eat exactly the same plant species, and new methods such as DNA metabarcoding of dung increasingly allow the quantification of these differences. However, integrating resource partitioning into insightful models of community dynamics, food webs and ecosystem dynamics requires some degree of aggregation of both herbivore species and their plant resources into functional groups. Previous studies on this question have gained important insights by aggregating consumers into grazers and browsers, into ruminants and non-ruminants, into migrants and resident species, and by studying their resource partitioning along body size gradients. The aggregation of resources and habitats typically follows this, as grasses versus woody species, high quality short stoloniferous grasses versus low quality tussock grasses, short shrubs versus tall trees, or dry season habitats versus wet season habitats. Such different aggregations of consumers and resources represent different (implicit) assumptions on resource competition versus resource partitioning and thus represent different niche structures, leading to different model outcomes. Using field-collected data from the Serengeti-Mara ecosystem, we explore the consequences of different levels of aggregation of consumers and resources for their assumed niche structure, and test the different outcomes against long-term time series observations of their population dynamics.

Keywords: Niche theory

Mini-symposium 5 - Vegetation modelling - optimality approach (General EEO and Plant Acclimation)



Predicting plant functional traits and ecosystem processes from eco-evolutionary optimality

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Ministry of Education Key Laboratory for
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^a – Presenting author

Process-based vegetation models have been developed to understand and predict the impacts of climate change on the structure and function of vegetation. The model's complexity has been increased tremendous in past decades, our understandings on vegetation dynamics however has not been advanced much yet. This is reflected by the persistence of large uncertainties in model prediction for the future and impose grand challenges for model development. Recent progresses have demonstrated the Eco-evolutionary Optimality (EEO) theory as a promising approach for generating novel, parameter-sparse representations of plant and vegetation processes in models. Here, we show that the EEO theory generates various parsimonious models successfully predicting the core traits and processes of organs (such as leaf economic spectrum traits), individual plants (such as the coordination between photosynthesis and hydraulics), and ecosystems (such as the carbon allocation and evapotranspiration). We also show that EEO theory can successfully be applied to agricultural ecosystems. With parsimonious parameters, it generates even better predictions than the complex process-based crop models. We therefore argue that by constraining the models with organizing principles, EEO theory can lead to a more robust basis for understanding and predicting the emergent functional properties of ecosystems under the changing environments.

Keywords: Optimality theory

Using Eco-Evolutionary Optimality Principles to Predict the Thermal Acclimation of the Optimal Temperature of Photosynthesis

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^a – Presenting author

Current models for the terrestrial biosphere do not capture the response of photosynthesis to global warming because they often do not account for thermal acclimation, the process by which plants adjust to long-term temperature conditions. However, there is increasing evidence for thermal acclimation that should be considered. This study covers the evaluation of the P-Model, a photosynthesis model that explicitly incorporates thermal acclimation, in terms of its predictions of the optimal leaf temperature of photosynthesis (T_{opt}), which is an essential indicator for whether plants may cope with rising temperatures under global warming. The results showed that the P-Model could capture globally observed T_{opt} , but it suffers from overestimation (i) when daily mean light is used as input instead of midday light conditions and (ii) due to a lack of constraints on light use efficiency at low temperature. The P-Model showed a high but limited capacity of plants to adjust T_{opt} with rising air temperatures. Therefore, it predicts a convergence of T_{opt} with growing-season air temperature. Plants in cold climates will experience air temperatures closer to their T_{opt} , while plants in warm climates may grow beyond their T_{opt} . However, when taking the uncoupling of air and leaf temperatures into account, the P-Model showed a greater thermal acclimation capacity of T_{opt} than when assessing it solely from air temperatures. Predicted growing-season leaf temperatures correlated closely with observed T_{opt} . This suggested that plants adjust their physiology to thermally regulate themselves to maintain an optimal leaf temperature close to their T_{opt} . This pattern was found across all temperature regimes, meaning that plants were predicted to operate at a leaf temperature close to their T_{opt} , even in warm climates.

Keywords: Optimality theory

Application of an optimality-based model to predict half-hourly carbon uptake and water release by ecosystem to include plant acclimation within a land-surface modelling framework

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Ascot, UK

² Geography & Environmental Sciences,
Reading University, Reading, UK

^a – Presenting author

Plants respond to environmental changes on different timescales. At leaf level there are photosynthetic processes that react instantaneously to external stimuli and others that occur at a slower (acclimated) timescale. Most of the current land surface models (LSMs) describe plants' instantaneous responses but it is important to consider both timescales to correctly predict plant assimilation. We develop a method to implement an existing optimality-based model, the P model, at sub-daily timesteps and thus to include acclimated responses within a LSM scheme. The resulting model correctly reproduces the diurnal cycle of gross primary production (GPP) as recorded by flux-tower measurements across different biomes. However, the model does not perform well in arid regions. There are two problems: an error in magnitude and in the shape of the diurnal cycle. The model overestimates GPP in dry areas and it does not capture the "midday depression" behaviour, noticeable from the observations. We adopt a process-based approach to include the effect of low soil moisture on simulated GPP in the P model. The main idea is to control GPP via hydraulics. We firstly assess the "demand"—the transpiration that would take place without any drought limitation—then we constrain the actual transpiration rate so that it does not exceed the canopy's hydraulic capacity to obtain the actual assimilation rate. Preliminary results comparing simulated transpiration and GPP to flux tower measurements at dry sites suggest that this is a promising way of correcting the observed biases in arid regions.

Keywords: Optimality theory

Relationships between resprouting and fire regimes

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² Imperial College London, Faculty of
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a – Presenting author

Resprouting is a resilience trait that allows individuals to regenerate rapidly following fire. It has profound effects on the speed of post-fire ecosystem recovery and therefore on water- and energy-exchanges with the atmosphere and the carbon cycle. However, the ability to resprout requires investing in carbon storage. Balancing the benefits of rapid recovery of photosynthesis against the costs of carbon storage implies that resprouting is an optimal behaviour in environments where fire is neither too frequent nor too infrequent. Although there is anecdotal support for this assertion, there has been little quantitative investigation of the types of fire regime where resprouting is an optimal strategy. In this study, we use data on the abundance of woody species in Europe, Australia and South America derived from the sPlotOpen database combined with information on whether the species present can resprout or not, derived from regional and global plant trait databases and field information, to examine how changes in the abundance of resprouting species varies with fire return interval and with fire intensity. We show that the proportion of resprouting species decreases as fire return intervals increase, while the abundance of resprouters is maximal at intermediate levels of fire intensity. This work suggests that it should be possible to model the occurrence and abundance of resprouting using an eco-evolutionary optimality approach based on balancing the costs and benefits of resprouting under different fire regimes.

Keywords: Optimality theory

rsofun: a combined canopy - dynamic vegetation model framework

Koen Hufkens^{a 1} and Benjamin D. Stocker¹

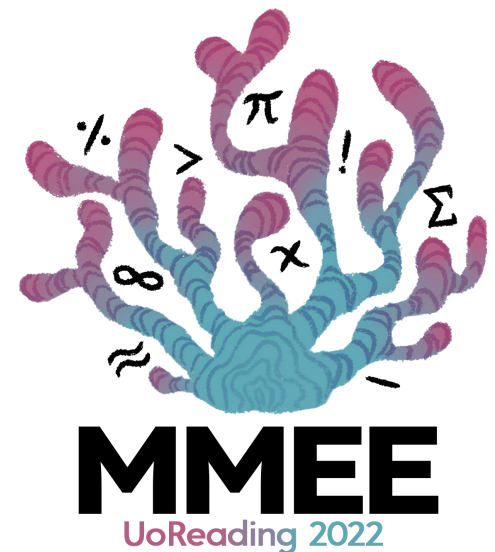
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Dynamic vegetation models and canopy level models serve two distinct functions within ecosystem science in support of hypothesis testing and furthering our understanding of vegetation responses to climate change. Here we present {rsofun} a Fortran implementation of both the P-MODEL (canopy scale) and LM3PPA (DVM) combined into an R package for easy model simulation and calibrations. Our implementation provides a convenient way to run or further develop models. We provide simple use cases to demonstrate this functionality as well as abbreviated instructions if users would want to change the underlying model code. We show that modelling with our setup is easy and fast, scaling from site level to global scales.

Keywords: Optimality theory

Mini-symposium 6 - Evolutionary Dynamics in the Soma



Stochastic model of tumor evolution for cancer etiology and risk

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a – Presenting author

We present a mathematical model of tumor evolution that includes all phases in the life of a tissue, from tissue development to cancer occurrence. The effects of a carrying capacity, different types of cell division, and different types of driver mutations are also accounted for. New analytical closed-form expressions are obtained from this mechanistic model, showing that the time to cancer can be approximated by a Weibull distribution, providing a simple probability distribution for the timing of a highly complex evolutionary process. The results of the mathematical model are then used both to provide key insights into cancer etiology, by assessing the role played by normal endogenous mutational processes, and to compare the cancer risk of repeated radiation exposures versus a single exposure to a high dose.

Keywords: Evolutionary models

Trade-off between reducing mutational accumulation and increasing commitment to differentiation determines tissue organization

Dr Gergely Szöllősi^{a1} and Imre Derenyi

¹ Institution

^a – Presenting author

Species-specific differences control cancer risk across orders of magnitude variation in body size and lifespan, e.g., by varying the copy numbers of tumor suppressor genes. It is unclear, however, how different tissues within an organism can control somatic evolution despite being subject to markedly different constraints, but sharing the same genome. Hierarchical differentiation, characteristic of self-renewing tissues, can restrain somatic evolution both by limiting divisional load, thereby reducing mutation accumulation, and by increasing cells' commitment to differentiation, which can ``wash out'' mutants. Here, we explore the organization of hierarchical tissues that have evolved to limit their lifetime incidence of cancer. Estimating the likelihood of cancer in the presence of mutations that increase self-proliferation we demonstrate that a trade-off exists between mutation accumulation and the strength of washing out. Our results explain differences in the organization of widely different hierarchical tissues, such as colon and blood.

Keywords: Evolutionary models

Immune selection and predictability of cancer evolution

Marta Luksza ***a***¹

¹ Institution

Abstract (14)

a – Presenting author

Keywords:

Population-level consequences of inheritable somatic mutations and the evolution of mutation rates in plants

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a – Presenting author

Plants lack a segregated germline, as reproductive organs emerge from vegetative parts during mating seasons. Therefore, plants acquire inheritable mutations in two ways, during gametogenesis and during somatic growth. Since the number of mitoses occurring in an individual's lifetime, that is the number of opportunities it has for somatic mutations to accumulate, varies widely between species with contrasting growth habits (say, trees versus annuals), somatic mutation accumulation may impact species' evolution differently depending on their life-history. In this project, I explored the consequences of the lack of germline segregation for the evolution of mutation rates in plants. I showed that the mutation rate per mutagenic event should be lower in more long-lived species at evolutionary equilibrium, because of the larger amount of deleterious mutations accumulating during growth in these species. Then, I studied whether somatic mutation accumulation could explain the higher inbreeding depression observed in perennials compared with annuals, given that perennials have lower per mutagenic event mutation rates at evolutionary equilibrium. I showed that somatic mutations contribute to generate higher inbreeding depression in perennials in this model, but that the generated increase quickly becomes negligible when meiosis is assumed to be more mutagenic than mitosis.

Keywords: Evolutionary models

Longitudinal Dynamics of Clonal Haematopoiesis

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¹ University of Edinburgh

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a – Presenting author

The prevalence of clonal haematopoiesis of indeterminate potential (CHIP) in healthy individuals increases rapidly from age 60 onwards and has been associated with increased risk for malignancy, heart disease and ischemic stroke. CHIP is driven by somatic mutations in stem cells that are also drivers of myeloid malignancies. Since mutations in stem cells often drive leukaemia, we hypothesised that stem cell fitness substantially contributes to transformation from CHIP to leukaemia. Stem cell fitness is defined as the proliferative advantage over cells carrying no or only neutral mutations. It is currently unknown whether mutations in different CHIP genes lead to distinct fitness advantages that could form the basis for patient stratification. We set out to quantify the fitness effects of CHIP drivers over a 12 year timespan in older age, using longitudinal error-corrected sequencing data. We developed a new filtering method to extract fitness effects from longitudinal data, and thus quantify the growth potential of variants within each individual, while taking into account individual mutational context. We show that gene-specific fitness differences can outweigh inter-individual variation and therefore could form the basis for personalised clinical management.

Keywords: Lineage tracing methods to measure evolutionary dynamics in cancer

Insights into evolutionary dynamics of B cells from a snapshot of the immune repertoire

Mr Natanael Spisak^{a 1}

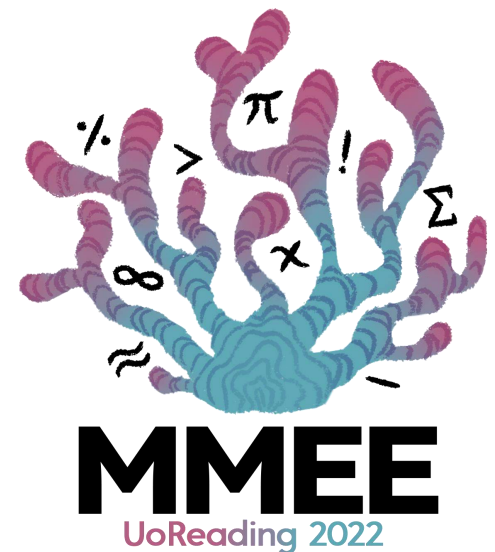
¹ Ecole Normale Supérieure, Paris, France

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B cells are central players of the adaptive immune response. Upon antigenic stimuli, they undergo an evolutionary process in which B-cell receptors, or antibodies, are subject to somatic hypermutations. The immune repertoire sampled in high-throughput sequencing experiments consists of products of very many affinity maturation processes. We will show how to disentangle independent evolutionary lineages by leveraging the extraordinary diversity of the naive (unmutated) repertoire. A high-fidelity partition of the data into families of related cells allows us to characterize the underlying evolutionary dynamics.

Keywords: Population dynamics

General Session 3 – Ecosystems Dynamics



Predator-Prey Model with Fear, Allee Effect and Z-Control

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^a – Presenting author

Prey-predator models with Allee and the fear effect on prey growth rate are developed and analyzed. We investigate a prey-predator model in which the predator uses a Holling type I functional response to predate the prey. We find four possible model equilibria and investigate their stability. The model exhibits Hopf-bifurcation for the co-existence equilibrium and transcritical bifurcation for the free predator equilibrium. Numerical simulations are carried out to show that after certain time the prey population has no effect since fear develops over time as a result of habituation. For small Allee effect the co-existence equilibrium is stable when it exists. Also, we find that as the Allee threshold increases the predator population increases. However after certain values of Allee threshold both populations become unstable and then go to extinct. Furthermore, three types of Z-control rules have been studied and explored to prevent species from extinction or to stabilize the ecological system.

Intervene or wait? An agent-based model to improve the timing of intervention in conservation conflicts management

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Alexander B. Duthie¹

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a – Presenting author

The timing of biodiversity managers' interventions can be critical to the success of conservation, especially in situations of conflict between conservation objectives and human livelihood, i.e., conservation conflicts. Given the uncertainty associated with complex social-ecological systems and the potentially irreversible consequences of delayed action for biodiversity and livelihoods, managers tend to simply intervene as soon as possible by precaution. However, refraining from intervening when the situation allows it can be beneficial, notably by saving critical management resources. We introduce a strategy for managers to decide, based on monitoring, whether intervention is required or if waiting is possible. To evaluate the performance of this strategy, we built an agent-based model of conservation conflict between a manager aiming to conserve an animal population and farmers aiming to maximize yield by protecting their crop from wildlife damage. We then simulated population dynamics and decision-making in budget-constrained adaptive management over time, while accounting for uncertainty around these processes. We showed that waiting strategies are worth considering in conservation conflicts, as they can facilitate equitable management with a more efficient use of resources, and even improve conservation outcomes under difficult budget constraints.

Anthropocene Community Assembly - spatial structure and mixing drive biodiversity

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Systems Analysis

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Community assembly, in which species are added one at a time to a community from a regional pool, is a well-established way to simulate stable complex ecosystems, circumventing the complexity-stability problem. Each community is assumed to be assembled in an almost entirely closed environment, leading to questions about how more open systems might assemble in reality. In particular, interactions between communities might drive new or unexpected behaviour, leading to more diverse or more homogeneous results dependent on the amount of community mixing. Here, we mediate interactions between communities by simulating size-biased and ecologically driven community assembly over a range of spatial structures. This produces different community combinations dependent on the spatial structure, reflected in changes in the biodiversity at both local and regional scales. These spatially induced trade-offs appear to reflect modern ideas of how humans are changing biodiversity and suggest that increased mixing associated with the Anthropocene can both increase local diversity while causing a collapse in regional diversity.

Variation in thermal sensitivity of metabolic traits can drive gradients of richness in microbial communities

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Predicting how species diversity changes along environmental gradients is an enduring problem in ecology. Previous work has posited that energy availability is a dominant mechanism that generates positive diversity-temperature gradients over space. However, this mechanism cannot explain the fact that microbial diversity often also shows a unimodal or declining response to temperature. Here, we show that variation in thermal sensitivity of metabolic traits (the change in trait value per unit change in temperature) across populations is likely to contribute strongly to temperature-richness gradients in microbial communities structured by competition. First, using a general mathematical model we show how the shape of richness-temperature relationship is determined by the population-level thermal sensitivity distribution. Next, we look at empirical data, to show that the variation in thermal sensitivity of metabolic traits across extant bacterial taxa is sufficient to generate the variety of their temperature-richness gradients observed in the real world. Our results provide a new mechanism that can help explain temperature-diversity gradients in ecological communities structured by competition.

Using game theory to model the dynamics of specialisms in ectomycorrhizal fungal communities

Dr Petra Guy^{a 1}

¹ Institution

^a – Presenting author

In mature temperate woodlands, most tree roots are colonised by ectomycorrhizal fungi (EMF hereafter) which supply nutrients and receive carbon from their host trees. Some specialist emf have a limited host range and tend to be found in association with a small number of tree species, whilst other generalist emf are ubiquitous and can be found in association with almost any tree species. Similarly, some evidence suggests that trees also display different traits in relation to their emf association, with some high receptivity trees hosting many more species than other low receptivity trees. It has been suggested that specialist emf may have co-evolved with their hosts to provide more nutrients and to receive more carbon. However, if specialists and high receptivity trees have co-evolved in this manner, why would they not have out-competed generalists and low receptivity trees? It is known that negative feedbacks within mutualisms allow partners of various qualities to co-exist. In this analysis, we model trees and emf as belonging to one of two guilds, low and high receptivity trees and generalist and specialist emf. We use replicator equations to express fitness relationships between the guild members which allow both guilds of trees and fungi to co-exist in a steady state. We then discuss these fitness relationships in relation to functional aspects of mutualisms in order to better understand woodland dynamics.

Role of trait variation in a savanna-woodland bistable system

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^a – Presenting author

Over the last decade, several studies have discussed the importance of individual and trait variation in natural populations. Individuals in nature interact with each other and their environment, giving rise to patterns and processes at the population, community and ecosystem level. However, individuals are generally treated to be identical in most theoretical studies, especially studies of bistable systems. We extend the mean-field model from Staver and Levin, 2012, *Am Nat*, to examine the role of individual variation in one such bistable system - with grassland, savanna and woodland as its alternative stable states. We specifically introduce variation in one functional and two demographic traits of savanna trees and saplings. Our study reveals that higher trait variation reduces bistability in the system, such that the woodland state is favored over the grassland state. Depending on the varying trait, the shift from one state to another can become less or more drastic. We also find that, at a particular driver value, even though the overall tree and grass cover remain the same for different initial conditions, the steady-state population trait distribution can be sensitive to initial conditions. Our findings show that individual variation in such systems can have important consequences for both ecological and evolutionary dynamics.

Impact of Seasonality on Bi-stable Ecosystem Dynamics

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a – Presenting author

Many studies have suggested that ecosystems may exhibit multiple stable states and abrupt responses to changes in underlying environmental conditions/drivers. Most mathematical modeling studies of multiple stable states and abrupt transitions ignore the role of seasonality associated with the environmental drivers. However, seasonal variations in environmental drivers can be important drivers of ecosystem states. In this study, we investigate the impact of driver seasonality on bistable ecosystems. To do this, we modify simple nonspatial models of ecosystems to incorporate a sinusoidal variation to the driver parameter of interest along with stochasticity. The timescale and the strength of the seasonality are varied to see how they affect the dynamics of the bistable ecosystem. We show that the seasonality imposed on the environmental driver may alter the qualitative nature of the histogram of the state variable. Specifically, we reveal that the timescale of the seasonal forcing relative to the intrinsic timescale of the system is crucial in determining the ecosystem dynamics and observed states. We argue how one could end up in wrong conclusions regarding the stable states of ecosystems if the seasonality is not accounted for.

Group reciprocity and the evolution of stereotypes

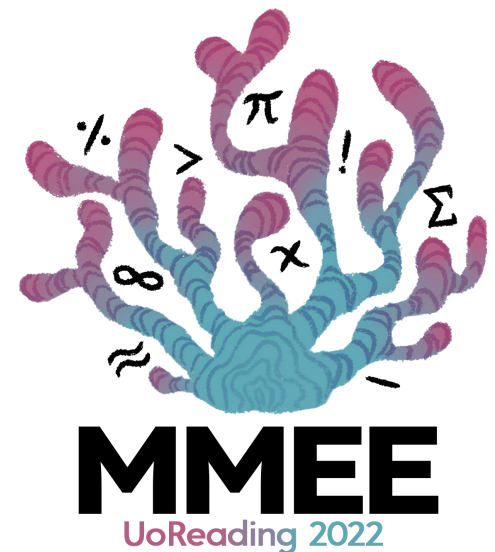
Dr Alexander Stewart^{a 1}

¹ Institution

^a – Presenting author

Stereotyping, in which a set of characteristics is attributed to all members of a group, shapes many social interactions. Such generalizations can reflect or even exacerbate inter-group tensions, leading in the extreme to de-humanization of out-groups. But the use of heuristics to guide social decision-making can often be a practical necessity. We study the evolution of stereotyping as a mechanism for cooperation under cognitive constraints. We consider a form of group reciprocity in which individuals make decisions about whether to cooperate with some people based on the average observed behavior of the identity group to which they belong (i.e. the group's stereotype). We explore the evolution of social circles - i.e. the number of people who are not stereotyped, but are instead judged only by their individual behavior. We also study the evolution of stereotypes themselves - i.e the degree of coarseness or specificity in the stereotypes people employ. We show that the co-evolution of social circles and stereotype groups undergoes two critical transitions, depending on the cognitive costs associated with remembering individual identities, as well as the benefits of cooperation. When costs are low, social circles are large and stereotypes are positive. When costs are intermediate, social circles are smaller, while stereotypes are coarse but generally positive. However when costs are high, social circles shrink and stereotypes become very coarse and negative. We then explore the impact of environmental shocks on stereotypes. We show that although stereotypes that evolve as a mechanism for group reciprocity are often positive, when populations experience a "shock" that reduces the benefits of cooperation, positive stereotypes can become negative, resulting in a loss of cooperation.

General Session 4 – Miscellaneous



Functional Responses: From Individual Processes to Feeding Experiments

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Ecological systems are tremendously complex, and can be regarded as ever-adapting, large networks of individuals interacting in a finite number of ways. These systems are characterized by different levels of stochasticity, associated to the discrete nature of their components and to the scale at which the system is looked at. At the population level, functional responses are non-linear functions commonly used to describe the variation in the rate of consumption of resources by consumers. They have been widely used in both theoretical and empirical studies, but a comprehensive understanding of their parameterization at different levels of description remains elusive. To better characterize consumer-resource interactions, we build new theory for consumer-resource dynamics, developing a set of individual based population models and describing the emergence of functional responses at the population level. We also derive functional responses by focusing on the subset of reactions describing only the feeding process, fixing the total number of consumers and resources, in what we call chemostatic conditions. Building on our theoretical approach, we provide new analytical tools to infer functional response parameters in feeding experiments and point to potential errors in interpreting already existing empirical data. In our approach, we give a more rigorous, mechanistic, individual-based characterization of consumer resource dynamics and provide examples of its application to the design and realization of feeding experiments. From a purely theoretical perspective, the research presented paves the way to a new generation of aggregated models of community dynamics, with potential applications to biodiversity assessment across scales. Our stochastic approach builds on fundamental ecological processes and has natural connections to basic ecological theory. Finally, we will also present potential generalizations to include evolutionary theory.

Keywords: Community Ecology

Stochastic Control of Ecological Networks

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The aim of the following work is to model the maintenance of ecological networks in forest environments, built from bioreserves, patches and corridors, when these grids are subject to random processes such as extreme natural events. The management plan consists in providing both temporary and sustainable habitats to migratory species. It also aims at ensuring connectivity between the natural areas without interruption. After presenting the random graph-theoretic framework, we apply the stochastic optimal control to the graph dynamics. Our results show that the preservation of the network architecture cannot be achieved, under stochastic control, over the entire duration. It can only be accomplished, at the cost of sacrificing the links between the patches, by increasing usage of the control devices. This would have a negative effect on the species migration by causing congestion among the channels left at their disposal. The optimal scenario, in which the shadow price is at its lowest and all connections are well-preserved, occurs at half of the course, be it the only optimal stopping moment found on the stochastic optimal trajectories. The optimal forestry policy thus has to cut down the timing of the practices devoted to biodiversity protection by half.

Keywords: Eco-evolutionary responses to environmental change, dynamics and structure of large ecological networks, bioeconomics, forest management, ecological networks, biodiversity, stochastic optimal control

Waggle dance distributions quantify collective foraging in honey bee colonies

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¹ Institution

^a – Presenting author

Honeybee foraging is a collective behaviour that is directed through the waggle dance communication system, whereby colony foraging effort is allocated through a series of feedback loops using both social and private information. Yet, despite its complexity, accumulating evidence suggests benefits of using social information vary across environments and are sometimes even negligible. Here, we present a mathematical model that can quantify the relative use of private and social information, by inferring the proportion of 'scout' and 'recruit' dances on a hive's dance floor. After applying this methodology to waggle dance data from twenty hives, we show that social information is used less in environments where resources are sparse, potentially because colonies are required to send out more scouts to find food in these circumstances. Our methodology provides an innovative new tool to quantify social information use in undisturbed hives at a much larger scale than hitherto has been possible.

Keywords: Behavioural Ecology

Modelling bacteria-phage interaction with temperature-dependent lysogeny under global climate change

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^a – Presenting author

Phages are bacterial viruses, they are the most abundant biological entity on Earth, and they impact all aspects of bacterial evolution and dynamics. Recent empirical studies have revealed crucial facts regarding phage control of bacteria. However, some of those facts have not been properly addressed in mathematical models of bacteria-phage interaction. For example, this concerns the recently discovered condition-dependent lysogeny, where the type of infection cycle of phage (lytic or lysogenic) is determined by the environmental conditions such as the temperature or others. Constant fluctuation of temperature on different timescales (daily, monthly, or seasonally) results in a constant switch between lytic or lysogenic infection cycles making bacteria-phage interaction extremely complex. The ongoing global climate change would highly affect bacteria-phage interaction in the case the infection cycle is determined by the ambient temperature. Mathematical modelling is currently considered to be an efficient tool to address the complexity of bacteria-phage interaction with condition-dependent lysogeny under various scenarios of temperature variation. In this study, we model natural control of a highly pathogenic bacteria - *Burkholderia pseudomallei* - by its phage. *B. pseudomallei* causes the infectious disease called melioidosis, which is among the most fatal diseases in Southeast Asia and across the world. We use homogeneous (ODEs based) and spatially heterogeneous (reaction-diffusion PDEs) models to predict the eventual spread of zones of endemicity of the disease due to global climate change. We consider realistic model parameters taken from lab experiments and field observation, as well as current forecast on the temperature raise within next 20 years. To model the recent cases of melioidosis reported during recent years, we implement the historic time series of the temperature and the UV radiation. Our model predicts an overall increase in the pathogen load in Southeast Asia within next 20 years which can be explained by reduction of the control of bacteria by the phage caused by global climate change. The model also emphasises the role of enrichment of the environment and the extensive use of those agrochemicals that kill phages in success/failure of the natural control of *B. pseudomallei*.

Predicting bee activity levels and pollination services in Ireland under climate change with a mechanistic model of thermoregulation

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Ireland

^a – Presenting author

As providers of pollination services, bees are critical in ensuring ecosystem functioning and food security for the future. It is well known that weather affects bees' activity levels, causing concern that climate change will have a detrimental effect on already declining bee populations and the pollination services that they provide. Metabolic heat production allows bees to keep their thorax above the minimum temperature necessary for flight under most conditions. However, flight continues to produce large amounts of heat even as air temperature increases, and so bees have developed a variety of cooling mechanisms. We have developed an ordinary differential equation model for the thorax temperature of bumblebees and honeybees as a result of the heat flux caused by metabolic heat production, behavioural cooling mechanisms, solar radiation, thermal radiation, and convection. We use this model to predict bees' body temperatures, and therefore ability to fly, under a variety of weather conditions that correspond to current conditions and projected conditions 20-40 years into the future under varying climate change scenarios. We use these predictions to provide insights into the effects of climate change on bee activity and pollination services.

Keywords: Mechanistic Modelling

Biodiversity and Trade Data Reconciliation

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^a – Presenting author

Consumption and production of traded commodities can have a significant impact on local biodiversity in regions of production. Environmentally-extended trade models utilise reported trade data to understand trade networks, enable policy makers to inform their decisions, and address this impact. One issue that affects the outcome of such models is uncertainty within trade data; importers and exporters often report different volumes for a given trade flow, so quantities need to be selected which will represent the flows in the model. The easiest solution is to select the quantities from one set of trade data, but there are methods available for choosing these quantities based on multiple data sources, i.e. 'reconciling' the data. It is, however, unclear whether these methods are appropriate because they are often applied to large real-world datasets where the reasons for the data discrepancies are buried. Here we apply these methods to smaller synthetic datasets which simulate trade data discrepancies that arise from controlled causes. We are then able to evaluate the efficacy of existing reconciliation methods and posit a method for 'reconciling' a dataset, allowing the biodiversity impacts to be more accurately assessed.

Keywords: Biodiversity and trade networks

Stressor interactions at the community level: explaining qualitative mismatches between observations

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^a – Presenting author

Understanding the ecological impacts of global change forces us to consider the antagonistic and synergistic interactions between the multiple stressors that ecosystems may face. At the community level, such interactions are quantified based on the responses of various ecosystem-functioning or diversity metrics. Worryingly, in empirical data, we find that community metrics often observe opposite interactions between the same two stressors - sometimes even systematically. Here, we investigate this puzzling pattern via a series of geometrical abstractions. By representing stressors and their interactions as displacement vectors in community state-space, and community metrics as directions in this space, we show that the angle between two directions determines the probability, over random stressor combinations, that the metrics will observe opposite interactions. We find that diversity and functioning can easily be associated to opposing directions, which explains the systematic mismatches seen in empirical data. Our work offers a platform from which to study stressor interactions at the community-level, explaining why qualitative mismatches are to be expected, but also revealing what can be learned from those mismatches about underlying population-level processes.

Keywords: Community Ecology

Analytical approximation for invasion and endemic thresholds in spatially explicit individual-based models

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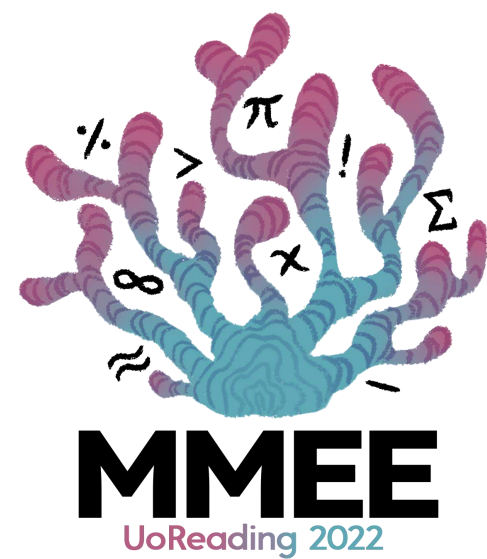
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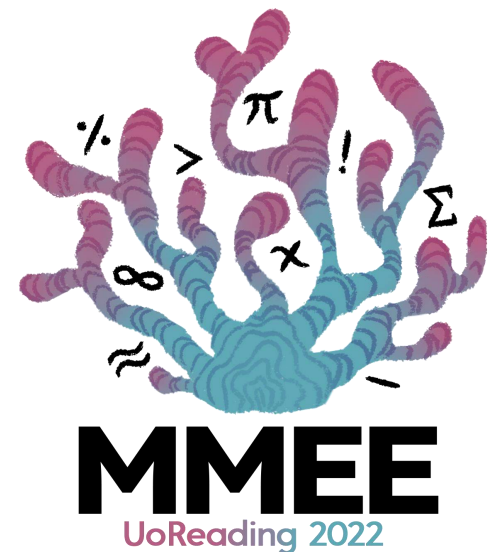
Within the recently introduced general mathematical framework for analysis of individual-based models we derived an analytical approximation to a general epidemiological, stochastic, spatially explicit SIR(S) model where the infection is dispersed within a given static host landscape according to a finite-ranged dispersal kernel. We derived an analytical expression for infection rate, and analytical conditions for a pathogen to invade a spatially explicit host population and to become endemic. The results provide general insights about: the likely impact of the host landscape on the size of an epidemic; the likely impact of optimal control strategies on invasion and persistence; a trade-off between the 'spatial' and 'non-spatial' control measures and a vaccination strategy; the optimal strategy to control invading and endemic diseases with minimal socio-economic cost across all possible parameter combinations. The modelling framework presented here can be applied to a wide class of individual-based models of diseases in populations of humans, animals and plants.

Keywords: Epidemiology, Spatial Ecology

Day 2



Mini-symposium 7 - Applications of Evolutionary Game Theory - Cancer treatment



Tumour containment for Norton-Simon models

Dr Yannick Viossat^{*a* 1}

a – Presenting author

Some clinical and pre-clinical data suggest that treating some tumors at a mild, patient-specific dose might delay resistance to treatment and increase survival time. A recent mathematical model with sensitive and resistant tumor cells identified conditions under which a treatment aiming at tumor containment rather than eradication is indeed optimal. One of the assumptions is however problematic, namely, that the growth-rate of sensitive cells is non-increasing in the size of the resistant population. This article shows how to dispense with this and other assumptions, to generalize results to Norton-Simon models and others. This is achieved by a novel mathematical analysis which compares across treatments the total tumor size as a function of the resistant population size.

Keywords: Population dynamics

Stochastic dynamics of evolutionary informed cancer therapies

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a – Presenting author

Intra-tumour genetic heterogeneity is a natural outcome of the cancer evolutionary process. It is a leading contributor to treatment resistance and disease progression. In the past decade, novel personalised therapy schedules have been developed that explicitly consider cancer as a speciation process to improve patient outcomes. These evolutionary informed therapies are based on mathematical models, and with only a few exceptions are described by a set of deterministic differential equations. However, these models must make assumptions on the population sizes of resistant clones at the time of diagnosis and ignore stochastic aspects of the dynamics. In my talk, I will introduce a stochastic branching process, including competition between cancer cells and mutation events. I will present the expected heterogeneity of resistant clones at the time of diagnosis and during treatment and discuss possible thresholds of stochastic extinction of resistant subpopulations with and without treatment.

Mutation accumulation waves in ecological models

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Mutation accumulation is a natural product of somatic evolution. The patterns of mutation frequency distributions are often used to estimate evolutionary parameters such as selection strength, which are otherwise hard to measure in vivo. Analytical solution of the mutation frequency distribution both in growing (cancer) and constant (healthy) populations are continuous with power-law shapes. Mutation frequencies exceeding the expected average are often considered a signal of positive selection. However, in single evolutionary trajectories, the mutation distribution is non-continuous and many especially high frequencies are entirely void of mutations. We explain this observation by introducing the concept of "mutation waves", where mutations jointly move towards high frequencies. We analyse the time these waves are present, the mean size of these waves as well as their distribution. Using the "mutation waves", we explain how this average behaviour of mutation frequency distribution emerges from an effectively bi-modal process in single evolutionary repeats. This indicates that a mutation frequency distribution exceeding the expected average by large margins in real sequencing data is not necessarily an aberration in need of an explanation, but instead can be a regular occurrence even in the absence of selection.

Keywords: Evolutionary models

Game theory to improve treatment of non-small cell lung cancer

Dr Monica Salvioli^{a1}

^a – Presenting author

We use a dataset of 590 Non-Small Cell Lung Patients treated with either chemotherapy or immunotherapy to determine whether a game-theoretic model can capture the tumor dynamics better than classical mathematical models of population growth (exponential, logistic, classic Bertalanffy, general Bertalanffy, Gompertz, general Gompertz). While the latter ones describe only the population growth and ignore the cancer evolutionary dynamics, our game-theoretic model encompasses both the ecological and the evolutionary dynamics, where the evolving trait is the therapy resistance. Our results show that the game-theoretic model provides a better fit than any of the non-evolutionary models and is able to provide predictions of tumor growth based on just a few initial measurements. Subsequently, we extend the model into a Stackelberg (leader-follower) evolutionary game, where the cancer cells, as followers, evolve resistance to therapy and the physician, as a rational leader, determines the optimal treatment following different pre-defined criteria, for example minimizing the final tumor burden. Our work shows how therapeutic protocols based on game-theoretic modeling have the potential to predict tumor growth better than other models and therefore improve the patient outcome.

Keywords: Evolutionary models

A game-theoretic approach to contain cancer

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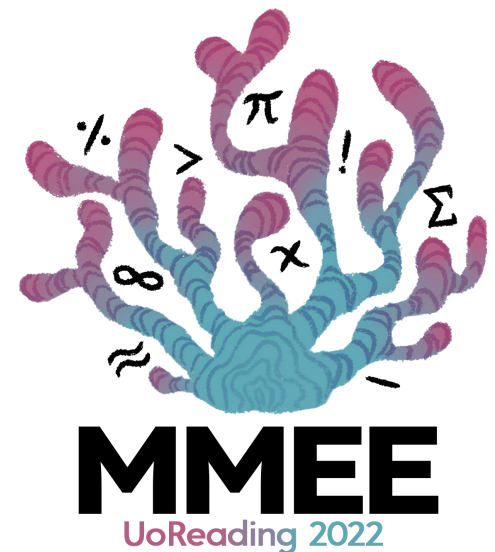
a – Presenting author

Cancer is a complex dynamic system. Several different approaches, including game theory, control theory, and machine learning, have been developed to model and understand cancer and design better treatments. Dynamic game-theoretic approach enables us to analyze complex eco-evolutionary dynamics of cancer and model dynamic interactions between a physician and cancer. Here we model cancer treatment as a Stackelberg evolutionary game between the physician and cancer cells. In this game, physician selects the treatment, including its dosing and timing, to maximize patient's quality of life. Cancer cells may respond to this treatment by evolving treatment-induced resistance. We consider a model which describes eco-evolutionary dynamics of two cancer cell types: a fully treatment-sensitive type and a type with evolving treatment-induced resistance. First, we will investigate stability of the equilibrium points via Lyapunov approach. Second, by defining an appropriate quality of life function, we will compare Nash and Stackelberg strategies with maximum tolerable dose that corresponds to the standard of care to show the effectiveness of the mentioned strategies. Since some parameters used in the dynamic models of cancer are varied by changing treatment or are estimated imprecisely in the model identification phase via real data, a sensitivity analysis is needed. We will perform this sensitivity analysis, using robust control techniques, to find upper bounds for the Euclidean norm of the mentioned uncertainties or errors in the parameters of the dynamical model of cancer. If the uncertainties and errors go beyond these upper bounds, the equilibrium points will enter a region which is dangerous for the patient. We define this region to be the area in which the number of cancer cells exceeds a predefined threshold. We will show how sensitive the treatment protocols are.

Keywords: Evolutionary models, Population Dynamics

Mini-symposium 8 - Vegetation modelling

- optimality approach optimality approach
(Carbon and Nitrogen Cycles)



Towards a resource economics paradigm for modelling carbon-nitrogen cycle interactions in terrestrial ecosystems

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^a – Presenting author

Nitrogen (N) limitation of plant growth and carbon (C) sequestration appears to be widespread in terrestrial ecosystems, yet a substantial global sink of photosynthesis-derived C has persisted in recent decades where CO₂ has continuously increased. This appears paradoxical in view of Liebig's conceptual model of the Law of the Minimum, which posits that plant growth is ultimately limited by the most limiting resource. It also poses a challenge for process-based Dynamic Vegetation Models (DVMs) that simulate a strong N limitation of the land C sink. The interpretation of phenomena observed in field studies and the formulation of DVMs commonly conceptualise N limitation as a mismatch between supply (from the soil) and demand (by the plant) of reactive N. However, C allocation is highly flexible and plants thereby control mechanisms by which a shortage of N supply may be relieved. Mechanisms include symbiotic N fixation, plant-soil interactions stimulating N availability to plants, and the aversion of N losses from the ecosystem through effective scavenging of available N. Here, we propose a resource economics paradigm to account for the energetic (C) cost of these adaptations and contend that eco-evolutionary optimality of plant functioning leads supply and demand to ultimately balance. A parsimonious model of optimal root and shoot allocation to balance C and N acquisition predicts that a leaf-level enhancement of photosynthesis under elevated CO₂ leads to a shift towards relatively more belowground C allocation. This shift may set in motion a cascade of feedbacks that ultimately accelerates the rate of N cycling, increases net primary productivity and reduces the openness of the N cycle, albeit at an increasing C cost of N acquisition. We investigate observations from CO₂ manipulation experiments to test the predicted shift towards relatively more belowground C allocation and the existence of a feedback cascade that counters progressive N limitation and tends to relieve N limitation at longer time scales. This provides key mechanistic insights to reveal whether tight N constraints on CO₂ fertilisation and the land C sink may be overestimated when flexible allocation and its effects on C-N cycling are ignored in models. We argue that process-based DVMs should be re-formulated to account for C-N tradeoffs and plant adjustments to balance N supply and demand.

Keywords: Optimality theory

Eco-evolutionary optimality-based modelling of leaf area index

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^a – Presenting author

Terrestrial vegetation helps to regulate atmospheric CO₂ through photosynthesis, and increasing photosynthesis is responsible for the current land carbon sink. The fate of this sink, however, remains highly uncertain under the combination of still-rising CO₂ and continued global warming. Assessing and mitigating potential risks of global environmental change requires the accurate characterization of vegetation biophysical and biochemical processes and responses to change in environmental drivers. The amount of leaf area, quantified by the leaf area index (LAI), is a key variable determining these processes. Despite many successes, global vegetation models are still subject to systematic failures and divergences between model projections, indicating a need to develop and test more reliable representations of vegetation-climate interactions. LAI in particular is not well simulated by current models. Here we apply eco-evolutionary optimality (EEO) principles to derive a parsimonious approach to the prediction of LAI by balancing net carbon gain and water loss. Plants allocate carbon to foliage in order to absorb light and acquire CO₂ by photosynthesis, while risking hydraulic failure and desiccation if transpiration is too high. We hypothesize that plants optimize the trade-off between these two processes, with LAI limited by the minimum of two values determined by the energy supply for photosynthesis and the water supply by precipitation, respectively. With simple equations, requiring far fewer parameters than typical complex models, we demonstrate a gridded simulated annual maximum LAI that is broadly consistent with a similar measure derived from remotely sensed observations. Further development of this model over different time scales, and its incorporation into vegetation models, would be beneficial to achieve better carbon cycle projections in a changing world.

Keywords: Climate change, Eco-evolutionary Optimality, Leaf Area Index, Optimality theory

Quantifying the coupled carbon and nitrogen metabolism of terrestrial ecosystems

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^a – Presenting author

The coupling between carbon (C) and nitrogen (N) cycling in terrestrial ecosystems is incompletely understood, yet critical to predicting land CO₂ uptake under climate change. Biomass production efficiency (BPE) and nitrogen use efficiency (NUE) relate ecosystem N uptake (N_{up}) to gross primary production (GPP). We used a global field-measurement dataset to derive empirical models for biomass production and allocation, tissue stoichiometry (C:N ratio) and N resorption efficiency as functions of climate, stand age and soil fertility. These were applied in a global framework to simulate C and N uptake. Modelled global GPP was 124 ± 42 PgC/yr, and N uptake 790 ± 220 TgN/yr. GPP accounted for 75% of variance in N uptake. The C and N cycles are partially decoupled, as shown by an inverse relationship between BPE and NUE: where soil fertility limits plant growth, assimilated C is used less efficiently (and N more efficiently) to produce biomass.

Keywords: Optimality theory

Modelling leaf responses to soil nitrogen variability: insights from model-data explorations using eco-evolutionary optimality theory

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^a – Presenting author

Experiments have shown that leaf traits, including those that are the basis of leaf economics, respond significantly to changes in soil nitrogen availability. However, there is a significant amount of variation in those responses, likely due to complex individual plant allocation decisions that vary over space and time. Eco-evolutionary optimality (EEO) theory provides a framework to better understand mechanisms underlying this variability. EEO theory revolves around the idea that natural selection will eliminate uncompetitive trait combinations in a given environment. Here, we present work using quantified theory that falls under the umbrella of EEO in concert with experimental nitrogen manipulation studies to better understand leaf-level responses to nitrogen availability. Data from a globally distributed nutrient addition experiment (Nutrient Network) indicated that leaf nitrogen responses to nitrogen addition were much better predicted by site climate than by nitrogen addition treatment. However, while a theoretical model based on site climate could predict some of the variation in leaf nitrogen, significant additional information was provided by soil nitrogen availability and through estimates of changes in aboveground biomass. This suggests that whole-plant allocation responses to nitrogen availability are important for predicting leaf-level responses. Using photosynthetic data at targeted experiments, we found that leaf photosynthesis is not impacted by nitrogen availability, both in closed canopy forests and in open canopy greenhouse experiments. However, there was a stimulation of leaf nitrogen, providing evidence for allocation to non-photosynthetic leaf processes, which cannot be currently quantified by EEO theory. All together, these findings suggest that soil nitrogen availability is a small, but significant driver of leaf traits and that further EEO theory development on non-photosynthetic nitrogen allocation is needed to understand these responses.

Keywords: Optimality theory

Environmental controls of leaf carbon and nitrogen stoichiometry

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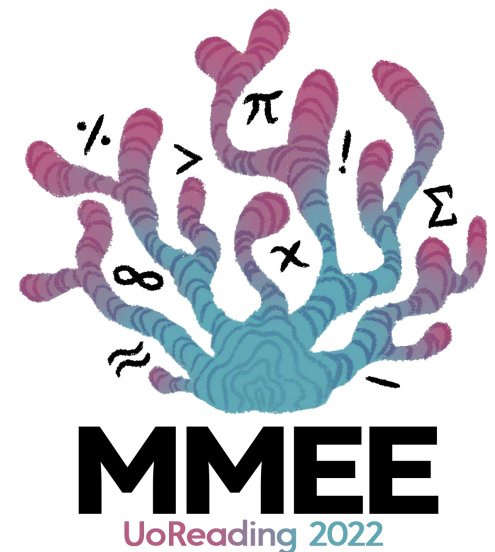
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a – Presenting author

Leaf stoichiometric traits are central to terrestrial ecosystem function and biogeochemical cycling, yet there is no broadly accepted theory to explain their variation along environmental gradients. We used the China Plant Trait Database version 2 to examine the climatic and taxonomic controls of leaf carbon (C) and nitrogen (N) contents per unit mass (C_{mass}, N_{mass}) along climatic gradients using mixed-effects models, with evergreen and deciduous taxa treated separately. Temperature and moisture optima and tolerances of major woody genera were characterized. An eco-evolutionary optimality model was proposed to predict N_{mass} independently, for comparison. Climate explained 4–12% of leaf stoichiometric trait variation among species but up to 40% among communities, indicating the key role of species replacement in mediating the community-level response. Deciduous species separated primarily along the moisture gradient, evergreen species along the temperature gradient. C_{mass} increased with irradiance, but decreased with moisture and temperature. N_{mass} declined with all three variables. C:N ratio variations were dominated by N_{mass}. The coefficient relating N_{mass} to its predictor – the ratio of maximum carboxylation capacity at 25 °C, V_{cmax25} to leaf mass per area, M_a – increased with leaf area index. The optimality model captured 68% and 53% of variations in V_{cmax25} and M_a respectively, 30% of variation in N_{mass} when leaf area index effect was included. Across-community stoichiometric trait variations along climate gradients are achieved by species replacement. Variations in leaf C:N ratio are mainly determined by N rather than C. Optimality-based modelling shows useful predictive ability for community-mean N_{mass}. This finding should help to improve the representation of C:N stoichiometry in land-surface models.

Keywords: Optimality theory

Mini-symposium 9 - Mathematical Models of Reproductive Dormancy



The effects of dormancy in population genetics and population dynamics

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^a – Presenting author

Throughout the tree of life, populations have evolved the capacity to contend with suboptimal conditions by engaging in dormancy, whereby individuals enter a reversible state of vanishing metabolic activity. The resulting "seed banks" serve as long-lived reservoirs of genetic and phenotypic diversity. Of particular relevance is the case of microbial dormancy, which has a fundamental impact on the evolutionary, ecological and also pathogenic character of microbial communities.

However, despite its ubiquity in nature, dormancy is a rather new subject for stochastic individual based modeling and interacting particle systems. Here, it leads to novel effects, in particular based on the introduction of memory, resilience and diversity into the underlying systems. The resulting probabilistic structures are surprisingly rich, already when considering simple 'toy models', and lead to new universal scaling limits.

In this talk, after providing some background on dormancy, I will present and discuss recent models for dormancy and seed banks in population genetics (including several coalescent structures) and population dynamics. Along the line, I will sketch areas for future mathematical and interdisciplinary research.

A new plant metapopulation model with recurrent extinction events and a seed bank component

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² CMAP, Ecole Polytechnique, France

^a – Presenting author

The k-parent Wright-Fisher metapopulation model with a seed bank component is a model for plant metapopulations living in a fragmented environment in which local extinction events are frequent. Examples of such environments are agroecosystems or urban tree bases. This model is an intermediate between population dynamics models with a seed bank component, based on the classical Wright-Fisher model, and Stochastic Patch Occupancy Models (SPOMs) used in metapopulation ecology. Its main feature is the use of "ghost" individuals, which can reproduce but with a very strong selective disadvantage against "real" individuals, to artificially ensure a constant population size and make it possible to reconstruct genealogies. Letting reproduction, dormancy and extinction events happen on the same timescale, I show the existence of an extinction threshold above which persistence of the subpopulation of "real" individuals is not possible, and investigate how the seed bank characteristics affect this extinction threshold. This result has implications for plant dynamics in highly fragmented and disturbed environments. I also show the convergence of the model to a SPOM under an appropriate scaling, bridging the gap between individual-based models and occupancy models.

Keywords: Population dynamics

Inference of dormancy traits evolution from whole genome sequence data

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of population genetics

^a – Presenting author

Dormancy is observed in many species across the tree of life. To understand why dormancy is frequently observed, much theoretical work has been done suggesting that specific biotic or abiotic stress may lead to the evolution of dormancy as a bet-hedging strategy. However, precise measure of dormancy can be difficult to obtain as experimental design can be hard to set up, too costly or too slow (e.g. several years). In addition to this, experiments can only inform us on the current dormancy rate and not on its evolution through time. To solve those issues, we build a statistical tool (teSMC) making use of full genome sequence data, mutation and recombination rate to estimate the variation of dormancy of a population through time. We demonstrate the accuracy of our approach on simulated data and apply our method on wild tomato data, unveiling its evolutionary history of dormancy.

Keywords: Ancestral Recombination Graph, Kingman coalescent, Population Genetics

Dormancy with heavy tail

Dr Dario Spano^{a 1}

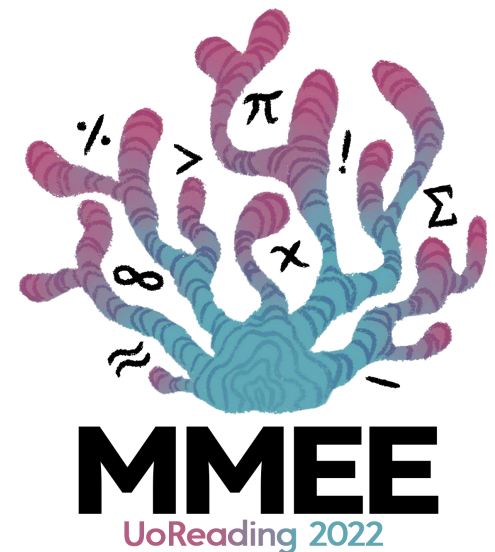
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The most studied population genetic models of dormancy describe populations with spontaneous switch-on/switch-off from active to dormant state and feature exponentially distributed return times to an active state. Very little is known about models where the seedbank effect is heavy-tailed. It is conceivable that heavy-tailed dormancy could describe populations where inactive reservoirs are arranged in complex structures (e.g. marine biofilms). To capture such complexity, we will illustrate various possible extensions of the seedbank model yielding a more extensive description of the phenomena of persistence and latency, encompassing regions of gradually decreasing metabolic activity rather than binary on-off switching pattern of dormancy, and heavy-tailed return times to full activity. We will also discuss their statistical tractability.

Keywords: Population dynamics

General Session 5 – Evolutionary Models I



Social Distancing as a Social Dilemma Game

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Since the outbreak of the global COVID-19 pandemic, social distancing has been known to everyone and recommended almost everywhere every day. Social distancing has been and will be one of the most effective measures and sometimes, the only available one for fighting epidemics and saving lives. However, it has not been so clear how social distancing should be practiced or managed, especially when it comes to regulating everyone's otherwise normal social activities. The debate on how to implement social distancing often leads to a heated political argument, while research on the subject is lacking. In this talk, I will discuss a theoretical framework for the understanding of the scientific nature of social distancing by considering social distancing as a social dilemma game played by every individual against his/her population. From this perspective, every individual needs to make decision on how to engage in social distancing, or risk being trapped into a dilemma either exposing to deadly diseases or getting no access to necessary social activities. As the players of the game, the individual's decisions depend on the population's actions and vice versa, and an optimal strategy can be found when the game reaches an equilibrium. I will show how an optimal strategy can be determined for a population with either closely related or completely separated social activities and with either single or multiple social groups, and how the collective behaviors of social distancing can be simulated by following every individual's actions as the distancing game progresses. The simulation results for populations of varying sizes and complexities will be presented, which not only justify the choices of the strategies based on the game theoretic analysis, but also demonstrate the convergence of the individual actions to an optimal distancing strategy in silico and possibly in natura as well, if every individual makes rational distancing decisions.

First passage time analysis of spatial mutation patterns reveals sub-clonal evolutionary dynamics in colorectal cancer

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The signature of early cancer dynamics on the spatial arrangement of tumour cells is poorly understood, and yet could encode information about how sub-clones grew within the expanding tumour. Novel methods of quantifying spatial tumour data at the cellular scale are required to link evolutionary dynamics to the resulting spatial architecture of the tumour. Here, we propose a framework using first passage times of random walks to quantify the complex spatial patterns of tumour cell population mixing. First, using a simple model of cell mixing we demonstrate how first passage time statistics can distinguish between different pattern structures. We then apply our method to simulated patterns of mutated and non-mutated tumour cell population mixing, generated using an agent-based model of expanding tumours, to explore how first passage times reflect mutant cell replicative advantage, time of emergence and strength of cell pushing. Finally, we analyse experimentally measured human colorectal cancer, and estimate parameters of early sub-clonal dynamics using our spatial computational model. We uncover a wide range of sub-clonal dynamics, with mutant cell division rates varying between 1 and 4 times the rate of non-mutated cells across our sample set. Some mutated sub-clones emerged after as few as 100 non-mutant cell divisions, and others only after 50,000 divisions. The majority were consistent with boundary driven growth or short-range cell pushing. By analysing multiple sub-sampled regions in a small number of samples, we explore how the distribution of inferred dynamics could inform about the initial mutational event. Our results demonstrate the efficacy of first passage time analysis as a new methodology in spatial analysis of solid tumour tissue, and suggest that patterns of sub-clonal mixing can provide insights into early cancer dynamics.

Selection gradient on life history traits in host-associating microbes

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Microbial communities extend the host functional repertoire, thus making the host and its associated microbes a functional unit. We are only beginning to decipher how host and microbe fitnesses are intertwined: while it is now clear that the microbiota has a vast potential to affect the host physiology, less focus has been put to the microbial perspective, i.e. to understand what benefit or cost can microbes retrieve from their interaction with their host. In contrast to the common hypotheses of strong and continued coevolution proposed to explain the emergence of such elaborate symbioses, we focus here on the steps that can lead a microbial population to transition from a free-living life-style to an association with a host. In particular, we aim at understanding what selection pressures apply to microbes following a biphasic life cycle, in which they can regularly transit in and outside a host. We study three simple models of such biphasic life cycles. In the first model, we study a homogeneous microbial population transiting between a host and its environment and perform a sensitivity analysis to show the existence of two different regimes: one where the effect of migration from the environment to the host dominates, and a second where the within-host replication rate matters most. The second model is an SI-inspired compartmental model, which accounts for the habitats' dynamics. We show that microbial propagation across habitats depends on the product of the transmissibilities, which we propose as a new holistic measure of microbial fitness - bearing similitudes with the R_0 of epidemiology. In the third model, we combine microbial population and habitats dynamics and derive predictions that are consistent with experimental observations of an increased ability to form biofilms in bacteria evolved in biphasic conditions with *C. elegans*.

Modelling the impact of epithelial structure and dynamics on the evolution of cooperation

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Cooperation is usually considered a social phenomenon, but it also occurs on the cellular level. For example, there are several mutations associated with malignancy that rely on the production of diffusible growth factors, and thus confer a shared fitness benefit. It is well-established within evolutionary graph theory that the success of cooperation depends on the structure and update dynamics of the host population. However, tissue dynamics are not easily represented by fixed graph models. We use the Voronoi tessellation model to consider the invasion of cooperative mutants in epithelial cells. This approach allows us significant freedom compared to evolutionary graph theory models, to consider how realistic population structure and tissue update dynamics affect the success of cooperation in a homeostatic epithelium.

A mathematical framework for evo-devo dynamics

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Natural selection acts on phenotypes constructed over development, which raises the question of how development affects evolution. Classic evolutionary theory indicates that development affects evolution by modulating the genetic covariation upon which selection acts, thus affecting genetic constraints. However, whether genetic constraints are relative, thus diverting adaptation from the direction of steepest fitness ascent, or absolute, thus blocking adaptation in certain directions, remains uncertain. This limits understanding of long-term evolution of developmentally constructed phenotypes. Here we formulate a general tractable mathematical framework that integrates age progression, explicit development (i.e., the construction of the phenotype across life subject to developmental constraints), and evolutionary dynamics, thus describing the evolutionary developmental (evo-devo) dynamics. The framework recovers evolutionary dynamic equations in gradient form and describes the evolution of genetic covariation from the evolution of gene expression, phenotype, environment, and mutational covariation. This shows that genetic and phenotypic evolution must be followed simultaneously to yield a well-defined description of long-term phenotypic evolution in gradient form, such that evolution described as the climbing of a fitness landscape occurs in geno-phenotype space. Genetic constraints in geno-phenotype space are necessarily absolute because the degrees of freedom of genetic covariation are necessarily limited by genetic space. Thus, the long-term evolutionary dynamics of developed phenotypes is strongly non-standard: in particular, developmental constraints determine the admissible evolutionary path and evolutionary outcomes do not generally occur at fitness landscape peaks in geno-phenotype space, but at peaks in the admissible evolutionary path where "total genetic selection" vanishes if exogenous plastic response vanishes and mutational variation exists in all directions of gene-expression space. Our framework provides an alternative method to dynamic optimization (i.e., dynamic programming or optimal control) to identify evolutionary outcomes in models with developmentally dynamic traits. These results show that development has major evolutionary effects.

Beyond Fitness Decoupling: Tradeoff-breaking during Evolutionary Transitions in Individuality

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Evolutionary transitions in individuality (ETIs) involve the formation of Darwinian collectives from Darwinian particles. The transition from cells to multicellular life is a prime example. During an ETI, collectives become units of selection in their own right. However, the underlying processes are poorly understood. One observation used to identify the completion of an ETI is an increase in collective-level performance accompanied by a decrease in particle-level performance, for example, measured by growth rate. This seemingly counterintuitive dynamic has been referred to as “fitness decoupling” and has been used to interpret both models and experimental data. Using a mathematical approach we show this concept to be problematic in that the fitness of particles and collectives can never decouple: calculations of particle and collective fitness performed over appropriate and equivalent time intervals are necessarily the same. By way of solution, we draw attention to the value of mechanistic approaches that emphasise traits as opposed to fitness and tradeoffs among traits. This trait-based approach is sufficient to capture dynamics that underpin evolutionary transitions. In addition, drawing upon both experimental and theoretical studies, we show that while early stages of transitions might often involve tradeoffs among particle traits, later—and critical—stages are likely to involve rupture of such tradeoffs. Tradeoff-breaking thus stands as a useful marker for ETIs.

Trajectories of adaptation and how to exploit them

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Populations of microbial pathogens or cancer cells possess enormous adaptive potential. Such adaptations regularly lead to the failure of treatment, with drastic consequences for individual and public health. From a reductionistic viewpoint, the fundamental processes in such microbial populations are replication, mutation and death. Characterizing these processes by traits allows us to understand adaptation as an uphill walk on a fitness landscape spanned by replication rate and death rate, with mutation rate dictating the walking speed in this picture. Different treatment types exist to tamper with any of these fundamental processes. How such treatment types affect the trajectory of adaptation in trait space is not clear. In this contribution, I will tackle this question and present i) which exact trajectory a population takes in a trait space spanned by replication rate and death rate, ii) how this trajectory is affected by treatment, and iii) how treatments that target either the population size via bottlenecking or the traits via static and toxic drugs differ. Further, I will discuss the fitness gradient(s) that prescribe the adaptation and show that the information on such fitness gradients can guide effective treatment strategies.

A theory of multi-site evolutionary rescue/resistance applied to gene drive suppression systems

Bhavin Khatri ^{a 1,2} and Prof Austin Barn¹

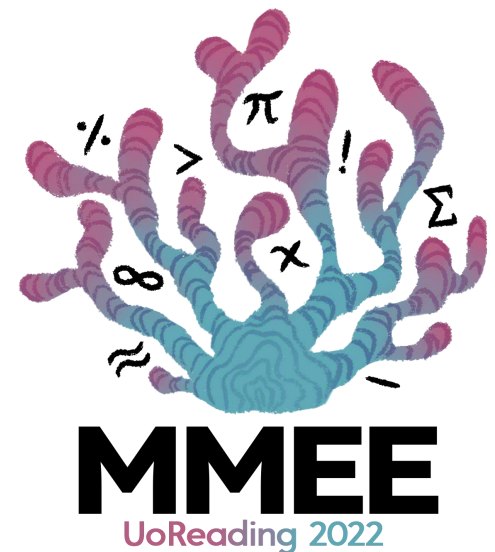
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Evolution of resistance is a major barrier to successful deployment of gene drive systems to suppress natural populations, which could greatly reduce the burden of many vector borne diseases. Multiplexed guide RNAs that require resistance mutations in all target cut sites is a promising anti-resistance strategy, since in principle resistance would only arise in unrealistically large populations. Using novel stochastic simulations that accurately model evolution at very large population sizes, we explore the probability of resistance. Our results highlight the importance of natural genetic standing variation and the complexity of the mutation-selection-drift balance between haplotypes with complete resistance and those with an incomplete number of resistant alleles, which is not tractable in the multi-allelic diffusion approximation with uni-directional mutation. Using heuristic analysis, we find this leads to a qualitatively new phenomenon where weakly deleterious naturally occurring variants greatly amplify the probability of multi-site resistance compared to de novo mutation. This challenges the intuition that many target sites would guarantee prevention of resistance, where in the face of standing genetic variation, it can be probable even in not very large populations. This result has broad application to resistance arising in many multi-site evolutionary scenarios including multi-drug resistance to antibiotics, antivirals and cancer treatments, as well as the evolution of vaccine escape mutations in large populations.

General Session 6 – Population Dynamics I



Role of a seed bank for dynamics and control of *Sorghum halepense*

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Perennial weed species like *Sorghum halepense* are a bane on agricultural produce and lead to significant economic losses. Such weeds can spread quickly and are particularly hard to control due to their ability to reproduce sexually via seeds as well as asexually through rhizomes. Control strategies are frequently investigated through field experiments in the short run. However, mathematical modelling has proved to be a valuable approach to studying the long-term population dynamics of weeds. Still, only a few models have dealt with perennial weed species because of their complex life cycle. In this talk, I will present a population-based model of seed and rhizome propagated perennial weeds. The model focuses on *Sorghum halepense* as an example. Herbicide application and tillage, commonly used to control *Sorghum halepense*, are integrated into the model to evaluate the extent of control they provide and the evolution of resistance against the herbicide. Herbicide resistance is modelled as target-site resistance based on a single resistance allele. I will emphasise the pivotal role of a seed bank for the persistence and rapid adaptation of *Sorghum halepense*. In particular, I will illustrate how a seed bank helps to preserve genetic diversity under recurrent selective pressure imposed by herbicides. Moreover, I will highlight the potential of a seed bank to ensure population survival under control by delaying extinction and increasing the probability that resistant mutants establish.

Keywords: Ecosystem Dynamics, Evolution of Herbicide Resistance, Population Dynamics, Seed Bank

Revealing long-transients in simple discrete models of population dynamics

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Traditionally, mathematical modelling of population dynamics has been focused on long-term, asymptotic behaviour (systems attractors), whereas the effects of transient regimes has been largely disregarded. However, currently there is a growing appreciation of the role of transients both in empirical ecology and mathematical modelling of population dynamics. Among important challenges are identification of mechanisms of transients in various dynamical systems and derivation of the corresponding scaling law of the transient's lifetime. Prediction of the lifetime of ecological transients is of a vital practical importance for long-term ecological forecasting and regime shifts anticipation. In this study, we reveal various patterns of transients occurring in few simple discrete population models which are mathematically described by discontinuous maps. We start with a single population model with a logistic (or Ricker function) local growth and a density-dependent dispersal. In this model, we demonstrate the possibility of various types of transient dynamics within a wide range of system parameters. This includes crawl-by dynamics, chaotic saddles, ghost attractors, and various intermittency regimes. For each type of transient, we have investigated the corresponding scaling law of the transient's lifetime. Then we considered a discrete predator-prey model with a discontinuous dispersal of both populations. In this system, we show the possibility of complex patterns occurring as a cascade of transients of different types. We show that the final attractor of the system becomes highly unpredictable from the time series, which is of great importance for ecosystem management. In the space of the key model parameters, we show where particular types of long transients can be expected. Finally, we show the possibility of complex long transients in discrete food web models with higher dimensionality (3-D models).

Bayesian inference frameworks to infer selection strength of extra-chromosomal DNAs

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Cancer is a complex (epi)genetic disease characterized by variation, selection and adaptation. Several recent studies have highlighted the importance of extra-chromosomal DNA (ecDNA) in fostering tumour progression. As opposed to chromosomal DNA, ecDNA copies are thought to be randomly segregated between daughter cells during cell division, causing extremely high cell to cell copy number heterogeneity. In turn, selection can act on this heterogeneity, e.g. by regulating oncogenic expressions in the absence or presence of treatment, thereby changing the cancerous cell's phenotype. The heterogeneity of the ecDNA copy number poses a great challenge to current cancer therapies, and a better theoretical characterisation of this process is needed. The goal of the project is to understand the evolutionary dynamics of ecDNA driving tumour evolution using mathematical and computational modeling. We study the stochastic dynamics of ecDNA in an exponential growing tumour population. By implementing approximate Bayesian computation approaches, we infer the strength of selection based on the ecDNA copy number distribution. This framework builds on the evolutionary dynamics of ecDNA with the hope to detect predictors of poor prognosis.

Keywords: Evolutionary models, Phylogenies and evolutionary genetics, Population dynamics

Quasi-stationary behavior of the Crump-Young model of chemostat

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The Crump-Young model consists of two fully coupled stochastic processes modeling the substrate and micro-organisms dynamics in a chemostat. Substrate evolves following an ordinary differential equation whose coefficients depend of micro-organisms number. Micro-organisms are modeled though a pure jump process whose the jump rates depend on the substrate concentration. It is known that this model extincts almost-surely in the sense that micro-organism population vanishes. However, despite its simplicity, the long-time behavior of this process is not well understood. The existence (but not the uniqueness) of quasi-stationary distribution (QSD) as well as some regularity properties of these QSD were proved in the literature. Nevertheless, the long-time behavior of the process before extinction was, until now, unknown. In this work, we prove that there exist a unique QSD and that, conditionally on the non-extinction, the Crump-Young model converges exponentially fast to this QSD. Convergence to quasi-stationary distribution is usually proved though Hilbert techniques. However, our process is not reversible making these techniques difficult to deal with. To overcome this problem, we use recent results [Champagnat-Villemonais 17 & 20, Bansaye-Cloez-Gabriel-Marguet 19] which are a generalization of usual techniques to prove convergence to stationary distribution. The proof is mainly based on hitting time estimates and Lyapunov functions bounds. Due to the deterministic part, the dynamics of the Crump-Young model is highly degenerated. The proof then consists of technical sharp estimates.

Individual based models in adaptive dynamics: the case of small and frequent mutations

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Adaptative dynamics theory is based on biological assumptions which are assumptions of rare and small mutations and of large population leading to the mathematical justification of an ODE approximating the population evolution dynamics : the Canonical Equation of Adaptive Dynamics (CEAD). Despite its success, the proposed approaches are criticized by biologists since they are based on a non-realistic assumption of rare mutations. The goal is to correct this biological controversy by proposing more realistic probabilistic models and mathematical approaches. We will focus mathematically, under a simultaneous double asymptotic of large population and small mutations, on the consequences of a new biological assumption of frequent mutations on the canonical equation. The aim is to determine, from a stochastic individual-centered model, the long time behavior of the average phenotypic trait of the population. The question we ask is reformulated into a slow-fast asymptotic analysis acting on three eco-evolutionary time scales where we identify the fast component as measure-valued diffusion which is interpreted as a centered Fleming-Viot process.

The multi-type bisexual Galton-Watson process with superadditive mating

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The bisexual Galton-Watson process [Daley, '68] is an extension of the classical Galton-Watson process, but taking into account the mating of females and males, which form couples that can accomplish reproduction. Properties such as extinction conditions and asymptotic behavior have been studied in the past years, but multi-type versions have only been treated in some particular cases. In this work we deal with a general multi-dimensional version of Daley's model, where we consider different types of females and males, which mate according to a 'mating function'. We consider that this function is superadditive, which in simple words implies that two groups of females and males will form a larger number of couples together rather than separate. One of the main difficulties in the study of this process is the absence of a linear operator that is the key to understand its behavior in the asexual case, but in our case it turns out to be only concave. To overcome this issue, we use a concave Perron-Frobenius theory [Krause '94] which ensures the existence of eigen-elements for some concave operators. Using this tool, we find a necessary and sufficient condition for almost sure extinction as well as a law of large numbers. Finally, we study the convergence of the process in the long-time through the identification of a supermartingale.

A coarse-graining model for the evolution of cooperation and the impact of environment

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Cooperative breeding occurs when an individual helps to raise the offspring of others. It is typically considered to be costly for helpers who lose or postpone the opportunity for personal fitness gains. This behaviour is widespread, occurring in both benign and harsh environments. Moreover, phylogenetic data suggests that environmental conditions play a role in promoting and hindering cooperative breeding. Several theoretical studies have tried to capture the role of environment in the development of helping. However these studies model cost of helping in ways that limit the impact of environmental conditions. To better understand the influence of environment, we built a kin selection model where individuals choosing to help their parents pay an opportunity cost by having different abilities for an extended period of their life history. Thanks to the persistent nature of the cost, we uncover new environmental impacts on the evolution of cooperative breeding. Specifically, by computing the inclusive fitness of this kin selection model, we were able to show that the environment, described by the opportunity cost of helping, has an influence over the emergence and development of altruistic behaviour in the population.

Keywords: Evolutionary Models

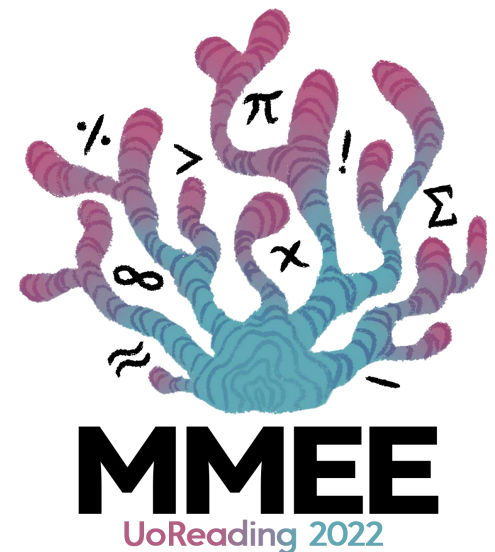
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The design of mechanisms that encourage pro-social behaviour in populations of self-regarding individuals is recognised as a major theoretical challenge within several areas of social, life and engineering sciences. In this context, cooperation is typically assumed to emerge from the combined actions of individuals within these systems. However, in many scenarios, such actions are advocated and promoted by an external party, which does not participate in these interactions, calling for a new set of heuristics capable of engineering emergent behaviour in self-organised complex systems. Several heuristics have been found to be efficient at promoting pro-sociality at minimal costs, but these studies neglect underlying complex network structures which often define real-world populations. In the case of such socially diverse populations, previous findings have shown that investment is non-trivial, and that recklessly rewarding cooperators can sometimes lead to a decrease in cooperation. Here, we have extended these models and tested the robustness of their findings to stochastic social learning paradigms. Akin to real-world decisions on how to distribute endowments, we study several incentive schemes, considering information about the overall population, local neighbourhoods, or the level of influence that a cooperative node has in the network, selectively rewarding cooperative behaviour according to these metrics. Following a transition towards a more realistic, stochastic update rule, we found that carelessly promoting cooperators can often lead to their downfall in socially diverse settings. Previously, these findings were restricted to very particular combinations of parameters, but stochastic dynamics highlight the pitfalls of inconsiderate incentives in a variety of settings. As result, defector communities grow before eventually collapsing due to their inability to reciprocate. These emergent cyclic patterns not only damage cooperation, but also decimate the budgets of external investors. Our findings highlight the complexity of designing effective and cogent investment policies in socially diverse populations.

Mini-symposium 10 - Applications of Evolutionary Game Theory - Structured populations



Models and measures of animal aggregation and dispersal

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The dispersal of individuals within an animal population will depend upon local properties intrinsic to the environment that differentiate superior from inferior regions as well as properties of the population. Competing concerns can either draw conspecifics together in aggregation, such as collective defence against predators, or promote dispersal that minimizes local densities, for instance to reduce competition for food. In this talk we consider a range of models of non-independent movement. These include established models, such as the ideal free distribution, but also novel models which we introduce, such as the wheel. We will also discuss several ways to combine different models to create a flexible model to address a variety of dispersal mechanisms. We further discuss novel measures of movement coordination and show how to generate a population movement that achieves appropriate values of the measure specified. The movement framework that we have developed is both of interest as a stand-alone process to explore movement, but also able to generate a variety of movement patterns that can be embedded into wider evolutionary models where movement is not the only consideration.

Keywords: Evolutionary models

Modeling aggression in realistic populations: The multiplayer Hawk–Dove game on evolving networks

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We model a mobile population of Hawks and Doves interacting over a network. Individuals choose strategically to either stay at the current location or move to a neighboring location depending on their inherent staying propensity trait and the composition of the group at the current location. The Hawk–Dove game interactions involve all individuals at the same location and may feature groups of arbitrary size. We investigate the effects of network topology, movement cost, population size, and reward-to-cost ratio on the evolution of the population. We find that unlike in the public goods game, stability is rare, and Doves tend to do better than Hawks for low movement costs on complete and circle graphs but for high movement costs on the star graph. The threshold of the reward-to-cost ratio after which Hawks dominate Doves is lowest for the star graph and highest for the circle graph. This is a continuation of our ongoing investigation of multiplayer interactions on evolving networks, which features a novel model of the multiplayer Hawk–Dove game in a mobile structured population.

Keywords: Evolutionary Models

More can be Better: An analysis of single mutant fixation probability functions under 2x2 games

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The self-organization of collective behaviour is a topic of interest in numerous research fields, and in its context, evolutionary game theory has proved to be a powerful probing tool. Even though initial evolutionary models with frequency-dependent fitness assumed infinite populations, it has been shown that the stability of a strategy may depend not only on the game's payoff matrix but on the size of the finite population. To perform a systematic analysis of 2x2 games in well-mixed finite populations, we start by proving that 9 of the 24 possible payoff orderings always lead to single mutant fixation probability functions decreasing monotonically with population size as they trivially do under fixed fitness scenarios. However, we observe a diversity of fixation functions with increasing regions under 12 other orderings, which included anti-coordination games (e.g. Hawk-Dove/Snowdrift game), the fixation of unbeatable strategies (e.g. Defectors in the Prisoner's Dilemma), and the fixation of Stag Hunters under that game (the only exception in coordination games). Fixation functions that increase from a global minimum up to a finite asymptotic value are pervasive, and we suggest that these have been easily concealed by the weak selection limit. We prove under which payoff matrices it is possible to have fixation increasing for the smallest populations and find three different ways this can happen. Finally, we describe two distinct fixation functions having two local extremes and associate them with transitions from ones with one global minimum.

Keywords: Evolutionary models

Evolutionary graph theory derived from eco-evolutionary dynamics

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A biologically motivated individual-based framework for evolution in network-structured populations is developed that can accommodate eco-evolutionary dynamics. This framework is used to construct a network birth and death model. The evolutionary graph theory model, which considers evolutionary dynamics only, is derived as a special case, highlighting additional assumptions that diverge from real biological processes. This is achieved by introducing a negative ecological feedback loop that suppresses ecological dynamics by forcing births and deaths to be coupled. We also investigate how fitness, a measure of reproductive success used in evolutionary graph theory, is related to the life-history of individuals in terms of their birth and death rates. In simple networks, these ecologically motivated dynamics are used to provide new insight into the spread of adaptive mutations, both with and without clonal interference. For example, the star network, which is known to be an amplifier of selection in evolutionary.

Keywords: Evolutionary Models

Collective beliefs and trust in structured populations

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Collective beliefs can catalyse cooperation in a population of selfish individuals. This effect is present even when the stories that constitute the belief lack any moralising aspect. The sole fact of altering one's perception of reality can provoke the development of cooperative behaviour. Introducing an arbitrary mythology system in a finite, well-mixed population can transform a collection of egoists into a trusting cooperative. However, human populations are not always well mixed. Social and cultural identities often bias the network of interactions. Random networks are typical caricatures of human societies. Hence, we further develop this model by applying the setup assuming a structured population. The person perpetuating a belief might have different degrees of connectedness. We aim to understand the speed at which trust builds in a network when the myth originator has low or high connectedness. A belief frequently involves a complex system of stories. It is unlikely to appear in society spontaneously in the same way as actions can change within a generation. Consequently, we assume that actions and myths spread at different rates. Lastly, we plan to study the spread of trust when the myths explicitly condone specific actions. The project will explore different network structures, and this ongoing work will be presented.

Keywords: Population dynamics

Ultimatum game in adaptive networks with asymmetric relations

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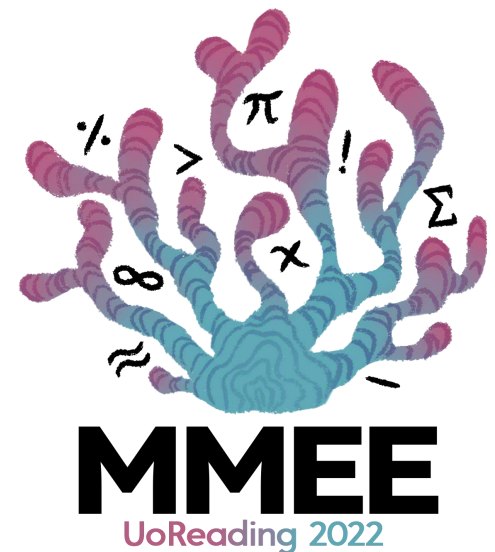
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The ultimatum game is a commonly used paradigm for studying the emergence of fairness in the population. In the game, the "proposer" splits a given reward, and the "responder" can either accept or reject it. If the responder rejects, neither player receives anything. Experimental evidence reveals behaviour inconsistent with the conventional assumptions of rational, self-interested, and utility-maximising players, as people commonly refuse low non-zero offers. There is ongoing research on the influence of cultural, emotional, and other contextual aspects on the offer and rejection thresholds. In this work, we study the evolution of populations of players and their interaction networks. The networks can have complex topology and are adaptive. The players alter their links according to the behavior of their neighbours in the game. Additionally, each player is assigned a dynamic variable called "status" that influences how likely a player is to take the role of proposer or responder. We consider a functional relation between income and status and investigate how interaction networks of asymmetric relations and strategies co-evolve. We report on the effect of different network topologies, evolutionary update rules, income-status feedback, and initial strategy distributions in player populations. In particular, we compare hubs and low-degree nodes in the networks in terms of their offer and rejection thresholds, as well as their value of status.

Keywords: Evolutionary models, Population dynamics

Mini-symposium 11 - Vegetation modelling - optimality approach (Hydraulics & Plant Water Regulations)



Towards a unified theory of plant photosynthesis and hydraulics

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^a – Presenting author

We present P-hydro, a trait-based theory unifying plant photosynthesis and hydraulics, based on optimality principles, to simultaneously predict the stomatal and biochemical responses of plants to developing water stress. Our theory is comprehensively tested against published data from drought experiments on 18 species. With just two latent parameters, it successfully predicts stomatal conductance, assimilation rates, leaf internal CO₂ concentrations, carboxylation and electron-transport capacities, and leaf water potentials in response to soil moisture, temperature, light intensity, CO₂ concentration, and vapour pressure deficit (VPD). Signalling an advance over most previous models, predictions of our theory related to plant hydraulic strategies (particularly, the predicted responses to VPD) are consistent with the latest empirical findings. The theory can be readily plugged into vegetation models, and thus has the potential to significantly enhance our ability to predict vegetation responses to changing climates, especially for unprecedented, out-of-sample environmental conditions.

Keywords: Optimality theory

Regulation of plant water status. The complementary problem

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^a – Presenting author

Being rooted in a soil medium while having their aerial organs exposed to the atmosphere above the soil, most terrestrial plants live in a hydraulic continuum whose water potentials range from those of soil liquid water to the often highly negative values of water vapour in the atmosphere. In one sense, regulation of plant water status entails the opposite function of the regulation of plant stomatal behaviour, and the identification of the optimal degree of plant hydration may represent the complementary problem to the maximization of photosynthesis under some hydraulic or water relations constraint. Plant physiologists have long identified a continuum of strategies from the isohydric to the anisohydric extremes of water status regulation. The isohydric/anisohydric spectrum of water status regulation is well established but available approaches suffer from several limitations. Firstly, they are undefined at the daily time scale. Importantly, this does not allow to consider the effects of VPD, atmospheric vapour pressure deficit. Secondly, they do not quantify the equivalent to a plant water status property, as separate from additional environmental effects. Finally, they do not quantify water status regulation per se, but rather the degree of coupling between pre-dawn and midday water potentials under a specific set of environmental conditions. These limitations impact our ability to relate plant traits with metrics of plant water status regulation in vivo as well as our interpretation of plant-to-pixel canopy water status metrics as obtained by radar remote sensing. I will present a new approach aiming to develop a metric that a) separates the effect of VPD, b) can be applied at intra-daily time scale, c) provides a null reference against which to assess internal plant regulation of water status.

Keywords: Optimality theory

An Investigation of Optimality in Applications to Land Surface Models

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^a – Presenting author

With the advance in our understanding of the soil-plant-atmosphere continuum, more and more important processes involved have been identified and introduced into various models. With the increase in models' completeness, so is the increase of the models' complexity and the number of model parameters involved for estimation. Employing optimality principles is an effective way of reducing the number of model parameters related to plants, especially for situations with limited available observations. The challenge is, however, which optimality principle should be used. In this study, we extend the idea of modeling strategy presented in Luo et al. (2013) by simultaneously using multiple plausible expressions, derived from different perspectives in representing the same processes, to investigate the capabilities and potential limitations of individual optimality rules. As an illustration, we employ the expressions of the least-cost optimality theory from the original formulation of Prentice et al. (2014), after extending it to include water-limited conditions, and also the updated semi-empirical Ball-Berry-Leuning formulation (Tuzet et al., 2003). Both are implemented into VIC+ land surface model. Detailed behaviors and the uncertainties of the model simulated variables of assimilation, latent heat flux, stomatal conductance, leaf water potential, CO₂ concentration in leaf, soil moisture and relevant parameters are analyzed using hourly time series of multiple years with data from two sites in the U.S. The interpretation of the results, specifically regarding the reasonableness of the variable combinations and parameters are discussed and their implications are explored.

Keywords: Optimality theory

Drought impacts on water use and ecosystem productivity underestimated by earth system models

Julia K. Green ^a¹ and Trevor F. Keenan¹

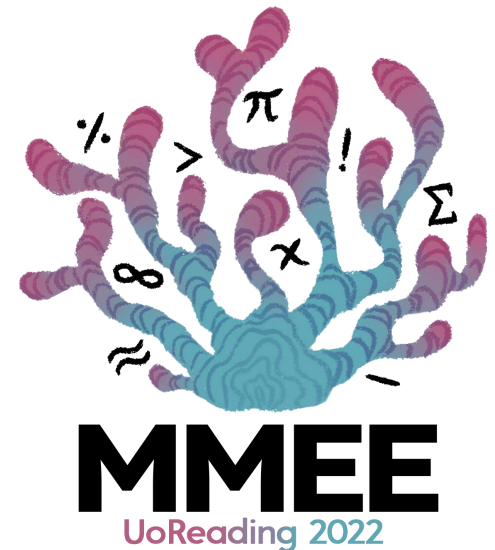
¹ University of California, Berkeley

^a – Presenting author

Plants have the ability to open and close their stomata in response to both water supply deficits as well as high water demand to prevent hydraulic failure. However, model misrepresentation of this plant response to water stress is a major source of uncertainty in our future climate projections. Here we use observational and reanalysis data to create a new emergent constraint for canopy conductance sensitivity to moisture availability, and find that models tend to underestimate this sensitivity. Based upon the strong relationship between vegetation stomatal conductance and gross primary production, this suggests that models are also overestimating carbon uptake during dry anomalies. By incorporating more mechanistic representation of canopy conductance sensitivity to moisture anomalies in models using eco-optimality principles, we can improve this representation.

Keywords: Optimality theory

Mini-symposium 12 - Phylogenetic simulation and inference models uncover deep-time dynamics in island biogeography



The limits to ecological limits to diversification

Prof. Rampal S. Etienne **a** 1

a – Presenting author

While the theory of micro-evolution by natural selection assigns a crucial role to competition, its role in macroevolution is less clear. Phylogenetic evidence for a decelerating accumulation of lineages suggests a feedback of lineage diversity on diversification, i.e., ecological limits to diversification. However, does this feedback only occur between close relatives, or do distant relatives also influence their diversification? In other words: are there phylogenetic limits to these ecological limits? Islands form ideal systems to answer these questions, because their boundedness facilitates an overview of all potential competitors. The DAISIE (Dynamic Assembly of Island biota through Speciation Immigration and Extinction) framework allows for testing the presence of diversity-dependence on islands given phylogenetic data on colonization and branching times. The current inference models in DAISIE assume that this diversity-dependence only applies within a colonizing clade, which we term clade-specific (CS) diversity-dependence. Here we introduce a new DAISIE model that assumes that diversity-dependence applies to all species regardless of their ancestry, i.e. diversity-dependence applies both to species within the same clade and between different clades. We call this island-wide (IW) diversity-dependence. Here we present a method to compute a likelihood for this model and develop a statistical procedure based on likelihood ratio bootstrapping to compare it to the likelihood of the CS model in order to overcome biases known for standard model selection. We apply it to the diversification of *Eleutherodactylus* frogs on Hispaniola. Across the Greater Antilles archipelago, this radiation shows repeated patterns of diversification in ecotypes which are similar across clades. This could be suggestive of overlapping niche space and hence between-clade interactions, i.e. IW diversity-dependence. But it could also be suggestive of only within-clade interactions, because between-clade interactions would have blocked the same ecotype re-appearing. We find that the CS model fits the data much better than the IW model, indicating that different colonizations, while resulting in similar ecotypes, are sufficiently distinct to avoid interacting strongly. We argue that non-overlapping distributions between clades (both spatially and in terms of ecotypes) cannot be used as evidence of CS diversity-dependence, because this pattern may be a consequence of IW diversity-dependence. By contrast, by using phylogenetic data rather than distributional data our method does allow for inferring the phylogenetic limits to ecological limits to diversification. We discuss how our new IW model advances our understanding also in other ways, ranging from identifying priority effects to modelling the spread of an epidemic in island-like systems, such as schools or hospitals.

Keywords: Island Biogeography

Island-wide diversification dynamics emerging from an individual-based model of competition and immigration

Mr Theo Pannetier ^{*a*}

a – Presenting author

Diversity-dependent diversification has emerged as a prime hypothesis for interpreting diversity patterns in molecular phylogenies and the fossil record, offering a universal model for how competition at the ecological level may regulate evolution on geological timescales. It is often assumed that diversity-dependence operates in a clade-specific manner, with members of a clade competing exclusively with one another. Islands present the ideal ecological setting to explore the consequences of relaxing this assumption, with their finite set of resources and clearly identifiable, polyphyletic communities. Here, we use an individual-based model with Lotka-Volterra competition to simulate diversification on an island. Evolutionary branching emerges from competition, so that immigrating populations eventually form a community with multiple clades, and the island's niche space is progressively partitioned among their descendants. We explore the conditions that lead to successful establishment and diversification of immigrating species, and the eventual coexistence of multiple clades competing in the island's niche space. Where such polyphyletic biotas persist, we study whether the diversity-dependent character of diversification is detected when considering clades separately, or together, using the DAISIE likelihood framework, and if diversity-dependence is found to operate in a clade-specific, or island-wide basis.

Keywords: Evolutionary models

Approximate Bayesian Computation in Island Biogeography models

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Island biogeography models play an important role in understanding evolutionary patterns and processes of species on isolated systems. While many simulation models have been developed in island biogeography, a major challenge is to estimate evolutionary and biogeographical parameters such as colonization, speciation and extinction from phylogenetic data. A maximum likelihood approach has been used to estimate parameters of the island biogeography model DAISIE (Dynamic Assembly of Island biota through Speciation, Immigration and Extinction). However, with the increasing model complexity required for more mechanistic hypotheses in island biogeography, it is often not possible to develop likelihood functions to gain tractable solutions and information in the data may be limited for estimating large numbers of parameters. Approximate Bayesian Computation (ABC) has been proposed as a likelihood-free method to overcome these difficulties. Here, we develop an ABC framework for the island biogeography model DAISIE, with the aim of estimating parameters from complex evolutionary scenarios. We test the inference ability of the ABC approach and investigate what the most informative summary statistics are. Furthermore, we apply the ABC framework to an extension of the DAISIE model with trait state-dependent colonization and diversification rates, to study whether trait dynamics affect the diversity of island species.

Keywords: Approximate Bayesian Computation, Island Biogeography

Robustness driven model development in island biogeography

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^a – Presenting author

Islands are model systems for understanding biodiversity, ecology and evolution. Tackling outstanding questions on the colonisation and diversification histories of species in island communities requires statistical inference models to understand the rates of (macro)evolutionary processes and select among different models to determine the most probable explanation. This can be done either by deriving new models tailored for specific questions or by applying models that already exist but may not be ideally suited for the question at hand. Here we test whether a general model of island biogeography is applicable to new areas of island biogeography, by examining how it performs when its assumptions are violated. The model (DAISIE) can estimate rates of colonisation, speciation and extinction (CES rates) on islands and detect whether these rates are diversity-dependent. DAISIE was developed for studying phylogenetic data from oceanic islands (never connected to the mainland) and assumes island area is constant through time. We tested whether the model is robust to changes in island area and connectivity through time, either via geological changes to the island, or sea-level oscillations.. We identify that the model fails to reliably estimate CES rates when islands were previously connected to the mainland (continental islands), in which cases a new inference model is required. We then develop this continental model of island biogeography and apply it to simulated data to show whether initial species presence on the island can be detected and whether these signatures exist in empirical data from continental islands.

Keywords: Evolutionary Genetics, Phylogenetics

Rethinking Phylogenetic Diversity

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Phylogenetic Diversity is one of the most prominent measures of biodiversity. It is used routinely in studies of macroecology and macroevolution and in real-world conservation applications. Recent work, both empirical and theoretical, has investigated the link between Phylogenetic Diversity and Functional Diversity producing mixed results. This talk will revisit the conceptual origins of Phylogeny Diversity in the context of its link to Functional Diversity. We will show how the link between Phylogeny Diversity and Functional Diversity could potentially be strengthened, with some tweaks. Along the way we will visit other questions in the field, how does Phylogenetic Diversity translate through to phylogenetic networks and groups of extinct species? Are 'living fossils' real and how do they relate to phylogeny? We will close by exploring rich possibilities for the application of Phylogenetic Diversity in the future.

How do landscape dynamics in oceanic archipelagos affect lineage accumulation and phylogenetic tree imbalance?

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a – Presenting author

Several recent theoretical studies showed that simple landscape dynamics influences how species diversify, which may result in an imprint of past landscape dynamics on phylogeny shape. Oceanic volcanic archipelagos have more complex landscape dynamics, with several islands successively emerging, changing in size and in connectivity, continuously affecting the evolutionary processes building diversity. Here, we build a model to determine if such complex geoenvironmental dynamics leave a distinguishable signature on phylogeny shape. The model is individual-based and ecologically neutral. Several islands emerge in succession with a typical volcanic ontogeny. We consider both mainland and inter-island dispersal. Geographically isolated lineages diverge over time, possibly speciating. This model simulates microevolutionary processes from which speciation and extinction are emergent processes, and we study the corresponding phylogenies. We showed that lineage accumulation in the recent past accelerates as total size of the archipelago increases, with sudden jumps when new islands emerge. We demonstrated that this is due to evolutionary radiations occurring when new empty space can be colonised. We observed that tree imbalance increases until the archipelago reaches its maximum size, because increase in archipelago size benefits mainly to the most abundant lineage who is also the one generating most of archipelago diversity. Consistently, we observed that archipelagos with larger inter-island distances, thus with weaker inter-island migration, generate more balanced trees and that less remote archipelago decrease the speed of lineage accumulation. These results show how geoenvironmental dynamics in oceanic archipelagos may explain contrasted diversification patterns and how this may reflect into phylogenies.

Keywords: Phylogenies and evolutionary genetics

Simulating the dynamics of Darwin's evolutionary wedges

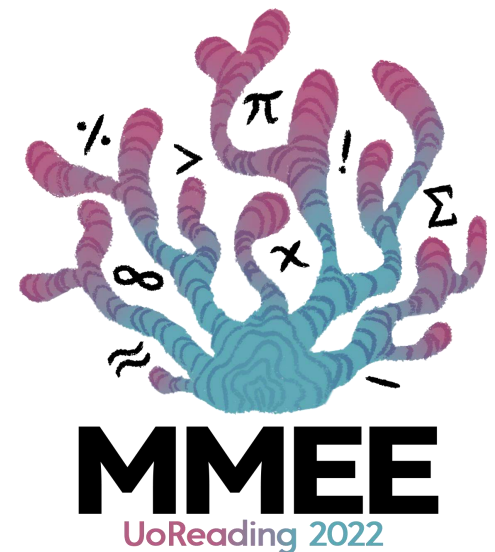
Dr Alex Pigot^{**a**1}

a – Presenting author

From character displacement, to community assembly rules and the taxon cycle, islands have been central to both theory and empirical tests of how competition between species shapes the evolution and distribution of biodiversity. However, inferring how and to what extent, competition regulates biodiversity over macroevolutionary timescales remains a major challenge because most models do not explicitly account for how species interact in space and time. In this talk, I will discuss recent simulation results from our group, showing how differences in the nature of competition – including both the timing and direction of interactions between invading and resident species – can give rise to highly variable signatures in the structure of ecological communities and adaptive radiations. I will discuss the implications and prospects of these results for inferring the historical role of competition from phylogenetic, functional and geographic data of extant species.

Keywords: Phylogenies and evolutionary genetics

General Session 7 – Evolutionary Models II



Plasmid-mediated heterozygosity, multidrug resistance, and evolutionary rescue in bacteria

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^a – Presenting author

Bacterial plasmids are extra-chromosomal, independently replicating DNA elements in bacteria, which may carry genes that affect the fitness of their hosts, in particular antibiotic resistance genes. Because many plasmids exist in multiple copies per cell, they can carry multiple distinct alleles, allowing for heterozygosity not possible for loci on the haploid chromosome. Plasmid-mediated heterozygosity of antibiotic resistance alleles can produce multidrug resistance, in which a single bacterial strain is resistant to multiple antibiotics, a serious problem in the clinical context. However, plasmid-mediated heterozygosity is also subject to constant loss due to random segregation of plasmids on cell division: each division has some probability of producing a homozygous daughter cell. We present mathematical models of evolutionary rescue in bacterial populations through the emergence of multidrug resistance from alleles on plasmids. Based on branching process theory, we derive the minimum threshold on the selective advantage of heterozygotes required to overcome segregative loss and make rescue possible. This threshold decreases with increasing copy number of the plasmid. These results contribute to our understanding of the evolution of antibiotic resistance in complex selective environments.

Revisiting the role of behavior-mediated structuring in the survival of populations in hostile environments

Miss Simran Sandhu^{a 1}

¹ Institution

^a – Presenting author

Increasing the population density of some target species is a major goal in ecosystem and agricultural management. This is especially challenging in hostile environments characterized by a high abundance of natural enemies such as parasites and predators. Until recently, creating safe locations with lower mortality was thought to be an appropriate strategy to enhance the species' population density in hazardous environments. Here we challenge this common opinion. We use mathematical modelling and empirical data on the defensive tactics of salmonid fish in the presence of their parasites to investigate the role of behavioral structuring in hostile environments. Experimentally, we show in the system comprising of rainbow trout and its parasite, the trematode eye-fluke *D. pseudospathaceum*, more reactive fish individuals show a reduced infection load. We find that the susceptibility of individual fish to infection remains over time. Using either shoaling or sheltering as a defensive strategy generally reduces the infection load compared to staying solitary, with sheltering more effectively reducing the infection load compared to shoaling. Then, inspired by experimental results, we build a theoretical model to explore the role of safe zones in a hostile environment in shaping the population density. The model predicts that adding an insufficient number of safe zones reduces the population density of the species due to a combination of emergent dynamical behavioral structuring, in terms of anti-predator strategies taken by individuals, and strong intraspecific competition. Non-plastic structuring in individuals' reactivity and/or boldness largely reduces the mentioned negative effects. We demonstrate a possible mechanism for the emergence of such structuring: evolutionary branching of a monomorphic population into a dimorphic one with slow/fast (shy/bold) strains. In this study, we re-considered the role of safe zones in the survival of populations in hostile environments. Our general conclusion is that having an insufficient number of safe zones (shelters) would result, counter-intuitively, in reducing the population numbers due to dynamical behavioral structuring of the population, which can be partly compensated by non-plastic structuring. Our findings are of particular importance for commercial fish farming and restoration of threatened natural populations through artificially improving their natural habitats.

The best of both worlds: combining population genetic and quantitative genetic models

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¹ Institut Camille Jordan, UCBL/CNRS

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^a – Presenting author

Traits under migration-selection balance are increasingly shown to exhibit complex patterns of genetic architecture, with allelic differences of varying magnitude. However, studying the influence of a large number of small allelic effects on the maintenance of spatial polymorphism is mathematically challenging, due to the high complexity of the systems that arise. Here we propose a new methodology that allows us to take into account the combined contributions of a major locus and of a quantitative background resulting from small effect loci, inherited according to the infinitesimal model. In a regime of small variance contributed by the quantitative loci, we found new arguments of convex analysis to justify that traits are concentrated around the major alleles effects according to a normal distribution, which leads to a slow-fast analysis approach. By applying it to a symmetrical two patch model, we predict an undocumented phenomenon of loss of polymorphism at the major locus despite strong selection for local adaptation under some conditions, where the infinitesimal quantitative background slowly disrupts the fast established symmetrical polymorphism at the major locus, which is confirmed by individual-based simulations. We also provide a comprehensive toolbox designed to describe how to apply our method to more complex population genetic models. (The talk is based on the paper available at the following link: <https://arxiv.org/abs/2111.11142>).

Keywords: Population Dynamics

Tempo of adaptation under limited dispersal

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^a – Presenting author

How likely and how quickly beneficial alleles can fixate through selective sweeps are central questions to the population genetics of adaptation. Such sweeps may be hard - where the fixating allele originates from a new mutation - or soft, in which the fixating allele comes from the species' pool of standing variation. The mean time taken by these different sweeps is accurately described in well-mixed populations. Many natural populations, however, are subdivided and dispersal-limited. Here, we show how the probability and mean time of hard and soft sweeps are affected by both inbreeding and kin-competition. These effects are modulated in structured diploid populations by the allele genetic dominance, which is considered in the interval $0 \leq h \leq 1$. We find that limited dispersal attenuates the classical effects of genetic dominance on hard sweeps - i.e., that deviations from the additive case ($h=0.5$) increase the mean time to fixation. Regarding soft sweeps, we find that its mean time increases monotonically with the genetic dominance under highly limited dispersal; whereas, slightly limited dispersal accelerates the fixation dynamics of both (nearly) recessive and (nearly) dominant alleles in structured populations. Expanding previous findings about inbred populations, our results demonstrate that when kin-competition is considered in addition to inbreeding, the fixation dynamics of dominant alleles are also affected by population structure. These results are endorsed by individual-based simulations. This work puts forward our understanding of the pace and molecular signatures of genetic adaptation under the influence of limited dispersal, population structure and genetic dominance - especially in the case of (partially) dominant alleles.

Long-time behavior of a PDE replicator equation for multilevel selection in group-structured populations

Dr Daniel Cooney^{a 1}

¹ Institution

^a – Presenting author

In many biological systems, natural selection acts simultaneously on multiple levels of organization. This scenario typically presents an evolutionary conflict between the incentive of individuals to cheat and the collective incentive to establish cooperation within a group. Generalizing previous work on multilevel selection in evolutionary game theory, we consider a hyperbolic PDE model of a group-structured population, in which members within a single group compete with each other for individual-level replication; while the group also competes against other groups for group-level replication. We derive a threshold level of the relative strength of between-group competition such that defectors take over the population below the threshold while cooperation persists in the longtime population above the threshold. Under stronger assumptions on the initial distribution of group compositions, we further prove that the population converges to a steady state density supporting cooperation for between-group selection strength above the threshold. We further establish long-time bounds on the time-average of the collective payoff of the population, showing that the long-run population cannot outperform the payoff of a full-cooperator group even in the limit of infinitely-strong between-group competition. When the group replication rate is maximized by an intermediate level of within-group cooperation, individual-level selection casts a long shadow on the dynamics of multilevel selection: no level of between-group competition can erase the effects of the individual incentive to defect. We further extend our model to study the case of multiple types of groups, showing how the games that groups play can coevolve with the level of cooperation.

Biased ecological inheritance towards kin can promote ecological polymorphism

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Organisms continuously modify their environment, often impacting the fitness of future conspecifics. When such ecological inheritance disproportionately affects kin, selection favours environmental modifications that increase the fitness of downstream individuals. This can in turn steer the evolution of ecologically-relevant traits, e.g. enhancing the maintenance of a niche. How selection shapes variation in such traits within populations, however, remains poorly understood. Here, we investigate the coevolution of multiple traits in a group-structured population when these traits affect the group environment, which is then bequeathed to future generations. We examine when such coevolution leads to polymorphism as well as the type of associations among traits that are favoured by selection. We find that due to ecological inheritance towards kin, a positive association among two traits is favoured (i) when these traits have synergistic effects on the environment (which increases fitness); or when one trait improves the environment while the other (ii) has synergistic effects with the environment on fitness; or (iii) increases the likelihood that future kin benefit from this environment. To illustrate this, we model the coevolution of (a) the attack rate on a renewable resource, which deteriorates environmental conditions for future generations, with (b) dispersal between groups, which reduces the likelihood that kin suffers from such deterioration. We find that this often leads to the emergence of two highly-differentiated morphs: one that readily disperses and depletes local resources; and another that maintains these resources and tends to remain philopatric. Remarkably, these two consumer types coexist in spite of relying entirely on the same resource. Beyond this example, our results suggest that ecological inheritance can contribute to variation of functional traits and lead to complex ecological polymorphism.

Revisiting the Role of Hyperparasitism in Evolution of Virulence

Dr Andrew Morozov^{a 1}

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^a – Presenting author

Hyperparasitism denotes the natural phenomenon where a parasite infecting a host is in turn infected by its own parasite. Hyperparasites can shape the dynamics of host-parasite interactions and often have a deleterious impact on pathogens, an important class of parasites, causing a reduction in their virulence and transmission rate. Hyperparasitism thus could be an important tool of biological control. However, host-parasite-hyperparasite systems have so far been outside the mainstream of modelling studies, especially those dealing with eco-evolutionary aspects of species interactions. Here we theoretically explore the evolution of life traits in a generic host-parasite-hyperparasite system, focusing on parasite virulence and the positive impact hyperparasitism has on the host population. We also explore the co-evolution of life history traits of the parasite and hyperparasite, using adaptive dynamics and quantitative genetics frameworks to identify evolutionarily singular strategies. We find that in the presence of hyperparasites, the evolutionarily optimal pathogen virulence generally shifts towards more virulent strains. However, even in this case, the use of hyperparasites in biocontrol could be justified since overall host mortality decreases. An intriguing possible outcome of the evolution of the hyperparasite can be its evolutionary suicide.

Modeling Coevolution of Host and Microbiome

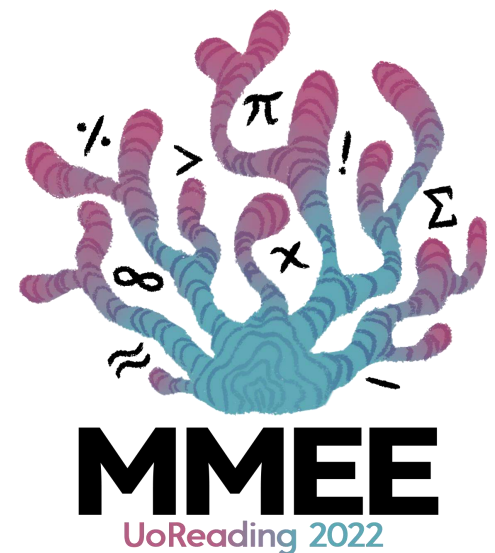
Mr Taom Sakal^{*a* 1}

¹ Institution

^{*a*} – Presenting author

Scientists have done much to discover how microbiomes influence their host's fitness. But we have done little to study how this affects the coevolution of host and microbiome. Few mathematical models exist, and fewer still give strong analytical results or extend to large numbers of host/microbe species. We introduce a new framework to remedy this, one which tracks both host and microbe frequencies and allows fitness of an individual host/microbe to be an arbitrary function of the host-microbiome combination they are in. We then share some preliminary results concerning equilibria, conditions for cyclic dynamics, and the behavior of the system under a matrix of random fitness parameters.

General Session 8 – Population Dynamics II



Analysis of the stable steady states of multispecies non-local advection-diffusion models using energy functionals

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² University of Alberta, Alberta, Canada

^a – Presenting author

In many biological systems, it is essential for individuals to gain information from their local environment before taking decision: through sight, hearing or smell, animals detect the presence of food, water or other individuals, and adjust accordingly their behavior. Interestingly, this feature is not only restricted to higher level species, such as animals, but is also found in cells. For example, some human immune cells are able to interact non-locally by extending long thin protrusions to detect the presence of chemicals or signaling molecules. The process of gaining information about the presence or absence of significant elements in the environment is intrinsically non-local and mathematically the non-local sensing leads to non-local advection terms in continuum models. In this talk, I will focus on a class of nonlocal advection-diffusion equations modeling population movements generated by inter and intra-species interactions. I will show that the model supports a great variety of complex spatio-temporal patterns, including stationary aggregations, segregations, oscillatory patterns, and irregular spatio-temporal solutions. However, if populations respond to each other in a symmetric fashion, linear stability analysis shows that the only patterns that emerge from small perturbations of the stable steady state are stationary. In this case, the system admits an energy functional that is decreasing and bounded below, suggesting that patterns remain stationary for all time. I will show how to use this functional to gain insight into the analytic structure of the stable steady state solutions. This procedure reveals a range of possible stationary patterns, including various multi-stable situations, which we validate via comparison with numerical simulations.

Bridging local interactions and physiology in populations: an alternative approach for dynamic energy budget individual-based models

Mr Wissam Barhdadi^{a 1}

¹ Institution

^a – Presenting author

Understanding how ecosystems respond to changing environmental conditions has become a crucial priority. Mechanistic modelling approaches are increasingly favoured for understanding and augmenting the predictive capacity of ecological models under novel conditions. More specifically, individual-based models (IBMs) that track individuals' energy budgets in a population are useful for projecting dynamics across different environmental conditions based on physiological constraints. To model the individual bioenergetics, so-called dynamic energy budget (DEB) models are increasingly used as a consequence of their generality and firm theoretical foundations. Still, classical DEB-IBMs adopt a top-down system-level thinking to incorporate individual behaviour, disregarding key IBM features such as local interactions and heterogeneity. This overlooks the significant influence of individual behaviour on life-history and fitness, with subsequent impacts on population dynamics. We therefore propose a general IBM approach where individuals are modelled in a fine-scale spatially explicit environment in which they forage for energy and allocate it following DEB-rules to their growth, reproduction and development. Using experimental data for the marine nematode *Halomonhystera disjuncta*, we conduct a case study to highlight the model's potential for gathering mechanistic insights into how populations respond to environmental changes. We find that by adopting different movement strategies for the foraging of individuals, different population-level patterns emerge compared to those emerging from classical DEB-IBMs. Moreover, compared to classical DEB-IBMs where all individuals behave according to the same functional response, a distribution of functional response curves emerge from the implemented fine-scale DEB-IBM. With the increasing availability of individual-level data on behaviour, this framework could allow to integrate such data in order to generate understanding of ecological patterns at higher scales. These developments for the DEB-IBM framework could therefore greatly contribute to the development of mechanistic ecological models of ecosystems facing environmental changes.

Chemical contamination mediated regime shifts in planktonic systems

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Abrupt transitions leading to algal blooms are quite well known in aquatic ecosystems and have important implications for the environment. These ecosystem shifts have been largely attributed to nutrient dynamics and food web interactions. Contamination with heavy metals such as copper can modulate such ecological interactions which in turn may impact ecosystem functioning. Motivated by this, we explored the effect of copper enrichment on such regime shifts in planktonic systems. We integrated copper contamination to a minimal phytoplankton–zooplankton model which is known to demonstrate abrupt transitions between ecosystem states. Our results suggest that both the toxic and deficient concentration of copper in water bodies can lead to regime shift to an algal-dominated alternative stable state. Further, interaction with fish density can also lead to collapse of population cycles thus leading to algal domination in the intermediate copper ranges. Environmental stochasticity may result in state transition much prior to the tipping point and there is a significant loss in the bimodality on increasing intensity and redness of noise. Finally, the impending state shifts due to contamination cannot be predicted by the generic early warning indicators unless the transition is close enough. Overall the study provides fresh impetus to explore regime shifts in ecosystems under the influence of anthropogenic changes like chemical contamination.

Forecasting in stochastic eco-evolutionary networks

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^a – Presenting author

Ecological systems are typically structured by trophic relationships which manifest at the microscopic level through different sorts of interactions between individuals. However, in order to gain an understanding of the resulting aggregate dynamics, one usually seeks a more coarse-grained description in terms of phenotype counts. The traditionally most popular approach is by deterministic macroscopic models, which essentially describe an infinite-population limit through reaction-rate-ODEs. On the other hand, experimental evidence suggests that most populations are locally rare, making the case for stochastic mesoscopic models that are able to incorporate finite population effects such as demographic noise. Continuous-time Markovian reaction networks are mesoscopic models which allow to stringently carry over microscopic assumptions to the aggregate level but require more involved mathematics than macroscopic models. In particular, the stochastic forecasting problem is considerable more intricate than its deterministic counterpart as it requires to estimate the conditional probability distribution of a high-dimensional stochastically evolving state vector given a history of lower-dimensional observations. This problem has not received much attention in ecology despite the contemporary need to forecast ecological scenarios in the face of global change and ecosystem collapse. Fortunately the conditional state estimation problem has an extensive track record in the physical sciences and mechanical/electrical engineering where it is commonly referred to as Bayesian filtering. While closed-form solutions are usually not available, there is a host of well-developed computational methods such as the extended Kalman filter, various particle filter methods and the adaptive Gaussian mixture filter, to name just a few. In this talk I will discuss the suitability of different filtering schemes for ecological Markovian reaction networks with a focus on an eco-evolutionary host-parasite scenario. I will then discuss the theoretical limits of forecasting in this setting and touch upon ramifications for experimental design.

The role of environmental variation on the population dynamics of Atlantic salmon (*Salmo salar*)

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The anadromous Atlantic salmon life cycle can be described as stage structured due to its discrete life stages as well as distinct river and marine phases, however, individuals can also vary in body size within life stages. Such details need to be depicted when modelling the population dynamics of these species and can therefore be explored using structured population models, such as Integral Projection Models (IPM). IPMs are useful tools to investigate population-level processes from individual demographic rates, estimated using vital rate regression models. However, many IPM approaches typically lack a mechanistic representation of the biological processes that produce the observed demographic variation. This lack of a mechanistic underpinning limits the ability of these models to predict future dynamics under novel environmental conditions. To overcome this and create a more mechanistic population model, I will incorporate metabolic traits to parameterise an IPM. The metabolic rate of an individual can be determined by its body mass and temperature and such individual-level processes have been shown to be a fundamental biological rate that influences Atlantic salmon life history. I will therefore demonstrate how metabolic theory can be used to develop a structured metabolic population model to predict population dynamics of Atlantic salmon and help understand the impact of temperature variation. This will enable an understanding of the fundamental drivers of Atlantic salmon dynamics. Predictions from the model will be compared to empirical data, to validate its application.

Keywords: Integral Projection Models, Structured Population Models

Eco-Evolutionary Dynamics in Structured Populations

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a – Presenting author

We introduce a generalization of stage- and age-structured populations called state-structured populations, which are ubiquitous throughout biology from cells entering and exiting various cell states to species in a metapopulation migrating among habitats. Though the mathematical framework for modeling age- and stage-structured populations under density and frequency independence is somewhat well developed, the same cannot be said for state-structured populations. In the context of matrix theory, evolutionary game theory, and the G function framework, we herein develop the mathematics needed to simulate and analyze the ecology and evolution of state-structured populations. For simplicity, we consider the case of two discrete states in the population and focus on difference equation implementations of the relevant matrix population models. We broadly investigate ecological (long-term and transient) and evolutionary dynamics of state-structured populations under density- and frequency-dependence. An expository example of the application of such a framework in biology is provided in the modeling of cell plasticity and therapeutic resistance in cancer.

Keywords: Evolutionary Models, Size-structured Ecosystems

Arranging Pre-commitment to Enhance Coordination Among Firms Adopting Technology

Ndidi Bianca Ogbo^{a1} and The Anh Han¹

¹ Teesside University, UK

^a – Presenting author

Over the years, different mechanisms have been put in place to study and promote the emergence of cooperation. Ranging from group and kin selection, memory and reputation-based reciprocity mechanisms, social diversity and context-based reactions and several other mechanisms used to understand human behaviours and how they cooperate. These methods used to promote cooperation are of great importance, but they are not sufficiently enough especially in the case of our technology adoption scenario where the expected payoff is asymmetric and firms need to be coordinated to participate in the game. To achieve coordination among agents in this type of scenario, extra mechanisms may need to be applied to enforce cooperative behaviour. Establishing a pre-commitment in terms of posterior benefits and consequences from those engaging in it provides an important mechanism for securing cooperation. We studied using methods from Evolutionary Game Theory (EGT) how arranging pre-commitments can also be adopted as a tool for enhancing coordination when its outcomes exhibit an asymmetric payoff structure, in both pairwise and multiplayer interactions. Arguably, coordination is more complex to achieve than cooperation since there might be several desirable collective outcomes in a coordination problem (compared to mutual cooperation, the only desirable collective outcome in cooperation dilemmas). Our analysis shows that whether pre-commitment would be a viable evolutionary mechanism for enhancing coordination and the overall population social welfare depends on the collective benefit, cost of the pre-commitment deal and severity of competition, and more importantly, how asymmetric benefits are resolved in a commitment deal. We first start our study in a well-mixed population and progressed to a more realistic setting of a structured population. Our results are almost similar in both settings; showing that pre-commitment can enhance coordination and the overall population payoff, especially when the cost of commitment is justified against the benefit of coordination.

Title

Mr Marcus Krellner **a** **1**

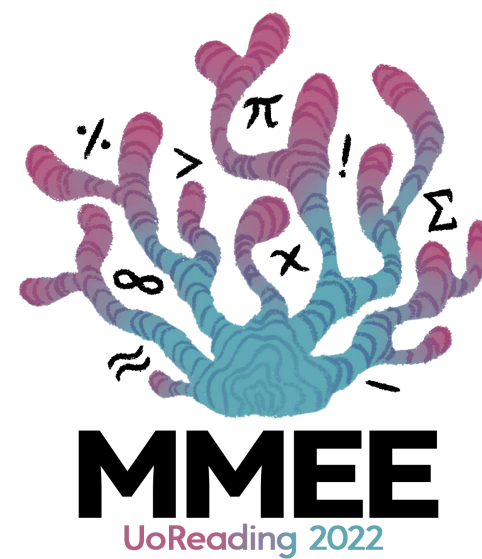
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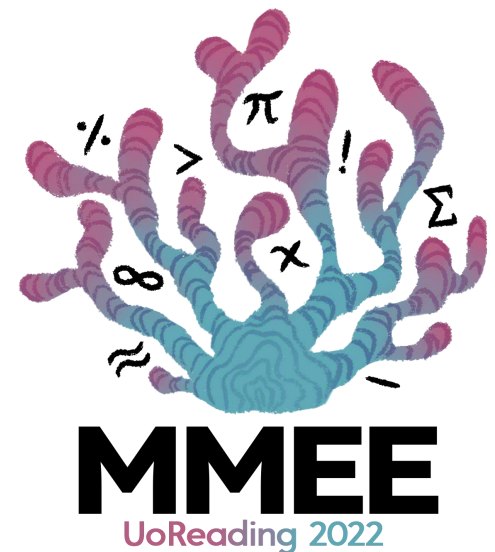
Altruism is not supposed to exist, yet we are glad it does. And not just between closely related individuals, but even between strangers. An explanation for this is indirect reciprocity. If I help you, I will earn a good reputation and, in the future, somebody else will help me. Yet this simple principle does not work under realistic conditions. Others who should recognize my helpfulness may not notice or misunderstand my actions. The biggest problem becomes identifying a justified refusal to help. People, who never choose to help, should not receive help themselves. But if we monitor each other's reputations privately, we can never be sure if someone we deem unhelpful is truly so, or if we just failed to recognize it. It was shown that we cannot sustain indirect reciprocity if we assess privately. But lately, three new lines of research give reasons for optimism. First, it was shown that a little bit of information exchange can effectively solve the problem. When I decide to help or refuse someone, I only need to ask a few other people about their opinions. If I act as their majority would do (i.e. if I please them), I significantly improve my own reputation and hence the help I will receive. Similarly, another study showed, that if I sometimes choose to help a bad player (i.e. if I adopt a generous strategy), I can also improve my reputation. In both cases, these improvements in one's own reputation had positive effects on the indirect reciprocity within the whole population. The last kind of scientific progress was the development of analytical models of indirect reciprocity under private assessments. Before that, studies had to rely on simulations and hence limit their scope. New exhaustive analyses suggested some new strategies, but they also confirmed known strategies.

Keywords: Evolutionary models

Day 3



Mini-symposium 13 - Random matrix theory and the dynamics and coevolution of microbiomes



Formation of host-microbe associations

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^a – Presenting author

Many microbes form specific and beneficial associations with host animals, thereby promoting both host fitness and their own prevalence within the hosts. But how do those associations form in the first place? And is an increased within-host prevalence, compared to the environment, necessarily a sign of a generally positive interaction between microbe and host? To address these questions we develop a stochastic model of hosts and microbes developing in and dispersing across a patchy habitat. We show that even when the microbes decrease host fitness compared to the microbe-free state, their overlapping life-histories can allow certain microbial types to get enriched in the hosts. This result emphasizes that within-host enrichment has to be interpreted in the specific environmental context, and is not per se a reliable indicator of a beneficial host-microbe interaction. Nevertheless enrichment and stronger interactions can provide the foundation for the subsequent evolution of mutually beneficial coevolved symbioses.

Keywords: Population dynamics

Horizontal gene transfer and ecological interactions jointly control microbiome stability

Dr Katharine Coyte^a¹

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^a – Presenting author

Genes encoding resistance to stressors such as antibiotics are widespread across microbiomes, often encoded on mobile genetic elements. Yet despite their prevalence, the impact of these resistance genes upon the dynamics of microbial communities remains largely unknown. Here we develop new eco-evolutionary theory to explore how resistance genes alter the stability of diverse microbiomes. We show that adding resistance genes to a microbiome typically increases its overall stability, however, the impact of resistance genes upon the stability of individual taxa varies dramatically depending upon the identity of individual taxa, the mobility of the resistance gene, and the network of ecological interactions within the community. Crucially, we confirm each of our key theoretical predictions experimentally. Together these findings highlight the importance of the interplay between ecological interactions and horizontal gene transfer in driving the eco-evolutionary dynamics of diverse microbiomes.

Keywords: Ecosystems dynamics

Can we infer the degree of collective integration of ecological communities?

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^a – Presenting author

Species interactions are key drivers of the dynamics of ecosystems. However, the staggering complexity of living systems makes the problem of inferring interactions very challenging. Yet, the study of disordered many-species dynamical models suggest that aggregate features of a system are driven by aggregate features of the interaction network, and are thus not sensitive to fine scale details (that would be inaccessible in practice). I propose to investigate whether or not we can leverage this intuitive idea to determine which interaction features can be reliably inferred from abundance data across environmental gradients. The goal is to clarify what information about interactions is theoretically present in observational data, tackling the classic problem of inferring processes from patterns. This abstract is a contribution to the minisymposium "Random matrix theory and the dynamics and coevolution of microbiomes".

Keywords: Ecosystems dynamics

Fluctuation spectra of large random dynamical systems reveal hidden structure in ecological networks

Professor Tim Rogers^{*a*1}

¹ Institution

a – Presenting author

Understanding the relationship between complexity and stability in ecosystem dynamics remains a key open question which has inspired a rich body of work developed over more than fifty years. The vast majority of this theory addresses asymptotic linear stability around equilibrium points, but the idea of 'stability' in fact has other uses in the empirical ecological literature. The important notion of 'temporal stability' describes the character of fluctuations in population dynamics, driven by intrinsic or extrinsic noise. In this talk I will apply tools from random matrix theory to the problem of temporal stability, deriving analytical predictions for the fluctuation spectra of complex ecological networks. I will show how different network structures leave distinct signatures in the spectrum of fluctuations, and demonstrate the application of our theory to the analysis of ecological time-series data of plankton abundances.

Keywords: Ecosystems dynamics

The Feasibility and Stability of Large Lotka Volterra Models with interaction structure

My Xiaoyuan Liu^{a 1}, Jon Pitchford and George Constable

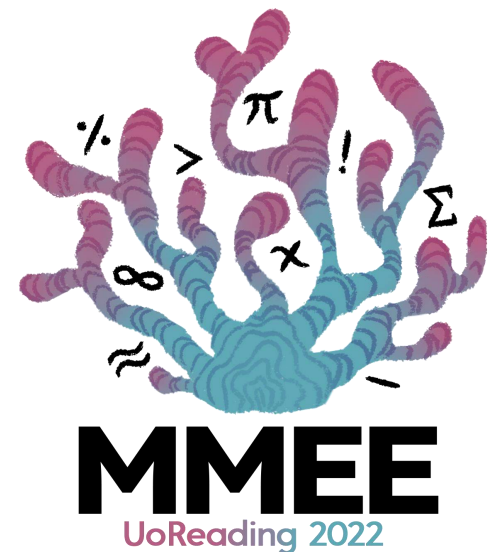
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The mathematical study of ecological stability has a long history dating back to the work of May in 1972. Since then, many advancements have been made to May's linear RMT (random matrix theory) model of stability to account for biological realism as well as improving accuracy. Some models accounted for interaction structure while others focused exclusively on relating May's linear model to specific ecological models, such as the GLV (generalised Lotka-Volterra) model. Few studies have simultaneously accounted for the interaction structure while relating May's RMT model to specific ecological models. For an ecological model to make sense biologically, it must be feasible, which is the condition where all equilibrium abundances of the model take on positive values. In my talk, I will present my work on analytically investigating the feasibility of random GLV systems with particular interaction structures, such as predator prey, mutualism and competition. These structures are proven to have significant effects on the feasibility of the GLV model as well as linear stability. I will also demonstrate how an understanding of the feasibility of random systems has the power to refine our understanding of their stability, using a recent method of stability analysis.

Keywords: Ecosystems dynamics

Mini-symposium 14 - Social evolution under uncertainty



Private assessment of indirect reciprocity changes the landscape of cooperation

Professor Isamu Okada^{a 1}

^a – Presenting author

This talk will consider a private assessment scheme of indirect reciprocity. Indirect reciprocity is one of the main principles of evolving cooperation in a social dilemma situation. In reciprocity, a positive score is given to cooperative behaviour while a negative score is given to non-cooperative behaviour, and the dilemma is resolved by selectively cooperating only with those with positive scores. However, many studies have shown that non-cooperation with those who have not cooperated also downgrades one's reputation; they have called this situation the scoring dilemma. To address this dilemma, the notion of justified punishments has been considered. The notion of justified punishment allows good individuals who defect against bad co-players to keep their standing. However, in a private assessment scheme, this solution occurs a new type of dilemma because reputations may be downgraded when the intent of punishment is not correctly communicated. In this talk based on a published paper, we identify sufficient conditions to overcome each of the three dilemmas including the dilemma of punishment to maintain stable cooperation by using the framework of evolutionary game theory. This condition includes the principle of detecting free riders, which resolves the social dilemma, the principle of justification, which resolves the scoring dilemma, and the principle of generosity, which resolves the dilemma of punishment. A norm that satisfies these principles can stably maintain social cooperation.

Exploring incentive strategies in public goods dilemmas

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^a – Presenting author

Public cooperation is imperative for the sustainable management of common resources in human societies. However, the way how cooperation emerges in a population of rational individuals poses a puzzle: why should cooperators incur a cost to benefit others? Social institutions charged with administering incentives, such as rewards and punishments, are widely recognized as successful means of solving the problem in human societies. In this talk, I will first provide an overview of several hot topics about social incentives in the research area, and then introduce our recent works about exploring the incentive strategies using evolutionary game theory for solving the problem of cooperation.

An integrated model of upstream and downstream reciprocity

Dr Tatsuya Sasaki^{a 1}

¹ Department of Community Development, the Koriyama Women's University, Koriyama, Japan

^a – Presenting author

Indirect reciprocity is one of the major mechanisms for the evolution of cooperation in human societies. Furthermore, there are two branches of indirect reciprocity, upstream reciprocity and downstream reciprocity. The two reciprocal approaches to cooperation can be characterized in terms of signs of grace. Cooperation in future is causally realized in downstream reciprocity: “I save you, and someone else will save me.” A good sign through cooperative toil in downstream reciprocity represents the cause of salvation: “Because I save someone, I have a good sign, and someone else will save me.” Cooperation in future is predicted in upstream reciprocity: “You save me, and I’ll save someone else.” Upstream reciprocity is not so simple, and its use of signs is abductive: “Someone saved me. This leads me to infer that I have a good sign, so I am tempted to save someone else in order to give a reason to having deserved this good sign.” We here propose a standard model that reintegrate the two branches and analyze it. The model connects the future that has been predicted in upstream reciprocity and the future that has been causally realized in downstream reciprocity

The effect of environmental information on cooperation in stochastic games

Dr Maria Kleshnina^a

^a – Presenting author

In stochastic games, the environment changes depending on the choices made by the interactants in iterated encounters. Stochastic games are therefore a generalisation of repeated games, where the environment is constant and the same payoff matrix applies in every round. Here we study evolution of cooperation in stochastic donation games with two states, each representing a different environment. We consider pure memory-1 strategies: the next move depends on the outcome of the previous round. However, we distinguish two cases: (i) players receive no information about the state; or (ii) players do receive information about the state. Analysing all possible two-state stochastic games we find and characterise settings where receiving information about the state of the environment is (i) better (ii) neutral or (iii) worse for evolution of cooperation.

Keywords: Evolutionary models

A unified framework of direct and indirect reciprocity

Mr Christian Hilbe^a

^a – Presenting author

Direct and indirect reciprocity are key mechanisms for cooperation. Direct reciprocity means individuals use their own experience to decide whether to cooperate with another group member. Indirect reciprocity means they also consider the experiences of others. Although the two mechanisms are intertwined, they are typically studied in isolation. Here, we introduce a framework that unites both kinds of reciprocity. Individuals can choose whether to take into account third-party information about their interaction partner. We find that they learn to draw on such information when any two individuals only meet occasionally, when information is reliable, and when strategy mutations are rare. In that case, group members can adopt a simple and intuitive strategy, termed ‘Generous Scoring’, to sustain cooperation in a Nash equilibrium. Our results highlight how individuals choose between information from different sources, and how they learn to cooperate when both direct and indirect reciprocity are available.

Keywords: Evolutionary models

Evolutionary dynamics of cooperation in collective index insurance

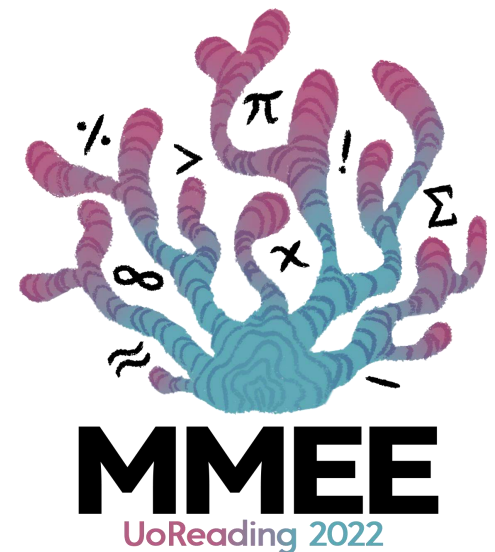
Dr Fernando P. Santos^{a 1}

^a – Presenting author

The uncertainty associated with extreme weather events often prevents low-income farmers from accessing high-return technologies that would enhance their productivity. As a result, they often fall into poverty traps, a problem likely to worsen as the frequency of weather disasters increases due to climate change. Insurance offers, in principle, a solution for this conundrum and a means to guarantee households' wellbeing. Group collective index insurance constitutes an alternative to indemnity or individual index insurance and has the potential to alleviate basis risk through within-group informal transfers. In this talk, I will present an evolutionary game theoretical model to study the dynamics of index insurance adoption. With such a model, we show that collective index insurance introduces a coordination dilemma of insurance adoption: socially optimal outcomes are obtained when everyone adopts insurance; however, a minimum fraction of contributors is necessary before the effects of basis risk can be averaged out and individuals start taking up insurance. We further show that additional mechanisms—such as local peer monitoring and defector exclusion—are necessary to stabilize informal transfers and collective index insurance adoption

Keywords: Evolutionary models

Mini-symposium 15 - Eco-evolutionary responses to environmental change



Eco-evolutionary community dynamics

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^a – Presenting author

Ecological and evolutionary processes can occur over similar temporal and spatial scales and might frequently interact. Studies on eco-evolutionary dynamics often focus on evolutionary changes in a single species, and how this can influence population, community and ecosystem dynamics. However, in natural systems, species are embedded within complex communities in which multiple species interact. Hence, in the face of environmental change, species within the community respond and evolve simultaneously, with each of these responses having further consequences for the community. A synthesis by M. Vellend points toward the links between evolutionary biology and community ecology, i.e., that both fields can be organized along four key processes. By explicitly considering interactions between these processes of evolutionary biology and the processes of community ecology, it may facilitate our understanding of eco-evolutionary dynamics in multi-species communities. Focusing on interactions between processes of evolutionary biology and community ecology may enable explorations of the full range of eco-evolutionary community dynamics, may provide a way forward to reveal generalities and formulate hypotheses about eco-evolutionary community dynamics and guide the design of novel theoretical models that explicitly take these interactions into account.

Models for Eco-Evolutionary Extinction Vortices under Balancing Selection

Mr Peter Nabutanyi ^{a 1} and Meike J. Wittmann¹

¹ Bielefeld University, Bielefeld, Germany

^a – Presenting author

The smaller a population is, the faster it loses genetic diversity as a result of genetic drift. Loss of genetic diversity can reduce population growth rate, making populations even smaller and more vulnerable to loss of genetic diversity. Ultimately, the population can be driven to extinction by this “eco-evolutionary extinction vortex.” While there are already quantitative models for extinction vortices resulting from inbreeding depression and mutation accumulation, to date extinction vortices resulting from loss of genetic diversity at loci under various forms of balancing selection have been mainly described verbally. To understand better when such extinction vortices arise and to develop methods for detecting them, we propose quantitative eco-evolutionary models, both stochastic individual-based simulations and deterministic approximations, linking loss of genetic diversity and population decline. Using mathematical analysis and simulations, we identify parameter combinations that exhibit strong interactions between population size and genetic diversity and match our definition of an eco-evolutionary vortex (i.e., per capita population decline rates and per-locus fixation rates increase with decreasing population size and number of polymorphic loci). We further highlight cues that may be exhibited by such populations but find that classical early-warning signals are of limited use in detecting populations undergoing an eco-evolutionary extinction vortex.

Keywords: Eco-evolutionary models, Evolutionary models

Evolutionary rescue by horizontal gene transfer

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^a – Presenting author

Many bacteria contain extra-chromosomal DNA elements, co-called plasmids. Plasmids are passed down from the mother cell to the daughter cells at cell division. In addition, some types of plasmids – termed conjugative plasmids – can horizontally transfer between neighboring cells, even between cells belonging to different species. In this way, beneficial traits can rapidly spread within bacterial populations and communities. However, if the potential recipient cell is already colonized by another plasmid, successful transfer may be prevented (incompatible plasmids). To understand under which conditions horizontal transfer helps bacterial populations to escape extinction following environmental change, we study adaptation through *de novo* mutations on conjugative plasmids and through immigrant plasmids that are either compatible or incompatible with a resident plasmid. A careful analysis based on branching process theory and stochastic computer simulations reveals subtle complexities in the effects of horizontal gene transfer in the presence of plasmid competition and plasmid costs. We finally consider the evolution of antibiotic drug resistance in the human gut via transfer of a resistance plasmid from commensal to pathogenic bacteria, accounting for ecological interactions between the two species and antibiotic treatment.

Keywords: Ecosystems dynamics

Ecological limits to evolutionary rescue

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⁴ Carnegie Institution for Science,
Department of Global Ecology

a – Presenting author

Environments change, for both natural and anthropogenic reasons, which can threaten species persistence. Evolutionary adaptation is a potentially powerful mechanism to allow species to persist in these changing environments. To determine the conditions under which adaptation will prevent extinction (evolutionary rescue), classic quantitative genetics models have assumed a constantly changing environment. They predict that species traits will track a moving environmental optimum with a lag that approaches a constant. If fitness is negative at this lag, the species will go extinct. There have been many elaborations of these models incorporating increased genetic realism. Here, we review and explore the consequences of four ecological complications: non-quadratic fitness functions, interacting density- and trait-dependence, species interactions and fundamental limits to adaptation. We show that non-quadratic fitness functions can result in evolutionary tipping points and existential crises, as can the interaction between density- and trait-dependent mortality. We then review the literature on how interspecific interactions affect adaptation and persistence. Finally, we suggest an alternative theoretical framework that considers bounded environmental change and fundamental limits to adaptation. A research programme that combines theory and experiments and integrates across organizational scales will be needed to predict whether adaptation will prevent species extinction in changing environments.

Changes in Ecological Coexistence with a Shifting Environment

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¹ University of Illinois at Urbana-Champaign, Illinois, USA

² Purdue University, Indiana, USA

^a – Presenting author

Ecological communities consist of a multitude of species which persist in their interactions across space and time, a phenomenon known as ecological coexistence. Coexistence between and among species is largely determined by their adaptations. As environmental shifts like climate change occur, they bring about fitness changes for species by favoring species with certain adaptations over others, by having species evolve in their adaptations in response to the shifts, or via both mechanisms. The resulting change in species fitness will necessarily impact ecological coexistence. In this study, I seek to see how measures of coexistence like niche and fitness differences change with shifting environments with and without evolutionary responses. Using an evolutionary game theoretic version of an annual plant model, several multispecies in-silico communities are generated. These communities are then subjected to a shifting environment with various measures of coexistence tracked over time. In one scenario, the environmental change is assumed to happen so quickly that species do not have time to evolve and so remain fixed. In the second scenario, environmental change happens slowly enough that species evolve in response to the environmental change. We can compare these responses to disaggregate the effects of the mismatch between species and environment (which affect fitness differences) from the effects of the evolutionary response to understand (which should maintain fitness differences but also change niche differences) on evolutionary coexistence. This work will give us a greater understanding of the ways in which multispecies community will be affected and respond to environmental shifts.

Keywords: Evolutionary models

Species interactions and the eco-evolutionary response of communities to climate change

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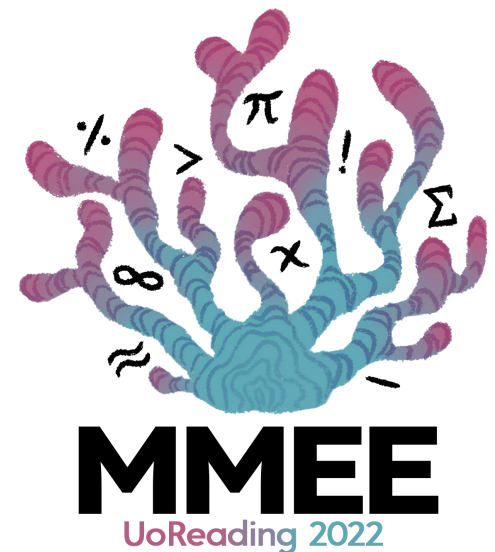
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^a – Presenting author

Eco-evolutionary dynamics are essential in shaping the biological response of communities to ongoing climate change. Here I present a spatially explicit eco-evolutionary modelling framework which integrates species interactions, evolution, and dispersal. The approach accounts for species interactions within and between trophic levels, and for the strength of interspecific competition possibly changing due to increasing temperatures. The modeling framework captures previously reported ecological responses to climate change, and also reveals two key results. First, interactions between trophic levels as well as temperature-dependent competition within a trophic level mitigate the negative impact of climate change on biodiversity, emphasizing the importance of understanding biotic interactions in shaping climate change impact. Second, adopting a trait-based perspective reveals a strong positive relationship between the within-community variation in preferred temperatures and the capacity to respond to climate change. In particular, temperature-dependent competition consistently results both in higher trait variation and more responsive communities to altered climatic conditions. Overall, the study aims at emphasizing the importance of species interactions in an eco-evolutionary setting, and at expanding our knowledge of the interplay between ecological and evolutionary processes.

Keywords: Ecosystems dynamics

General Session 9 – Evolutionary Models III



Evolutionarily stable levels of aposematic defence in prey populations

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a – Presenting author

Our understanding of aposematism (the conspicuous signalling of a defence for the deterrence of predators) has advanced notably since its first observation in the late nineteenth century. The aim of this talk is two-fold: first, to determine the relationship between evolutionarily stable levels of defence and signal strength under various regimes of background mortality and colony size. Second, to compare these predictions with simulations of finite prey populations that are subject to random local mutation. We compare the roles of absolute resident fitness, marginal mutant fitness and stochasticity in the evolution of prey traits and discuss the importance of population size in the above. The work presented here provides new insight into Wallace's first recorded "warning colouration" process in animals. Indeed, it extends the scope of a well-established game-theoretical model of this very same process both from the analytical standpoint (by considering regimes of varying background mortality and colony size) and from the practical standpoint (by assessing its efficacy and limitations in predicting the evolution of prey traits in finite simulated populations). Both of these constitute new contributions to the theory of aposematic signalling.

Title

Raneem Ayman Aizouk *a* ¹

¹ Institution

a – Presenting author

In this talk, we consider a model of a dynamically evolving network of interactions between individuals, where each individual has an optimum level of social engagement with other group members. A randomly selected individual will form or break a link to obtain the required contacts. These interactions were formulated as a graph realisation problem. Broom and Cannings considered a game-theoretical version of this model together with examples. One of these examples was an apparently simple three player game following the sequence 111, where they found three Nash equilibria, believing this was the complete solution set. One aim was demonstrate the complexity of the game for all but very small examples like this, where they found three Nash equilibria. We revisit the example sequence 111 and show that even here the game is complex, much more so than previously thought. We define a general expression for the payoff functions for all possible strategy combinations. In addition to the three Nash equilibria previously found, we identify a stable set of strategies that led to another six cyclic Nash equilibria for the game and the original three solutions. We have found no other solutions, although the possibility of more solutions is an open problem.

The replicator dynamics for state based and age structured game theoretic models

Dr. Krzysztof Argasinski^{a1}

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^a – Presenting author

We present an attempt to integrate the classical evolutionary game theory based on replicator dynamics and the state-based approach of Houston and McNamara. In the new approach, individuals have different heritable strategies; however, individuals carrying the same strategy can differ in terms of state, role or the situation in which they act. Thus, the classical replicator dynamics is completed by the additional subsystem of differential equations describing the dynamics of transitions between different states. In effect, the interactions described by game structure, in addition to the demographic payoffs (constituted by births and deaths), can lead to the change in state of the competing individuals. Special cases of reversible and irreversible incremental stage-structured models, where the state changes can describe energy accumulation, developmental steps, are derived for discrete and continuous versions. The special limit cases of the switching dynamics, describing the age structured models, are equivalent to Leslie Matrix (for discrete state space) and McKendrick von Foerster model (for continuous state space). This leads to the coupled PDE-ODE systems. Then, on the attracting manifold of the age structure dynamics, the Euler-Lotka equation of classical demography is satisfied. The new approach is illustrated using the example of the Owner-Intruder game with explicit dynamics of the role changes. The opponents in the game are drawn from two separate subpopulations consisting of Owners and Intruders. Here, the Intruders check random nest sites and play the Hawk-Dove game with the Owner if they are occupied. Meanwhile, the Owners produce newborns that become Intruders, since they must find a free nest site to reproduce. An interesting feedback mechanism is produced via the fluxes of individuals between the different subpopulations. Different strategies may have different distributions of states, which may seriously affect their payoffs.

Coordination games in cancer

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a – Presenting author

We propose a model of cancer initiation and progression where tumor growth is modulated by an evolutionary coordination game. Evolutionary games of cancer are widely used to model frequency-dependent cell interactions with the most studied games being the Prisoner's Dilemma and public goods games. Coordination games, by their more obscure and less evocative nature, are left understudied, despite the fact that, as we argue, they offer great potential in understanding and treating cancer. In this paper we present the conditions under which coordination games between cancer cells evolve, we propose aspects of cancer that can be modeled as results of coordination games, and explore the ways through which coordination games of cancer can be exploited for therapy.

Parthenogenesis and the Evolution of Anisogamy

Dr George Constable^{a 1}

¹ Institution

^a – Presenting author

Explaining the origin of the size dimorphism in the familiar sperm-egg system is a much celebrated success story in evolutionary ecology. However, classic models for the evolution of anisogamy (different sized gametes) do not take into account the possibility of parthenogenesis (development without fertilization), despite the fact that sex is facultative in many relevant taxa (e.g., algae). In this talk I will discuss the consequences of this additional modelling consideration. First parthenogenesis can stabilise isogamy relative to the obligately sexual case. Second, parthenogenesis can lead to biased sex ratios that are sufficiently extreme that one type can displace the other, leading to de facto asexuality for the remaining type that now lacks partners to mate with. Finally, and perhaps most interestingly, we also find scenarios in which parthenogens have an intrinsic survival advantage yet facultatively sexual isogamous populations are robust to the invasion of asexuals, despite us assuming no genetic benefits of recombination. I will conclude by contextualising the results of our model with some biological examples.

A trade-off between two tolerance strategies of the host leads to evolutionary branching

Ms Prerna Singh^{a1} and Dr Alex Best¹

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^a – Presenting author

There are crucial distinctions between tolerance to the effects of infection-induced deaths (mortality tolerance) and tolerance to the parasite-induced reduction in the reproduction of infected hosts (sterility tolerance). Theoretical studies have discussed the negative correlation between tolerance and resistance mechanisms, but such a correlation within different modes of tolerance is rarely looked upon. Here we consider a host population subjected to a pathogen that adversely affects both aspects of the host's fitness; fecundity and mortality. We assume that the host responds by evolving tolerance to both forms of parasitic impact and obeys a sterility-mortality tolerance trade-off. We extend a classic host-parasite SIR model and use adaptive dynamics framework to model the evolution of two forms of tolerance as host defense strategies. Existing theory claims that a direct trade-off within two defense strategies do not allow evolutionary branching unless there is an additional cost to some host life-history trait. However, we discover that a trade-off between two tolerance strategies drives the host population to branch into extreme dimorphic strains, i.e., branching occurs. As such, the strain in which infected hosts are sterile but have low mortality can coexist with the strain in which infected hosts are fully fertile and have a high mortality rate. In this talk, we will discuss the variation in tolerance investments corresponding to different ecological parameters. We will also compare disease prevalence patterns with and without evolving host defense and discuss the possibilities of evolutionary branching.

A mathematical model to study the sheltering effect of mating types and selfing

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Large regions of suppressed recombination encompassing genes involved in reproduction (sexual genes or mating-types genes) have been observed in many species. The mechanisms underlying the expansion of such regions beyond sex-involved genes are still debated. One of the hypotheses suggested is the sheltering of deleterious alleles : in species where the sex-involved gene is always heterozygous, the suppression of recombination may be extended to encompass segregating recessive deleterious alleles and guarantee their heterozygosity. However, the dynamics of deleterious mutations partially linked to a sex-involved gene are not yet well understood, especially in finite populations. In particular, whether or not deleterious mutations are likely to be maintained for long enough to eventually trigger recombination suppression is yet to be evaluated. Using a branching process approximation, we studied the fate of a single deleterious mutation in a diploid two loci-two alleles population, one locus carrying mating-types alleles that are always heterozygous. We obtained analytical and numerical results on the probability and time of purging of the deleterious mutation under two selection scenarios (recessive deleterious or overdominant allele). In particular, we investigated the impact of recombination between the two loci and of various mating systems (outcrossing and intra and inter-tetrad selfing) on the maintenance of the mutation. We found that the presence of a mating type locus always shelters deleterious mutations, i.e. it generally decreases the purging probability and increases the purging time of deleterious mutations. We also observed rare events of maintenance of deleterious mutations during strikingly long evolutionary times, suggesting that deleterious mutations can indeed accumulate near the mating-type locus on evolutionary time scales.

Keywords: Deleterious mutation, Mating type locus, Multitype Branching Process, Sheltering effect

Title

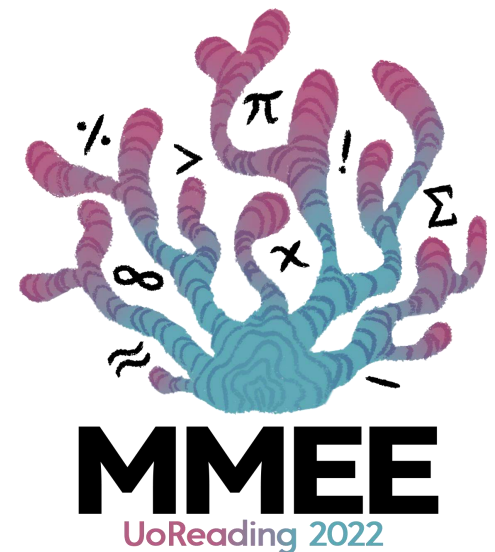
Mr Ewan Flintham ***a*** **1**

1 Institution

a – Presenting author

Sexual conflict arises when males evolve traits that improve their mating success but in so doing harm females. By reducing female fitness, male harm can impair recruitment and even lead to population extinction. Current theory on harm is based on the assumption that an individual's phenotype is entirely determined by its genotype. But most sexually selected traits show condition-dependent expression such that individuals in better condition can express more extravagant phenotypes. Here, we develop demographically explicit models of sexual conflict evolution where individuals vary in their condition. We show that condition-dependent expression readily evolves for traits underlying sexual conflict, so that conflict is more intense in populations where individuals are in better condition. This intensified conflict can reduce mean fitness and thus generate a negative association between condition and population size. We find that the impact of condition on demography is particularly deleterious where condition has a genetic basis that coevolves with sexual conflict. This occurs because sexual selection favours alleles that improve condition (the "good genes" effect), producing a feedback between condition and sexual conflict that drives the evolution of intense male harm. More broadly, our results suggest that the good genes effect via sexual interactions leads at best to limited improvements in mean fitness, and may in fact be detrimental if not fatal in the presence of male harm.

General Session 10 – Population Dynamics III



Modelling the patients flow into, through and out off hospital

Dr. Tahani Al-Karkhi^{a1}

¹ Institution

^a – Presenting author

Health care is becoming increasingly complex, especially in secondary care. Hospital bed numbers per capita in the United Kingdom (UK) are lower than many European countries, and often represent the limiting factor in delivering secondary care. Mechanisms to improve the efficiency of their use (and reduce opportunity costs) are therefore important managers. There have been attempts to model bed usage in departments (micro-level) and across health systems (macro-level), however so far, there have been few models developed allowing reliable description and analysis of hospital bed use across a whole hospital (looking at the interactions between parts of a hospital as patients move through) from admission to discharge or death. Patients with serious medical conditions (e.g. COVID-19) pass into, through, and out of, hospital. We plan to apply to this problem the tools developed during PhD studies, in which the equilibrium between three types of microplankton controlled by modulating chemical signals were modelled. Considering the hospital as a multicompartment system, we will derive relevant equations to allow a description of these departments' dynamic relationships. These relationships are determined by many factors, some known, some unknown, and many interdependent. We do not need to, and indeed cannot, know all of these factors (as needed for discrete event simulation, or agent-based modelling), but will merely look at the net changes between compartments (i.e. a 'system dynamics' approach). When we achieve a stable model, we intend to obtain data of bed usage from a UK hospital to try to validate it. If the model works, we would then plan to obtain bed usage data from another hospital to see if the model is as generalizable as expected. If successful, this methodology could then be adapted to most hospitals, and allows exploration of the impact of changing admission, transfer and discharge thresholds on throughput.

The role of trait variation in determining the risk of vector borne disease

Mr. Dominic Brass ^{a 1,2}, Professor
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Dr. David Ewing⁴, Professor Amanda
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^a – Presenting author

The incidence of vector-borne is on the rise globally and understanding drivers of this change, and the risk posed by vector populations, is critical for planning future control efforts. The life-history traits of insect vectors are often highly sensitive to changes in environmental conditions, altering the ability of these populations to maintain disease outbreaks. Current predictive approaches often make broad simplifying assumptions about how vector trait varies with environment. It is common to assume that the trait dynamics of vector populations can be represented by an average trait value determined by the instantaneous abiotic environmental conditions. This overlooks the complex series of historical environmental conditions and population states that contribute to the vector population's trait structure and therefore risks mis-estimating disease risk. We develop a mathematical modelling framework that uses a system of stage-phenotypically structured delay-differential equations to account for the effect of mechanisms of individual variation on disease risk. Using this framework, we derive a model that accurately predicts the dynamics of the invasive dengue vector *Aedes albopictus* in the field over the species global range, independently of the populations we validate against. When incorporated into a Susceptible - Infected - Resistant (SIR) model we find that these predictions are sufficient to predict the timing, magnitude, and location of dengue outbreaks. We demonstrate that the vector population's trait structure is critical in producing predictions that are generalisable through space and time. This demonstrates the importance of considering the effects mechanisms of individual variation on a species population dynamical processes and provides insights in to the evolving risk posed by *Aedes albopictus* to public health.

Heterogeneity in behaviour and movement can influence the stability of predator-prey periodic travelling waves

Mr Renato Andrade^a and Professor
Christina Cobbold

^a – Presenting author

Cyclic predator-prey systems are often observed in nature. In a spatial setting these can manifest as periodic traveling waves (PTW). Environmental change and direct human activity are known to, among other effects, increase the heterogeneity of the physical environment in which prey and predator inhabit. Aiming to understand the effects of heterogeneity on predator-prey PTWs we consider an one-dimensional infinite landscape Rosenzweig-MacArthur reaction-diffusion model, with alternating patch types and study the PTWs in this system. Through known techniques such as asymptotic homogenisation and reduction to normal form, the PTW solutions of the model are analysed close to a Hopf bifurcation. Our results show how heterogeneity can both stabilise and destabilise PTW solutions. We illustrate how the effects of heterogeneity can be understood and interpreted using Turchin's concept of residence index (encapsulating diffusion rate and patch preference). In particular, our results show that heterogeneity in predator movement alone does not change PTW stability, while heterogeneity prey movement does. Moreover, when there is heterogeneity in both prey and predator movement, prey heterogeneity acts to modulate the effects of predator heterogeneity, by this we mean that as prey increasingly spend more time in one patch type over another the greater the effect that heterogeneity in predator movement has on the PTW stability. Therefore, prey movement and behaviour play a fundamental role in predicting the stability, and hence, predictability of predator-prey PTWs in heterogeneous landscapes.

Keywords: Ecosystems dynamics, Spatial ecology

Spatial spread of suppression, eradication and replacement drives

Ms Léna Klay^{a 1}

¹ Institution

^a – Presenting author

Understanding the temporal spread of gene drive alleles (alleles that disrupt the laws of heredity by biasing their own transmission) through modeling is essential before any field experiments. And taking into account spatial structure and demography is a step towards more realistic models. In this talk, I will present results from a deterministic reaction-diffusion model, describing the interplay between demographic and allelic dynamics. I will address the following questions: Does the drive invade the wild-type population? If it does, then at which speed? What are the demographic consequences? Under certain conditions, we observe the existence of a release threshold: the drive alleles only spreads when the number of introduced individuals is large enough. In contrast with non-spatial models, the value of the threshold depends on demographic parameters. We also note that an eradication drive is able to spread in the population, leading to global extinction. However to do so, it must counteract a demographic flux, which can sometimes hamper its spread. In a second part, I will consider various timings of gene conversion (considering conversion can happen in the zygote or in the germline) and different probabilities of gene conversion (instead of assuming 100% conversion). Numerical simulations show intriguing results: in some cases without release threshold, the speed of invasion and the final allele proportions appear to be fully independent upon demographic parameters. I will present preliminary analytical results supporting these heuristic findings and put into perspective the necessity of considering demographic dynamics in the models.

Evolution of Decision-Making Rules

Ms Anna Sigalou^{*a* 1}

¹ Institution

^{*a*} – Presenting author

Social animals live in uncertain environments and rely on cues to navigate them. To make decisions, they use public and social information which they process using decision-making strategies. This process is often modelled by observing collective behaviour, and finding a model that leads to these collective dynamics. Here we attempt the opposite: we first try to identify plausible individual decision-making rules, and then see how they can lead to the observed collective behaviours. We investigate how individual decision-making affects the group's collective behaviour, how this group reaches optimal and evolutionary stable behaviour, and we explore how the different decision-making strategies compete with each-other.

Higher order interactions in invasion dynamics

Dr Aisling Daly^{a 1}

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^a – Presenting author

Understanding and predicting how the impacts of invasive species propagate through recipient communities remains a key challenge in ecology. Determining individual-level traits that characterize successful invaders, such as high rates of resource consumption, may fail to fully quantify such impacts because they do not account for how invaders interact with each other and with other species in recipient communities. There is growing evidence for the dominance of trait-mediated indirect interactions over density mediation. These are examples of higher-order interactions: interactions that are modified by other species, which can significantly affect coexistence either positively or negatively. Ecological modelling studies have largely neglected the questions of how and when higher-order interactions emerge, and how they affect a community's coexistence and stability. The classical (pairwise) invasion criterion, stating that an invasive species can successfully establish in a community if its population growth rate is positive at low densities, is defined for short-term invasion success. But this overlooks the long-term effects of the invader's presence in the community: as the invading population increases, it affects the abundance of other species, which will indirectly affect its own growth rate (i.e. feedbacks via higher order interaction). We model this density dependence using a higher-order interaction framework, where interactions between species are not strictly pairwise and hence per capita density dependence is no longer additive across species, in order to predict long-term invasion success beyond the initial establishment phase.

Is evolution an efficient algorithm?

Dr Per Kristian Lehre **a**¹

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a – Presenting author

Computer scientists have since the 1960s taken inspiration from biological principles of natural selection when designing optimisation algorithms. So-called evolutionary algorithms (EAs) have been successfully applied in a wide range of optimisation domains, including scheduling, logistics, drug design, and the automotive industry.

Over the last two decades, theoretical computer scientists have developed a theory attempting to characterise the efficiency of evolution. Analogously to how computer scientists study how the running time of algorithms grows with the problem instance size (time complexity analysis), we would like to estimate the expected time required by an evolutionary algorithm to obtain genotypes on the global fitness peak -- as a function of the number of genes in the model (the "problem instance size".)

This talk gives an introduction to our recent work in this area. In particular, we will discuss analytical techniques that aid in analysing the time complexity of evolutionary algorithms. These are based on martingale theory, concentration of measure, branching processes etc. We will then consider some applications of the techniques, particularly in understanding how characteristics of the fitness landscape and model parameters (mutation rate, population size, selection pressure etc.) influence the time complexity of evolutionary algorithms.

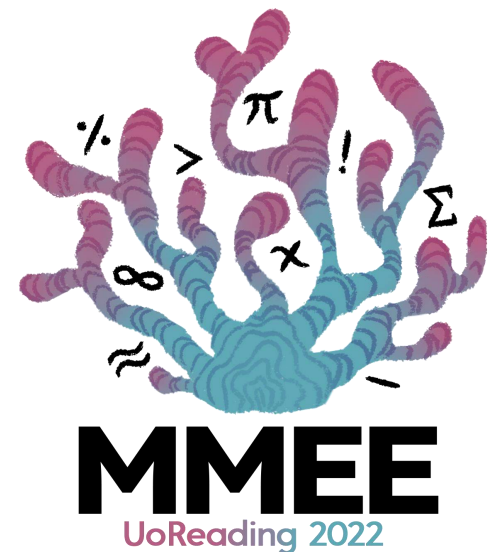
Reward AND Punishment

Miss Calina Durbac^{*a*}

^{*a*} – Presenting author

External institutions such as UN and NATO can provide incentives to enhance cooperation in a population in which this behaviour is infrequent. This process however requires spending optimisation as it can be costly. Such a problem can be mathematically formulated as a multi-objective optimisation problem where one wishes to minimise the cost of providing incentives while ensuring a minimum level of cooperation, sustained over time. We provide a rigorous analysis of this optimisation problem, in a finite population and stochastic setting, studying both pairwise and multi-player cooperation dilemmas. We prove the regularity of the cost function for providing incentives over time, characterise their asymptotic limits (infinite population, weak selection, and large selection) and show that employing both reward and punishment incentives is cheaper than implementing one or the other. We have numerical proof that the mixed cost function exhibits a phase transition phenomenon when the intensity of selection varies. Numerical simulations are also provided to demonstrate analytical observations. It is of crucial importance for real-world applications of institutional incentives since intensity of selection is often found to be non-extreme and specific for a given population.

Mini Symposium 16 – Applications of Evolutionary Game Theory



A Cancer Evolutionary Tumor Board: Simple models and big decisions

Professor Joel Brown^{a 1}

^a – Presenting author

Tumor boards provide valuable services to patients and the treating oncologists. A physician and health team present a patient's case to a panel of experts. The panel then provides assessments and advice regarding the patient's disease and treatment options. The Moffitt Cancer Center has developed a novel and presently one-of-a-kind tumor board: an Evolutionary Tumor Board (ETB). The multi-disciplinary team of clinical oncologists, pathologists, radiologists, mathematicians, basic science researchers, and evolutionary biologists consider consenting patients without curable options. The board uses first principles of ecology and evolution to develop and apply evolutionary therapies. Such therapies rely on Stackelberg evolutionary games (Stanková et al. 2019, JAMA: Oncology doi:10.1001/jamaoncol.2018.3395) where the goal is to anticipate and steer the eco-evolutionary dynamics of the patient's cancer. In these games, the physician is the leader who can select therapies based on anticipated trajectories of the disease. The cancer cells evolve resistance in response to therapy. They are followers in the sense that they evolve in response to and not in anticipation of therapy. The ETB provides patient-specific mathematical modelling. Each patient is modelled separately by integrating their data with retrospective data and known knowledge of the disease. The patient-specific decision tool evaluates the possible consequences of different treatment options. It proves valuable in determining therapeutic options, how to sequence therapies, and when to switch therapies.

Keywords: Evolutionary models

Bifurcations in eco-evolutionary models of adaptive therapy

Mr Frederik Thomsen^{a1}, Johan Dubbeldam¹

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a – Presenting author

The major obstacle in the design of effective treatment strategies for cancer therapy is the emergence of drug-resistance. Strategies aiming to eliminate the maximum volume of cells through continuous application of treatment are doomed to fail as, inevitably, an initially small subpopulation of at least partially drug-resistant cells becomes dominant by competitive release. Adaptive therapy is a new paradigm aiming to delay treatment failure by instead dynamically adapting the drug-dosage in response to the current total population state and utilizing competitive interactions between cell types. Recent mathematical models of adaptive therapy couple fast ecological population dynamics to a slowly evolving resistance in continuous, low-dimensional dynamical systems. The time-scales are typically assumed to be entirely separate such that the coupling reduces to a simple algebraic constraint. In this work we compare different classes of minimal eco-evolutionary models, including the standard Lotka-Volterra or Gompertzian type population dynamics, where the separation of time-scales is incomplete using geometric singular perturbation theory. An aspect largely ignored in the literature is the importance of bifurcations which occur dynamically through both the changing resistance and the adaptation of the drug-dosage. We demonstrate how a successful adaptive therapy strategy relies on such bifurcations to create robust, structurally different flows between treatment levels and identify optimal parameter regimes. In addition, we show how special canard solutions, inherent to the fast-slow population dynamics, will impact the containment of trajectories within given tolerance regions in the state space. Our results provide new insights into the mechanisms underlying adaptive therapy and compliment other approaches using optimal control.

Keywords: Evolutionary models

Parasite-like interactions between tumour subclones

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^a – Presenting author

Diversity within tumours influences tumour growth rate, treatment resistance, and metastasis, yet we know remarkably little about how cells from different subclones interact. I will present results of experiments to determine both the nature and mechanisms of subclonal cellular interactions between two murine mammary cancer cell lines in vitro. My mathematical analysis of the results reveals that, compared to monoculture, growth of the “winner” was enhanced by the presence of the “loser” cell line, whereas growth of the latter was reduced. These interactions are mediated by the production of paracrine metabolites resulting in the winner subclone effectively “farming” the loser. Simple mathematical analysis within the framework of evolutionary game theory nevertheless shows that, when accounting for microenvironmental heterogeneity, our inferred parameter values are plausibly consistent with long-term clonal coexistence. These findings add a new level of complexity to the mechanisms underlying subclonal growth dynamics.

Keywords: Evolutionary models

Combined mathematical and experimental analysis of cancer adaptive therapy with kinase inhibitors

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Montpellier – France

a – Presenting author

Adaptive therapy aims to control tumour burden by exploiting competition between therapy-resistant and -sensitive cells. We tested this strategy using a model of resistance to Epidermal Growth Factor Receptor Tyrosine Kinase Inhibitors (EGFR TKIs). We found that a low dose outperforms higher dose and maximum tolerated dose (MTD) therapy in controlling resistance in monolayer culture. In tumour spheroids, where cell-cell competition is more spatially confined, low dose therapy outperforms MTD in both controlling resistance and minimising tumour burden. By combining mathematical modelling and Bayesian inference methods, we have quantified key parameters of this system to inform planned preclinical and clinical trials of adaptive therapy.

Keywords: Mathematical Oncology

Epidemic patterns of emerging variants

Golsa Sayyar ^{a1} and Gergely Röst¹

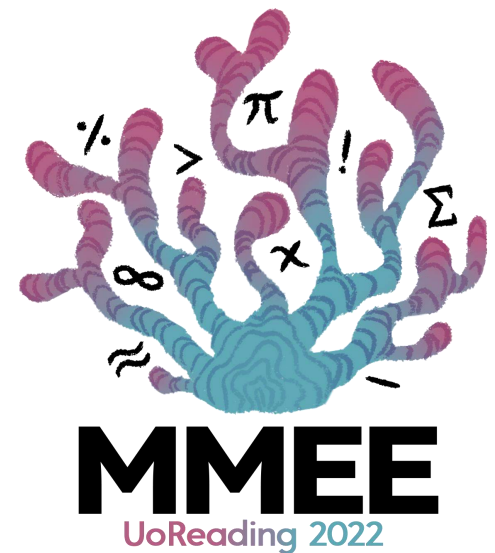
¹ University of Szeged, Szeged, Hungary

^a – Presenting author

Motivated by the emergence of new variants during the COVID-19 pandemic, we consider an epidemiological model of disease transmission dynamics, where by mutation novel strains of a virus appear. In the model, disease prevalence is modulated by social distancing. We study the different patterns that are generated under different assumptions. If recovery from a given strain gives immunity against all previous strains, but not against more novel strains, then we observe a very regular sequential pattern of strain replacement where newer strains gain dominance, and their waves are increasingly wider. However, if protection upon recovery holds only against that particular strain, we find a much more complicated dynamics with potential recurrence of earlier strains, and co-circulation of various strains. Finally, we compare the observed patterns with what we have seen during COVID-19.

Keywords: Epidemiology

Poster Session



Modelling the evolution of structured populations under coordinated movement

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United Kingdom

^a – Presenting author

In recent years, classic evolution models have been extended to incorporate more realistic features. A recent series of papers have developed a new evolutionary framework including structure, multiplayer interactions and movement. However, so far movement distributions have only involved independent movement e.g., without herding behaviour. In this presentation we develop a model to investigate the evolution of such a population under movement distributions where individuals are influenced by the movement of others. The interactions between individuals are modelled using the multiplayer public goods game. By incorporating these new movement distributions into existing evolutionary models, we demonstrate that certain levels of aggregation benefit specific types of individuals. Moreover, by extending the home fidelity parameter which is the measure of preference individuals have for staying at their home vertex to any positive value, we investigate a general approach of novel models such as the wheel to a wider class of structures.

Keywords: Evolutionary models

Parasite-Host coevolution with alternative modes of transmission

Mr George Shillcock^{a 1}

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^a – Presenting author

Parasites able to transmit from mother to offspring (vertically) and between unrelated hosts (horizontally) can survive a larger range of ecological conditions and are subject to different selective pressures. Vertical transmission is widely accepted to decrease virulence in the long run by making parasites more invested in host fecundity. However, most studies dismiss host response; important when host and parasite evolve on comparable timescales. Because vertical transmission also decreases the inclusive fitness of a host, it might not always align evolutionary interests. To tease apart these tensions we use game theory to model coevolution. We find vertical transmission does not necessarily promote benign parasitism but can whenever (i) horizontal transmission quickly saturates (ii) it is expensive for the host to retaliate, and (iii) the intrinsic growth rate of the host population is low.

Keywords: Evolutionary models

Evolutionary Indices for Classifying Modes of Tumour Evolution

Mr Veselin Manojlovic^{a 1}

¹ Institution

^a – Presenting author

Trees are a useful mathematical tool in evolutionary theory, especially when describing the structure of an evolving population. To quantify certain properties of trees, such as diversity or symmetry of branching events, one may employ evolutionary indices. When it comes to tree balance, the most popular indices have certain shortcomings, including that they are not suited to applications to the tree types used to describe the evolution of tumours, microbial populations, and cell lines. Thus, we define a new class of robust, universal tree balance indices which take a form similar to Colless' index while taking into account node sizes, include trees with arbitrary degree distributions, and enable a better comparison of trees with different numbers of leaves. Additionally, we explore properties of one such Colless-like index and its connection to Sackin's index on full m-ary cladograms, thus bringing the two most popular indices together. Furthermore, we examine specific properties of the new class of robust balance indices. We conclude by showing how and why the new class of indices could replace ones in current use.

Keywords: Phylogenies and evolutionary genetics

Macroevolution of mutualistic interactions on islands

Ms Yang Shen^{a 1}

¹ Institution

^a – Presenting author

Islands are seen as "natural laboratories" by many biologist, ecologists and geologists as they help understand global scale biodiversity patterns with a relatively isolated status. The flora and fauna of islands are particularly interesting to study because within such well-defined borders, enabling ecologists to capture macroevolutionary dynamics and step to study community assembly. Species in ecological communities are embedded in networks of interacting species. Using the concept "networks" to engage two entities (usually plant and animal species in mutualistic interaction) improves the analysis of ecological inter-species interaction mechanism. On evolutionary scale, species immigrating from mainland and successfully establishing on island are influenced by multiple factors. These inner or outer reasons are mainly related to affect the rates of immigration, speciation and extinction. Here we construct a species dynamic model on island involved mutualism and consider these three processes (i.e. immigration, extinction and speciation). With this approach, we are aiming to understand mutualism on evolutionary scale and to study how mutualism affect species assembly on island.

Keywords: Evolutionary models

Testing the optimality framework with empirical data of rising CO₂ levels on *Solanum dulcamara*

Ms Astrid Odé^{a1}, KT Rebel¹, MJ van der Ploeg², HJ de Boer¹

¹ Utrecht University, Copernicus Institute of Sustainable Development, Environmental Sciences

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The optimality framework of Prentice et al. (2014) predicts relationships between photosynthetic traits and leaf gas exchange of plants. Photosynthesis and gas exchange traits, such as V_{cmax} , g_s , g_{smax} , and J_{max} , depend strongly on morphological characteristics, including leaf hydraulics (Brodribb et al., 2007) and the conservative g_s/g_{smax} ratio (McElwain et al., 2016). This research aims to relate adaptations of these morphological features to adaptations of photosynthetic traits (mainly g_s/g_{smax} and V_{cmax}) over different timescales. Here we present empirical data to test predictions of this optimality model on the effects of changing CO₂ concentrations. Two genotypes of *Solanum Dulcamara* were used; the 'dry' genotype is adapted to well-drained sandy soil, and the 'wet' genotype is adapted to poorly-drained clayey soil. Seeds were grown under 200, 400, or 800 ppm CO₂ in climate chambers. The optimality model predicts a trade off between the costs of transpiration and the costs of photosynthesis. The v_{cmax} decreased in both genotypes at higher CO₂ concentrations. The dry genotype had a higher Huber value and lower V_{cmax} , in comparison to the wet genotype, and the dry genotype also showed the highest down-regulation of V_{cmax} under high CO₂, while the wet genotype displayed the highest down-regulation of g_s . Vein density and guard cell length were strongly correlated, and had the clearest response to different CO₂ levels. Effects on stomatal density were absent, but it was correlated to the guard cell length. The results of the photosynthetic traits and g_s are in line with the optimality model, while leaf morphological traits appear less consistent with the theory.

Keywords: Optimality theory

The effect of nutritional constraints on plant functioning; Studying stoichiometry for optimality theory testing

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Evolution is a process favouring the optimally adapted individuals. Applying Eco-Evolutionary Optimality (EEO) models provide simple and accurate representations of leaf level processes. EEO approaches are scarcely applied to whole plant levels, while this addition will prove useful in modelling plant- and ecosystem interactions and dynamics. The increasing anthropogenic emissions of CO₂ alongside changing nutrient availability prove a challenge for modelling as nutritional limitations constraining global plant productivity will change significantly. Relieving certain nutritional limitations will impose restrictions of other essential nutrients on plants. Interacting effects of elevated CO₂ and limitation of essential nutrients are thought to affect plant tissue concentrations, organ growth rates, and photosynthetic capacities. However, it remains uncertain how this optimality at leaf level translates to optimality in total plant functioning. In an exploratory study plants were treated with three different CO₂ treatments and two different phosphorus (P) treatments in a factorial design. It is hypothesised that (I) the effect of P deficiency on total plant biomass accumulation is stronger in plants grown in higher CO₂ concentrations, and (II) increase in CO₂ concentrations will decrease relative allocation of nitrogen (N) and P towards leaves to optimize the relation between photosynthesis and respiration. Three different species, *Panicum miliaceum*, *Solanum dulcamara*, and *Holcus lanatus* were grown at either high (800ppm), ambient (450ppm) or low (150ppm) CO₂ concentrations. They were treated with sufficient P (an N:P ratio of 1:1) or low P (an N:P ratio of 45:1, with similar N), and were measured for photosynthetic traits. Preliminary analysis suggests P deficiency both negatively affects growth and maximum photosynthesis rate, with an increased effect in low CO₂ conditions. In addition to the existing analyses, leaf N and P concentrations will be assessed alongside electron transport rate and maximum carboxylation rate to determine leaf stoichiometry, relative allocation and their effects on photosynthesis.

Keywords: Optimality theory

Models of Leishmania transmission and control at multiple scales

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Leishmaniasis is a neglected tropical disease endemic in many regions around the globe. It is responsible for thousands of deaths each year [1] and is caused by parasites of the Leishmania genus. Leishmania parasites can infect many mammalian species [2] but depends upon sand flies as a vector. Despite efforts to understand leishmaniasis transmission, particularly in humans, rodents and canines, the transmission dynamics are yet to be fully uncovered. Recent work has further developed our understanding of the complex life cycle of Leishmania parasites in their sand fly vector [3] and highlighted the importance of the distribution of parasites in the skin of the mammalian host [4]. The interaction between patchy skin parasite distributions, variability in sand fly feeding behaviour, parasite population dynamics in the sand flies may be crucial to leishmaniasis transmission [5]. My focus is on understanding the influence of heterogeneity at various scales on transmission, from the micro-scale of parasite uptake and deposition [5] to the macro-scale distribution of cases across regions such as Brazil, and on the implications that this has for controlling the disease in endemic regions. I will present results based on multi-scale modelling of the transmission process in heterogeneous environment. I will also show some new statistical approaches which we are developing with the aim of prioritising public health interventions.

Keywords: Epidemiology

Title

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Microbes play crucial roles in a wide range of ecosystem functions and constitute a large proportion of Earth's biodiversity. However, ecologists are yet to come to a consensus on the trends and underlying mechanisms of microbial species diversity along temperature gradients (e.g. across latitudes). I investigated the species richness pattern that merges in mesophilic bacterial communities assembled at different environmental temperatures using a general, metabolically-constrained mathematical model parameterized with real data. I find that species richness after assembly declines with increasing temperature, irrespective of the strategies that microbes adopt. This decline with warming is mainly governed by differential extinction of species' metabolic strategies driven by resource competition in the face of changing temperature. Specifically, species with higher intrinsic carbon use efficiencies (CUE) are favored especially at higher temperatures, which is the combination of higher thermal sensitivities in uptake rate and lower thermal sensitivities in respiration rates. As metabolic rates increase exponentially with temperature, effective competition among species increased for the fixed amount of resources available, so relatively higher facilitation and higher resources partitions (lower resource overlaps) are favored. These results suggest that even if the species thermal physiologies vary independently, the emergent community CUE would still increase with temperature as a result of species sorting. To the best of my knowledge, this is the first theoretical study on the effect of temperature on diversity and its link with CUE of complex microbial communities. This study provides new mechanistic insights into the geographical patterns of microbial diversity and their relation to carbon cycling.

Keywords: Population dynamics

Validating a Lotka-Volterra approximation to the Microbial Consumer Resource Model

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The use of mathematical models for simulating microbial communities has become an important tool to predict the outcomes and drivers of community assembly. However, models such as these are often analytically intractable and computationally demanding, calling for the use of approximations which, in turn, require that researchers make non-trivial assumptions about the behaviour of the system. One such instance is the microbial consumer-resource model (MCRM), often approximated as a generalized Lotka-Volterra model given the assumption that resource dynamics equilibrate faster than those of consumers. Unfortunately, the “fast” resource dynamics assumption has not been characterized for nutrient supply regimes typically used in microbial culturing techniques. In this poster I outline the validity of the Lotka-Volterra approximation to the MCRM and evaluate nutrient regimes which satisfy the “fast” resource dynamics assumption.

Keywords: Population dynamics

Coevolutionary Stability of Host-Symbiont Systems

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The existence of an Evolutionarily Stable State (ESS) in a host-symbiont interaction at ecologically stable coexistence is studied in the framework of a two-player game. Our basic objective is to obtain an evolutionary insight into the transmission behaviour of symbionts (which can be either parasitic or mutualistic) which are obligate and host-specific. To address this scenario, a general problem of coexistence of host and symbiont is considered with both vertical and horizontal transmission at the same time. The evolutionary success of the vertically transmitted symbionts is given by the evolutionary success of their infected host lineage. Furthermore, our selection situation belongs to the multi-species group selection models as the symbionts and the host together form a “group”. The novelty of our study is that the dynamics of group formation is not based on interactions between the host and the symbiont, and also that the horizontal infection and clearing of infection are independent. Age-structured population based on the general kin demographic selection with dependence between infected and non-infected lineages is considered. The main idea of this model is that the evolutionarily best phenotype maximizes its phenotypic long-term growth rate. We derive the population dynamics of the system based on this model and find a two-species stable ecological state. For the evolutionary stability of the resident system, we require that each mutation introduced at the stable state will die out by ecological selection. A game between the obligate symbiont and the host, with payoffs dependent on long-term growth rates of the lineages, is examined at this ecological stable state of the host-symbiont coevolutionary selection dynamics. The objective is to establish the existence of a strict Nash equilibrium and thereby an ESS for the host-symbiont interaction which in turn illustrates the final state of co-evolution.

Keywords: Evolutionary Game Models, ESS, Structured Population Dynamics

An Ocean Biochemical Model With Chemical Interactions Between Planktons

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Harmful phytoplankton release toxins that inhibit growth and reproduction of their competitors. This phenomenon, referred to as allelopathy, was confirmed in previous studies through laboratory experiments and models of interspecific competition. Large-scale ocean biogeochemical models have been developed and are widely used in various studies on plankton dynamics in marine ecosystems. However, the role of allelopathy and the effects of phytoplankton toxins on zooplankton, have not been explicitly represented in these models. Therefore, this research aims to fill the above-mentioned gap by incorporating allelopathy and algal toxicity into MEDUSA, an ocean biogeochemical model of intermediate complexity. Firstly, each of the two phytoplankton functional groups in MEDUSA was subdivided into toxic and sensitive groups to create four new groups: toxic and sensitive diatoms, toxic and sensitive non-diatoms. Secondly, the default dynamic equation for each phytoplankton group was expanded to include allelopathy. Following this, the amended MEDUSA was coupled to a 1D hydrodynamic model to simulate the influence of allelopathy on phytoplankton dynamics. In the next step, dynamics of toxins in the plankton pool will be added to facilitate explicit representation of allelopathy in the model. A detailed description of the modified biogeochemical model representing these chemical interactions, along with some preliminary results from the 1D model simulations, will be presented in this conference. Going forward, the updated biogeochemical model will be coupled to a 3D hydrodynamic model and deployed for detailed studies on dynamics of marine phytoplankton in selected regions.

Applications of heat stress indices for ecology

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Extreme heat is a growing risk to both human and planetary health. Examples include, impacting specie migration patterns especially types of bird and impacting the diversity of species across ecosystems. The latest physical basis of the IPCC report states that they are now very confident that heatwaves are linked to climate change over both the land surface and in the oceans. One aspect of extreme heat is heat stress, the build-up of body heat as a result of external environment and/or exertion. Heat stress has a profound impact on global ecosystems both on land and in a marine environment. In the Pacific Northwest heatwave in June 2021, over 1,000 people lost their lives at the same time as over 1 billion marine animals died. thermofeel is a python library that was developed at the European Center of Medium-Range Forecasts (ECMWF) to be able to model and forecast heat stress whilst adhering to open data principles, it is currently in pre-operations. Here, the discussion of which heat stress indices could be applicable across human health and planetary health will be explored and how a OneHealth approach to heat stress modelling could improve our understanding of the intersections of this deadly hazard.

Improving Treatment of Metastatic Cancers Through Game Theory and Dynamical Systems Theory

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Here we investigate whether in a model of Pressley et al., a low constant dose can stabilize the tumor at a viable tumor burden and maximize the patient's quality of life. When stabilization of the tumor is possible, the constant lower dose is calculated based on Stackelberg evolutionary game setting presented by Salvioli. We prove that for all models in Pressley et al.'s work at the equilibrium cancer population is always descending as drug dosage increases. Therefore, the stabilization of the tumor with a lower constant dosage is only possible if MTD stabilizes the tumor. This changes if we include competition coefficients in this model. Furthermore, in the Pressley et al.'s model at the equilibrium point of the polymorphic population one cell type would go extinct. With competition coefficients, neither cell type contains the other kind and they can coexist. In the Stackelberg evolutionary game model, the physician as the leader selects the treatment dose to optimize the patient's quality of life if the viable stable cancer population can be reached. For each of the models without competition coefficients and the extended model with direct competition between different cell types, the Stackelberg solution (corresponding to evolutionary treatment) and Nash solution (corresponding to ecological treatment) are investigated. We show that Stackelberg strategies lead to the best results in terms of patient's quality of life, followed by Nash strategies, with MTD leading to the worst quality of life. The stability and reachability of the Nash and Stackelberg solutions are also analyzed. Our research demonstrates that game theory is a useful tool for optimizing treatment within the context of evolutionary therapies.

Dating a lineage without fossils: A case study of Amaryllidaceae

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Amaryllidaceae J.St-Hil. sensu APG III (2009) has a cosmopolitan distribution and comprises three subfamilies (Agapanthoideae, Allioideae, and Amaryllidoideae) with approximately 90 genera and between 1700-1800 species. Amaryllidaceae includes many economic and horticulturally important genera including *Narcissus* L. (daffodils), *Allium* L. (onions) and *Agapanthus* L'Her. (African lilies). Previous research indicates Amaryllidaceae diverged somewhere in Africa, however, estimates of when and exactly where this divergence occurred are limited. A particular challenge of dating Amaryllidaceae is the lack of fossils attributable to the family and so divergence estimates are based on other monocotyledon lineages. Current estimates of Amaryllidaceae divergence are between 62.5 – 45 MYA. These dates are derived from high level studies of monocotyledon and broader angiosperm lineages. Due to the very limited representation of Amaryllidaceae in these studies, divergence dates within the family have not been accurately estimated and the date of the family is uncertain. Here we generate a dataset of 78 plastome protein coding genes from a total of 162 samples covering 59 Amaryllidaceae genera. This extensive sampling of the family makes it possible to estimate more accurately the divergence of the family, subfamilies and genera. Both maximum likelihood and Bayesian analysis have been conducted to determine evolutionary relationships within Amaryllidaceae. Preliminary divergence analysis suggests Amaryllidaceae diverged in the early Eocene (47 MYA) during a period of warmer and wetter conditions.

Keywords: Amaryllidaceae, Molecular Dating, Phylogenetics

Climate change and harmful algal growth using laboratory experiments and biogeochemical modelling

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Climate change is expected to alter the growing conditions in aquatic ecosystems, and, as a consequence, an imbalance in ecosystem dynamics due to changes in algal or cyanobacterial growth rate and toxin production is expected. This imbalance can cause major environmental impacts such as the occurrence of harmful algal blooms, creation of dead zones in aquatic habitats and altering the productivity of fisheries. Therefore, it is important to investigate the effects of multiple factors that may simultaneously impact algal growing conditions. Key environmental conditions that influence the growth rate and toxicity of algal species are temperature, light intensity, nutrient concentration, and pH level. However, previous laboratory studies focused on one or two factor(s) in relation to algal toxin production. This study aims to monitor all the factors simultaneously by modelling algal growth and toxin production in laboratory conditions. To achieve this, the impact of each environmental condition on the growth rate and toxin production was identified by analyzing experimental data reported in the literature. The growth rate and toxicity of algal species were found to increase when the temperature was between 20°C and 25°C. When the light intensity was about 100 $\mu\text{mol m}^{-2} \text{s}^{-1}$, both growth rate and toxicity increased. Algal growth and toxin production was also found to positively correlate with high nutrient concentration. Finally, it was reported that a pH level of 8 is optimal for the growth rate and toxin production of algal organisms. These findings will be presented and the optimal conditions for growth and toxin production will be discussed. This forms a preliminary step for conducting a set of experiments to identify how a combination of multiple environmental conditions may impact growing conditions and population dynamics. The laboratory data will then be used to develop a new model of algal growth rate and toxin production.