Stochastic Evolution of Populations in Fluctuating Environments

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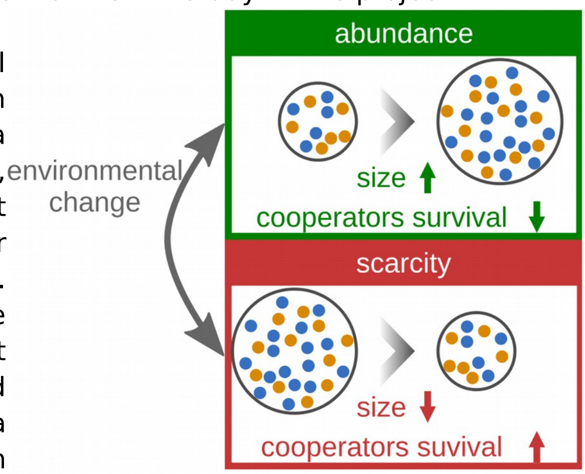
Why does cooperation abound in Nature? Why are there so many coexisting species and not just a few dominant ones? These are issues of paramount importance in biology and ecology and are among the “big questions facing science” [1]. In fact, while there are many examples of cooperative behaviour in Nature, these are challenges to Darwinian evolution since altruism increases the fitness of a population at a cost for the single individual: In the absence of appropriate mechanisms, cooperation is not sustained by evolution. Furthermore, how the interactions between organisms and between the environment and the species shape the biodiversity remains a fascinating puzzle: Some ecological system are composed by a very large number of coexisting species and others by much fewer, and species diversity can greatly vary within an ecosystem.
It is well established that birth and death events by which the composition of a finite population changes yield demographic fluctuations that are ubiquitous and can lead to the extinction of some species and to the survival of others [2-4]. Moreover, organisms of an ecosystem generally move and form spatial arrangements that often help maintain their coexistence [5]. In addition to demographic fluctuations and spatial effects, natural populations face ever-changing environmental conditions (e.g. temperature, light, pH, …) that can influence their evolution. The changes in external conditions are often modelled by environmental noise whose impact has been studied in a number of systems where demographic noise was assumed to be independent of the environmental changes, see e.g. [6]. However, the dynamics of the population composition is often coupled with the evolution of its size, which results in a *coupling between demographic fluctuations and environmental noise.* This is particularly relevant to microbial communities, which can experience sudden and extreme environmental changes, and leads to a number of challenging mathematical and modelling issues that we will study in this project.

The class of problems that we will study is well illustrated by the following example based on Ref.[2], in which a population consisting of a two strains of bacteria compete for resources, a fast strain (free riders) has a constant selective advantage over the other (cooperators) that produces a public good. While free riders always prevail in the absence of randomness [3], the probability that cooperators take over is greatly enhanced when the population size is driven by a carrying capacity that randomly switches from a state of abundance in which the population size is large to a state of scarcity in which the population shrinks: When the population size is small (scarcity of nutrients), demographic fluctuations are stronger than when nutrient is abundant which counterbalances the selection pressure and enhances the chance for cooperation to prevail, see Cartoon and the supporting videos [2].



Intertwined evolution of the population and its composition in the model of Ref.[2]: Slow and fast strains (blue and yellow) interact according to a birth-death process [3-5], while the carrying capacity randomly switches between two values and drives the population size. Demographic fluctuations are coupled to environmental randomness.

Objectives

Evolutionary game theory (EGT) describes the dynamics of populations in which the success of one type depends on the actions of the others. In EGT, selection pressure varies with the species densities and thus the population composition as well each species' fitness change continuously in time. EGT provides a suitable framework to model the evolution of cooperative behaviour that is generally formulated in terms of Markov birth-death processes such as the Moran model in which at each time-step two randomly-picked neighbours interact and the offspring of one replaces the other with a probability proportional to their relative fitness [3,4]. While EGT models have been extensively studied, little is known about the joint effect of coupled environmental and demographic randomness on the evolution of cooperation, and even less is known about their effects in a spatial setting. Important objectives of this PhD project are therefore the following:

- An interesting starting point will be to generalize the approach of Ref.[2] and analyse how environmental randomness affects the evolution of paradigmatic EGT models in various cooperation scenarios [3,4]. For this we will consider the prisoners' dilemma, the snowdrift or the stag-hunt games, and public goods games in finite well-mixed populations of fluctuating size, e.g. driven by a randomly switching carrying capacity [3,2]. We will thus study the probability that cooperation prevails and the mean time for this to happen. We will also investigate how the population size evolves when its internal composition changes (what is its long-time distribution?)

- It is known that space and movement play important roles in population dynamics and can drastically affect the evolution of cooperation [3]. We will thus investigate the spatially-extended counterparts of the above EGT cooperation scenarios by considering that the population is arranged on a lattice consisting of interconnected patches of fluctuating size between which individuals can move. By combining computer simulations with approximate analytical calculations we will investigate under which circumstances space favours or hinders the evolution of cooperation.

- We will also investigate the role of environmental noise on species diversity by studying the voter model with speciation when the population size fluctuates [7,8]. This is a reference neutral model used to understand what shapes biodiversity and species coexistence across scales when randomness is the prime evolutionary force (selection is assumed to be negligible) [9,10]. In this model, closely related to the Moran models used in EGT, an organism is randomly killed and replaced with some probability by an offspring of a neighbour or, with a complementary probability, by an individual of a new species. Here, we plan to study the voter model with speciation in a metapopulation consisting of a lattice of patches connected by migration and endowed with a fluctuating carrying capacity. We will be chiefly interested in determining the species-area relationship that measures how the number of observed species increases upon enlarging the sampled area [9,10].

The ultimate goal of the project will be to have gained a thorough understanding of the biologically-relevant and mathematically-challenging situations where populations evolve being subject to randomness stemming from a realistic coupling between fluctuating environmental factors and demographic stochasticity. It is expected that the theoretical advances will lead to predictions that could be tested experimentally, e.g. in microbial communities with suitably engineered switching strains [11].

Potential for high impact outcome

The proposed project branches out from a recent work [2] that has just been published in a high-impact journal (Physical Review Letters) and has already attracted significant attention. One of the reasons is the resonance of the research topic across various disciplines (e.g. in biology, ecology, physics, behavioural and environmental science) and possible applications. Furthermore, both supervisors have a track record of publishing in high-impact journals. We therefore anticipate the project generating several papers with at least one being suitable for submission to a high impact journal.

Training

The student will work under the supervision of Drs Mauro Mobilia and Sandro Azaele within he Department of Applied Mathematics. This project provides a high level of specialist scientific training in: (i) stochastic modelling (analytical and computational); (ii) applications of statistical mechanics methods to models of evolutionary game theory and theoretical ecology; and (iii) high-performance computing (HPC) to perform large-scale simulations of spatially extended systems. Co-supervision ill involve weekly formal meetings with Drs Mobilia and Azaele as well as more frequent meetings with either supervisors when necessary. The PhD student will have access to the various training workshops put on by the Staff and Departmental development Unit at the University of Leeds and will also be encouraged to undertake the training on HPC provided by the Leeds Advanced Research Computing (http://arc.leeds.ac.uk/training/). This project builds on a long-standing collaboration with the group of Professor Erwin Frey (https://www.theorie.physik.uni-muenchen.de/lsfrey/group_frey/index.html) at the University LMU of Munich of which the PhD student will certainly benefit.

Student profile & pre-requisites

The student should have a solid background in a mathematical subject such as applied mathematics or theoretical physics. They should have a taste for interdisciplinary applications of mathematics and computational methods, especially with relevance to biology and ecology. As in all scientific endeavour, intense motivation and genuine curiosity are essential. Applicants should thus have:

- A genuine interest in applications of mathematical modelling to biology and ecology.
- A strong mathematical background: a degree in a mathematical subject (e.g. physics, computer science).
- Experience with programming or computational modelling is not obligatory but the candidate must be willing to learn required computational techniques. Prior knowledge of R, Matlab, C++ or Python will be valuable.

References

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