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Abstracts of Plenary and Invited Lectures

Section:

0. Plenary Lectures

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The Population Dynamics of Conflict and Cooperation

Among the wide-ranging applications of mathematical modelling to biological problems, those dealing with ecology and evolution have proved particularly challenging for stochastic processes and dynamical systems. This lecture attempts a survey, emphasising the major feedback mechanisms acting on the densities of the interacting populations and keeping mostly to the framework of ordinary differential equations. (Time delays, spatial heterogeneities and stochastic fluctuations have a major impact in many applications.)
Even the simplest Lotka-Volterra models of three interacting species display a strong propensity for instability, for instance chaotic oscillations (in the one-predator, two-prey case) or heteroclinic attractors (for three competing species). Stability notions in the sense of Lagrange are often more appropriate than Lyapunov stability for population ecology. Basic questions concern permanence (can small perturbations lead to the extinction of some populations?) and invadability (will a population grow if introduced in small numbers?). Contingency and history-dependence play an essential role in the assembly of ecological communitities (keystone predators mediate the diversity of the ecosystem, species can invade but alter the community in such a way that they become extinct and cannot be re-introduced, a set of stably co-existing species cannot be obtained through sequential invasion by these species alone etc.)
Competition among conspecifics drives natural selection. Game theory allows to investigate the relative success of different behavioural types in conflicts within and between species (when fighting for resources, for instance, or investing in offspring). The interactions of individuals lead to collective dynamics of populations, regulating key parameters like sex ratio, clutch size or dispersal rate. The simplest dynamics, the replicator equation, is equivalent to the Lotka-Volterra dynamics. It is based on the assumption that strategies 'breed true' and are transmitted to offspring proportionally to the payoff currently achieved. Other dynamics take account of the intricacies of Mendelian inheritance, and still others are based on transmission via imitation and learning. The latter approach – adaptation by cultural means – allows to apply evolutionary game theory to economics and social sciences, to analyse its relation with the equilibria concepts of classical game theory and to stress the importance of non-equilibrium outcomes. Adaptive

dynamics (based on assuming that replication is only almost exact) provides a tool for describing long term evolution by mutation and selection.
Of biomedical relevance are applications to epidemiology, immunology and virology. Mathematical models help to understand the course of infectious diseases both within organisms and within populations, and suggest guidelines for treatment and vaccination. Within individual organisms, pathogens elicit immune responses which then attack the pathogens in much the same way as prey and predators interact. Within the population, the interactions of infected, susceptible and immune organisms lead to endemic or epidemic forms of the disease.
The evolution of virulence (i. e. the parasite-induced mortality of host organisms) has attracted particular attention. Pathogens use the bodies of their hosts both as resource and as vehicle. Mathematical models show that by having to spread within and between organisms, parasites often face conflicting demands on transmission rate and long-term exploitation. In the case of co-infection, i. e. when several strains compete, selection on parasites need not optimise the exploitation of the host (or the basic reproductive rate, i. e. the number of infected hosts produced by an infected individual in a population of susceptibles). Game theoretical arguments help in analysing such situations.
The parasite ecology is further complicated by countermeasures of the hosts. Due to their short generation times, parasites are usually at an advantage – witness the rapidly evolving resistance to antibiotics – but sexual reproduction allows host organisms to recombine immunotypes and thus to present shifting targets to the pathogens trying to enter the cells. Mathematical models for the resulting arms races display a profusion of limit cycles, irregular oscillations and heteroclinic cycles and make evolution look like a treadmill rather than a ladder.
Nevertheless, evolution has been punctuated by some major transitions to new levels of organisation, for instance self-replicating molecules, chromosomes, cells, multicellular organisms, colonies and societies. In most cases, this emergence of nested hierarchies was due to the fusion of formerly independent units into entities of higher order (which remain threatened by exploitation through mutinies of 'selfish' units). Evolutionary game theory provides a tool for the analysis of such feats of cooperation: catalytic loops of RNA molecules exhibit limit cycles, the suppression of 'outlaw genes' within the genome leads to heteroclinic repellors, etc.
In particular, direct and indirect reciprocity, which play a basic role in human societies, can be understood by means of repeated interactions. Mutual aid emerges through learning rules, moralistic emotions, social pressure and reputation. Thus biological evolution leads game theory back to its original economic motivation.