Evolutionary Games

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1 Overview of the Field

Since the workshop held at BIRS in 2006 on the same topic, evolutionary game theory has continued to expand in the directions identified there as well as in several new directions. There seems to be a tendency to reach out from the founding concept of an evolutionarily stable strategy, towards related concepts such as continuously stable strategies and stochastically stable strategies, towards the analysis of polymorphic equilibria and complex population structures, towards a dynamic underpinning of the evolutionary process based on different transmission mechanisms, towards the investigation of how individual information and ongoing interactions impact population behavior, towards a reinterpretation of existing models of population dynamics using a game-theoretic perspective. These directions lead to a large variety of stochastic processes and deterministic dynamics whose interrelation is far from being fully understood.

The 2010 workshop aimed to bring together people with different modeling approaches and to allow them to appraise the state of the art in the neighboring fields. This seems all the more useful as evolutionary games have been approached within several different disciplines with very different traditions and also different channels of communication (journals, conferences etc). We mention here classical, economy-based game theory versus biology-driven evolutionary models; probabilistic reasoning based on finite population models versus ordinary differential equations assuming infinite, well mixed populations; equilibrium concepts versus complex attractors; long-term versus short-term evolution; frequency-dependent population genetics versus learning models based on imitation, or endogenous aspiration levels, etc.

To give some specific examples, extensive-form games have for decades been analyzed entirely by static classical game theory techniques based on rationality assumptions, but have recently been exhaustively studied from a dynamic perspective in a monograph [8] on evolutionary games and applied to existing models such as signaling games[19]. Classical stochastic processes used in genetics, as for instance the Moran process, have provided the basis for an entirely new analysis of evolutionary dynamics in games in finite populations[15, 23], using concepts such as substitution and fixation. There are surprising relations between different types of deterministic game dynamics, as for instance between the orbits of the best-reply dynamics and the time-averages of solutions of the replicator equation[18]. Non-linear payoff functions are increasingly well understood, for instance through adaptive dynamics[20]; population games have been investigated in depth[28]; games with continuous strategy spaces become increasingly important, and often lead to other predictions than in the discrete case[17]; games on graphs [22, 25] and dynamic graphs [14, 26] are of obvious importance for the evolution of cooperation. The phase-transitions in spatial games attract more and more investigators wielding the tool-box of statistical mechanics and power laws[31], etc.

The main focus of the workshop was on mathematical methodology. However, since most of the new methods have been devised by applying them to very concrete examples from biology or experimental games, it was important to also have several lectures concentrating on new applications. These include the study of animal movement between spatially separated patches through the habitat selection game[1] . Such new directions enhance our understanding of evolutionary methods that predict individual behavior modeled by game interactions.

In addition, experimental work on the evolution of cooperation in Public Goods and Prisoner's Dilemma games pioneered by Fehr, Gächter, Milinski, et al. [12, 13] are gaining new impetus in the last couple of years. New results from groups led by Nowak and Cressman point to interesting cross-cultural similarities and differences.

2 Presentation Highlights

During the workshop week, there were two concurrent programs: one on Evolutionary Games and the other on Inclusive Fitness in Evolutionary Modeling. Many of the topics discussed in both workshops are of mutual interest to all participants, hence there were many interactions between the two workshop during open discussion sessions in the Max Bell Lecture Hall as well as informally in the lounge and dining hall.

In the first half of the morning, both workshops gathered together for lectures from the Inclusive Fitness group. David Queller (Rice University) spoke on non-additivity, joint effects, frequency dependence and green beard effect; Andy Gardner (University of Oxford) on the genetic theory of kin selection; Mike Whitlock (University of British Columbia) on applications of evolutionary model in discrete and spacial population to evolution of recessive alleles and social evolution; Sébastien Lion (University of London) on inclusive fitness theory applied to complex and realistic ecological dynamics; Samuel Alizon (ETH) on kin selection methods in evolutionary epidemiology; and finally Suzanne Alonzo (Yale University) on how interactions within and between sexes affect the evolution and ecology of reproductive traits, paternity and male tactics, sexual conflict and selection using phenotypic and genetic modeling approaches with ocellated wrasse as the focal species.

The rest of the day was filled with Evolutionary Games talks, with occasional visits from the Inclusive Fitness group as well from the Focused Research Group on Discrete Probability. All of our twenty participants gave talks covering a wide spectrum of themes:

- A few of our speakers presented work of interest to both workshops in attendance.
  - Jeff Fletcher (Portland State University) affirmed his belief that inclusive fitness is an accounting method, not a fundamental mechanism. He argued that various theories of the evolution of altruism rely on the same underlying requirement for sufficient assortment between the genotype in question and help from others.
  - Feng Fu (Harvard University) presented a minimal model of in-group favoritism in homogeneous populations. The population is divided in groups according to each individual's randomly assigned tag. Each individual has the same level of in/out group helping tendency. Individuals' tags and behavioral strategies are both heritable traits that are subject to mutation and selection. Feng derived an analytical condition for cooperation to evolve under weak selection using coalescent theory. The critical benefit-to-cost ratio reaches minimum when individuals only help in-group members and refrain from helping out-group members.
  - Sabin Lessard (Montréal University) discussed the effects of relatedness and population subdivision on long-term evolution based on interactions in finite group-structured populations[21].
  - Recent work of Hisashi Ohtsuki (Tokyo Institute of Technology) on evolutionary games in island model is of particular interest to the inclusive fitness group. Hisashi investigated the evolutionary dynamics of games played in a subdivided population which follows the Wright's island model. He found that limited dispersal produces positive association among neighbors' strategies, hence coefficients of relatedness appear in the main equation. His results can be interpreted in terms of inclusive fitness, and several previous results follow this setup.

- Theoretical studies of evolutionary games continues to flourish.
  - Tibor Antal (Harvard University) presented his recent work with Fu, Nowak, Ohtsuki, Tarnita, Taylor, Traulsen, Wage and Wakeley using perturbation theory to study games in phenotype space under weak selection[2, 3]. The main focus is on determining the strategy that is most abundant in the long run. The technique developed can be applied to games with multiple strategies and games in structured populations.
  - Joseph Apaloo (St. Francis Xavier University) gave an overview on the mathematical theory for describing the eventual outcome of evolutionary games involving single species as well as multi-species evolutionary models[4].
- The effect of reputation, reward, and punishment on the evolution of cooperation and altruism remains a fascinating topic. Prisoner's Dilemma and Public Goods games have become the mathematical metaphors for game theoretical investigations of cooperative behavior in respectively pairs and groups of interacting individuals. Cooperation is a conundrum because cooperators make a sacrifice to benefit others at some cost to themselves. Exploiters or defectors reap the benefits and forgo costs. Despite the fact that groups of cooperators outperform groups of defectors, Darwinian selection or utilitarian principles based on rational choice should favor defectors.
  - Indirect reciprocity is one of the main mechanisms to explain the evolution of cooperation. Ulrich Berger (Vienna University of Economics Business Administration) introduced a new notion of "tolerant scoring", a first-order assessment rule with built-in tolerance against single defections, to understand the evolution of cooperation in Prisoner's Dilemma Game[6]. The upshot of the analysis in this framework is that all individuals are discriminators and most cooperate.
  - There have been much interest and progress in experimental study [11, 12, 13, 27] on the evolutionary of cooperation. Ross Cressman (Wilfrid Laurier University) reported results from two experiments [34] that test the effects of punishment and/or reward schemes on the cooperative behavior of players in repeated Prisoner's Dilemma (PD) and Public Goods (PGG) games. Subjects for both game experiments were university students in Beijing. For the PD experiment, costly punishment does not increase the average level of cooperation compared to the control experiment where this option is not available. This result contrasts with several similar experiments conducted in western societies. On the other hand, in the PGG control experiment (i.e. the standard repeated PGG without reward or punishment), the average contribution levels to the public good match closely those found in the same control conducted in Boston. The PGG experiment shows that combined reward and punishment schemes are most effective in increasing contributions, followed by punishment on its own and that reward on its own has no significant effect on contributions. These results differ from those in Boston that exhibited little difference in contribution levels when players reward, punish, or reward and punish each other between rounds. The experiments are discussed in relation to cultural differences in attitudes to a player's reputation and to institutional incentive schemes to increase the cooperative behavior of its members.
  - Christoph Hauert (University of British Columbia) outlined his recent work with Peter Forsyth, an undergraduate student, on incentives for cooperation which may defeat the social dilemma of cooperation. Negative incentives based on the punishment of shirkers are efficient in stabilizing cooperation once established but fail to initiate cooperation. In the complementary case of positive incentives created by rewarding those that did contribute to the public good, cooperation can be initiated in interaction groups of arbitrary size but, in contrast to punishment, can not be stabilized. In fact, the dynamics of reward is complex and dominated by unpredictable oscillations.
  - József Garay (Eötvös University) considered the four behavioral traits: envy (reducing the fitness of more successful individuals at one's own cost), charity (increasing the fitness of less successful individuals at one's own cost), spitefulness (decreasing others' fitness unconditionally at one's own cost), and selfishness (neither decreasing nor increasing others' fitness). He found that when damage is additive, envy dominates selfishness if the cost of envy is low, envy and selfishness

can replace spitefulness when cost of damage is high, moreover, envy is selected in a mixed population of all four strategies. When damage is multiplicative, coexistence of selfish and envious strategists is possible. Envy is a conditional spiteful strategy, so in envious groups there is less damage than in spiteful groups, hence envy decreases the total cost of the spiteful competition. In a simple kin-selection scenario the envious-spiteful strategists (envious within its kin and spiteful outside its kin) outperform selfish and spiteful ones as well.

  - Karl Sigmund (University of Vienna) provided yet another perspective on the effect of punishment in the evolution of cooperation. Karl and his colleagues analyzed the effect and dynamics of peer versus pool punishment in public goods games. It is well known that sanctions promote collaboration in public goods games, but since they are themselves a public good, second-order free riders, who do not punish defectors, can exploit this and subvert cooperation. The punishment of second-order defectors is called second-order punishment. Most experiments use peer punishment, which is ill suited for second-order punishment[9, 30]. But another form of punishment, called pool punishment, is better suited to the task. In an open competition of peer with pool punishment, the latter prevails if and only if second order punishment is included. Pool punishment trades efficiency for stability. It is an implementation of the self-financed contract enforcement mechanisms which are frequently found in real-life institutions implementing the 'governance of the commons'.

- Michael Doebeli discussed his recent work with Ispolatov on the origin and maintenance of phenotypic diversity in a population or species[10]. They extend the classical Gaussian model for frequency-dependent competition from one to many phenotypic dimensions. Their analysis indicates that for a number of phenotypes, each of which is under stabilizing selection and frequency-dependent selection, where frequency-dependence is sufficiently weak to induce maintenance of diversity along any of the phenotypic components in isolation, then any interaction between phenotypes strongly increases the tendancy for diversification.

- Vlastimil Krivan (Academy of Sciences of the Czech Republic) analyzed models of optimal foraging theory with respect to evolutionarily stability of optimal strategies[1]. An improvement is made on the original prey and patch models introduced by Charnov which assume frequency independent fitness functions that are proportional to energy intake rate by a single consumer. In the dynamic setting with frequency dependent fitness functions and corresponding evolutionarily stable strategies, partial preferences for food types arise.

- At our 2006 workshop, Hauert, Lieberman, and Ohtsuki showed a simple rule ($r > k$) for the evolution of cooperation on graphs and social networks[25], namely the benefit to cost ratio must exceed the average degree of a node. Since then, Pacheco and Santos showed that social diversity promotes the emergence of cooperation in Public Goods Games, particularly with fixed contribution[29].

  - Building upon these work on games on graphs, Cong Li (Chinese Academy of Science) together with Cressman and Tao explored three main questions: How does network structure affect the evolution of cooperation? Do different network structures work similarly? Which is the best network structure for the promotion of cooperation? Many biological, technological and social networks lie somewhere between two extremes which are regular and random networks. Watts and Strogatz [33] found these systems can be highly clustered, like regular lattices, yet have small characteristic path lengths, like random graphs, and they called these networks the 'small-world' networks. Barabási and Albert [5] also noticed that a common property of many large networks is that the vertex connectivities follow a scale-free power distribution, i.e., $P(k) \sim k^{-\gamma}$, where $P(k)$ is the probability that a vertex in the network interacts with other vertices. Cong and his colleagues found that for 'small-world' networks, network structure makes no difference in promoting cooperation under weak selection, regular graphs does best in PG games, promotion of cooperation is however sensitive to network structure under strong selection, and fixed contribution works to promote cooperation in 'small-world' and random graph for PD games but not for PG games under weak selection. For scale-free networks, the simple rule $r > k$ fails for some PD and PG games, and furthermore, scale-free network promotes cooperation more efficiently than regular, small-world, and random network.

- Jacek Miękisz (Warsaw University) discussed the Prisoner's Dilemma game on the Barabási-Albert scale-free network with costs of maintaining links. He showed that a population of players undergoes a sharp transition from the cooperation phase to a mixed cooperation/defection phase as the cost passes through its critical value. In the random matching model, players are randomly matched with a finite number of opponents - equal to the number of neighbors in the corresponding spatial model. Jacek showed that for the snow drift game, spatial structure promotes cooperation much better than the random matching of players.
- György Szabó (Research Institute for Technical Physics and Materials Science) talked about his work on social dilemmas in spatial systems with collective strategy updates[32]. Social dilemmas are studied with players following unconditional cooperative or defective strategies. The players are located on a square lattice and each player's income is collected from 2×2 games (including Prisoner's Dilemma, Stag Hunt and Hawk-Dove games) with the four nearest neighbors. The evolution of strategy distribution is governed by random sequential strategy updates. During an elementary process several players choose new strategies at random in a way favoring the income increase of a group they belong to. The strategy update is stochastic and the magnitude of noise is characterized by a "temperature" parameter using the Fermi-Dirac function that provides smooth transition from 0 to 1 in the strategy adoption probability. Systematic investigations are performed to determine the average frequency of cooperators in the stationary state when varying the payoffs, the size of group, and also the number of players who can modify their strategy simultaneously for a fixed noise level. The present dynamical rules support the maintenance of cooperation in two ways. On the one hand, cooperators and defectors can form chessboard like structure providing optimum income for the whole society if the sum of sucker's payoff and temptation to choose defection is sufficiently high. On the other hand, the enforcement of group interest supports cooperation within the region of Prisoner's Dilemma even if only one or two players can choose new strategy within an elementary step.

- Evolutionary game dynamics continue to spark interesting work, both in existing and new directions.

  - Marius Ochea (Tilburg University) , an economist, studied repeated Prisoner's Dilemma game under logit dynamics[24], focusing on five strategies: AllC (unconditional cooperators), AllD (unconditional defectors), TFT (reactive players), GTFT (Generous Tit-for-Tat), and Pavlov (Win-StayLoseShift). He discovered that the Rock-Paper-Scissors (RPS) phenomenon is abundant in the 3×3 ecologies involving Pavlov and GTFT players, and in the 4×4 ecology without GTFT, RPS cycles coexists with a chaotic attractor. AllC is detrimental to the TFT, GTFT, and Pavlov players in the 4×4 ecologies leading to AllD monomorphism, and Pavlov players succeeds in the 4×4 ecologies without AllC and goes to extinction in the 5×5 setting with AllC.
  - Another economist, Bill Sandholm (University of Wisconsin), discussed his recent work on sampling best response dynamics and deterministic equilibrium selection. Bill and his colleagues consider a model of evolution in games in which revising agents observe the strategies of k randomly sampled opponents and then choose a best response to the distribution of strategies in the sample. They prove that under the resulting deterministic evolutionary dynamics, which they call k-sampling best response dynamics, any iterated $(1/k)$- dominant equilibrium is almost globally asymptotically stable. They show as well that this sufficient condition for stability is also necessary in super-modular games. Since the selection occurs by way of a deterministic dynamic, the selected equilibrium is reached quickly; in particular, the long waiting times associated with equilibrium selection in stochastic stability models are absent.

    Bill also demonstrated the latest version of his shareware program **Dynamo**, a suite of easy-to-use Mathematica notebooks for generating phase diagrams, vector fields, and other graphics related to evolutionary game dynamics. The software is a great tool which provides intuitive and geometric perspective for researchers. The software is publicly available at

    `http://www.ssc.wisc.edu/~whs/dynamo/index.html`

Bill's forthcoming book, Population Games and Evolutionary Dynamics, offers a systematic, rigorous, and unified presentation of evolutionary game theory, covering the core developments of the theory from its inception in biology in the 1970s through recent advances. It will be a valuable resource for students and researchers in the field.

- Evolutionary game dynamics of two players with two strategies has been studied in great detail. These games have been used to model many biologically relevant scenarios, ranging from social dilemmas in mammals to microbial diversity. Some of these games may, in fact, take place among an artbitary number of individuals and not just between two. Two participants presented interesting work on the dynamics of multiplayer games.
  - It is often difficult to determine the exact payoffs in a game, furthermore, payoff values are frequently variable rather than constant. In finite random games, where there are n players, each having finitely many strategies with payoffs that are independent and identical continuous distributions, cooperation is preferable when a Nash equilibrium is not Pareto-optimal. Christine Taylor (Harvard University) gave a brief overview on the Pareto-inefficiency of Nash equilibrium solutions in finite random games[7], and then explored the relationship between cooperation and self-interest in certain classes of two-player multi-strategy games and multi-player two-strategy symmetric games. She found that cooperation is more advantageous in two-player multi-strategy random games as the number of strategies increases, and as the correlation between the two player's payoffs increases. For symmetric multiplayer two-strategy random games, cooperation becomes more beneficial as the number of players increases.
  - Arne Traulsen (Max-Planck-Institute for Evolutionary Biology) studied game dynamics of symmetric two-strategy multiplayer games[16]. In this setting, one can calculate fixation probabilities and compare them to each other or to neutral selection in the spirit of the $1/3$-rule. For games with multiple players and more than two strategies, some statements derived for pairwise interactions no longer hold. For example, in two player games with any number of strategies there can be at most one isolated internal equilibrium. For d players with n strategies, there can be at most $(d-1)^{n-1}$ isolated internal equilibria. Multiplayer games show a great dynamical complexity that cannot be captured based on pairwise interactions. The results hold for any game and can easily be applied to specific cases, such as public goods games or multiplayer stag hunts.

Many of the presentation slides are posted online at

`http://temple.birs.ca/~10w5020/`

3 Outcome of the Meeting

We are most grateful to BIRS for the opportunity to bring together a group of researchers from scientifically as well as geographically diverse areas to the majestic setting of Banff National Park again, 4 years after our 2006 workshop. All participants have enjoyed learning the latest work of their colleagues, not to mention the incredible views, great selection of food in the dining hall, excellent lodging, and inviting atmosphere of the common lounge. As the presentation summaries illustrate, our colleagues have made considerable advances in various branches of evolutionary games since our previous meeting, along the paths highlighted in our 2006 workshop and in new directions. We are particularly appreciative of the hospitality and administrative support from Brenda Williams and her staff. The organizers are unanimous that the efficient BIRS staff has made the BIRS workshops the easiest conference to organize.

The reduced group size for this workshop has not dampened the enthusiasm of participants. Many fruitful exchanges took place during the presentations, as well as in the lounge, dining hall, not only within Evolutionary Games workshop, but also with members of the Inclusive Fitness workshop. BIRS workshops, as always, have left participants feeling refreshed and inspired to forge new collaborations. We are already looking forward to meeting again to discover our progresses at the next Banff workshop.

The rainy weather for most of the week kept participants working together longer than otherwise. A large number of our workshop participants, who stayed on to attend the 14th International Symposium on Dynamic

Games and Applications conveniently held in Banff immediately after our workshop, reported that they were rewarded with sunny skies and great hikes at the week's end.

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