The role of polymorphism in the evolution and stability of cooperation

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PhD dissertation thesis book

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1. Introduction and background

A typical social dilemma develops when the benefits of cooperation can be exploited by cheaters, that is by individuals who enjoy the benefits without reciprocating (Trivers 1971). We use the term cooperation, if the reciprocal interaction takes place between conspecifics (West et al. 2007), meaning that partners are usually also in competition with each other. When the two or more interacting individuals are from different species, we term such interactions as mutualisms, or interspecific cooperation. Both cooperation and mutualism faces analogous dilemma (West et al. 2007): as best characterized by the famous Prisoner's Dilemma game (Trivers 1971), each participant would be better off cooperating, but cheating pays off even better, thus cheater strategies spread, and consequently the population ends up in the worst outcome, that is no cooperation (Nowak 2006a,b).

Cooperation research has offered various explanations, and has proposed several mechanisms that may promote the evolution and stability of cooperative behavior despite its disadvantage against cheaters (Nowak 2006b; West et al. 2007). Foremost, evolutionary game theory has proven to be an efficient and prominent tool for the study of social interactions, and can be used to describe social dilemmas both of cooperation and mutualism (Bshary & Bronstein 2004; Doebeli & Hauert 2005; Nowak 2006a). Accordingly, studies applied different types of games as metaphors for the wide variety cooperative behavior that can be observed in nature (Dugatkin 1997; Bergstrom et al. 2003). Classical game theoretical approaches, however, made several simplifying assumptions, or made the fewest assumptions required to evolve (or maintain) cooperation: these models generally assumed dyadic games with two players interacting, static and random interaction topology where partners picked randomly, fixed, static investment strategies, and homogeneous environment (Bergstrom et al. 2003; Bshary & Bronstein 2004; Doebeli & Hauert 2005). Also, primarily the Prisoner's Dilemma game has emerged as metaphor, many times become the only considered metaphor, to describe diverse biological and social situations (Archetti & Scheuring 2012). Empirical observations, however, depicted a more sophisticated and complex picture of cooperative behavior in nature (Bergstrom et al. 2003; Bshary & Bronstein 2004; Kiers & Denison 2008; Kiers et al. 2011).

The aim of the dissertation was to investigate models in which one or more of the simplifying assumptions made by classical, "minimal" models of evolutionary game theory are relaxed (Sachs et al. 2004). After over-viewing the pioneering models developed and analyzed in order to explain the conundrum of cooperation, new game theoretical approaches are proposed for a more precise description of specific types of social interactions. The focus was on two aspects of cooperation: non-linear *N*-person games, and conditional strategies in cooperative interactions. In particular, the study investigated the effect of relaxing some of the simplifying assumptions made in “minimal” models in the evolution and stability of cooperation.

Numerous biological situations can best be described as *N*-person dilemmas (Nunn & Lewis 2001; Kitchen & Beehner 2007) with non-linear benefit functions (Pacheco et al. 2009; Boza & Számadó 2010; Archetti & Scheuring 2012). In these situation, the successful cooperative effort is achieved only if the number of cooperating individuals reaches a given threshold. A multilevel selection model is proposed to study the evolution and stability social interactions in group living species, where collective action is modeled as an *N*-player Threshold Public Good Game (Bach et al. 2006), and selection acts both at the individual and at the group level. It was showed, that depending on the threshold value and the cost of cooperation a cooperative equilibrium exists where cooperators and defectors coexist. While these situations assume that groups of individuals engage in an interaction which may or may not end in successful cooperation, these groups themselves often compete with each other. Thus, the main aim of the study was to propose and analyze a model that integrates Threshold Public Goods Game with multilevel selection approach, both in well-mixed and spatially explicit populations structures, where competition occurred both at the individual and at the group level (Boza & Számadó 2010).

The second part of the dissertation concentrated on the study of stability of cooperation with conditional strategies. Any potential interaction between partners can be divided into three phases: *assortative*, *interactive* and *allocative* (Dugatkin 1995). During the *assortative* phase, individuals decide with whom to interact with, during the *interactive* phase, strategies individuals follow determine how to invest, and during the *allocative* phase, individuals may decide how to divide the resource (Dugatkin 1995). In all phases conditional strategies might prove more appropriate to describe cooperative behavior in many types of social interactions, compared to the traditionally assumed static or fixed strategies. Accordingly, conditional strategies in the *assortative* and in the *interactive* phases are considered, relaxing the assumptions of random interaction topology and fixed, static investment behavior of “minimal models” of cooperation (Kun et al. 2010; Boza et al. 2012)

By introducing conditional strategies in the process of choosing the suitable partners in the *assortative* phase, individuals, both cooperators and defectors, could choose to keep or break connection with partners. Thus partner choice affected only with whom to maintain connection, but the network connection topology was unchanged (Kun et al. 2010). As not only cooperators, but defectors could also follow conditional partner choosing/ rejecting behavior, the question was open such simple conditional behavior promotes of hinders cooperation.

In the second part of the study, a model with conditional strategies determining the investment behavior was assumed in order to relax the fixed and static investment strategy assumed in *interactive* phase. In particular, the study presented a comprehensive analysis of a continuous reciprocal investment game between mutualists, both in well-mixed and spatially structured populations. In particular, the role of spatial structure in stabilizing interspecific mutualism, especially when considered as plastic investment behavior, was largely debated, and not fully understood (Boza & Scheuring 2004; Boza et al. 2012).

2. Models and methods

The investigations were carried out in individual based models. The fitness of an individual depended on the outcome of its interaction with a member of the same population in the case of cooperation models, or with the member of another population in the case of mutualism model, while competition occurred between members of the same populations in all cases.

Individuals occupied lattices of a rectangular grid, or nodes of a regular, and a scale-free graph in the case of spatially explicit population structures. In the case of cooperation models, the focal individual interacted with the closest neighbors in the lattice or in the graph. In the case of mutualism model, the two populations inhabited two separate lattices, and interaction took place between individuals from the corresponding lattices. Competition occurred between the neighboring individuals from the same populations. In well-mixed populations both interaction and competition partners were picked randomly from the populations.

In the *N*-player Threshold Public Good Game, besides individual level competition, group level competition occurred, in which case neighboring groups in the spatial model, or random groups in the well-mixed model, competed for territories, the grids of a regular lattice, according to the average payoff of the participating group members, and the winner replaced the outcompeted group in the territory.

In the partner choice model, individuals could follow two strategies, cooperate or defect, and partner choice was defined as a dynamical re-linking of network connections depending on the composition of the local neighborhood. Here the probability of re-linking was controlled by an external parameter, and the defined re-linking rules.

In the models of collective actions and of mutualisms, each individual was represented by one or two heritable, adaptive traits, which defined the individual's strategy in the interaction. In the case Threshold Public Good Game, the traits defined an individual's propensity to participate in the two collective actions, separately. Participating individuals payed the cost of cooperation. If the collective action is successful, every participant received an equally shared benefit, regardless of their cooperative efforts.

In the case of mutualistic investments, each individual's strategy was specified by two (non-negative) quantitative adaptive traits: the unconditional investment (a, determining the initial offer), and the conditional investment (b, determining the reward rate). Thus, the strategy of Mutualist A was given by the pair ($a_{\mathrm{A}}, b_{\mathrm{A}}$), and the strategy of Mutualist B was given by the pair ($a_{\mathrm{B}}, b_{\mathrm{B}}$). The initial offer was an unconditional, fixed investment in the mutualistic interaction, and the reward rate determined how the investment changed depending on the last payoff gained from interaction with the current partner.

The presented results were obtained by numerical calculations with multiple repetitions, and by investigating all important dimensions of the parameter space.

3. Theses

N-person Threshold Public Goods Game

1) The results obtained confirm the findings of other studies, namely that the population can evolve into stable levels of cooperative polymorphism, where cooperators and free riders can stably live together. The equilibrium ratio of cooperators depends on the cost of cooperation, the threshold value, the group size, and on initial rate of cooperation. The described dynamics holds for a wide range of sigmoid benefit functions, not only for strict deterministic stepwise threshold function.
2) Division of labor can evolve in multiple collective actions, by assuming multilevel selection, and multiple collective actions. In the case of multilevel selection, laggards–cheaters–can actually play an important role in resource allocation at the group level. In the case of multiple collective actions, such as collective hunt and territory defense,

division of labour may evolve where cooperators in one action switch roles, and can act as laggards in another collective action, while other individuals follow alternated strategies.

3) Spatial population structure promotes cooperation in Threshold Public Goods Games, as invasion of cooperators is easier in spatially confined populations. Also the hysteresis point can disappear in spatially explicit populations, thus cooperation can be a stable outcome even for high cost values.

Conditional partner choice model

4) Simple conditional rules of partner choice, such as “Get rid of defectors” or “The friend of my friend is my friend” can promote cooperation, even in cases when the interaction topology remains unaffected, and only the composition of the interaction neighborhood is allowed to change.

Conditional investments in interspecific interactions

5) In mutualistic interactions modeled as continuous reciprocal investment game, partners invariably follow investment cycles, during which mutualism first increases, before both partners eventually reduce their investments to zero, so that these cycles always conclude with full defection.
6) The key mechanism for stabilizing mutualism is phase polymorphism along the investment cycle. Although mutualistic partners perpetually change their strategies, the community-level distribution of investment levels becomes stationary. Strategy-diversity thresholds, different for well-mixed and spatially structured mutualistic communities, indicate the necessary rate of polymorphism for maintaining mutualism.
7) A comprehensive analysis of the model considering the relevant parameters, such as the benefit-to-cost ratio, updating method, population structure, or the effect of mutational variability, revealed that the assumption of mutational variability has the most significant effect on the stability of mutualistic investments in the model. The emerging phase polymorphism and underlying strategy diversity recurrently retrigger evolutionarily increasing levels of cooperative investments in some portion of the community, a process that is essential for maintaining high investment levels.
8) In spatially structured populations, the maintenance of polymorphism is facilitated by a dynamic mosaic structures, in which mutualistic partners form expanding and collapsing spatial bubbles or clusters. Most importantly, insulating boundary layers between adjacent spatial bubbles can hinder the invasion of strategies, and hence can promote strategy polymorphism.

9) Spatial environmental heterogeneity can catalyze the emergence of insulating boundary layers, and thus promote the stability of mutualistic investments. Hence patchy costly environment need not lead to the breakdown of mutualisms, rather results in stabilizing mutualistic investment at the population level.

4. Conclusions

Identifying the mechanisms maintaining polymorphism in natural communities, provides a significant step towards understanding the coevolution and population dynamics of many types of social interactions. The model proposed in the dissertation can provide a potential explanation for the observed polymorphism in natural societies in threshold game like situations. In conclusion, what was regarded as cheating at the individual level is in fact can play a significant part in the optimization at the group level. Furthermore, assuming conditional strategies, such as the proposed, or similar, conditional partner choice mechanisms, can provide basis for understanding social networks in animal and human societies. The presented results also demonstrate that interspecific mutualism, when considered as plastic investment behavior, can be unstable, and, in agreement with empirical observations, may involve a polymorphism of investment levels, varying both in space and in time. The long-standing notion of social interactions being static is becoming extended as new findings, both experimental and theoretical, broaden our understanding. The results and conclusions of the models proposed in the current study, combined with empirical observations, can provide a prosperous basis for further research, both for the empirical and the theoretical sciences.

5. Publication list

RELEVANT PUBLICATIONS

Boza, G., Kun, Á., Scheuring, I. & Dieckmann, U. (2012) Strategy diversity stabilizes mutualism through investment cycles, phase diffusion, and spatial bubbles. *PLoS Computational Biology,* 8: e1002660.

Boza, G. & Számadó, Sz. (2010) Beneficial laggards: multilevel selection, cooperative polymorphism and division of labour in Threshold Public Good Games. *BMC Evolutionary Biology* 10: 336.

Kun, Á., **Boza, G.** & Scheuring, I. (2010) Cooperators Unite! Assortative linking promotes cooperation particularly for medium sized associations. *BMC Evolutionary Biology* 10: 173.

Boza, G. & Scheuring, I. (2004) Environmental heterogeneity and the evolution of mutualism. *Ecological Complexity* 1: 329–339.

SELECTED RELEVANT CONFERENCE AND WORKSHOP PRESENTATIONS

Boza, G. & Számadó, Sz. (2010) Cooperation and multilevel selection in *n*-player Threshold Public Goods Games. Presentation at INCORE Conference “Cooperation: an Interdisciplinary Dialogue”, 2010 September 17-18, Collegium Budapest, Budapest, Hungary.

Boza, G., Kun, Á., Scheuring, I. & Dieckmann, U. (2009) Mutualism and exploitation: a theoretical approach. Presentation at the 8th Hungarian Congress of Ecology, August 26-28 2009, Szeged, Hungary.

Boza, G., Kun, Á., Scheuring, I. & Dieckmann, U. (2009) The evolution and stability of conditional mutualistic interactions: model and reality. Presentation at the 5th Annual Plant Biology Symposium “Mutualism: Plants and the Evolution of Cooperation & Trading, (TECT)”, May 7-9 2009, Harvard University, USA.

Boza, G., Kun, Á., Scheuring, I. & Dieckmann, U. (2008) Investigation of a general model of mutualism. Presentation at the TECT General Meeting, EUROCORES Programme TECT, Barcelona, November 23 2008.

Boza, G., Könnyű, B. & Számadó, Sz. (2007) Cooperation in *n*-player Prisoner’s Dilemma threshold game. Presentation at The 6th European Conference on Ecological Modelling, ECEM'07, November 27-30 2007, Trieste, Italy.

Boza, G. & Scheuring, I. (2004) The role of spatial heterogeneity on the evolution of mutualism. Poster at the Szeged Ecology Days Conference November 25-26 2004, Szeged, Hungary.

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