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Evolution of altruism: Exploring adaptive landscapes

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Summary

When tackling this thesis, my initial drive was to understand how far the genetic model of evolution suffices to explain human social behavior. The key interest in the genetic model is that mutation generates new social strategies independent from their fitness value – in contrast to cultural evolution where an agent can discard evidently unyielding strategies before using them. Cultural evolution thus allows a form of pre-selection. I emphasize that my interest in the genetic model is motivated by pluralism. I have no doubt that humans are in part cultural learners in social situations.

As example, take a population that socially interacts in that random pairs repeatedly play a game with the two actions ‘cooperate’ and ‘defect’. Two paradigmatic strategies in such games are unconditional defector (always defect) and Tit for Tat (cooperate in the first repetition and subsequently imitate the opponent’s previous action). For unconditional defector, a minimalistic genetic architecture requires no more than transcribing ‘defection’ in every repetition of the game. A mutation from such a genotype to Tit for Tat would then require mutation to the usage of 1) ‘cooperation’ as alternative action to ‘defection’ whereby this usage has to be 2) condition dependent. I emphasize that this mutation would generate an architecture transcribing conditional behavior from an architecture that does not. Viewed from the different perspective of a phenotypic level, unconditional defector could be the strategy of an individual who fails to grasp that ‘cooperation’ would be an option. This strategy, however, could also be chosen based on a sophisticated analysis à la homo economicus. Hence, simpleton and sophisticon could behave identically raising the question how selection would decide between them.

The scenarios described around unconditional defector and Tit for Tat illustrate that a modeler has a great deal of freedom with respect to chosen genetic underpinning. This choice thereby determines the types of mutant offspring can be expected from a certain parent strategy genotype (and possibly, the resulting evolutionary courses). The freedom in this choice and the associated modeling space, however, render answering the question if genetic models can explain human social behaviors beyond the scope my thesis. Still, the spirit of genetic modeling is factored in the chapters summarized in the following.

In a fully genetic model of sexual selection, preferences for mating partners are genetically determined and so is the attractive trait. If this trait is a handicap then the trait signaled via the handicap is also genetically determined. In Chapter 1, we present such a model where the attractive/handicap trait is altruism and the signaled trait is fitness. Altruism reduces the fitness of the altruist at the benefit of others. While the former effect is a characteristic of handicaps the latter effect is not found in non-altruistic handicaps. As an example, a – by its own – insufficiently fit individual might be able to express the handicap if its fitness is sufficiently increased by altruistic benefits. The influence of such effects of altruism on the evolution of altruistic handicaps under sex-

ual selection is studied in Chapter 1. We find that altruistic handicaps are favored whenever fit individuals benefit more from altruism than less fit individuals; altruistic handicaps are disfavored, otherwise.

Potential as invader is a common proxy for fitness. An example is opting out of repetitions in repeated Prisoner's Dilemma games. This option is argued to promote the evolution of altruism as conditional cooperators using this option (Out for Tat strategies) can be enhanced invaders of unconditional defector populations. Furthermore, loners (which always opt out) can also invade defector populations. Subsequent to such invasions, cooperation can evolve as cooperators are potent invaders of loner populations. The latter route to the evolution of cooperation sets doubt on the persistence of defector populations and hence, on the relevance of the former route. Using genetic architectures that transcribe general strategy sets, we find in Chapter 2 that opting out promotes the evolution of cooperation only over restricted parameter ranges: i.e. when opting out is lucrative over mutual defection but not too lucrative relative to mutual cooperation. Furthermore, we find that populations of Out for Tat strategies are less resistant to invasions than populations of certain classical conditional cooperator as Tit for Tat, i.e. the advantage as invader is often compensated by being more prone to invasions.

Apart from selection, the mutation regime and the recombination regime determine which phenotypes can be expected in the next generation. As evolutionary biologist, I thus hold these regimes as decisive quality of a genetic architecture. In Chapter 3, we study the case of asexual populations under frequency dependent selection. We thereby classify the effect of mutation on this selection by distinguishing direct effects – the fitness effect emerging from interacting with mutants – and indirect effects – the fitness effect emerging from interacting with descendants of mutants. The crux in indirect effects is that descendants from different types of mutants are differently affected by selection. By simulations, we show that indirect effects can result in cyclic and chaotic dynamics in populations that would evolve to an evolutionary stable state without mutation.

In biology, studying adaptation processes to heterogeneous environments has a long tradition. In Chapter 4, we show that this concept can be extrapolated to economics. A social norm constitutes the choice of complying with the norm. This choice can be increasingly compelling with increasing fraction of compliers e.g. because sanctioning norm-deviators increases in efficiency with this fraction. Such social norm is studied in Chapter 4 whereby this norm constitutes a heterogeneous environment as it fails to self-organize with some probability. Plastic traits as conditional behaviors are often the best form of adaptation to such environments. In the studied model, a preference for norm-adherence can indeed evolve towards ranges where the individuals comply only when the norm arises. Adherence then evolves to be a conditional behavior.

Lines of argumentation in evolutionary theory often focus on conspicuous locations in adaptive landscapes – e.g. the optima that constitute evolutionary stable states. An aim of my thesis is to divert attention outside these locations. For example, adding the outside option to the repeated Prisoner's Dilemma increases the number of strategies that mutation can generate by a manifold. Among these strategies can be conditional cooperators that are enhanced invaders of populations composed by defectors from the classical game. In Chapter 2, however, we exemplify that among these strategies can also be strategies that harm these conditional cooperators. Apart from harming effects, such strategies can be fairly inconspicuous, otherwise. In Chapter 3, an ap-

proach is proposed of how to integrate conspicuous and inconspicuous parts of adaptive landscape into analyses of evolutionary theory.

As (partially) cultural evolvers, humans focus on promising strategies and disregard evidently unyielding strategies in social situations. Analyzing a winning strategy like an evolutionary stable strategy is thus closer to us than analyzing a strategy off from peaks in the adaptive landscape. Mutation generating mutations arbitrary with respect to fitness or social yield (i.e. the genetic model) corresponds to the classical view on how 'evolution' functions as optimization process. Understanding if and how far evolutionary courses differ between cultural evolution and genetic evolution is in my view a promising approach for investigating the nature of evolution as optimization process.