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Evolution of altruism: Exploring adaptive landscapes

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Introduction

Evolutionary theory inspired the development of methods for combinatorial optimization, such as genetic algorithms and simulated annealing. Using such techniques, an engineer can find optimal solutions in an efficient manner thereby bypassing an otherwise unfeasible exhaustive search. Natural selection is indisputably an optimization process. As an evolutionary biologist, however, I ask whether I do a good job by restricting my view on evolution as an optimization process and, thus, by spotting optimal solutions only. Surpassing a valley to switch from one optimum to a higher one in an adaptive landscape (cf. Wright 1932) is a well-known allegory that is at the heart of combinatorial optimization. I wrote this Thesis as an invitation for a stroll in the (adaptive) regions around optima instead of heading right away for the top. This Thesis is therefore no attempt to rewrite the well-known catchphrase of evolutionary theory: ‘survival of the fittest’, but an attempt to display the possible insights that can be derived from evolutionary dynamics on the adaptive landscape.

‘Because it’s there!’ is the catchphrase of alpinism¹, but any alpinist knows the challenge is to get there by climbing. That the focus is on the path to peaks rather than the peaks in adaptive landscapes themselves, can be illustrated by bacterial strains with augmented mutation rates (Giraud et al. 2001; Pal et al. 2007): In constant fitness environments, such mutator strains are usually not beneficial because mutations on average tend to be detrimental. The mean fitness of mutator descendants is thus lower because of the higher incidence of mutations among them: their mutational load is higher. However, the likelihood of a beneficial mutation is also higher and this may make mutator strains perform better in variable environments (Giraud et al. 2001; Pal et al. 2007). The closer the population is to the top of the current fitness landscape, the higher is the fraction of detrimental mutations. Bacteria that mutate (back) to lower mutation rates can thus often outperform their mutator siblings with the result that mutator strains therefore tend to cycle in frequency (Giraud et al. 2001; Pal et al. 2007). Mutator strains paradigmatically show that costs are associated with adaptability and that adaptability constitutes an evolvable trait by itself (Giraud et al. 2001; Pal et al. 2007). Furthermore, they show that the path to peaks or rather, the pace on this path (mutators adapt faster) can be a competitive element in the evolutionary dynamics. After all, the term evolution stems from the Latin word ‘evolvere’ and not from ‘stare’.

Evolution is the outcome of selection acting on heritable variation. As is usually done in introductory text books on evolutionary biology, the essence of this definition can be captured by Fisher’s fundamental theorem of natural selection (Fisher 1930), the breeder’s equation (the response to selection $R = h^2 S$), and by the Price equation (Price 1970). These approaches share the characteristic that heritable variation and its effect on evolutionary change are represented by a scalar, i.e., the (heritable) variance

¹ Allegedly, George Mallory’s retort to the question ‘Why do you want to climb Mount Everest?’.

in Fisher's theorem and a function of the variance in the latter two frameworks. Here, heritable variation is handled as a quantity, e.g., mutational load of mutator strains. An adaptation process, however, is determined by beneficial mutations. Existence of such mutations, or not, is thus a decisive quality of heritable variation: In a competition between two bacteria differing only in the mutation rate, it can be decisive which bacterium first generates a beneficial mutant (i.e., a quality). The chance (i.e., a quantity) of generating this mutant is higher for the bacterium with the higher mutation rate. However, if the other bacterium first generates it then the fraction (i.e., a quantity) of offspring faithfully inheriting the beneficial mutation should also be higher (because of the lower mutation rate). In my opinion, whether one views heritable variation as a quality or rather as a quantity is at the heart of controversial discussions on Fisher's theorem (reviewed by Edwards 1994; Frank 1997, 1998; Grafen 2003) and on the Price equation (van Veelen 2005, 2009, 2011; Marshall 2011; Gardner et al. 2011). This introduction to my Thesis is not an attempt to start these discussions again, but serves rather as a guideline to develop questions underlying the chapters of this Thesis.

In this Thesis I focus on the question how heritable variation affects the evolution of altruism. Here, the key problem can be phrased as follows (for elaborate reviews see Henrich 2004; Lehmann and Keller 2006; Nowak 2006; West et al. 2007a,b): By acting altruistically, an individual reduces its own fitness (the cost of altruism) but enhances the fitness of other individuals. Evolution of altruism thus constitutes the conundrum of how (beneficial) altruistic behavior compensates for these fitness losses. Solutions to this problem come from theory based on green beard (or tag-based) processes, kin selection, group selection, (direct or indirect) reciprocity, and punishment (e.g., Henrich 2004). A further sub-categorization of these solutions could be obtained based on whether and to what extent the functioning of the solution is determined by environmental causes for variation or by heritable variation. For example in the case of group selection, a group could constitute of individuals on an island and competition between groups could be determined by the geography of the archipelago, i.e., by an environmental factor for variation between groups. In this Thesis I propose solutions that do not easily fall into the categories of Henrich (2004), as it was my aim to find new solutions beyond these categories. It is up to the reader to decide if I succeeded!

In the three sections below I describe the problems analyzed in the chapters of this Thesis. The first section corresponds to Chapter 1 and the third section to Chapter 4, whereas section 2 combines Chapters 2 and 3, being interrelated in that problems encountered in Chapter 2 inspired the analysis in Chapter 3.

1 Giving is sexy if you are good enough to give!

Costly status symbols are the handicap traits in human societies. For example, public fund raising for welfare organizations may serve as a status symbol for altruism and men possessing sports cars like a Ferrari may thereby become attractive partners for women (Sundie et al. 2011). It has been proposed that altruistic behaviors could have evolved as sexually selected handicaps (Zahavi 1977, 1995; Tessman 1995; Zahavi and Zahavi 1997; Miller 2000, 2007; Walker 2008; for a critical view see Driscoll 2006). Such altruistic behavior may serve to signal the individual's own superiority and the superiority of associated genes.

Altruism can benefit competitors, as is illustrated by the following example: if a guest pays rounds in a bar, then another guest could enjoy the double luck of having free drinks and going home with the lady of (the former guest's) dreams (possibly thanks to the free drinks). A non-altruistic handicap or status symbol would exclude benefiting competitor males. Instead, a Ferrari can be fun to ride, thereby benefiting the owner irrespective of its function as a 'status symbol'. Competitors need not be beneficiaries of altruism as is usually the case when spending money on welfare organizations. In my view, such benefiting is a characteristic unique to altruistic handicaps. The question is then if and how benefiting competitors affects evolution of altruistic handicaps relative to non-altruistic handicaps. In other words, big spenders should ask: is attractiveness acquired better by a Ferrari than by public altruism?

Altruism as a handicap is subject to the following scenario: Variation in fitness is signaled in that individuals with superior fitness act altruistically, individuals with inferior fitness do not, and altruists are preferred mating partners. In this scenario, superior individuals decrease their fitness by the cost of altruism while inferiors might increase their fitness by benefitting from the altruism of others. As a consequence, fitness differences between superior and inferior individuals decrease resulting in a decrease of the fitness variation to be signaled. Whereas a decrease in the fitness difference between superiors and inferiors is a qualitative effect, there is also a quantitative consequence thereof through changes in the frequencies of superior and inferior individuals. The qualitative effect influences the advantage of acquiring a superior mating partner. The quantitative effect modifies the success of competing mating preferences (e.g., the extent to which a preference for altruists could compete with being indifferent) in acquiring superior partners. Effects of the altruists on the variation in fitness can thus influence sexual selection on altruism.

Evolution of altruism as a sexually selectable handicap is modeled in Chapter 1. The idea of a handicap is to signal fitness superiority. Sufficient variability in fitness is required for the evolution of sexual selection on a handicap (see the discussion on the paradox of the lek: Kirkpatrick and Ryan 1991). Altruists change their own fitness because altruism entails a direct cost, but they also change the fitness of others because they receive the benefits of altruism. Thus, at the population level this means that altruists alter (e.g., as in the example above, reduce) variation in (relative) fitness. To study how this effect of altruism influences its evolution as a sexually-selected handicap, I have analyzed model versions that differ in the way of how fit and unfit recipients benefit from altruism.

2 Are evolutionary models constrained by the modeler's choice of heritable variation?

Some adaptation processes may not occur because the appropriate genotypes for phenotypes with high fitness are absent and will not emerge (i.e., a type of evolutionary constraint). Although constraints on variation may be a natural phenomenon, they may also be introduced in models for good or bad reasons. As a theoretician, I want to emphasize the role of such constraints in models of evolutionary theory. The modeler defines and thereby controls the genome. Of course, simplifying problems is a task faced by any scientist and keeping modeled genomes as simple as possible can be a

virtue. However, one should realize that this inevitably constrains the course of evolution.

Examples of constraints in models are parameters that could alternatively be modeled as evolvable variables. A realistic example could be the propensity to make an error in an evolutionary game by mistakenly playing an action that differs from the intended action. If this propensity is genetically determined and the propensity varies between individuals, then it can be subject to selection. Strong negative selection is plausible for erroneous behavior given that the consequences of making errors are often negative. If error-free behavior is, e.g., neurologically too costly, then the propensity should evolve under strong negative selection to an intermediate mean value with at least some variation. Treating the propensity as a fixed parameter value rather than as an evolvable trait would then be warranted if the mean propensity evolves to this value and its variation is sufficiently low. Indeed, several studies (Molander 1985; Sudge 1986; Boerlijst et al. 1997; Rand et al. 2009) model the propensity to make errors in (evolutionary) repeated games as a parameter (errors are then behavioral variation caused by the environment).

As outlined, constraints in models need not significantly affect the course of evolution. Constraints which do not fall into this category, however, constitute drawbacks for the interpretation of results. For example, the green beard solution for the evolution of altruism hinges on the constraint that all green beard carriers cooperate only with other green beard carriers (Dawkins 1976; i.e., altruism breaks down if green beard carriers who do not cooperate or who cooperate with non-green beard carriers occur). Henrich (2004) provides an overview of the constraints underlying the solutions to the evolution of altruism. My interest is to answer the question if constraints significantly alter the evolution of conditional behavior and in particular, conditional altruism in repeated games. Repeated games are the paradigmatic model framework for the study of such conditional behavior by the direct reciprocity solution (Trivers 1971) to the evolution of altruism.

In repeated games, the number of deterministic strategies is given by an exponential function of the number of repetitions (e.g., Cressman 1996). As was clear early on, investigating the strategy spaces thus readily constitutes an exhaustive search: Genetic algorithms were used as a method in the book by Axelrod (1984) on evolutionary repeated games. These algorithms do not define all strategies adjusted to the studied games and, hence, evolution is constrained if important strategies are left undefined. In the studies that followed, different scenarios for how to confront the exhaustive search were established. Famous is the example of Axelrod and Hamilton (1981) who asked peers to propose strategies. Evolution is constrained if important strategies were not proposed by these peers. An alternative approach is to restrict the strategy sets by confining memory (i.e., the number of previous repetitions on which game behavior can be conditioned) to the last few repetitions (Hauert and Schuster 1997). Evolution is constrained if strategies with higher memory are important (note that Hauert and Schuster conclude that they are likely not; see also Press and Dyson 2012). Furthermore, game theory provides comprehensive statements on the strategy space of repeated games like the backward induction argument and the Folk theorem. Similarly, several studies include comprehensive strategy spaces when arguing about evolutionary stability (Maynard Smith 1982) of strategies (e.g., Molander 1985; Boyd and Lorberbaum 1987) or alternative stability concepts (van Veelen and Garcia 2012; van Veelen et al. 2012). Confined within the strategy space of finite state automata, van

Veelen and Garcia (2010), Lindgren (1992) and van Veelen et al. (2012) performed numerical simulations with open-ended strategy evolution in the infinite space of repeated games with discounting (i.e., the length of the game is stochastically determined in that after a repetition is played, the game is continued for at least another repetition with a fixed probability or ended, otherwise).

Conditional behavior shares characteristics with reaction norms (i.e., a form of phenotypic plasticity): Innate conditional behavior is a reaction norm to the behaviors of opponents. The following approach to model reaction norms provides a good illustration of constrained evolution. Dieckmann et al. (2006) introduce the adaptive dynamics of function-valued traits. A reaction norm is a trait that functionally responds to an environmental factor and the method of Dieckmann et al. (2006) allows studying evolution of such function-valued traits. They describe differences in outcome between their approach and an approach where a predefined function (e.g., the exponential function or sine functions) evolves (fig. 1 of Dieckmann et al. 2006). A predefined function limits the range of function-shapes. Evolution is constrained if selection would otherwise favor shapes outside this range.

A conditional strategy in a repeated game can be understood as a function-type response to the behaviors of opponents (i.e., functions playing against each other). By excluding strategies, evolution can be constrained similar to the examples in fig. 1 in Dieckmann et al. (2006) because the corresponding function-type response is excluded. The approach of Dieckmann et al. (2006) extends the framework of adaptive dynamics (Metz et al. 1996; Geritz et al. 1998), which is a form of invasion analysis. When studying repeated games, demonstrating evolutionarily stable strategies (ESS; Maynard Smith 1982) follows from invasion analysis. Coarsely defined, an ESS is a function-type response that, after reaching fixation, can withstand invasions from any other function-type response (entering the population by mutation). An ESS thus constitutes of a best withstander of any alternative strategy. Although less used in the study of repeated games, I wish to point out another invasion analysis by Eshel (1983), which involves demonstrating continuously stable strategies (CSS) and includes optima as invaders.

ESS and CSS are comprehensive statements with regard to the strategy space in the sense that withstanding invasions concerns any strategy from this space. For example, Molander (1985) and Boyd and Lorberbaum (1987) are examples of ESS analyses for exhaustive strategy spaces. However, the optima are guaranteed only under restrictive assumptions (Maynard Smith 1982; Eshel 1983) on the heritable variation as quality – only a single strategy attempts to invade – and as quantity – the invader is sufficiently rare such that second order effects from its frequency can be ignored. Populations are assumed to be largely composed of one genotype and, only rarely, this homogeneity is interrupted by a mutation. Mutation is so rare that the destiny of a mutant – i.e., either vanishing or reaching fixation (or as discussed later, the third destiny that resident and mutant form a protected polymorphism) – should be determined before the subsequent mutation event. Biometry is too commonly used in behavioral ecology to justify excluding populations with more strategies than resident and invader, and populations with invader frequencies that are not rare. My impression is that empirical behavioral ecologists regularly face populations with a genotype frequency distribution that is noisy because all kinds of invader genotypes are found. I refer to variation in such populations as non-ESS variation. Non-ESS variation, for example, emerges in a sufficiently large population with finite mutation and if mutation can transform any geno-

type into any other genotype. The exclusion of strategies as a cause for constrained evolution constitutes a qualitative effect of heritable variation. This is not the case in ESS analyses as any strategy is considered as a potential invader (i.e., no exclusion). However, with non-ESS variation, two or more strategies might be able to co-invade an evolutionary stable state (i.e., a population otherwise homogeneously composed by an ESS). The stability of such a state then depends on the constraint that non-ESS variation is excluded. I propose the interpretation that such constrained evolution is a quantitative effect of heritable variation. Traditionally, biology is categorized within the inexact sciences because life is so noisy and fuzzy. Many methods of mathematical biology, however, reduce this noise to its minimum to increase tractability of analysis. Despite the elegance of tractability, I think the variation inherent to biological processes should not be disregarded as simple noise. At the very least, this assumption should be questioned now and then.

I have no doubt that invasion analyses constitute useful approaches in evolutionary theory. They allow keeping fairly complex evolutionary systems within tractable frameworks. Still, I think it is time to (additionally) venture outside these frameworks (for examples see Lindgren 1992; McNamara et al. 2004; Traulsen et al. 2009). What I have in mind is that we study how systems evolve without constraints in heritable variation, both as a quality and a quantity. I think attempting this is idealistic for two reasons: (1) systems are often intractable due to the sheer size of the strategy set, particularly in evolutionary versions of repeated games, and (2) leaving the framework of invasion analyses usually implies assumptions on the mutation regime, whereas the nature of such regimes is usually unknown. As a consequence, one would have to deal with a regime space that can be expected to exceed the strategy space in size. Despite the idealistic nature of the framework I propose, Chapters 2 and 3 are written in the spirit of attempting to study unconstrained evolution.

An analysis in evolutionary theory typically constitutes of analyzing potentials of a strategy phenotype as an invader (the continuously stable strategy of Eshel 1983) and as a withstander of invasions by other strategies after having attained population dominance (the evolutionary stable strategy of Maynard Smith 1982). In the literature one finds arguments that rely on either of the two potentials. For example, Batali and Kitcher (1995) argue that opting out in evolutionary repeated Prisoner's dilemma games (i.e., suspending a repetition) promotes the evolution of cooperation. The argument is based on the realization that – relative to classical conditional cooperators – Out for Tat strategies (i.e., conditional cooperators using this option) can be enhanced by invasion of unconditional defectors. Furthermore, populations dominated by unconditional defectors can also be invaded by strategies that persist in opting out (loners; Batali and Kitcher 1995; Hauert et al. 2002). Cooperators can then invade loner-dominated populations, thereby opening up a further route for the evolution of cooperation. But if loners readily invade unconditional defector-dominated populations then Out for Tat strategies are hardly ever in the position to invade such populations. The two routes for the evolution of cooperation thus undermine each other. Opting out additionally can constitute a cheap way to signal remorse by cooperating in repetitions where the opponent opted out. This characteristic casts doubt on the potential of Out for Tat strategies to withstand invasions from strategies that (falsely) signal remorse in this way. In Chapter 2, I reevaluate the enhancing effect of opting out on the evolution of cooperation.

I consider Chapter 3 to be at the heart of what is expressed in the title of this Thesis. In this chapter, a method is proposed for how to study effects of mutation on frequency-dependent selection in asexual populations under recurrent mutation. We thereby take advantage of simplified cladistics where each individual with a genotype distinct from the parental genotype due to mutation founds a new clade. This provides a perspective on the effect of founders (mutants) on frequency-dependent fitness. For many mutation regimes, this allows to trace which phenotypes benefit from interacting with mutants. Effects of mutation are more lasting whenever mutants faithfully reproduce. The approach taken also provides another perspective on the effect of non-founders on frequency-dependent fitness. Using these two perspectives, it is tested how general earlier propositions (McNamara et al. 2004 and 2008; Eriksson and Lindgren 2005; Traulsen et al. 2009) are concerning the enhancing effect of mutation on the evolution of cooperation. Using the evolutionary game of the finitely repeated Prisoner's Dilemma, Chapter 3 shows how cooperation evolves via interactions with founders and via interactions with descendants of founders.

3 Variable social norm behavior as cause or consequence of heterogeneity in a social norm

Chapter 4 is published in an economics journal. A key contribution to this work I did together with Christian Traxler was my expertise on adaptation processes in heterogeneous environments (Spichtig and Kawecki 2004). The topic of Chapter 4 concerns the question how a social norm that is established in some but not in all generations, adapts to temporal heterogeneity. A social norm is a rule of conduct, which is enforced by internal or external sanctions (Coleman 1990). Norms can differ between societies or change within societies over time. An individual – commuting between societies or not – is thus confronted with the choice of adopting local or current norms potentially against his or her customs. Variation is thus between societies or within a society over time and social norm behavior can vary over a life time. If not all individuals comply with the norm, then such behavior deviating from the norm constitutes a source of variation within society. Whether, where, and when such variable behavior evolves in the context of social norms is studied in Chapter 4. Here, the evolvable trait is a preference that can be understood as an aversion towards sanctions associated with deviating from the norm. The individual uses this preference to weigh the sanctions relative to the cost of complying with the norm. Such weighing determines if avoiding sanctions is worth the cost of complying. In this decision process the individual has to take into account that the sanctions tend to increase in strength, the higher the compliance. Because of this association between compliance and strength of sanctioning, a form of divergent selection can emerge: Either preferences are beneficial that weigh avoiding sanctions as worth the compliance costs and the population evolves towards full compliance as a consequence, or vice versa and the social norm erodes. The study in Chapter 4 focuses on conditions where for a given genetic composition of the preference trait, the population can assume states with low or high compliance. This allows a scenario where over generations the population fluctuates between such states. The question is then if norm compliance can evolve as a conditional behavior.

4 Summarizing the goals of my excursions

I started the introduction by proposing a critical view on evolution as an optimization process and by emphasizing how this process is influenced by the presence (maintenance) of heritable variation.

The first section concerns the evolution of altruism as a sexually attractive handicap. A handicap is aimed to signal superiority (in fitness). As a handicap entails a cost, superiority should be distinguished enough to render signaling worth the handicap. Put differently, a sufficient fraction of the population being suboptimal is required for handicap signaling to evolve (the paradox of the lek): Evolution is quasi needed not to be too effective as an optimization process. Altruism, however, can alter the difference in fitness between superiors and inferiors (e.g., if inferiors increase their fitness due to altruistic benefits). How such changing fitness differences feed back on the evolution of altruistic handicaps is investigated in Chapter 1.

Limiting heritable variation in number and frequency is common in models of evolutionary theory as it improves tractability of the analysis. However, biometry would be obsolete if heritable variation was so exceptional in nature. Furthermore, limiting heritable variation can bias results if a course of evolution is not pursued because plausible genotypes are discarded by the modeler. In Chapters 2 and 3, examples are given of argumentations in evolutionary theory – with a focus on optimization – that turned out to be invalid after limits on heritable variation are relaxed. I view Chapter 3 as a particularly good example of how to deal with unrestricted heritable variation.

How heritable variation is protected by environmental heterogeneity is a discussion in biology spanning decades. In Chapter 4, I project this discussion on economics. Here, I analyze how compliance to a social norm evolves when overall compliance to the norm varies over time.

A discussion on the overarching theme ‘optimization process’ is based on the results presented in the four intermediate chapters and concludes the Thesis.

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