Symmetry and Collective Fluctuations in Evolutionary Games

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Preface

Today evolutionary population models are being applied to a wide variety of problems, reaching from traditional organism competition and reproduction upward to include demes and species, and downward into cellular and molecular dynamics and to mechanisms responsible for development and regulation. Evolutionary modeling has expanded laterally into domains of social and cultural dynamics, economics, and theories of learning and optimal inference. The expanding scope of evolutionary explanations and metaphors has led to renewed interest in the nature, and the origin in real systems, of abstractions such as individuality, which are the foundation for Darwinian dynamics. Improved understanding of the role of partial autonomy and competition in creating developmental programs, and of group-level coordinated action in ecosystems, has led to efforts to incorporate modern understanding of development and ecology more integrally within the population-based framework that formalizes evolutionary dynamics.

The statistical sophistication of evolutionary modeling has also increased in the past two decades. Topics of interest include multiple forms and levels of individuality, dynamics at many scales of time or of aggregation, strong selection and feedbacks through population states, interactions among multiple genes or multiple criteria of selection and a more statistical approach to the gene concept itself. The wish to apply evolutionary models as more than proofs of concept—as falsifiable quantitative theories of the causes of order—has also led to efforts toward less parametric and hence less biased model selection, and to inference from incompletely specified models.

These developments create collaborative opportunities for physics, as biologists, economists and others are independently reformulating basic concepts of entity, agency and interaction in statistical terms, along lines similar to those that condensed matter and quantum mechanics followed for particles and forces in the latter half of the 20th century, as well as studying new kinds of dynamical order in populations that have no direct analogs in equilibrium. In parallel, the past decade especially has seen significant advances in the large-deviations theory of non-equilibrium stochastic processes, by both mathematicians and physicists. While technical difficulties abound, it is becoming possible to speak of a coherent non-equilibrium thermodynamics based on sound first principles of path ensembles and path entropies, and in the process to understand equilibrium statistical mechanics in terms that are less dependent on mechanics and more plainly rooted in inference.

In this monograph we bring together a conceptual treatment of evolutionary dynamics and a path-ensemble approach to non-equilibrium stochastic processes. Our framework is evolutionary game theory, in which the map from individual types and their interactions to the fitness that determines their evolutionary success is modeled as a game played among agents in the population. Our approach, however, is not anchored either in analogy to play or in motivations to interpret particular interactions as games. Rather, we argue that games are a flexible and reasonably generic framework to capture, classify and analyze the processes in development and some forms of inter-agent interaction that lie behind arbitrary frequency-dependent fitness models. Games are generic in evolutionary dynamics in the same way as abstractions such as the individual or the gene are; the scientific problem is to decompose their structure and understand what dynamics different structures imply.

Readers familiar with the conceptual shifts in condensed matter physics and quantum field theory in the 20th century will anticipate that symmetry and collective fluctuations will be central to determining which distinctions among games matter qualitatively, and their consequences for dynamics. We explain why symmetry plays this role and illustrate with several examples that are in some ways similar to cases in equilibrium thermodynamics and in other ways conceptually new and intrinsically dynamical.

The presentation is meant to introduce quantitative methods while emphasizing the concepts they capture rather than mere computational technique. The mathematical development is self-contained and all results can be reproduced by the reader from the inputs provided, mostly with elementary methods. We do not, however, provide pedagogical introductions to basic ideas of evolutionary dynamics, game theory, or statistical mechanics. Readers who have had an introductory exposure to each of these topics will find the material here more familiar and intuitive than it will be to those for whom this is a first exposure.

Our work grew from more than a decade of stimulating exchange with colleagues and friends at the Santa Fe Institute, including Cosma Shalizi, David Krakauer, Steve Frank, Martin Shubik, Jessica Flack, Walter Fontana, Doug Erwin, Martin Nowak, Duncan Foley, Jeremy van Cleve and Sam Bowles. Each of them, through years of patience, guidance to literature and shared work, explained to us aspects of evolutionary theory, stochastic processes, game theory, or the scientific problems that were most central in applying these ideas to a variety of disciplines.

Early stages of work by ES were carried out under the generous hospitality of Martin Nowak and the Harvard Program for Evolutionary Dynamics, and the last year was hosted by George Mason University. ES also acknowledges two month-long visits to Stockholm in 2012 (hosted by the Theoretical Computer Science department of the Royal Institute of Technology (KTH)) and in 2014 (hosted by the KTH ACCESS Linnaeus Center, School of Electrical Engineering, Royal Institute of Technology (KTH)). Finally, ES is grateful for financial support from Insight Venture Partners and from William Melton. SK acknowledges funding from the Swedish Research Council.

Author biography

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Eric Smith received his BSc in Physics and Mathematics from the California Institute of Technology in 1987 and his PhD in Physics from The University of Texas at Austin in 1993, with a dissertation on problems in string theory and high-temperature superconductivity.

He has worked as a post-doctoral researcher at the Los Alamos National Laboratory, the Applied Research Labs at the University of Texas at Austin, and the Santa Fe Institute. Since 2006 he has been a faculty member of the Santa Fe Institute and since 2012 has been a Research Professor at George Mason University.

His work is broadly concerned with the origin of robust order in physical, chemical, biological and social systems. Specific areas of interest include the origin and role of institutions in economic dynamics and the transition from the geochemistry of the early earth to the first levels of biological organization.
(Photo credit Nerissa Escanlar.)

Supriya Krishnamurthy

Supriya Krishnamurthy received her BSc and MSc degrees in Physics from Hansraj College, Delhi University and the Indian Institute of Technology Kanpur, respectively, and her PhD, in non-equilibrium statistical mechanics, from the Tata Institute of Fundamental Research in Bombay in 1998. After her PhD she worked as a post-doctoral researcher in Paris at the Ecole Supérieure de Physique et de Chimie Industrielles, at the Theoretical Physics Department of the University of Oxford and at the Santa Fe Institute. She has worked at the Swedish Institute of Computer Science (SICS), Stockholm, as a senior researcher (2004–2009) and as an assistant professor at the Royal Institute of Technology at Stockholm (2006–2008). Currently, she is an associate professor at the Department of Physics at the University of Stockholm (2008–). She was also associated with the Santa Fe Institute during 2005–2011 as external faculty.
Her research interests include understanding both fundamental as well as inter-disciplinary applications of non-equilibrium statistical mechanics.

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Symmetry and Collective Fluctuations in Evolutionary Games

Eric Smith and Supriya Krishnamurthy

Chapter 1

Introduction: bringing together Darwinian evolution and games

Evolutionary game theory describes a class of population models in which the individuals subject to Darwinian selection are also the agents who play games to determine their fitnesses. The merger of the two domains has been a fertile source of models which can be given many interpretations. Our subject is statistical estimation and stochastic dynamics of evolutionary systems, in which games provide a taxonomy for major families of structure and behavior. Here we introduce the central concepts of symmetry, collective fluctuation, robustness and scale dependence that will be the themes of the following chapters. The technical problems of computing robust forms of scale-dependent stochastic dynamics will lead us to reconsider the basic abstractions that unify population models and games. We argue in favor of a statistical formulation of concepts such as individuality and agency, similar to the reformulation of the concepts of particles and forces in 20th century statistical physics, and a good match to modern efforts to incorporate principles of developmental biology integrally within our understanding of evolution.

1.1 The content and interpretation of evolutionary games

Evolutionary game theory [1–12] refers to a class of population models that bring together the formalization of evolutionary dynamics from population genetics and the structured models of interaction from game theory. At a minimum, the connection between population genetics and games is made at two points: the elementary entities in the evolving population (when described at an appropriate resolution) are the agents who play the games and the payoffs that result from play define their levels of fitnesses in the evolutionary dynamic. Depending on the model employed and the question of interest, many other points of contact may also be formed, drawing from the diverse inventory of game structures and the many kinds

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of possible interaction among individuals in populations. We will discuss some of these connections in later chapters.

The move to combine evolutionary dynamics with games can be approached as an extension or refinement from within either evolutionary theory or game theory. Within population-genetic formalizations of evolution, fitness models are effectively 'black boxes', chosen arbitrarily along with other models for heredity and for the mechanisms that generate variation. Games provide a structured way to unpack those black boxes, assigning meaning to the way interactions among individuals generate fitness from an individual's type in a population context. They may also offer ways to link the interactions that create fitness with mechanisms that generate variation, thus embedding knowledge about developmental programs or ecological interactions more integrally within the formalization of evolutionary dynamics.

Within game theory, many different solution concepts[1] may be applied to the same structured interaction; which solution concept is used determines which strategies or collections of strategies will be favored. Evolutionary updating provides an alternative solution concept to rational-choice solutions, which has many desirable properties statistically and, for some applications, empirically.

Evolutionary game theory potentially offers a very rich synthesis of concepts and tools. It can draw on all the methods to treat assortation, replication, transmission and selection formalized within modern population genetics [15–21], representing much of what is understood about the multilevel structure of interactions that converts the general mechanism of selection into the panoply of distinct evolutionary situations [22, 23]. It may also employ the full range of descriptions of structured individual and group interactions from game theory [14, 24, 25]. These include the extensive form [26], which maps out the dynamics and sub-structure during the course of a particular interaction, and cooperative solution concepts [13], which abstract some forms of institutional agreement or other group-level constraints on joint actions.

1.2 The approach to evolutionary games in this monograph

1.2.1 The foundation in prior work

Compared to either of its parent fields, mathematical population genetics and rational-choice game theory, evolutionary game theory is still a relatively young field. At present, a growing list of example models has been worked out (reviewed in [4, 7, 8]); some classification has been carried out based on symmetry, particularly from a dynamical-systems perspective; and suites of analytic methods now exist, drawing from the established fixed-point analysis of strategic games [25], from non-linear dynamics [4, 7, 12], and to a limited extent from stochastic process theory [3, 6].

[1] A *solution concept* is any formal procedure that uses the specification of the game and the assignment of payoffs to select a strategy or a distribution over strategies [13]. Solution concepts may employ the normal (also called 'strategic') form, the extensive form, or the coalitional form representation of the game. For a sense of the diversity of solution concepts that may be defined within any one of these representations, see [14].

A large amount of analysis has been carried out for games in the strategic form[2] (also called 'normal' form) and some work has been done using the extensive form [26]. Since the extensive form is a refinement of the strategic form in which the *structure* of play is made explicit [13], the relatively limited treatment it has received represents only a very early stage of exploration of a potentially rich and important topic.

The majority of the existing literature on evolutionary games grows out of the study of either fixed points or dynamical systems and has been based on the classical *replicator equation* [4], which is a mean-field equation[3]. The concept of *evolutionary stability* of equilibria, introduced by Maynard Smith and Price [27], is defined in terms of infinitesimal perturbations about the solution given by the replicator equation. Some research has been carried out on non-infinitesimal population fluctuations (inevitable in finite-sized populations and, as we will show, sometimes important even in infinite-population limits). Work on fluctuations divides into studies concerned with refining equilibrium selection to exclude ambiguity and studies that treat ongoing dynamics as an empirical consequence of ambiguity that models should not seek to exclude.

In general, games will admit multiple Nash equilibria or evolutionary stable states [28–31]. A tradition in economics has been to seek *equilibrium refinements* [14], which reduce this multiplicity by placing further restrictions to rule out sub-sets of equilibria in different contexts. In the presence of finite fluctuations, the long-run probabilities for a population to be found within basins of attraction of different equilibria will generally differ and the ratios of these probabilities can generally be made to diverge with large population size or small fluctuation strengths[4]. Therefore, by a process analogous to annealing, stochasticity may be used to reduce the number of equilibria that are populated with non-zero measure in the long run [32], providing an evolutionary argument for refinement. Adopting an alternative emphasis, a few studies have been performed in which stochastic dynamics in the presence of multiple equilibria was the primary focus [33–37]. As in the study of the extensive form in evolutionary dynamics, the topic of stochastic aggregate dynamics is an exceedingly broad and important area into which only introductory forays have been made. It will be our main area of emphasis.

1.2.2 Using symmetries to classify and understand the robust forms of stochastic dynamics

We will study evolutionary game theory in its stochastic form. Stochasticity arises from the population-level events which are already recognized in population

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[2] The *strategic form* of a game is the most widely seen representation in terms of 'payoff matrices', in which entire strategies simply appear as indices to the rows and columns (and further indices, for k-player games), without reference to the structure of play that the strategy represents.

[3] To the extent that one views all evolutionary game phenomena as fundamentally stochastic—a point of view that we will strongly advocate—the replicator equation is more importantly a form of mean-field *approximation*.

[4] An important exception to this generalization arises when multiple equilibria reflect the presence of an underlying *symmetry* and this will be one of the reasons symmetry is important in our treatment that follows.

genetics: sampling of individuals who will interact (here, by playing a game together), culling (death) and replacement (replication). In some of the examples we will also consider stochasticity within the course of play of a single game. In games for which strategies consist of moves that could be shuffled as part of the reproductive process, the place at which crossover occurs is an additional source of randomness. Beyond the mean-field analysis of the replicator equation, new phenomena arise that are not possible in deterministic systems. We are also led to ask which outcomes predicted by the replicator dynamic are robust in the presence of fluctuations, a seemingly innocent question that in statistical mechanics and field theory has led to a radical reconceptualization of the nature of objects and interactions [38–40].

In suitable weak-fluctuation limits, we will recover standard results from the replicator analysis concerning bifurcations to multiple equilibria or limit cycles (other attractors could be included but are not pursued here). These phenomena are an important source of multilevel dynamics in ontogeny[5] and evolution. They cause individual dynamics, through mutually reinforcing cooperative effects, to become entrained by population states which then take on dynamics of their own. We classify bifurcations according to symmetry, as is done in the dynamical-systems approach [4]. However, making a slightly different emphasis than the typical one from dynamical systems, we view bifurcations not as fundamental changes of symmetry groups, but as changes in the *representation* of symmetries by dynamical states. The presence of underlying symmetries that are merely hidden, in the stochastic domain, is the basis for proofs that multilevel dynamics is a *robust* property against all orders of fluctuation corrections, even if we cannot compute or efficiently simulate them. The existence of hidden symmetries causes multiple equilibria to escape the filters of equilibrium refinement *inherently*, allowing us to use stochastic approaches such as annealing [32], not with the goal of singling out a unique static equilibrium, but to identify sources of long-run dynamics that are not sensitive to fine modeling assumptions. We will recover important symmetry-derived theorems of condensed matter physics and field theory, such as *Goldstone's theorem*, and show the forms that they take in evolutionary dynamics, particularly as these result from new roles of time in irreversible stochastic processes.

We then consider effects that cannot be produced at all in the deterministic approximation, including fluctuation-controlled dynamical regimes that persist in infinite-population limits, creep and forms of symmetry breaking that resemble glass phases, where the number of ordered macrostates and the complexity can be 'open-ended'. The potential for open-ended complexity is an often cited property of evolving systems [41] that simple bifurcations do not possess, so it is important to have examples in evolutionary game theory where at least the rudiments of an unlimited diversity of macrostates can be exhibited.

[5] *Ontogeny* refers to the entire sequence of events in the life of an organism, which occur between its origin through replication and its death or fissioning into offspring.

1.3 Empirical bases for the abstractions behind models and model selection

To a large extent evolutionary game theory has been used as a cornucopia of 'toy models'—proofs of concept demonstrating certain types of dynamics that might occur—but only in rare cases [42] have these been required to serve as empirically calibrated analytic frameworks to show that a certain causal explanation *must* hold. Most conventional use of evolutionary game theory thus stands in contrast to other areas of quantitative evolutionary modeling, such as quantitative genetics [43], which aspire to less mechanistically rich descriptions of processes than games (they employ merely linear regressions on identified alleles), but which seek to show that any correct account must be equivalent to, or a refinement of, a statistically defended regression model.

An exploration of toy models is an essential part of developing the phenomenology of a domain as rich as the merger of population genetics and game theory, but on its own it leaves a literature that is to some extent a collection of ad hoc cases[6], rather than the application of a set of overarching principles. The motivation for game models is often drawn heavily from the scientific narrative for each particular case [8, 27], obscuring the role that games *as a system* play in modeling evolutionary dynamics. Toy modeling fills the level of ∃ (there exists) in propositional logic, whereas an empirical defense of causality must fill the role of ∀ (for all). Proofs of concept therefore do not expose the basic abstractions of a theory to certain tests of robustness or generality that more quantitative methods require. Although it may not be apparent upon first consideration, 'stress-testing' the choice and interpretation of models, especially against the pervasive effects of stochastic perturbations, can lead to a reconceptualization of the basic abstractions underlying a theory, ultimately making it better able to incorporate advances in understanding in other areas.

1.3.1 Introducing games from a starting point in regression modeling of population processes

We will be interested in common mathematical elements of evolutionary game theory as a system for studying evolutionary dynamics, with an eye toward empirical applications. Therefore, we will bypass the appeals to scientific narratives that often play a large role in the motivation of game models for particular cases. We focus instead on the consequences of stochasticity that must affect the choice and interpretation of *all* game models from empirical observations. Any attempt to use evolutionary games to understand natural phenomena will inevitably include sampling fluctuations from observations and hence uncertainty in model identification[7], as well as stochasticity in model dynamics that will affect analysis and prediction.

[6] Here the term ad hoc—literally 'for this'—does not carry a pejorative connotation. In final applications, all models must be justified by appeal to the details of the particular case.

[7] In the most general case, model identification includes not only parameter estimation, but specification of the basic concepts of agency, move and interaction sequence that define the structure of a model and its connection to observations [42].

De-emphasizing narrative forces us to ask what can be justified statistically in the choice and interpretation of a game model, in the presence of uncertainty, noise and error. By defining games statistically, we obtain a clearer abstraction of the role of games as a general framework in evolutionary dynamics: we will argue that the proper abstraction for the role of games is as models of development, which complement the models of information dynamics formalized in population genetics. We will introduce the problem of identifying a game model as a problem of non-linear regression following the empirically motivated methods of Fisher's theorem [44] and the more general Price equation [45–47]. Regression estimates begin with the lowest-order (generally linear) models of fitness and recursively *construct* the dynamics of the game through the addition of higher-order interaction terms as required. We will thus embed evolutionary game theory within the larger suite of formal evolutionary methods, so that approaches such as quantitative genetics coincide (tautologically) with the lowest-order estimators for games. Since any finite sample supports the inference of only a limited number and precision of model coefficients, we will be forced to address the problem of justifying models that formally involve infinite hierarchies of coefficients (even when these are all set to zero, they nonetheless exist as modeling choices[8]), and the related problem of determining which predictions from a statistically estimated model are robust.

1.3.2 Symmetry and scale

An immediate consequence of incorporating stochasticity in all elements of model selection, analysis and interpretation is that regression coefficients generically come to depend on *scale*. Relevant scales may be the population size, or the time interval or number of interaction events over which samples are drawn. The scale dependence of regression coefficients that is readily demonstrated in models reminds us that scale is also an inherent property of empirical observations. Therefore the concept of calibrating the coefficients in a game model to describe a natural system is one that inherently invokes the scale at which the model is to be estimated and analyzed. We will go further to propose that the *meaning* of the fundamental abstractions of evolutionary game theory, such as individuals, genes, or strategies, should come to be understood as scale-relative concepts, for the same reason that elementary particles and forces are now understood to be scale-relative concepts in physics.

In a modeling framework where the detailed model description becomes scale-dependent, symmetries take on elevated importance because they are the invariant properties that identify systems across all scales. The changes of symmetry representation by population states, as population size or interaction strength are changed, then define the robust dynamical regimes or *phases* in which variation, interaction, replication and selection act. This view is very compatible

[8] This is the fundamental insight behind *effective field theory* [40]. Although first appreciated in the contexts of condensed matter and elementary particle physics, the statistical arguments that force the effective-theory interpretation apply equally to population processes. Current work in other areas of population genetics [15, 16, 48–52] is already re-deriving similar results, in the course of defining statistically valid methods to treat multilocus interactions, strong selection and other phenomena.

with the modern understanding of multilevel selection [47, 53, 54] and the hierarchical role played by evolutionary dynamics in the evolution of developmental complexity [22, 23]. We believe it leads to a conceptualization of the fundamental abstractions of evolutionary game theory in keeping with the best understanding in modern evolutionary theory. In addition to demonstrating some qualitative categories of scale-dependent description, and showing why they matter, we derive methods to quantitatively compare model descriptions that differ at multiple scales because they incorporate different degrees of correlation and we show that these methods match well against simulation results, even in some cases of large fluctuations.

1.4 A summary of the key ideas and the topics to be developed

The following is a brief summary of the major conceptual commitments that we believe underlie a systematic and principled understanding of evolutionary games, and which will guide our presentation of a general framework and a few illustrative examples in the following chapters. We provide an overview here without attempting full explanations, so that readers from different backgrounds will see the relation of some topics that they will know as familiar foundations with others that may be new to them. Complex topics for which we can only provide a brief summary description in this list are developed in detail in later chapters. The list below is not exhaustive of concepts that could be developed in this area, but we believe it provides a reliable foundation that can be elaborated without needing to be overturned.

1.4.1 The Price equation: accounting identities, fitness and closures in population genetics

We construct evolutionary game theory as a general framework to classify and interpret fitness models—their quantitative dependence on population state and, if desired, explicit representations of the interaction sequences that determine fitness—within the axiomatic structure of population genetics. We begin in chapter 2 with the *Price equation*, an accounting identity for any process satisfying the assumptions of population genetics, in which *fitness* universally appears as a summary statistic [47].[9]

Fitness is defined in terms of the number of offspring relative to the number of their parents, grouped by the parents' type. It is a descriptive statistic, which can be computed for any given realization of an evolutionary process. If the purpose of an evolutionary account is not only description or historical reconstruction of a particular instance, but also estimation of a process model for change, then fitness (as well as other parameters) must be given a model in terms of properties of individuals and populations. The model estimation problem is to determine what

[9] Economists will appreciate the importance of accounting identities as non-trivial constraints, despite their 'tautological' nature: by construction they apply to all well-formed models in the domain for which they are derived; and thus they identify that domain.

structure and what coefficients can be justified from empirical observation. Once a population process model is chosen, one must often also define *closures* for it[10], which are approximations that permit calculations from finite orders of terms or parameters. The empirical calibration of fitness models leads to the approach of Fisher [44] and Price [45], who replace fitness (the summary statistic) with models that are meant to match regression coefficients of fitness on individual and population states, obtained from statistical samples. Since regressions can be performed on interaction terms of arbitrarily high order, in principle this approach provides a full basis for the identification of those aspects of a process that affect fitness; one can then ask in a principled way how much detail is supported by empirical evidence and attempt to systematically construct least-committal models [55, 56] for undetermined parameters.

1.4.2 The incorporation of information and development are the two complements that govern evolutionary dynamics

The mechanism of heredity in any population process determines which consequences of events affecting parents persist as features of the population state of the offspring. Since the filter of natural selection—the part of the population process represented explicitly in population-genetic models—acts to narrow the distribution of properties of offspring, population genetics comprises the information incorporating aspects of evolutionary dynamics[11]. The formal equivalence between the replicator equation and Bayes's theorem for updating probability distributions [58] provides a way to quantify this concept of information and also to show that selection is a statistically *optimal* method for incorporating information within a population about its environment.

Not all properties of organisms are directly preserved by mechanisms of heredity and the difference between what is preserved and what is generated and acted on by selection is the difference between genotype and phenotype. The complement to the information transmitted via a distribution of genotypes is the collection of all other aspects of phenotype, which are constructed through non-heritable interactions within generations. We will refer to these as *development*, broadly construed. From the perspective of classical population genetics, development consists simply of a genotype/environment → phenotype/fitness map, but we are concerned with the actual generating processes responsible for that map.

The complementarity between the information incorporating function of selection and heredity, and the constructive role of development, for us *defines* the respective roles of population genetics and games within evolutionary game theory.

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[10] 'Closure' is used as a general term in economics; in population genetics it normally refers to the more specific problem of *moment closure*, which we will show can be handled in a variety of ways.

[11] Here we are referring specifically to those aspects of information incorporated and preserved within the Darwinian paradigm. Other modes of propagation of ordered states—in particular modification of an environment that persists through mechanisms different from replication by populations of individuals undergoing Darwinian competition—are also relevant to evolutionary dynamics but they are a different topic [57] which we leave out of the scope of this discussion.

1.4.3 The emergence of games as a framework to systematically model development

Starting from the Price equation and a need for closures, a general polynomial expansion of frequency-dependent regression models for fitness is equivalent, at order k, to treating development as a k-player normal-form game with uniform matching of individuals. This equivalence is a tautology, meaning both that the normal-form game interpretation is always available and at the same time that it is highly ambiguous about the mechanism that constitutes the 'game' and about its interpretation. If, beyond the aggregate statistics of fitness, we are given more information about the frequencies with which individuals are sampled to interact in the population, we may resolve the normal form into contributions from assortative matching and a set of payoffs which differ from the mere coefficients in the fitness function. If we know more about the internal structure of interactions—which may be temporal sequence, signaling or imitation, or even just linkage—then we may refine the normal form to a particular extensive-form game [26]. Further elaborations, to include constraints on joint actions by multiple individuals, could be developed to make contact with the coalitional-form representation from cooperative game theory, but we do not pursue those systematically in this monograph. The sequence of one-to-many mappings, from the normal-form to the extensive-form and the coalitional-form solution concepts, constitutes a well-understood approach to refining the definition and interpretation of games in classical game theory [13] and we think it provides a useful level of discipline also for the interpretation of evolutionary games.

In this way games emerge as a highly general, if not all encompassing, framework to model development.

1.4.4 Symmetry and collective fluctuations in evolutionary games

A central theme in our approach to the topic of evolutionary games is that interactions among individuals in single events may produce population behaviors that, in aggregate, are describable with games of a similar form but with coefficients that may differ from those that the individuals directly experience. Most obviously, individual traits may polarize population states or lead to distributions of fluctuations that feed back so that higher-order correlations become part of the best average estimates for individual fitness.

In the domain of toy models, we often have the option to regard such differences as artifacts of the adoption of coarse-grained descriptions, but we think that if games are to become a serious tool for the analysis and interpretation of empirical phenomena, it is better to start to think of such scale dependence of parameters as an essential feature of the *definition* of such concepts as individuality, agency and interaction. Such a revision in the notion of what constitutes an elementary particle have been fundamental to a radical reformulation of the conceptualization of objects and interactions in physics [38–40]. Modern writing on evolution makes a serious effort to understand the way structured interactions, replication and selection interact at many scales, to produce multiple novel levels of individuality both in development [22] and as levels of selection [47, 53, 54]. We believe that a statistical notion of individuality and interaction is already inherent in modern biology and we make that integral to the way we present game models.

When the use of evolutionary games is altered from toy modeling of a hypothesized 'fundamental' interaction and its scale-dependent approximations, to an attempt to represent data in which all estimation and prediction problems involve uncertainties that depend on scale, a different approach is required to specifying what constitutes a model of a particular actual phenomenon, *at all scales of interest*. We therefore introduce fitness models and their classification in terms of *symmetry groups and the representation of symmetries by population states*. Symmetries are scale-invariant properties of systems and changes in their representations (known as *symmetry breaking* [59–61]) imply robust predictions for multiscale dynamics.

Stochasticity and correlation are the causes of parameter change in models of the same system at different scales and the stochastic effects that are robust within symmetry classes (and that lead to symmetry breaking) are *collective fluctuations* [62]. We introduce in chapter 2, and develop in detail in chapters 5–8, a set of examples of major classes of symmetry groups and categories of symmetry breaking and show how each implies a distinctive form of scale dependence in fitness or dynamics. These include the emergence of new units of selection or of coalitional behavior from interactions that are non-cooperative at the scale of individual interactions.

1.4.5 Large-deviations theory as the central organizing concept for calculations

The preceding four points provide a set of abstractions of evolutionary games that frees the fundamentals of the theory from arbitrary narratives invoked to justify particular cases and also acts as a guard against over-interpretation. However, these points are not useful in practice without ways to identify the relevant classes of collective fluctuations or their consequences for the expression of symmetry and for parameter changes across scales.

Evolutionary population processes are extended-time, irreversible Markov processes. In general, their distributions over collections of events could be too complicated to permit *any* robust characterizations. However, a feature of even moderately large populations or times that can make such processes tractable and can make games a stable and useful class of models is the tendency for probability distributions to converge toward a small number of exponential families. Within these families, the combinatorics of large numbers of agents or events may produce leading-log probabilities of fluctuations with a scaling relation known as the *large-deviations property*, in which the dependence on system scale separates from the dependence on the structure of the fluctuation [63].

Chapter 4 is devoted to a derivation of the large-deviations theory of discrete population processes tailored to the structure of evolutionary game models introduced in chapter 2. We show how the large-deviations limit singles out classes of collective fluctuations and how their properties can be computed to connect game descriptions across scales.

Good treatments of the consequences of large numbers and aggregation exist for evolutionary dynamics [3, 6] and for population processes more generally [64, 65].

Many of these draw from the probability literature and are concerned with convergence and laws of large numbers. Our approach will be one more familiar to physicists and will emphasize the extraction of terms most directly responsible for multiscale dynamics and multilevel selection.

These first five points have addressed general conceptual foundations of evolutionary game theory. The next four points concern particular applications, which are nonetheless of wide interest within either population biology or game theory.

1.4.6 The event structure of single interactions and uses of the extensive form

For many applications of evolutionary games it is not necessary (or not empirically warranted) to go beyond the normal form and the assumption of random matching. For others, though, the sub-structure of play when a collection of agents is brought together in a single interaction is central to the question being asked. The standard way to represent event sequences and information conditions in game theory [13, 25] is to refine the normal form to the *extensive-form* representation, most familiar as a 'game tree'.

Therefore, after introducing the general role of games in population processes in chapter 2, we provide a non-exhaustive but systematic introduction to extensive forms in chapter 3. A dedicated treatment of the extensive form is given in [26] and many more applications still could be developed. Here we will mostly be concerned with the two concepts of *neutrality* and *repetition*.

Neutrality [66–71] arises in evolutionary dynamics when distinct genotypes have the same fitness in populations that they themselves produce. It is an important form of symmetry under interchange of agent types, and a property that complex developmental programs can be expected to produce very frequently. A summary of some combinatorial counts of game trees enables us to provide explicit examples.

Repetition is a property of game interactions studied extensively in the economics literature [72–75] to model the relation between long-term and short-term incentives. We consider it because it is a source of some very well-known models of neutral evolution, for which we can demonstrate new consequences of collective fluctuations. A widely used framework to study repetition in rational-choice game theory is the *repeated game*, a particular kind of extensive form built up by recursive attachment of a normal-form *stage game* to build up the game tree. Repeating the play of a stage game is the simplest and most generic way to produce complexity and with it the problems of understanding error and limitations on strategic capacity.

The next three topics consider other, more specific, uses of the extensive form and of repetition.

1.4.7 The statistical gene in relation to modularity in development

Mendelian heredity—the property that the sources of traits are replicated as discrete units which are shuffled like cards rather than being mixed like paint—was one pillar of the modern evolutionary synthesis [54, 76] and is incorporated as an essential assumption within standard population genetics. The convention of formalizing evolution in terms of invariant hereditary 'particles' has presented one of two important challenges to the use of evolution to describe social, behavioral, or institutional dynamics [36, 77].[12]

Given the importance of particulate heredity to current evolutionary thinking, we briefly consider its origin in biological systems. We argue that the standard invariant hereditary unit in biology—the *gene* understood as a non-recombining region of DNA—results not from the properties of DNA as a system for storing information, but from modularity in development which is either reinforced by selection or recapitulated in transmission mechanisms. The extensive form of a game inherently produces a kind of modularity in the sequence of play and offers a natural set of elementary units (the moves) to vary through mutation or to shuffle via crossover. We show, first in chapter 7 and in a different way in chapter 8, how the 'gene' description that arises out of the modularity of game trees leads in the presence of crossover to a multilevel evolutionary dynamic that must select both genes and their covariance within genotypes. In this way we connect the use of the extensive-form game as a general framework to the statistical and developmental origins of modularity that justify the gene concept in biology.

1.4.8 Repetition in evolutionary and rational-choice game theory: re-directing the forces of selection

The repeated games, with payoffs accumulated from the moves in each stage of play, have become a standard framework, in both evolutionary [8, 11, 79] and rational-choice game theory [25, 72, 74], to study the relations between short-term and long-term rewards for nominally equivalent move profiles. Repeated games are most often invoked as a framework to study the 'paradox of cooperation'.

In the play of a repeated game, correlations between moves in different stages can re-direct the force of selection (in the evolutionary context), or the non-cooperative equilibrium condition (in the rational-choice framing) to favor outcomes very different from those that would be favored by the stage game in isolation. The approaches to repeated games in evolutionary and rational-choice game theory have diverged sharply in the study of how repetition produces these differences. The divergence of approaches is at first surprising because for finite normal-form games, a result known as the *fundamental theorem of evolutionary game theory* [7][13] asserts that the evolutionary stable strategies are the same fixed points as Nash equilibria. The forward looking self-consistency of rational choice and the recursive filtering of natural selection might thus be expected to yield the same solutions.

Rational-choice repeated game theory, however, concerns cases with a very large or even infinite degeneracy of Nash equilibria, or with ambiguities in the way

[12] The other difficulty, perhaps more fundamental, is the possibility that a given offspring may draw inherently from multiple parents, obviating the existence of fitness as a universal summary statistic in the Price equation, which we take to be a defining feature of the classical population-genetic formalization of evolutionary dynamics. This difficulty is particularly evident in attempts to characterize technological innovation with evolutionary terms [78].

[13] Sometimes this is alternatively referred to as the *'folk' theorem of evolutionary game theory*.

equilibrium should be formalized, typically arising from an infinite or indefinite number of stage repetitions and associated normal forms that are not finite. Ambiguities in equilibrium selection are treated with a poorly formalized notion of 'prior agreement', which requires only conditions of feasibility and individual rationality of outcomes[14]. A set of results known as *(the) folk theorems* [75] of repeated game theory show that any outcome in the large set of feasible and individually rational move profiles can be supported as an equilibrium.

In evolutionary models with repeated games, the notion of prior agreement is replaced by direct specification of the set of strategies that may exist within evolving populations and the ways they are generated. Depending on how strategies are restricted, or on the dynamics of type changes, limited sets of marginally stable or even unique stable equilibria may be selected.

In chapter 9 we construct the mapping between the evolutionary and rational-choice approaches to strategy selection in repeated games. We show how different forms of coordination in the repeated game, which appear as features of development in the evolutionary setting, may also be cast as signaling about strategy types, or even as kinds of public information that have been introduced in rational-choice game theory to expand the notion of Nash (*aka* non-cooperative) equilibrium to include correlated equilibria. Our interest is to use the explicitly dynamical and constructive approach to strategy generation in the evolutionary approach to define systematic approximations to the concepts of indefinite repetition and prior agreement in the rational-choice setting and to understand how these approximations imply bounds on strategic complexity.

1.4.9 Evolutionary mechanics and thermodynamics

The classical *replicator equation* [4] often used to study evolutionary games is very restrictive: by omitting explicit fluctuations, it is effectively a single-scale description. It also uses a particular set of closure assumptions, known as *mean-field assumptions*, which can sometimes be invalid even in infinite-population limits. For us, the stochastic population process is fundamental at all levels because stochasticity is the basis for criteria of robustness.

It is now well understood that the large-deviations scaling limit is the essential property behind the concept of entropy and thermodynamic limits [62, 63, 80]. A game model at the scale of individual interactions is the mechanical description, from which a (possibly different) game model of the aggregate population behavior is derived as the corresponding thermodynamic limit. The difference between individual and aggregate models results from *entropy corrections*, equivalent to those in any thermodynamic theory, but derived for extended-time irreversible Markov processes. A low-dimensional example in which the control over dynamics is shifted from

[14] Compared to the emphasis of every other aspect of game theory on the precise formalization of models of interaction [11], the notion of prior agreement is so permissive as to be almost unformalized. It is something like a solution concept with a potentially infinite set of distinct choices that the players are not forced but are simply declared to 'agree upon' before play. The way the choices are made then selects one rather than another equilibrium.

deterministic parameters (mean fitness and mutation) to fluctuation entropies is solved in detail in chapter 7. We expect that the most important and common use of evolutionary entropy will come not from low-dimensional systems with imposed symmetries, but from the high-dimensional neutrality produced by complex developmental trajectories, sketched in chapter 3.

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