Working Paper

Can adaptive dynamics invade?

Ulf Dieckmann

WP-96-152
December 1996

International Institute for Applied Systems Analysis ◻ A-2361 Laxenburg ◻ Austria
Telephone: +43 2236 807 ◻ Fax: +43 2236 71313 ◻ E-Mail: info@iiasa.ac.at

Can adaptive dynamics invade?

Ulf Dieckmann

WP-96-152
December 1996

IIASA International Institute for Applied Systems Analysis □ A-2361 Laxenburg □ Austria
Telephone: +43 2236 807 □ Fax: +43 2236 71313 □ E-Mail: info@iiasa.ac.at

IIASA STUDIES IN ADAPTIVE DYNAMICS NO. 14

The Adaptive Dynamics Network at IIASA fosters the development of new mathematical and conceptual techniques for understanding the evolution of complex adaptive systems

Focusing on these long-term implications of adaptive processes in systems of limited growth, the Adaptive Dynamics Network brings together scientists and institutions from around the world with IIASA acting as the central node.

Scientific progress within the network is reported in the IIASA Studies in Adaptive Dynamics series.

THE ADAPTIVE DYNAMICS NETWORK

The pivotal role of evolutionary theory in life sciences derives from its capability to provide causal explanations for phenomena that are highly improbable in the physicochemical sense. Yet, until recently, many facts in biology could not be accounted for in the light of evolution. Just as physicists for a long time ignored the presence of chaos, these phenomena were basically not perceived by biologists.

Two examples illustrate this assertion. Although Darwin's publication of "The Origin of Species" sparked off the whole evolutionary revolution, oddly enough, the population genetic framework underlying the modern synthesis holds no clues to speciation events. A second illustration is the more recently appreciated issue of jump increases in biological complexity that result from the aggregation of individuals into mutualistic wholes.

These and many more problems possess a common source: the interactions of individuals are bound to change the environments these individuals live in. By closing the feedback loop in the evolutionary explanation, a new mathematical theory of the evolution of complex adaptive systems arises. It is this general theoretical option that lies at the core of the emerging field of adaptive dynamics. In consequence a major promise of adaptive dynamics studies is to elucidate the long-term effects of the interactions between ecological and evolutionary processes.

A commitment to interfacing the theory with empirical applications is necessary both for validation and for management problems. For example, empirical evidence indicates that to control pests and diseases or to achieve sustainable harvesting of renewable resources evolutionary deliberation is already crucial on the time scale of two decades.

The Adaptive Dynamics Network has as its primary objective the development of mathematical tools for the analysis of adaptive systems inside and outside the biological realm.

IIASA STUDIES IN ADAPTIVE DYNAMICS

No. 1 Metz JAJ, Geritz SAH, Meszéna G, Jacobs FJA, van Heerwaarden JS:
Adaptive Dynamics: A Geometrical Study of the Consequences of Nearly Faithful Reproduction.
IIASA Working Paper WP-95-99.
van Strien SJ, Verduyn Lunel SM (eds.): Stochastic and Spatial Structures of Dynamical Systems, KNAW Verhandelingen, North Holland, Amsterdam, pp. 183-231 (1996).

No. 2 Dieckmann U, Law R:
The Dynamical Theory of Coevolution: A Derivation from Stochastic Ecological Processes.
IIASA Working Paper WP-96-01.
Journal of Mathematical Biology (1996) 34, 579–612.

No. 3 Dieckmann U, Marrow P, Law R:
Evolutionary Cycling of Predator-Prey Interactions: Population Dynamics and the Red Queen.
Journal of Theoretical Biology (1995) 176, 91–102.

No. 4 Marrow P, Dieckmann U, Law R:
Evolutionary Dynamics of Predator-Prey Systems: An Ecological Perspective.
IIASA Working Paper WP-96-02.
Journal of Mathematical Biology (1996) 34, 556–578.

No. 5 Law R, Marrow P, Dieckmann U:
On Evolution under Asymmetric Competition.
IIASA Working Paper WP-96-03.
Evolutionary Ecology (1997) in press.

No. 6 Metz JAJ, Mylius SD, Diekmann O:
When Does Evolution Optimise? On the Relation between Types of Density Dependence and Evolutionarily Stable Life History Parameters.
IIASA Working Paper WP-96-04.

No. 7 Ferrière R, Gatto M:
Lyapunov Exponents and the Mathematics of Invasion in Oscillatory or Chaotic Populations.
Theoretical Population Biology (1995) 48, 126–171.

No. 8 Ferrière R, Fox GA:
Chaos and Evolution.
Trends in Ecology and Evolution (1995) 10, 480–485.

No. 9 Ferrière R, Michod RE:
The Evolution of Cooperation in Spatially Heterogeneous Populations.
IIASA Working Paper WP-96-29.
American Naturalist (1996) 147, 692–717.

No. 10 Van Dooren TJM, Metz JAJ:
Delayed Maturation in Temporally Structured Populations with Non-Equilibrium Dynamics.
IIASA Working Paper WP-96-70.

No. 11 Geritz SAH, Metz JAJ, Kisdi E, Meszéna G:
The Dynamics of Adaptation and Evolutionary Branching.
IIASA Working Paper WP-96-77.

No. 12 Geritz SAH, Kisdi E, Meszéna G, Metz JAJ:
Evolutionarily Singular Strategies and the Adaptive Growth and Branching of the Evolutionary Tree.
IIASA Working Paper WP-96-114.

No. 13 Heino M, Metz JAJ, Kaitala V:
Evolution of Mixed Maturation Strategies in Semelparous Life-Histories: the Crucial Role of Dimensionality of Feedback Environment.
IIASA Working Paper WP-96-126.

No. 14 Dieckmann U:
Can Adaptive Dynamics Invade?
IIASA Working Paper WP-96-152.

Issues of the IIASA Studies in Adaptive Dynamics series can be obtained free of charge. Please contact:

Adaptive Dynamics Network
International Institute for Applied Systems Analysis
A–2361 Laxenburg
Austria

Telephone +43 2236 807, Telefax +43 2236 71313, E-Mail adn@iiasa.ac.at,
Internet http://www.iiasa.ac.at/Research/ADN

Can Adaptive Dynamics Invade?

ULF DIECKMANN

International Institute for Applied Systems
Analysis, A-2361 Laxenburg, Austria

An international group of scientists gathered in August 1996 for a workshop in the Matra mountains of Hungary to report and assess recent developments and open research topics in the new field of adaptive dynamics. This paper provides a brief overview of basic adaptive dynamics theory, outlines recent work within the field and evaluates the prospects for the future.

1 Introduction

The emerging field of adaptive dynamics sets out to provide additional insights into the long-term dynamics of evolutionary and coevolutionary processes.

Ever since Haldane, Fisher and Wright laid the foundations for the Modern Synthesis of the 1930s, the pending integration of population ecology and evolutionary genetics has been debated. Progress into this direction proved difficult as it is not straightforward to implement into population genetic analyses ecologically realistic assumptions, for example regarding density dependence or interspecific interactions. When trying to do so, the resulting genetic models quickly become intractable.

Now population genetics' detailed knowledge, which reflects the chromosomal mechanisms of evolutionary change, can be complemented by a new framework for understanding the long-term consequences of phenotypic evolution. By trading genetic for ecological detail, adaptive dynamics theory links the interactions of individuals through the dynamics of populations to the evolution of communities. The adaptive dynamics approach goes beyond classical evolutionary game theory in several respects. It originates from two main lines of research: an extended classification scheme for evolutionarily stable strategies (Figure 1) and a network of evolutionary models linking classical evolutionary game theory to replicator dynamics and individual-based ecological models (Figure 2).

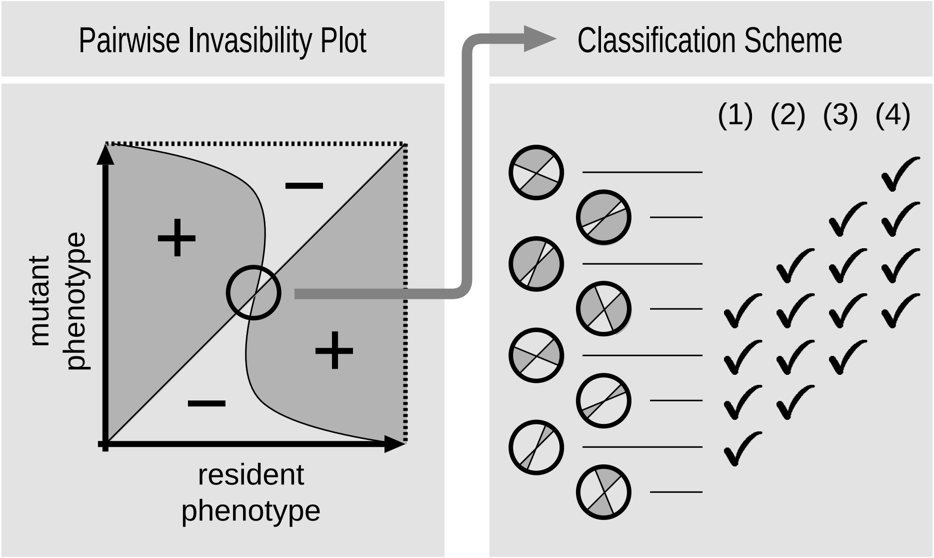

Figure 1 Pairwise invasibility plots and the classification of evolutionarily singular points. The adaptive dynamics invasion function of a particular ecological system defines a pairwise invasibility plot for resident and mutant phenotypes. When the invasion function is positive for a particular pair of phenotypes, the resident may be replaced by the invading mutant. Intersections of the invasion function's zero contour line with the 45 degree line indicate potential evolutionary end-points. Knowing the slope of the countour line at these singular points suffices to answer four separate questions: (1) Is a singular phenotype immune to invasions by neighboring phenotypes? (2) When starting from neighboring phenotypes, do successful invaders lie closer to the singular one? (3) Is the singular phenotype capable of invading into all its neighboring types? (4) When considering a pair of neighboring phenotypes to both sides of a singular one, can they invade into each other?

2 From Mutant Invasions to Adaptive Dynamics

Interactions between individuals are bound to change the environments these individuals live in. The phenotypic composition of an evolving population therefore affects its ecological environment, and this environment in turn determines the population dynamics of the individuals involved. It is this setting of resident phenotypes into which mutant phenotypes must succeed to invade for long-term evolution to proceed. Whether or not such an event may occur can be decided by adaptive dynamics' invasion functions: if the initial exponential growth rate of a small mutant population in an established resident population (a rate which one obtains as a Lyapunov exponent) is positive, the mutant phenotype has a chance to replace the former resident phenotype (Metz et al. 1992; Rand et al. 1994; Ferrière and Gatto 1995).

Once the invasion function of the evolving system is known, pairwise invasibility plots can be constructed (van Tienderen and de Jong 1986; Taylor 1989; Kisdi and Meszéna 1993; Metz et al. 1996, Geritz et al. 1997). In the simplest case mutant and resident phenotypes are distinguished by a single metric character or quantitative trait. When plotting the sign of the invasion function for each of the possible combinations of mutant and resident phenotypes, the shape of a zero contour line becomes visible, see Figure 1. This line separates regions of potential invasion success from those of invasion failure and its shape carries important information about the evolutionary process (Metz et al. 1996, Geritz et al. 1997). In particular, possible end-points of the process are located at those resident phenotypes where a zero contour line and the 45 degree line intersect.

In characterizing such potential end-points, also called singular points, classical evolutionary game theory emphasizes a single, fundamental dichotomy: either the resident phenotype is an evolutionarily stable strategy (ESS) or it is not. In the former case no mutant phenotype has a chance to invade into the resident population. In contrast, adaptive dynamics theory uses an extended classification scheme in which four different questions are tackled simultaneously.

1. Is a singular phenotype immune to invasions by neighboring phenotypes? This criterion amounts to a local version of the classical ESS condition.
2. When starting from neighboring phenotypes, do successful invaders lie closer to the singular one? Here the attainability of a singular point is addressed, an issue that is separate from its invasibility.
3. Is the singular phenotype capable of invading into all its neighboring types? Only if so, the phenotype at the singular point can be reached in a single mutation step.
4. When considering a pair of neighboring phenotypes to both sides of a singular one, can they invade into each other? Assessing this possibility is essential for predicting coexisting phenotypes and the emergence of polymorphisms.

All four questions are relevant when trying to understand the nature of potential evolutionary end-points. It is therefore remarkable how simple it is to obtain the four answers: all that is required is to take a look at the pairwise invasibility plot and read off the slope of the zero contour line at the singular phenotype (Metz et al. 1996, Geritz et al. 1997), see Figure 1.

3 Models of Phenotypic Evolution Unified

A large variety of phenotypic models has been used in the past to describe the dynamics of the evolutionary process. Within the adaptive dynamics framework these disparate approaches can be unified into a single network of linked descriptions (Dieckmann et al. 1995; Dieckmann and Law 1996). Starting from an individual-based account of birth, death and mutation processes, a stochastic model for the evolving polymorphic frequency distributions of phenotypes is constructed (Figure 2a). This dynamics can be applied either to a single population or to a community of coevolving populations. As the rates for birth, death and mutations are allowed to depend on any feature of these distributions, no limitations are imposed as to the kind of interspecific or intraspecific

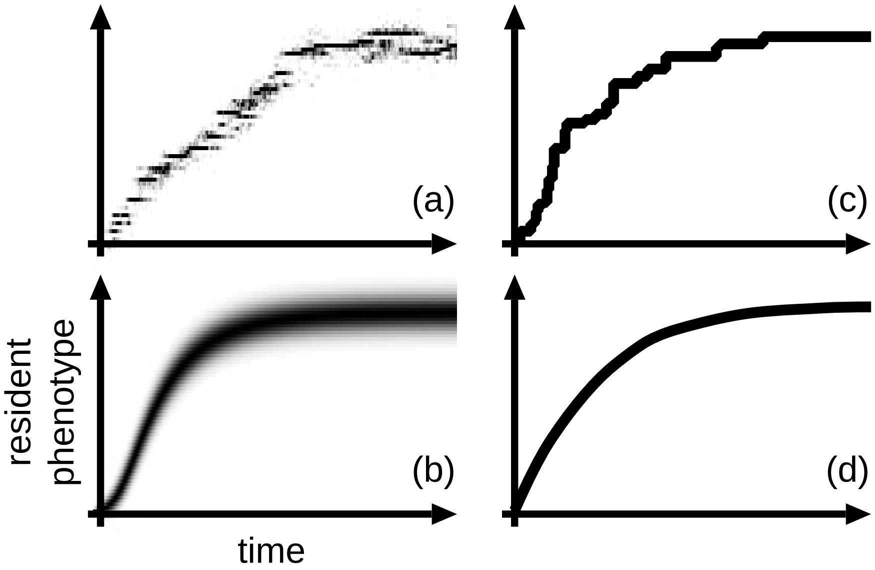

Figure 2 Generalized replicator dynamics and model reduction. Four types of models for phenotypic evolution are unified into a single network of linked descriptions: (a) individual-based birth-death-mutation process (polymorphic and stochastic), (b) reaction-diffusion model (polymorphic and deterministic), (c) evolutionary random walk (monomorphic and stochastic), (d) gradient ascent on an adaptive topography (monomorphic and deterministic).

interactions, and no type of density- or frequency-dependence in survival or fecundity is excluded.

From this model, which can be regarded as a generalization of the classical replicator equations (Schuster and Sigmund 1983) to nonlinear stochastic population dynamics with mutations, simplified models are derived. First, a reaction-diffusion approximation can be obtained for sufficiently large populations (Figure 2b). Second, if the conventional separation between the ecological and the evolutionary time scale is accepted, the evolutionary dynamics become mutation-limited and phenotypic distributions are monomorphic at most points in time (Figure 2c). The occurring phenotypic substitutions (although not their expected rates) can then be understood using classical evolutionary game theory complemented by pairwise invasibility plots. Sequences of such transitions bring about a directed evolutionary random walk in the space of phenotypes. Third, if mutational steps are not too large, the essence of the substitution process is captured by a deterministic dynamic (Figure 2d). This dynamic provides an underpinning for a class of models in the literature that are based on time-variable adaptive topographies (Hofbauer and Sigmund 1990; Abrams et al. 1993; Vincent et al. 1993).

4 Connections with Genetics

Adaptive dynamics theory predicts the existence of a type of evolutionary end-points that, on closer examination, turn out not to be end-points at all (Metz et al. 1996). Stefan Geritz and Hans Metz from the University of Leiden, the Netherlands, opened discussions on the phenomenon of evolutionary branching: starting from one side of a singular point, successfully invading phenotypes at first converge closer and closer to that singular point. Eventually, however, mutants leaping across the point also commence to invade on the other side. The two branches of phenotypes on both sides of such a singular point, once established, actually can coexist and will start to diverge from each other.

It has been suggested that the process of evolutionary branching could form the basis for an adaptation-driven speciation event (Metz et al. 1996). However, only when going beyond a merely phenotypic description of the evolutionary process by incorporating genetic mechanisms, two critical questions can be evaluated.

1. Does the phenomenon of evolutionary branching persist when diploid genetics and sexual reproduction are introduced?
2. Are there mechanisms that could cause genetic isolation of the evolving branches?

Contributions at the workshop indicated that both questions can be answered affirmatively. Work by Stefan Geritz and Eva Kisdi, Eötvös University Budapest, Hungary, shows that when either reproductive compatibility between two types of individuals or migration rates between two spatial patches are evolving, evolutionary branching can develop for diploid, sexual populations. Michael Döbeli from the University of Basel, Switzerland, and Ulf Dieckmann, IIASA Laxenburg, Austria, demonstrated that in a multi-locus genetic model an evolving degree of assortative mating is sufficient to allow for evolutionary branching at those phenotypes predicted by adaptive dynamics theory.

Other talks also were concerned with integrating phenotypic and genetic understanding of evolutionary dynamics. Carlo Matessi, IGBE-CNR Pavia, Italy, talked about the role of genetic canalization for selection in fluctuating environments. Tom van Dooren from the University of Antwerp, Belgium, and Stefan Geritz presented methods for extending the analyses of pairwise invasibility plots to systems with diploid inheritance.

5 Evolving Ecologies

The framework of adaptive dynamics is particularly geared to infer evolutionary predictions from ecological assumptions.

Richard Law from the University of York, U.K., showed how asymmetric competition between two ecological types can give rise to rich patterns of phenotypic coevolution, including the evolutionary cycling of phenotypes (Dieckmann et al. 1995) — patterns that are not expected from the simple presumption of character divergence. Guy Sella, Hebrew University, Jerusalem, Israel, and Michael Lachmann, Stanford University, USA, analytically investigated the critical effects of spatial heterogeneities in a grid-based prisoner's dilemma. Andrea Mathias, Eötvös University Budapest, Hungary, showed how the evolution of germination rates in annual plants exposed to randomly varying environments may result in two mixed strategies coexisting and may induce a cyclic process of evolutionary branching and extinction. Andrea Pugliese, University of Trento, Italy, presented an analysis of the coevolutionary dynamics of viruses and their hosts in which he explicitly allowed for within-host competition of viral strains. Vincent Jansen, Imperial College at Silwood Park, U.K., examined whether the damping effect which a spatial population structure can have on predator-prey cycles could be expected to arise under the coevolution of migration rates.

6 Adaptive Dynamics in the Wild

Several participants of the workshop reported on interpreting empirically observed patterns in terms of adaptive processes.

Paul Marrow, University of Cambridge, U.K., showed experimental data on the distribution of offspring numbers in Soey sheep and studied whether its variation with phenotypic state or population density could be understood as an outcome of optimized reproductive strategies. John Nagy, Arizona State University, USA, analyzed the adaptive dynamics of dispersal behavior in metapopulations of pika. Ido Pen, University of Groningen, the Netherlands, evaluated a set of competing adaptive explanations for the seasonal sex-ratio trend observed in the kestrel by devising a life-history model of the kestrel population and predicting the adaptive change by means of invasion functions. Mats Gyllenberg, University of Turku, Finland, analyzed to what extent the predator-prey cycles observed for voles and weasels in Northern Fennoscandia can be understood as a result of a predator-induced evolution of suppressed reproduction in the prey.

7 Remaining Challenges

Much progress has been made in setting up the adaptive dynamics framework over the past five years. Nevertheless, many interesting directions for future research remain widely open. Three examples illustrate this assertion.

Mikko Heino, University of Helsinki, Finland, and Géza Meszéna, Eötvös University Budapest, Hungary, independently reported findings which demonstrate the importance of environmental dimensionality. The environment closes the feedback loop from the current phenotypic state to changes in this state. How many variables are necessary to characterize this feedback? How can its dimensionality be assessed empirically? Issues of this kind appear likely to become more important in our understanding of adaptive outcomes than they are today.

Odo Diekmann, University of Utrecht, and Sido Mylius, Leiden University, both in the Netherlands, have analyzed the evolution of reproductive timing in salmons. Their model seems to show that adaptive dynamics' invasion functions can not always be obtained from the growth rates of mutants when these are rare. Under which conditions can attention remain focused on initial invasion dynamics when predicting phenotypic substitutions? The invasion-oriented approach to phenotypic evolution already has succeeded in advancing our understanding substantially (Diekmann et al. 1996), but its limitations still have to be evaluated in more detail.

Hans Metz, Stefan Geritz and Frans Jacobs, Leiden University, the Netherlands, are exploring the options of building a bifurcation theory of evolutionarily stable strategies. Similar to the bifurcation theory of ordinary differential equations, such a framework could enable qualitative predictions of evolutionary outcomes that are robust under small alterations in the underlying ecological settings. Although encouraging results for one-dimensional phenotypes already are available, a general account of evolutionary bifurcations is pending.

With problems of this calibre unsolved but now tractable, adaptive dynamics research promises to remain a fertile ground for innovative ideas on evolution, coevolution and complex adaptation in the years to come.

References

Abrams, P.A., Matsuda, H., Harada, Y.: *Evolutionarily unstable fitness maxima and stable fitness minima of continuous traits.* Evol. Ecol. **7**, 465–487 (1993)

Dieckmann, U., Marrow, P., Law, R.: *Evolutionary cycling of predator-prey interactions: population dynamics and the Red Queen* J. theor. Biol. **176**, 91–102 (1995)

Dieckmann, U., Law, R.: *The dynamical theory of coevolution: a derivation from stochastic ecological processes.* J. Math. Biol. **34**, 579–612 (1996)

Diekmann, O., Christiansen, F., Law, R.: *Evolutionary dynamics.* J. Math. Biol. **34**, 483 (1996)

Ferrière, R., Gatto, M.: *Lyapunov exponents and the mathematics of invasion in oscillatory or chaotic populations.* Theor. Pop. Biol. **48**, 126–171 (1995)

Geritz, S.A.H., Kisdi, E., Meszéna, G., Metz, J.A.J.: *Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree.* Evol. Ecol. in press (1997)

Hofbauer, J., Sigmund, K.: *Adaptive dynamics and evolutionary stability.* Appl. Math. Lett. **3**, 75–79 (1990)

Kisdi, E. Meszéna, G.: *Density-dependent life history evolution in fluctuating environments.* In: Yoshimura, J., Clark, C. (eds.) *Adaptation in a Stochastic Environment,* Lecture Notes in Biomathematics, Vol. 98, pp. 26–62, Berlin: Springer 1993

Metz, J.A.J., Geritz, S.A.H., Meszéna, G., Jacobs, F.J.A., van Heerwaarden, J.S.: *Adaptive dynamics: a geometrical study of the consequences of nearly faithful reproduction.* In: van Strien, S.J., Verduyn Lunel, S.M. (eds.) *Stochastic and Spatial Structures of Dynamical Systems,* pp. 183–231, Amsterdam: North Holland 1996

Metz, J.A.J., Nisbet, R.M., Geritz, S.A.H.: *How should we define "fitness" for general ecological scenarios?* Trends Ecol. Evol. **7**, 198–202 (1992)

Rand, D.A., Wilson, H.B., McGlade, J.M.: *Dynamics and evolution: evolutionarily stable attractors, invasion exponents and phenotype dynamics.* Phil. Trans. R. Soc. B **343**, 261–283 (1994)

Schuster, P., Sigmund, K.: *Replicator dynamics.* J. theor. Biol. **100**, 533–538 (1983)

Taylor, P.D.: *Evolutionary stability in one-parameter models under weak selection.* Theor. Pop. Biol. **36**, 125–143 (1989)

van Tienderen, P.H., de Jong, G.: *Sex-ratio under the haystack model — polymorphism may occur.* J. theor. Biol. **122**, 69–81 (1986)

Vincent, T.L., Cohen, Y., Brown, J.S.: *Evolution via strategy dynamics.* Theor. Pop. Biol. **44**, 149–176 (1993)