# Can adaptive dynamics invade?

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 in this direction proved difficult as it is not straightforward to incorporate ecologically realistic assumptions, for example, regarding density dependence or interspecific interactions, into population genetic analyses. When trying to do so, the resulting genetic models quickly become intractable.

The emerging field of adaptive dynamics sets out to provide additional insights into the long-term dynamics of evolutionary and coevolutionary processes. Now, detailed knowledge of population genetics, 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 (Fig. 1), and a network of evolutionary models linking classical evolutionary game theory to replicator dynamics and individual-based ecological models (Fig. 2). An international group of scientists gathered last summer for a workshop in the Matra mountains of Hungary to report and assess recent developments and open research topics in this new field.

## From mutant invasions to adaptive dynamics

Interactions between individuals are bound to change the environments that 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 that mutant phenotypes must invade for long-term evolution to proceed. Whether or not such an event may occur can be decided by the invasion functions of adaptive dynamics: if the initial exponential growth rate of a small mutant population in an established resident population (a rate that one obtains as a Lyapunov exponent) is positive, the mutant phenotype has a chance to replace the former resident phenotype[1-3].

Once the invasion function of the evolving system is known, pairwise invasibility plots can be constructed[4-7,15]. 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 Fig. 1). This line separates regions of potential invasion success from those of invasion failure, and its shape carries important information about the evolutionary process[6,7]. 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 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 phenotype? 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? This would be the only way the phenotype at the singular point can be reached in a single mutation step.
(4) If a pair of neighboring phenotypes lie either side of a singular phenotype, 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[6,7] (see Fig. 1).

## Models of phenotypic evolution unified

Many phenotypic models have been used 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[8,9]. 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 (Fig. 2a). This dynamics can
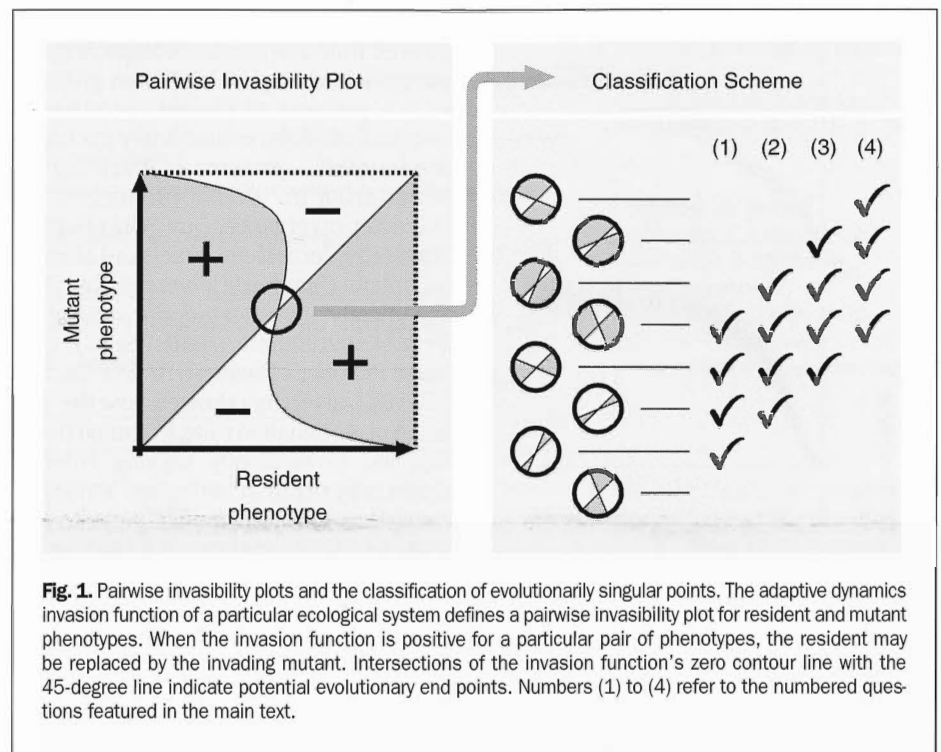


**Fig. 1.** Pairwise invasibility plots and the classification of evolutionarily singular points. The adaptive dynamics invasion function of a particular ecological system defines a pairwise invasibility plot for resident and mutant phenotypes. When the invasion function is positive for a particular 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. Numbers (1) to (4) refer to the numbered questions featured in the main text.

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 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[10] to nonlinear stochastic population dynamics with mutations, simplified models are derived. First, a reaction–diffusion approximation can be obtained for sufficiently large populations (Fig. 2b). Second, if the conventional separation between the ecological and the evolutionary timescale is accepted, the evolutionary dynamics become mutation-limited and phenotypic distributions are monomorphic at most points in time (Fig. 2c). The occurring phenotypic substitutions (although not their expected rates) can 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 (Fig. 2d). This dynamic provides an underpinning for a class of models in the literature that are based on time-variable adaptive topographies[11–13].

## 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[6,7]. Stefan Geritz and Hans Metz (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, can actually 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[6]. However, only when going beyond a merely phenotypic description of the evolutionary process by incorporating genetic mechanisms, can two critical questions be evaluated:
• Does the phenomenon of evolutionary branching persist when diploid genetics and sexual reproduction are introduced?
• 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 Doebeli (University of Basel, Switzerland) and Ulf Dieckmann [International Institute for Applied Systems Analysis (IIASA), Laxenburg, Austria]
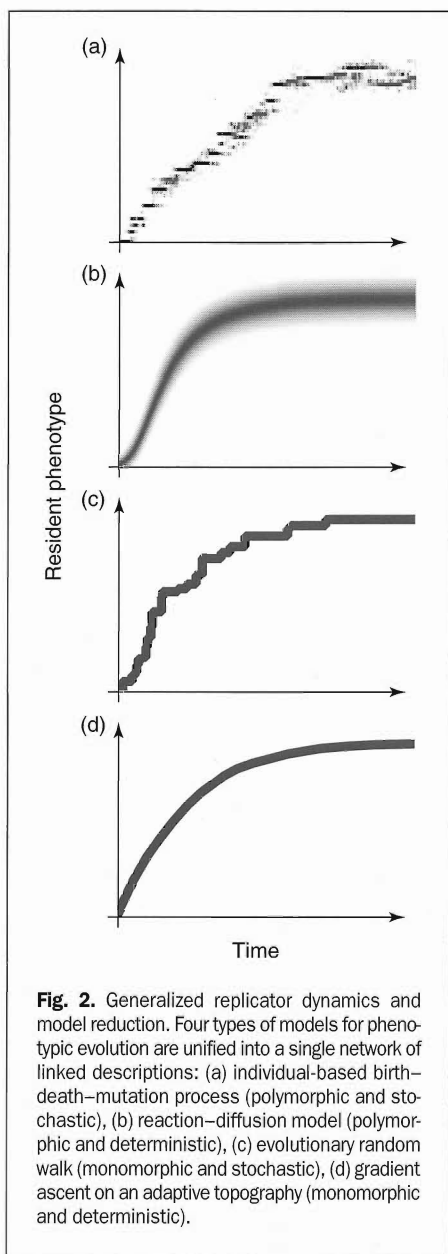
**Fig. 2.** Generalized replicator dynamics and model reduction. Four types of models for phenotypic evolution are unified into a single network of linked descriptions: (a) individual-based birth–death–mutation process (polymorphic and stochastic), (b) reaction–diffusion model (polymorphic and deterministic), (c) evolutionary random walk (monomorphic and stochastic), (d) gradient ascent on an adaptive topography (monomorphic and deterministic).

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 were also concerned with integrating phenotypic and genetic understanding of evolutionary dynamics. Carlo Matessi [Institute of Genetics, Biochemistry and Evolution, National Research Council (IGBE-CNR), Pavia, Italy] talked about the role of genetic canalization for selection in fluctuating environments. Tom van Dooren (University of Antwerp, Belgium) and Stefan Geritz presented methods for extending the analyses of pairwise invasibility plots to systems with diploid inheritance.

## Evolving ecologies

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

Richard Law (University of York, UK) showed how asymmetric competition between two ecological types can give rise to rich patterns of phenotypic coevolution, including the evolutionary cycling of phenotypes[9] – patterns that are not expected from the simple presumption of character divergence. Guy Sella (Hebrew University, Jerusalem, Israel) and Michael Lachmann (Stanford University, CA, USA) analytically investigated the critical effects of spatial heterogeneities in a grid-based Prisoner's Dilemma. Andrea Mathias (Eötvös University) 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, UK) examined whether the damping effect that a spatial population structure can have on predator–prey cycles could be expected to arise under the coevolution of migration rates.

## Adaptive dynamics in the wild

Several participants discussed the interpretation of empirically observed patterns in terms of adaptive processes. Paul Marrow (University of Cambridge, UK) showed experimental data on the distribution of offspring numbers in Soay sheep and studied whether 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 the extent to which 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.

## Remaining challenges

Mikko Heino (University of Helsinki, Finland) and Géza Meszéna (Eötvös University) independently reported findings that 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, The Netherlands) and Sido Mylius (Leiden University) have analyzed the evolution of reproductive timing in salmon. Their model seems to show that adaptive dynamics invasion functions cannot always be obtained from the growth rates of mutants when mutants are rare. The question is under which conditions can attention remain focused on initial invasion dynamics when predicting phenotypic substitutions? The invasion-oriented approach to phenotypic evolution has already succeeded in advancing our understanding substantially[14], but its limitations still have to be evaluated in more detail.

Hans Metz, Stefan Geritz and Frans Jacobs (Leiden University) are exploring the options of building a bifurcation theory of ESSs. 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 are already available, a general account of evolutionary bifurcations is pending.

With problems of this kind 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.

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