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PERSPECTIVES IN MATHEMATICAL BIOLOGY

Adaptive dynamics: a framework to model evolution in the ecological theatre

Éva Kisdi · Stefan A. H. Geritz

The astonishing diversity of life has evolved over many millions of years of natural selection. Yet natural selection, as often taught in introductory courses and textbooks on population genetics, seems to explain why diversity should *not* exist: the survival of the fittest is the loss of everything else. Simple models of natural selection predict the fixation of the best allele in every locus.[1] Yet the Earth (or any part of it) is not ruled by a single Darwinian monster.

Frequency-dependent selection (the advantage of an allele being rare, regardless of which allele it is) solves the problem of diversity, but then solves it all too well: by choosing the frequency-dependent fitness function appropriately, the model can produce *any* conceivable result and, hence, lacks predictive power.[2] In between the survival of the fittest and the survival of anybody, the problem of adaptive diversity slips away.

The solution to this paradox of classical population genetics is in the Ecology textbooks. Fitness describing survival and reproduction must be derived from realistic ecological interactions,[3] which explain how different genotypes or species coexist.

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[1] Save heterozygote superiority, which explains only within-species variation, is likely to be transient in long-term evolution, and is rare in fact.

[2] We used somewhat extreme words for clarity, but this extreme view is maintained in recent textbooks of population genetics (Hartl and Clark 2007, p. 230; Ewens 2004, p. 54).

[3] This point was also emphasised by the article of Lambert (2009) in this series of *Perspectives in Mathematical Biology*.

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É. Kisdi (✉) · S. A. H. Geritz
Department of Mathematics and Statistics, University of Helsinki, Helsinki, Finland
e-mail: eva.kisdi@helsinki.fi

S. A. H. Geritz
e-mail: stefan.geritz@helsinki.fi

This approach has been adopted in some exemplary cases with simple ecological assumptions (e.g., Christiansen and Loeschcke 1980; Levene 1953) but overall, there was for decades astonishingly little crosstalk between population genetics and ecology in the quest for explaining the evolution of diversity and explaining the coexistence of evolving species. And for good reason: taking the full extent of both genetic and ecological complexity on board would make a model impenetrable to any deep understanding.

Adaptive dynamics started out with an explicitly stated stance: let us trade genetic complexity for ecological complexity, and derive fitness from first principles of population dynamics (Metz et al. 1992). The analysis thus begins with calculating the birth and death rates (or other demographic parameters) as determined by resource competition, predation or other ecological interactions between individuals with different trait values in an explicit model of deterministic population dynamics, which describes how population size changes as a consequence of ecological interactions. Simple techniques, such as pairwise invasibility plots, can then be used to analyse the evolution of continuous traits via a sequence of mutations and invasions (Geritz et al. 1998). This analysis reveals that gradual evolution by small mutations can lead to a singular trait value at which the population undergoes *evolutionary branching*, i.e., splits into two lineages of distinct phenotypes that form two separate branches of the evolutionary tree (Geritz et al. 1998). Evolutionary branching has been found in models of many ecological scenarios including competition, predation, spatial structure, temporal stochasticity, host-pathogen interactions, and so forth (see bibliography at http://mathstat.helsinki.fi/~kisdi/addyn.htm). The emergence of adaptive diversity via evolutionary branching thus appears to be common.

Through its applications to many different ecological models, adaptive dynamics has proven itself a fruitful framework for modelling evolution as driven by ecological interactions. Delving into the mathematical theory of adaptive dynamics, however, one still encounters open problems in both ecological and evolutionary dynamics.

On the (fast) ecological time scale, the resident-invader dynamics needs a closer look. While the invasion fitness (i.e., the initial exponential growth rate of a rare mutant) is well defined and can be calculated under very general conditions (Metz et al. 1992), it provides no information about the outcome of an invasion event: the dynamics in the interior of the resident-invader population state space is typically invisible from the boundaries. This problem was dealt with on a case-by-case basis, until Geritz (2005) and Geritz et al. (2002) identified conditions under which the dynamics in the interior are implied by (and thus can be derived from) the dynamics near the boundary, provided that a mutation causes only a small change in the trait value. The generalization of these results to polymorphic resident populations (partially achieved in Dercole and Rinaldi 2008), to arbitrarily structured populations and to non-equilibrium systems remains an open problem.

On the (slow) evolutionary time scale, where trait values change as a result of many successive invasion events, the assumption of small mutation steps is again important: it allows us to use local approximations of the invasion fitness as a function of the mutant and resident trait values. Consequently, general theorems can be proven that do not depend on the details of the particular application but only on the local geometry of the fitness function. A good example is the classification of scalar-valued singular strategies into eight basic types (Geritz et al. 1998). An analogous classification for vector-valued traits, and in particular the formulation of necessary and sufficient conditions for evolutionary branching of vector-valued traits, remains one of the most important open problems of adaptive dynamics. Function-valued traits pose another set of novel challenges that, within the context of adaptive dynamics, have yet to be addressed (see Parvinen et al. (2006) for some results).

New mutants are initially present in such small numbers that the invasion dynamics cannot be realistically described by a deterministic model. Instead, we use a stochastic branching process (not to be confused with evolutionary branching) to calculate the probability of a successful invasion. The invasion probability together with the mutation rate and the probability distribution of mutational steps determine the probability distribution of the next evolutionary step in the trait space. While the distribution of evolutionary steps does not qualitatively affect the adaptive dynamics of scalar-valued traits in monomorphic populations, it has a significant effect in polymorphic populations as well as in the case of vector-valued traits. Adaptive dynamics motivates further research in the field of stochastic branching processes to find the probability of invasion for general (in particular non-equilibrium) population dynamics.

Mutation steps in adaptive dynamics are assumed to be small but not necessarily infinitesimally small. In the limit of infinitesimally small mutational steps and infinitely large resident populations, we obtain a system of ordinary differential equations, known as the canonical equation of adaptive dynamics (Champagnat et al. 2006; Dieckmann and Law 1996; Durinx et al. 2008) (for other possible limits of the underlying stochastic individual-level process, see for example Champagnat et al. 2008). The canonical equation describes the evolution of trait values as a continuous flow in the trait space. While it cannot capture the phenomenon of evolutionary branching, it does provide a useful tool for studying stability properties of evolutionary singularities (Leimar 2009) and cyclic or chaotic trait dynamics (Dercole and Rinaldi 2008).

Over the past decade, the clonal theory of adaptive dynamics has developed considerable breadth in terms of applications and is establishing a strong mathematical foundation. But how does it relate to population genetics and the evolution of diversity in diploid sexual organisms? With Mendelian inheritance, trait values are not inherited directly from parent to offspring. Alleles however are: alleles reproduce clonally, being transmitted from parent to offspring faithfully, except for mutations. One can thus use adaptive dynamics to study the evolution of allelic values (Kisdi and Geritz 1999) and to study population genetic phenomena such as the evolution of dominance (Van Dooren 1999) and gene duplication (Proulx and Phillips 2006) in one- or few-locus models. Evolutionary branching of alleles occurs under much the same conditions as evolutionary branching in clonal models, and can explain how the alleles of an adaptive genetic polymorphism initially arose.

To many researchers, the Holy Grail is not just explaining genetic or phenotypic diversity but explaining the origin of diverse species. For adaptive speciation to occur, two conditions must be met: natural selection must favour diversity; and reproductive isolation must evolve between the diverging lineages. Adaptive dynamics has helped to explain the former, but population genetics is vital for modelling the latter. In several recent models, adaptive dynamics has been used to study the evolution of reproductive isolation via assortative mating in diploid sexual organisms (Pennings et al. 2008;

Ripa 2009). The evolving mating system induces sexual selection because different genotypes are not equally likely to be chosen as mates and therefore to produce offspring. Sexual selection interacts with natural selection in a rather complicated way, producing unexpected phenomena such as evolution stalling half-way towards speciation (Matessi et al. 2001; Pennings et al. 2008). There is huge progress and many fresh ideas in speciation research, stemming from recent empirical findings and computational modelling efforts (reviewed in Bolnick and Fitzpatrick 2007). Adaptive dynamics can be one of the main guiding principles used to gain insight into the inherently complex process of speciation.

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