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COMMENTARY

# Has adaptive dynamics contributed to the understanding of adaptive and sympatric speciation?

S. GOURBIERE*,† & J. MALLET*

*Galton Laboratory, University College London, London, UK
†Laboratoire de Théorie des Systèmes, Université de Perpignan, Cedex, France

Adaptive dynamics (AD) theory (Dieckmann & Law, 1996; Metz *et al.*, 1996) has been widely used as an attractive extension of previous phenotypic approaches, namely evolutionary game theory and optimization models (Meszéna *et al.*, 2001). In the majority of AD models, the basis of evolution consists of replacement of a 'resident' population by a 'mutant' phenotype. Because fitness depends both on the mutant phenotype and the current state of the resident population, evolution proceeds in a continuously changing fitness landscape. This allows the dynamical attainability, the evolutionary stability and the invasion potential of mutants to be independent of one another. Earlier modelling approaches have also allowed these stability properties to combine in different ways, but AD provides an elegant mathematical framework unifying previous attempts. It is thus a convenient method deeply rooted both in evolutionary ecology to investigate frequency- and density-dependent evolution. As such, AD has been successful in investigating many evolutionary topics as well as in addressing important issues of conservation biology (http://www.iiasa.ac.at/Research/ADN).

One of the most intriguing situations investigated by AD is evolution towards fitness minima. In this case, a singular population state is both an attractor of the mutation-selection process and also, once reached, a repellor of the evolutionary dynamics. Such a phenotype or strategy is referred to as an 'evolutionary branching point', because in its vicinity different phenotypes can invade and undergo divergent evolution. The discovery that such branching processes can occur in a variety of ecological situations is touted as a major contribution of AD to the theory of sympatric speciation: the branching point can represent the ecologically-driven evolution, not only of polymorphisms, but also, in some cases, of separate species. Dieckmann and Doebeli's highly cited papers (especially Dieckmann & Doebeli, 1999; Doebeli & Dieckmann, 2000, 2003) argue that frequency-dependent ecological interactions can easily provide the selective environment required for assortative mating to evolve as a kind of reinforcement of ecologically driven post-zygotic isolation. One is then tempted to ask: 'Adaptive dynamics: is speciation too easy?' (Bridle & Jiggins, 2000). The review by Waxman & Gavrilets (2005) emphasizes that we should examine these models more carefully before accepting these contributions of AD to speciation theory. In this review, we ask: (1) Is AD an appropriate tool for modelling speciation? (2) What does AD really teach us about sympatric speciation?

*Correspondence:* Sébastien Gourbiere, Laboratoire de Théorie des Systèmes, Université de Perpignan, 52 Avenue Paul Alduy, 66 860 Perpignan Cedex, France.
Tel.: +33(0)4 68 66 17 63; fax: +33(0)4 68 66 17 60;
e-mail: gourbier@univ-perp.fr

## Is AD an appropriate tool for studying speciation?

Waxman & Gavrilets (2004) detail two important assumptions underlying much of the AD literature. First, AD is generally a theory of successive monomorphisms; where invading mutant phenotypes replace the residents. Secondly, AD rarely deals analytically with sex. Both of these points were highlighted as weaknesses in their model of speciation by AD practitioners themselves (Dieckmann & Doebeli, 1999). In those conditions, AD is a purely ecological framework and the best it can do is to predict conditions for branching points to occur. AD predictions then mainly provide a useful extension of ecological character displacement theory (which focused only on the role of competition), by investigating branching due to, e.g., mutualism and predation (Doebeli & Dieckmann, 2000).

As pointed out by Waxman and Gavrilets, a few studies have generalized the AD framework to diploid organisms with Mendelian genetics (but see Kisdi & Geritz, 1999; Geritz & Kisdi, 2000; Van Dooren, 2003). Fitness functions are here defined for alleles (instead of mutant phenotypes) and the branching process corresponds to the evolution of a genetic polymorphism. AD of monomorphic populations is identical under clonal and Mendelian genetics (provided that alleles contribute additively – e.g. Van Dooren, 2003). Consequently, evolutionary branching will occur under the same ecological conditions in both phenotypic and Mendelian frameworks (Kisdi & Geritz, 1999; Van Dooren, 2003).

However, the recognized contribution of AD to the speciation theory is not only in identifying conditions for branching, but also in investigating what happens after fitness minima have been reached. The major interest is of course in determining whether reproductive isolation develops between incipient species.

These investigations of speciation have mostly been done numerically, allowing straightforward inclusion both of population genetics and of mating processes. Typically, in Dieckmann & Doebeli's papers, polymorphic stochastic models involve a finite set of individuals interacting with respect to their ecological and mating phenotypes. Both ecological and mating traits are treated as quantitative characters determined by many additive diploid loci and are allowed to evolve via a stochastic

birth-death process where offspring inherit parent phenotypes with limited-mutational effects and free recombination.

Accordingly, the success of AD in investigating speciation mostly relies on numerical investigations of models coupling a simple genetic background with a detailed description of interactions generating natural and sexual selection. Whether or not these models are truly 'AD' is not so important. For clarity, one might restrict the use of the term AD to the analytical background provided for clonal or Mendelian genetics, which are definitively outstanding contributions to evolutionary biology. The individual-based models of speciation, set up to obtain realizations of the full stochastic mutation-selection process (Dieckmann *et al.*, 1995; Dieckmann & Law, 1996), are helpful and valuable but do not really qualify as AD, although they were inspired by AD models. Actually, similar individual-based models are used to investigate other evolutionary topics like, for instance, evolutionary genomics. Here, we will continue to refer to these models as AD in spite of this confusion, because of their roots in AD.

A more interesting question is whether these numerical results improve our understanding of speciation. Although individual-based models are useful in studying complex multilocus systems, they are hard to assess and make generalization difficult. This leads on to the second question:

## What does AD really teach us about sympatric speciation?

As Waxman and Gavrilets point out, the speciation scenarios investigated by AD practitioners have already been investigated in more traditional population genetic and evolutionary ecology frameworks. Competitive speciation (Dieckmann & Doebeli, 1999; Doebeli & Dieckmann, 2000), for example, has a venerable history and was proposed first by Rosenzweig (1978). Similarly, speciation along a gradient (Doebeli & Dieckmann, 2003) has its roots in the theory of clines (Haldane, 1948; Fisher, 1950) and has been investigated explicitly since Fisher (1930) and Endler (1977). The main contribution of AD is to provide a more formal investigation of coevolution between ecological traits and assortative mating than took place 30 years ago. But what is really needed from a quantitative approach is to give us insight into the thorny question of the likelihood of these possibilities in nature, and, as we shall show, it is unclear whether AD has achieved this any better than its forebears.

The AD workers claim that assortative mating evolves around branching points, whereas branching itself is claimed to be a general phenomenon that will occur in a wide range of ecological conditions (e.g. Dieckmann & Doebeli, 1999). In contrast, Waxman and Gavrilets argue that the robustness of AD speciation models is questionable: minor changes in parameter values or relaxation of some strong assumptions can strongly alter the outcome, and often prevent speciation.

Few tests of robustness are given in the key AD publications on speciation. Furthermore a number of the authors' claims for robustness (especially with respect to the number of loci determining traits, mutation patterns, form of assortative mating and level of competition between phenotypes, see Dieckmann & Doebeli, 1999) contrast with the results of other studies (Waxman & Gavrilets, 2004 and see below). One likely reason for these contrasting opinions is the sheer complexity of AD models. For instance, in the two Dieckmann and Doebeli Nature papers we found 12 and 18 parameters, with 7 and 11 of them taking on fixed values. The lack of sensitivity analysis is puzzling as some parameter choices are highly specific (e.g. the difference between the variances of assortative mating and disassortative mating functions, Dieckmann & Doebeli, 1999) and because some assumptions may be biologically unjustified (e.g. equal access to preferred mates of all phenotypes without regard to their abundance within the population – see 1 below).

In a few cases, we already have information about the effects of the model assumptions. The following four features of AD models have already been identified that can strongly alter the likelihood of sympatric speciation.

1. The frequency-independent mating process described in AD speciation models ensures that all individuals mate whatever their phenotypes. This is a rather unrealistic assumption as assortative mating is likely to generate strong sexual selection against rare phenotypes, because such individuals are less likely to find suitable mates. Recent investigations using both quantitative genetic (Drossel & McKane, 2000) and explicit genetic models (Gourbiere, 2004) demonstrate how important this assumption can be for competitive speciation models. For instance, considering five to 10 loci (as in the single-trait assortative mating model of Dieckmann & Doebeli, 1999; Doebeli & Dieckmann, 2000, 2003), the level of assortativeness required for speciation must be between 2.5- and 5-fold stronger under a realistic frequency-dependent mating scheme than under the frequency-independent mating scheme used in AD (Fig. 1).

2. Most of the AD results rely on simulations using very similar genetic architectures. Typically, ecological and mating characters are determined by five (or 10) diploid loci. The authors provide little analysis of sensitivity to the genetic architecture, and then only by decreasing the number of loci (Dieckmann & Doebeli, 1999). Interestingly, they observe a decrease in the waiting time for speciation when the number of loci is decreased. When one extends sensitivity analysis to an arbitrary number of loci, the assortative mating parameter range allowing for speciation decreases exponentially (Fig. 1). Accordingly, the required level of

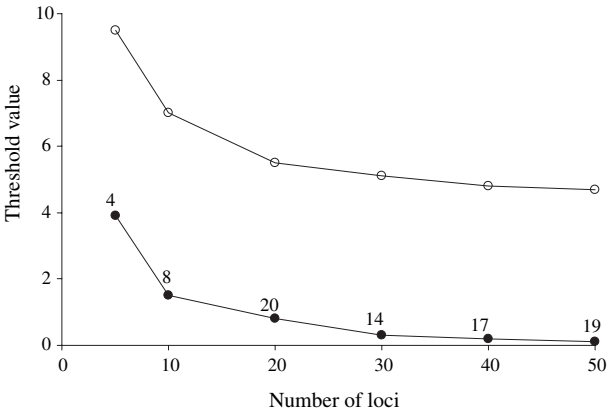


**Fig. 1** Importance of the genetic architecture and mating rule on sympatric speciation. In the model used here, there is a single quantitative trait that acts both as the trait used in mate choice, and the phenotype which causes the choice (emergence time or habitat preference could be examples). The *y*-axis corresponds to the minimal level of assortative mating (as measured by the width of the assortative mate choice distribution – the higher the value, the less strongly assortative is the mating) required to split an initially unimodal genotypic distribution into a bimodal distribution (the lower the threshold value, the stronger the assortative mating has to be). The *x*-axis corresponds to the number of loci ($n_l$) determining the phenotype involved in mate choice. The open and close circles stand for frequency-independent mating (all individuals have equal access to mates) and the more realistic frequency-dependent mating (rare phenotypes are less likely to find a mate), respectively. The level of initial genetic variance of the assortative mating trait required for speciation (when mating is frequency-dependent) is displayed above the close circles. All the results were obtained using an individual-based model corresponding to the quantitative genetic competition model of Doebeli (1996). Details of these two models can be found in Gourbiere (2004).

assortativeness must be doubled (for a frequency-dependent mating scheme) or increased 20-fold (for a frequency-independent mating scheme) when the number of loci is increased from five to 50. This indicates that speciation is much more difficult with larger set of speciation genes than the ones currently used in AD models.

3. An important result of AD is that competitive speciation occurs if the width of the competition distribution ($\sigma_\alpha$) is narrower than the width of the carrying capacity distribution ($\sigma_k$). Under these conditions, extreme phenotypes compete with fewer individuals than intermediate phenotypes. Such a selective advantage to extreme phenotypes compensates for any disadvantage due to lower carrying capacity and results in the disruptive selection promoting speciation. However, it has been ignored in the AD contributions to speciation theory that if $\sigma_\alpha$ is strongly decreased further, the competition occurs only between individuals with very similar phenotypes. Fitness differences between phenotypes are then mostly due to carrying capacities and the phenotypic distribution should simply evolve to fit the carrying capacity distribution, which is assumed to be unimodal. This argument implies that $\sigma_\alpha$ must be larger than some lower limit for speciation to proceed, as well as not larger than $\sigma_k$ (Gourbiere, 2004). In other words, as suggested by Waxman & Gavrilets, conditions for an ecological branching process do not by any means always correspond to conditions for speciation. They potentially include other kinds of genetic polymorphisms, such as a unimodal phenotypic distribution.

A related problem is that, in AD models, the genetic variance is to some extent a constraint imposed by the assumption of equal allele frequencies at a fixed number of two-allele genes, each with an identical contribution to the genetic variance. This constraint imposed by the genetic model ensures that the phenotypic variance itself cannot increase above the situation with all the loci at 50% allele frequency, and which, in the AD models used so far, ensures that $\sigma_\alpha < \sigma_k$ always. If mutation with variable, and, in particular, greater allelic effects were allowed, it seems likely that the phenotypic distribution might be able to broaden to match the carrying capacity distribution more exactly, obviating the pressure for the evolution of assortative mating to allow the population(s) to match the carrying capacity distribution more closely. Although these ideas have not been tested, it seems clear that this represents an important mechanism whereby natural populations can adjust to the prevailing environment without speciation.

4. All AD investigations of speciation consider alleles acting additively on phenotypes. This is a crucial assumption as evolution of dominance is an antagonist mechanism of assortative mating evolution (van Dooren, 1999; Kisdi & Geritz, 1999). Indeed, assortative mating evolves because of selection against highly heterozygous genotypes, and the evolution of dominance would be another means of removing such unfit phenotypes. Which of dominance or assortative mating might evolve first remains to be tested. This could also strongly impede the occurrence of sympatric speciation.

In addition to the lack of sensitivity analysis of AD speciation models to variations in assumptions and parameter values, there is no treatment whatsoever of sensitivity to initial conditions, although speciation strongly depends on initial conditions in numerous other models (for a simple example see Kirkpatrick & Ravigné, 2002). In the kinds of individual-based models implemented (Dieckmann & Doebeli, 1999; Doebeli & Dieckmann, 2000, 2003), likely sensitive initial conditions include numbers of individuals, phenotypic distributions and initial allele frequencies (any phenotype corresponds to a number of potential genotypes). All of these conditions affect the initial genetic variance. Interestingly, speciation does not depend on these initial conditions if mating is frequency-independent (as currently assumed in AD models of speciation – see 1

above). However, when rare-phenotype disadvantage is included in the mating scheme, the initial genetic variance must be larger than a threshold value (Fig. 1). This contributes to making speciation less likely than suggested by AD models.

In view of these various points, it seems that the likelihood of sympatric speciation has mostly been overstated by AD modellers. Accordingly, although AD and AD-derived individual-based numerical results provide a rare framework where population genetics and ecology are combined, robustness of the speciation results seems likely to be rather weaker than currently claimed by AD modellers.

## Conclusions

Technical constraints (see estimates of simulation times in Doebeli & Dieckmann, 2003) are surely responsible in part for the current lack of knowledge of the robustness of AD findings on speciation. Strikingly, it is almost impossible to reproduce AD models because, although the broad-scale ecological and genetic principles are described, there is insufficient description of the programming techniques implemented. Currently others can only implement similar (but probably nonidentical) polymorphic stochastic models; this situation is liable to contribute to the 'balkanization' of speciation theory (Kirkpatrick & Ravigné, 2002). Only the AD authors themselves can then really check the robustness of their results. Similar issues affect other branches of complex modelling, such as in astrophysics. Nevertheless, given the potential importance of AD results for speciation theory, it is damaging that the real contributions of AD cannot be readily checked or extended by other interested evolutionary biologists.

Our belief is that ecology is reasonably well implemented in AD, as the description of ecological interactions is deeply rooted in ecological character displacement theory. On the contrary, we think that a major area for investigation should be to extend AD models to more varied genetic architectures. Such theories will soon be desirable as genetic tools provide increasingly detailed empirical and genomic pictures of speciation. Furthermore, emphasis on greater realism in models of assortative mating would also be beneficial, by allowing a better understanding of the key process of reinforcement, and its interactions both with sexual selection and ecology in speciation.

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