

COMMENTARY

**'Adaptive Dynamics' vs.
'adaptive dynamics'**

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Various approaches that can be described as 'adaptive dynamics' arose from a need to describe the general features of evolutionary change under complex patterns of frequency dependence. Such frequency dependence often arises from ecological scenarios with several interacting species. Currently, the term, 'Adaptive Dynamics' (capitalized) is most often used to refer to a much more narrow body of theory based on models in which evolutionary change is mutation-limited and occurs on a time scale that is much slower than population dynamics. This note argues that the usefulness of all types of adaptive dynamics depends on their ability to provide approximate descriptions of systems in which their assumptions are not satisfied. The ability to approximate more complex situations can only be assessed by analysing more complex and realistic models. Some of Waxman and Gavrillets' criticisms of Adaptive Dynamics are based on unrealistic expectations from simple models, but they are probably correct in arguing that Adaptive Dynamics is insufficient to predict when sympatric speciation will occur.

Different approaches to the dynamics of adaptively changing characteristics

Community and ecosystem ecologists have largely ignored adaptive changes in the species that make up their objects of study. On the contrary, evolutionary ecologists have largely ignored adaptive change in all except for the simplest of ecological scenarios. These gaps have been noticed and commented on many times over the past several decades. Without some way of incorporating adaptive change into ecological models, their predictions are likely to be quite inaccurate, particularly for long-term change (Abrams, 1996; Thompson, 1998; Abrams & Vos, 2003; Matsuda & Abrams, 2004). Without some way of dealing with systems that have a reasonable number of species, evolutionary biology is unlikely to be able to explain spatial and temporal patterns in the characteristics of species that affect their interactions with other species (Brown & Vincent, 1992; Thompson, 1994, 1998; Abrams, 2000; Case & Taper, 2000; Day, 2000; Abrams & Chen, 2002). It is clear that we need to

combine ecological and evolutionary models using a simplified description of the dynamics of adaptive change in traits that determine ecological interactions. This need applies to all forms of adaptation, from behavioural change, through developmental plasticity, to changes in gene frequency. Achieving a full understanding of any of these mechanisms of adaptive change is likely to require a spectrum of models. It is also likely that some common features apply to most mechanisms, and one can hope that a simple framework for modelling might capture those common features. In the following, 'adaptive dynamics' (lower case; henceforth abbreviated as 'ad') will be used to refer to the dynamics of any adaptively changing traits. 'Adaptive Dynamics' (upper case; henceforth abbreviated as 'AD') will refer to a specific set of methods for analysing mutation limited evolutionary change developed by Metz and colleagues (Metz *et al.* 1996; Dieckmann & Law, 1996; Geritz *et al.*, 1997, 1998), and reviewed by Waxman & Gavrillets (2004). One objection to AD is its use of a very general term to describe a narrow spectrum of models of strictly evolutionary adaptation; a more modest appellation would be more appropriate.

As the mean phenotypic characteristics of individuals are key parameters of most ecological models, what is needed, at a minimum, is a description of the dynamics of those average characteristics that display adaptive change. One potential form of adaptive dynamics, models of gene frequency change, might seem to provide the appropriate framework for modelling adaptive evolutionary change. However, dynamic models of gene frequency change have not proven useful in the context of complex ecological scenarios because of lack of knowledge of the genetic basis of ecological characters, and of the translation between genotype and phenotype. On a practical level, such models are simply too complicated to deal with complex multi-species or multi-locus problems. Lande (1976) introduced phenotypically-based quantitative genetic models to evolutionary theory, initiating a wide range of applications to various evolutionary problems. Because breeding values are generally approximately normally distributed, one can describe the character state of a population in terms of the mean and variance of traits of interest. Quantitative genetics provides simple recursion relationships for the dynamics of means, variances, and covariances; the latter two are often assumed to be approximately constant. However, the initial applications of quantitative genetic recursions centred on biological scenarios where fitnesses were independent of frequency. The phenotypic recursions have an extra term for most scenarios that are characterized by frequency dependent fitness (Lande, 1976), and this can complicate the analysis. However, an approximation to these recursions has a simple form and seems to be widely applicable (Iwasa *et al.*, 1991; Taper & Case, 1992; Abrams *et al.*, 1993; Taylor & Day, 1997; Gomulkiewicz, 1998; Case & Taper, 2000; Abrams,

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2001, 2003). This approximation implies that the mean value of a trait changes at a rate approximately proportional to the slope of fitness as a function of an individual's trait (the individual's 'fitness gradient'). This slope is evaluated at the mean trait value in the population. Modifications are required when traits affecting different characters are correlated (Iwasa *et al.*, 1991; Abrams *et al.*, 1993). The approximation is most accurate when selection is relatively weak and the variance of the fitness function is greater than the variance of the phenotypic distribution of the character. In practice, the assumption is often reasonably good when some of these assumptions are violated (Abrams *et al.*, 1993), although there are certainly some cases where the approximation is not adequate (Gomulkiewicz, 1998).

Adaptive Dynamics assumes a particularly simple form for the underlying genetics. Populations are asexual and evolve by the replacement of nearly monomorphic populations by mutants having small phenotypic effects. This genetic model also produces phenotypic change that can be described by the fitness gradient dynamics described in the preceding paragraph. In this case, no approximations are required. However, the appearance of rigor is illusory, because the situations that might cause problems are not treated; selection is weak because the mutations have small effect, and phenotypic variance is assumed to be close to zero within a lineage. Evolution by the replacement of monomorphic populations by seldom-occurring mutations of small effect does not characterize change in ecologically important characters in most eukaryotes. To the extent that the results of AD models are useful in understanding natural patterns, it will usually be because the dynamics that are predicted are similar to those produced by a variety of other evolutionary mechanisms (Abrams, 2001).

The remainder of this article addresses some of the limitations of AD and then argues that the simplifications of all adaptive dynamics approaches are not so extreme as to prevent them from contributing to understanding the evolution of interacting individuals and species.

Limitations of AD

Does it matter that the underlying genetic assumptions of AD are seldom satisfied, given that AD often predicts the same form of phenotypic dynamics as a more general, but less rigorous, fitness-gradient approach? There are at least two circumstances where the AD assumptions are often seriously limiting or misleading. First, there are many cases where the stability of an equilibrium point hinges on the relative speeds of ecological and evolutionary (or other adaptive) processes (e.g. Abrams & Matsuda, 1997a, b; Abrams & Kawecki, 1999; Abrams, 1999; Ma *et al.*, 2003). The assumption (made by AD) that evolutionary dynamics

are very much slower than population dynamics is inappropriate here. In fact, evidence for rapid evolution is accumulating (Thompson, 1998; Hendry *et al.*, 2000), and recent experiments (Yoshida *et al.*, 2003) have confirmed earlier models (Abrams & Matsuda, 1997b) in showing that evolutionary change in prey can drive predator-prey population cycles. When there are population fluctuations because of any mechanism, selective pressures will almost always change over time, and the assumption of a separation of ecological and evolutionary times scales will often be misleading (Abrams, 1997). And, of course, slow adaptive dynamics never applies to cases where adaptation occurs via behaviour or developmental plasticity.

The second problem with a literal application of AD arises at 'branching points'; locally stable evolutionary equilibria that involve disruptive selection. The possibility of such equilibria was noted by Eshel (1983) and further explored in the context of population genetics by Taylor (1989) and Christiansen (1991). Some of the many ecological circumstances leading to such equilibria were outlined by Wilson & Turelli (1986) and Abrams *et al.* (1993), and in much of the recent AD literature discussed in Waxman & Gavrillets (2004). Early AD works assumed that such points would result in a branching of the evolutionary lineage into two distinct lineages (i.e. *de facto* speciation), and later work argued that speciation at branching points could occur in diploid sexual models (e.g. Dieckmann & Doebeli, 1999; Geritz & Kisdi, 2000; Doebeli & Dieckmann, 2003). However, the conditions for splitting of the lineage remain controversial (Waxman & Gavrillets, 2004) and are often likely to be restrictive, as first pointed out by Felsenstein (1979). Abrams *et al.* (1993) suggested that ecological scenarios leading to branching points could often lead to situations in which traits that minimize fitness are evolutionarily stable. The disruptive selection characteristic of branching points has been demonstrated in 3-spined sticklebacks (Bolnick, 2004), in one of many lakes where branching of the original marine lineage has not occurred. Speciation is a question of genetic isolation, and generally requires a more detailed genetic model than do many other questions in evolutionary ecology.

Are both AD and ad too simple to be useful?

Assume we broaden the term AD to include all methods applying fitness-gradient dynamics, making it a broader subset of ad. Further assume that analysing evolutionary trajectories in the vicinity of branching points requires more detailed models to determine whether splitting of a lineage occurs. Are the assumptions of the method still so great that they invalidate its application to most ecological scenarios? It is admittedly rather unlikely that such simplified models will provide precise forecasts of evolutionary trajectories for any real biological system.

However, they should enable us to understand at least some of the range of potential outcomes of perturbations to adaptively changing ecological systems. Certainly, the simplifications involved in such dynamics are no more extreme than the simplifications of most models in community ecology (homogeneous populations, no time lags, etc.). Of course, size- and age-structure and complicated, size-specific density dependence can alter the predictions of simple ecological models. This does not mean that simple models lacking these features are of no use in understanding the ecological process; simple models identify possible or probable outcomes in wider classes of complex models that cannot be analysed as thoroughly. Similarly, the simplifications involved in fitness gradient approaches are often likely to produce some quantitative errors for any particular system. However, these do not detract from the general insights that can be obtained. Waxman & Gavrillets (2004) are not justified in demanding that AD show that it makes empirically verifiable predictions that models with other genetic assumptions cannot easily make. Nor would this demand have been justified if applied to the more amorphous set of methods in ad. Simplified representations are necessary to understand complex scenarios in all areas of population biology. Such models would be useless if they made unique predictions that other models did not make.

The diversity of biological systems poses a major problem for evolutionary and ecological theory. Specific assumptions are likely to be violated in a major way in most systems. This means that it is seldom advisable to restrict oneself to models or methods that achieve simplicity or compact representation at the cost of making highly specific assumptions. Biological questions, rather than a goal of consistency with a set of rules should motivate model development. The case of initially successful invasions that eventually result in extinction of the invader is a case in point (i.e. the 'resident strikes back' phenomenon of Mylius & Diekmann, 2001). Geritz *et al.* (2002) have gone to some lengths to characterize fitness functions for which this outcome will not occur. This is because the 'standard procedure' in AD has been to assume that initially successful mutants always replace residents. No such assumptions apply to a more general set of ordinary differential equations describing changes in populations and traits, with the latter using a fitness gradient approach. Here one only needs to be aware of the well-known result that invasion does not imply persistence [stressed in an ecological context by Armstrong & McGehee (1980) among many others]. It would be unfortunate if the popularity of the AD approach led to neglect of those scenarios where the resident can 'strike back'. At the same time, characterizing such scenarios using AD (as in Geritz *et al.*, 2002) can provide guidance regarding the ecological circumstances where invasion analysis may be misleading in models that do not use the strict AD approach.

Conclusion

The main message of this commentary is that using fitness-gradient-based dynamics to describe the mean values of frequency dependent traits can provide great insight into the combined action of adaptive change and population dynamics in biological communities. Phenomenological approaches based on game-theory (Brown & Vincent, 1987; Vincent *et al.*, 1993; Nowak & Sigmund, 2004), phenotype-based quantitative genetic models (Lande, 1976; Taper & Case, 1992; Case & Taper, 2000) and AD (Geritz *et al.*, 1998) all support the use of such dynamics as a rough approach to understanding evolutionary questions involving frequency dependence. There is a less rigorous but still persuasive case that many behavioural traits can also be roughly described by the same general family of models (Abrams *et al.*, 1993; Taylor & Day, 1997; Ma *et al.*, 2003; Abrams & Matsuda, 2004). However, there seems to be no compelling reason to restrict the application of such fitness-gradient models to cases in which evolution proceeds by replacement of wild types by infrequently occurring mutants of small effect. And, as is true of all theory, more detailed models will often be needed to refine predictions for particular questions (e.g. speciation), particular species (e.g. those with size-related changes in ecological interactions and flexible growth), or particular evolutionary scenarios (e.g. narrow fitness functions and/or very strong selection).

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