

REVIEW

## Modelling the adaptive dynamics of traits involved in inter- and intraspecific interactions: An assessment of three methods

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### Abstract

In recent years, three related methods have been used to model the phenotypic dynamics of traits under the influence of natural selection. The first is based on an approximation to quantitative genetic recursion equations for sexual populations. The second is based on evolution in asexual lineages with mutation-generated variation. The third method finds an evolutionarily stable set of phenotypes for species characterized by a given set of fitness functions, assuming that the mode of reproduction places no constraints on the number of distinct types that can be maintained in the population. The three methods share the property that the rate of change of a trait within a homogeneous population is approximately proportional to the individual fitness gradient. The methods differ in assumptions about the potential magnitude of phenotypic differences in mutant forms, and in their assumptions about the probability that invasion or speciation occurs when a species has a stable, yet invadable phenotype. Determining the range of applicability of the different methods is important for assessing the validity of optimization methods in predicting the evolutionary outcome of ecological interactions. Methods based on quantitative genetic models predict that fitness minimizing traits will often be evolutionarily stable over significant time periods, while other approaches suggest this is likely to be rare. A more detailed study of cases of disruptive selection might reveal whether fitness-minimizing traits occur frequently in natural communities.

### Keywords

Adaptive dynamics, coevolution, evolutionarily stable strategy, frequency dependence, interspecific interaction, phenotypic evolution.

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### MODELLING THE DYNAMICS OF EVOLVING TRAITS OF INTERACTING SPECIES

The coupled evolution of traits related to inter- and intraspecific interactions within biological communities is an extremely complicated process. This complexity has led to a number of attempts to model the process in a way that captures the essential features of the process without losing mathematical tractability. This article reviews three related approaches to modelling the evolution or coevolution of interacting species that have been used in recent years, and examines their assumptions and limitations. Mathematical models must simplify reality in order to be useful. In ecology, one of the frequently used simplifications is the assumption of homogeneous populations; this assumption underlies most theory regarding

interactions between species. Until recently, evolutionary biologists have seldom simplified the evolutionary component of evolutionary scenarios in this way. However, a complete analysis of the dynamics of interacting and evolving individuals and/or species would require the analysis of a range of diploid multilocus genetic models, combined in a variety of ways with models of population dynamics. Such an approach has not been used, both because the genetic basis of traits involved in interactions is generally unknown, and because, had the genetics been known, the resulting models would probably have been hopelessly complicated.

Phenotypic models of traits related to interactions can be traced back to Leon (1974). This article was followed by a large number of related studies, all of which can be characterized as largely ignoring the details of the genetic

mechanism producing evolutionary change. These phenotypically based methods characterize a given species by the mean value of a trait or traits involved in the interaction, which is analogous to ecologists' assumption of homogeneous populations. However, they actually assume that there is some variation between individuals, which is what allows evolutionary change to occur. The phenotypic evolution models have had different underlying mechanisms, but all share the property that the rate of change of the mean trait value within a species can be approximated by the slope of the relationship between an individual's trait value and its fitness. This approximate relationship is potentially influenced by the mean trait value of the individual's species, the mean trait values of the interacting species and the population densities of all of these species. Because traits involved in interactions, either within or between species, are especially likely to have frequency dependent fitnesses, one of the earliest phenotypic approaches, the "CSS" approach proposed by Roughgarden (1976, 1979), frequently cannot be applied. The CSS method's assumption that the rate of change of the mean trait was proportional to the slope of the relationship between fitness and mean trait, assumes no intraspecific frequency dependence. There are many traits for which this assumption is justified (Lande 1976). However, the models of competitive coevolution to which it was applied by Roughgarden (1976, 1983b) logically required intraspecific frequency dependence of fitnesses, as pointed out by Brown & Vincent (1987), Taper (1988) and Abrams (1989). Some simple models of particular interaction-related traits lack within-species frequency dependence; e.g. models of predator-prey interactions by Roughgarden (1983a), Saloniemi (1993) and Abrams & Matsuda (1996), and the CSS approach is valid in these cases. However, more realistic models of predator-prey interactions imply frequency dependence (Matsuda & Abrams 1994a; Abrams & Matsuda 1997). These and most other models of interaction-related traits require a different approach.

The more recently proposed phenotypic methods are similar to Roughgarden's except for the crucial assumption that traits change at a rate proportional to the slope of the relationship between fitness and individual (rather than mean) trait value. These methods can often approximate the dynamics of traits with frequency-dependent fitnesses, and may greatly increase our ability to understand the evolution of ecological interactions. The approaches have been applied to the evolution of traits determining competitive ability within a species (Matsuda & Abrams 1994a,b; Abrams & Matsuda 1994; Kisdi 1999), competition between species (Taper & Case 1985; Case & Taper 1986, 1992a,b, 2000; Day 2000), predator-prey interactions (Brown & Vincent 1987, 1992;

Abrams & Matsuda 1996, 1997; Marrow *et al.* 1996; Gavrillets 1997), parasitoid-host interactions (Hochberg & Holt 1995; Hochberg 1997; Abrams & Kawecki 1999) and more complex food webs (Matsuda & Abrams 1994a,b; Abrams 1999, 2000). However, at present the three main approaches to phenotypic evolutionary modelling make significantly different predictions in many circumstances. This review will examine the assumptions and realms of applicability of these three approaches.

The major types of simplified coevolutionary models used in recent years differ primarily in their assumptions about the underlying genetic basis of the trait. The following are all simplified descriptions of methods that have been modified and elaborated since being introduced. Nevertheless, most articles published during the past decade can be classified as using one of the following three methods. More detailed descriptions are given in the following section.

**1** Methods based on sexual reproduction with phenotypic representations of quantitative trait evolution. These will be labelled "QG" (quantitative genetic) methods. They are most consistent with a genetic system where a large number of loci make small additive contributions to the trait (examples: Taper & Case 1992a; Abrams *et al.* 1993a, b; Abrams & Matsuda 1997a, b; Hochberg 1997; Case & Taper 2000). Most applications of these models assume that some additive genetic variation is maintained by processes (e.g. mutation) that are not explicitly included in the model. The variance may be assumed constant, or allowed to change under the action of natural selection. In any model, the variance must decrease as mean trait values approach the maximum or minimum potential individual trait values.

**2** Methods originally based on asexual reproduction with a low frequency of mutations, each having a small effect on the character (Metz *et al.* 1996; Geritz *et al.* 1997, 1998). These methods are labelled "AD" (adaptive dynamics), which is the term applied to them by their originators (Dieckmann 1997; Geritz *et al.* 1997), although all three methods discussed here represent some form of the dynamics of adapting traits. The AD methods have been extended to modelling allelic substitutions in diploid sexual species (Kisdi & Geritz 1999), but this represents a population genetic, rather than a phenotypic model of evolution.

**3** Methods that concentrate on finding a complete set of evolutionarily stable phenotypes, given one or a set of fitness functions. These will be labelled Evolutionarily Stable Strategy, or "ESS" approaches, which is again the term applied to them by their originators (Brown & Vincent 1987; Vincent & Brown 1988; Vincent *et al.* 1996; Cohen *et al.* 1999). The label is again somewhat misleading, because all three methods predict evolutionarily stable

strategies in some sense of that term. Under the ESS approach, the goal is to find a set of phenotypes where each maximizes fitness locally, and there is a distinct phenotype for every local maximum of the fitness function. Although reproductive mode is not specified, the ESS methods, like AD, are most consistent with asexual reproduction. In contrast to most applications of AD and QG, these methods have generally assumed that a given phenotype can give rise to mutants that have arbitrarily large phenotypic differences from the parental phenotype, or alternatively that invading species with such large differences enter the system.

This paper seeks to outline the similarities and differences between the evolutionary predictions produced by these methods. It also discusses some of the evidence that bears on which of the underlying sets of assumptions is most appropriate in different biological circumstances. I begin with a more detailed description of each of the three approaches.

## DESCRIPTIONS OF THE THREE METHODS

### The QG approach

The phenotypic QG models are derived from population genetic models that assume traits are determined by a large number of genetic loci with small additive effects on the character. This leads to the standard quantitative genetic recursion equations (Lande 1976) for the change in the mean phenotype under selection. The full expression for the change in the mean value  $z^*$  of a trait (which has a distribution of individual values  $z$ ) has the following form:

$$\Delta z^* = \frac{(V_A/V_T) \int (z - z^*) W(z, z^*) p(z, z^*) dz}{W^*} \quad (1)$$

where  $V_A$  is additive genetic variance for the trait in question,  $V_T$  is the total phenotypic variance,  $W$  is individual fitness,  $W^*$  is population mean fitness and  $p$  is the probability distribution of trait values  $z$  in a population with a mean trait of  $z^*$ ; this is usually assumed to be Gaussian. Mean fitness,  $W^*$ , is generally equal to one at an ecological equilibrium. The integral in (1) is taken over the full range of values of that trait in the population. This equation has been used to model the coevolution of competitors by Slatkin (1980), Taper & Case (1985), Milligan (1985) and Case and Taper (2000). By assuming that the trait distribution has a symmetric unimodal form, and is narrow relative to the variance of the fitness function, the following approximation to (1) results:

$$\Delta z^* = (V_A/W^*) (\partial W / \partial z)|_{z=z^*} \quad (2)$$

(Iwasa *et al.* 1991; Taper & Case 1992a; Abrams *et al.* 1993a, b). Thus, most of the simplified QG models of

coevolution describe the rate of change of each of the characters as being proportional to the slope of the relationship between individual fitness and the individual's character value (the individual fitness gradient) evaluated where the individual's trait is equal to the population mean. If there are multiple traits per species, genetic correlations between the traits influence the direction of change of all of the characters (Iwasa *et al.* 1991; Taper & Case 1992a). The additive genetic variance, which determines the rate of change of the mean character, may itself change as the mean trait value changes (Taper & Case 1985; Abrams *et al.* 1993b; Abrams & Matsuda 1996). The simplification leading to equation (2) assumes that the distribution of trait values in the population remains unimodal under the action of selection. This is what has been observed in multilocus genetic models with random mating, weak selection and many independent loci having additive effects on the trait (Felsenstein 1979). Bimodality can occur when there is assortative mating (Felsenstein 1979; Doebeli 1996a,b). This violates the assumptions underlying equation (2) and requires a more explicit population genetic model (Doebeli 1996a,b).

Applications of the simplified quantitative genetic approach have often assumed that the community consists of a fixed number of species (e.g. Matsuda *et al.* 1994; Abrams & Matsuda 1996, 1997). However, this is not a necessary component of the method; Taper & Case (1992a) investigated models of open communities in which there were continual invasions by species with mean phenotypes different from those of the residents. When there are invasions of new species, it is possible to assume that they have fitness functions the same as or different from those of the residents.

### The AD approach

AD models begin with some of the same assumptions as the QG models. Models of comparable ecological/evolutionary scenarios use the same function to describe the relationship between fitness and trait value. In addition, most AD models share the assumption that phenotypic variance is relatively small, so it is possible to characterize a species by its mean trait value. However, here the variation is generated by a stochastic mutation process, rather than assuming some fixed shape to the distribution of phenotypes. Each individual has a small probability of giving rise to a mutant having a slightly different phenotype. This basically asexual model implies that every mutant is an independently evolving lineage. Each of the types in the population changes in population size at a per generation rate determined by its fitness function; for type  $i$ , with phenotype  $z_i$ ,  $\Delta N_i = (W_i - 1)N_i$ , where fitness,  $W_i$  is a function of population density and

the distribution of trait values. The mean trait value changes as a consequence of the fact that some types increase more rapidly than do others. These basic dynamics are altered slightly by mutation, with each phenotypic class being assumed to give rise to descendents with slightly different phenotypes with a small probability. One can still describe the resulting set of asexual lineages as a single species if they form a relatively tight cluster in phenotypic space. This will generally be true if they experience stabilizing selection and mutational effects are small. Because of the large number of lineages and their random generation, such models are usually investigated by simulation (e.g. Geritz *et al.* 1997, 1998). However, the dynamics of the mean phenotype can again be well approximated by a dynamic model with the same form as equation (2) above (Dieckmann & Law 1996; Metz *et al.* 1996). The rate of change of the mean phenotype of a species is proportional to the gradient of individual fitness at the mean trait value (Dieckmann & Law 1996; Metz *et al.* 1996; Geritz *et al.* 1997, 1998). Here the constant of proportionality is again the additive genetic variance, making the basic trait dynamics the same as under Method 1. In this case variance is determined implicitly by mutation rate, the average phenotypic effect of mutations, and the strength of selection.

Because mutant types arise rarely and are usually assumed to differ relatively little from the parental type, the rate of evolutionary change is implicitly assumed to be much slower than the rate of change in population densities. This assumption has allowed the application of graphical techniques, such as “Pairwise Invasibility Plots” (Metz *et al.* 1996; Geritz *et al.* 1997), to determine the outcome of some single-trait models. Although the underlying mutational model can in theory allow for individual mutations that greatly change the phenotype, in such a case evolutionary change cannot in general be described by equation (2).

### The ESS approach

The ESS method has been used primarily by T. L. Vincent, J. S. Brown, and collaborators. It has been modified several times since first being introduced (Brown & Vincent 1987), and was most recently described in Cohen *et al.* (1999), following Vincent *et al.* (1996). The method assumes that a species is characterized by a particular fitness function, but that any number of independently reproducing populations can arise from such a species if natural selection favours such populations. These derived populations then effectively behave as new independent species. The ESS consists of the set of phenotypes within each fitness-function such that each phenotype has a greater fitness than any similar phenotypes, and the complete set cannot be invaded by any other phenotype (similar or dissimilar) sharing the same fitness

function. The generation of new populations (characterized by the same fitness function but a different phenotype) could be considered to be speciation or some type of population subdivision; Vincent and Brown usually refer to this process as speciation (e.g. Brown & Vincent 1992). The number and form of the fitness functions is fixed, and the number of distinct phenotypes (subpopulations or species) that can persist for each fitness function is determined by the form of those functions. The ecological interaction of all of the phenotypes is assumed to produce a locally stable equilibrium point of the population dynamics (Cohen *et al.* 1999). The dynamics of the change in numbers of individuals with a given phenotype is specified by the same fitness gradient equation (equation 2) that arises in the preceding two methods of modelling, with a fixed constant of proportionality analogous to the additive genetic variance in (2) (Cohen *et al.* 1993, 1999). Here distinct phenotypes are essentially treated as separate species, although some or all may share a common fitness function. A major feature of the approach of Vincent and collaborators is the assumption that every possible phenotype for a given fitness function occurs or arises frequently via mutation. These variants are not modelled explicitly. Instead, it is assumed that within a set of individuals sharing a common fitness function, a mutant type with the highest possible fitness will always invade a community if it is not already present (Brown & Vincent 1992).

Dynamics of traits were mentioned in some of the early ESS models (Rosenzweig *et al.* 1987), but were not formally added to the ESS approach until the article by Cohen *et al.* (1993). Cohen *et al.* (1993) invented a nongenetic dynamics of phenotypic classes that has many properties in common with the QG approach. It shares the characteristic that equation (2) describes the change in mean phenotype when the variance within a species is small enough. However, Cohen *et al.*'s (1993, 1999) approach adds the basic assumption of ESS models that a new species sharing the same fitness function as the original appears whenever it is able to invade. Cohen *et al.* (1999) also assume that evolutionary dynamics are sufficiently slower than population dynamics and that population densities are effectively always at their equilibrium values set by the current phenotypes. This, together with the assumption of stable population dynamics, allows Cohen *et al.* (1999) to arrive at a simplified criterion for system stability.

### WHAT ARE THE SIMILARITIES AND DIFFERENCES IN ASSUMPTIONS AND PREDICTIONS OF THE THREE APPROACHES?

All three approaches share the property that the dynamics of a trait within a population characterized by a

sufficiently narrow distribution of phenotypes can be approximated by the gradient of individual fitness evaluated at the mean phenotype (i.e. equation 2). There is no fundamental difference in the forms of the fitness functions used by the three methods, contrary to what is claimed in Cohen *et al.* (1999). The methods often do vary in the exact value of mean fitness when the distribution of trait values is wide relative to the fitness function. However, this frequently produces quantitative rather than qualitative differences in predicted phenotypes. Therefore, in some situations, all three of these methods will yield the same predictions about mean trait value when the same ecological scenario is assumed. Identical predictions should arise when the following conditions are satisfied: (1) the variance in trait values is narrow relative to the width of the fitness function; (2) there is a single ecological and evolutionary equilibrium (i.e. a set of population densities and trait values where the fitness gradients and per capita growth rates are zero); (3) the point equilibrium is globally stable; and (4) at this equilibrium, the trait values maximize the fitness of the respective species or strategies. Here, all three methods predict that mean trait value will attain the unique equilibrium specified by equation (2). There are certainly some evolutionary scenarios where there is only a single equilibrium, it is stable, and it maximizes individual fitness. However, there is no way of judging how commonly this is true of traits determining the nature of interactions in natural populations and communities. Some or all of these conditions have been violated in a number of previously analysed models of the evolution or coevolution of interacting species. For example, a combined ecological/evolutionary equilibrium is frequently not globally stable in the following analyses, among others: Schaffer & Rosenzweig (1978), Maynard Smith & Brown (1986), Frank (1994), Matsuda & Abrams (1994a, b), Matsuda *et al.* (1994), Abrams & Matsuda (1996, 1997), Abrams (1995, 1997, 1999), Abrams & Kawecki (1999).

The most important differences between the methods relate to the circumstances under which new independent evolutionary lineages arise, and the phenotype that such a lineage may have when it arises. Under all of the methods, the dynamics of traits within a lineage is either assumed to be given exactly by, or is often well approximated by equation (2) (or a multitrait or multispecies analogue). Deviations caused by large magnitude variation in traits are often small quantitative differences rather than qualitative ones (Taper & Case 1992a; Abrams *et al.* 1993b; Case & Taper 2000). However, qualitative differences are the rule when (1) there is an evolutionary equilibrium where one or more traits undergoes disruptive selection; or (2) there is an equilibrium trait value that represents a local, but not a global maximum of individual fitness.

When fitnesses are frequency independent, phenotypes that minimize fitness are evolutionary repellers; the mean phenotype will evolve away from such a value if it is initially larger or smaller than that value. However, when fitness is frequency dependent, there is the possibility of another type of equilibrium where the mean phenotype minimizes fitness, yet is a dynamic attractor because of frequency-dependent selection (Taylor 1989; Christiansen 1991; Taylor & Day, 1997). If the mean phenotype moves away from the point, the adaptive topography shifts to favour phenotypes closer to the original equilibrium. A wide variety of ecological scenarios can be expected to give rise to such equilibria (Abrams *et al.* 1993b). The trait undergoes disruptive selection at such a point. QG models predict that the mean phenotype may nevertheless remain at such a point in the absence of major perturbations to the community. This is because of the relative inflexibility of the trait distribution, which is restored to a unimodal form by sex and recombination each generation. Like any case of disruptive selection (Felsenstein 1979), stable, fitness-minimizing equilibrium points will usually be associated with an increase in the genetic variance over time when this is possible under the genetic system. In coevolutionary QG models, equilibria where fitness in one or more species is minimized may be characterized by cycles in which the phenotype varies above and below the equilibrium point (Abrams & Matsuda 1996; Marrow *et al.* 1996).

Because the asexual species assumed in the AD approach consist of many lineages, each undergoing mutation, it is possible for the trait distribution to take on almost any form depending on the shape of the fitness landscape. Bimodal trait distributions are frequently produced at a fitness-minimizing point that is maintained by frequency dependence. These can evolve to become independent evolutionary lineages (i.e. new species) when the phenotypic distributions become nonoverlapping. Evolutionary attractors characterized by locally minimal fitness have thus been termed "branching points" (Metz *et al.* 1996). There are a variety of consequences that may follow branching in an AD model, including further branching, or extinction of one of the two new lineages followed by another branching event (Geritz *et al.* 1998; Kisdi & Geritz 1999). The AD approach uses simulation to determine whether splitting of the evolutionary lineage actually occurs at a branching point. Splitting has occurred in most cases analysed, although some coevolutionary AD models have shown that evolution of the interacting species can prevent branching in a focal species (Marrow *et al.* 1996). The ESS models assume that sympatric speciation or invasion of a new species sharing the resident's fitness function always occurs when an equilibrium of the trait and population dynamics equations can be invaded by any other phenotype sharing that

fitness function (Cohen *et al.* 1999). Thus, branching occurs by definition at a branching point under the ESS approach. However, unlike AD models, the ESS approach allows the splitting of lineages to occur via an immediate large magnitude shift in the character of one of the descendent lineages. AD models that allow mutations with large enough phenotypic effects can also produce similar outcomes (T. Day, in preparation). In addition, AD models can produce new lineages with initially very different character states, if it is assumed that invasion of another species rather than speciation produced the second population.

QG models in their simplest form assume that there is no sympatric speciation and no invasion of new species. However, the QG approach can describe such phenomena by introducing a new, independently reproducing species with an initial mean phenotype different from the resident whenever conditions suggest that sympatric speciation or invasion of independently reproducing but similar species is likely. Taper & Case (1992a) use a QG model to investigate taxon cycles in competitive communities, and assume that new invading species have phenotypes that maximize fitness. These are generally quite different than the phenotype of the resident species. In one sense, introducing new species also introduces an element of arbitrariness into the analysis. Of the three methods, only the AD approach generates new lineages as an integral part of the adaptive dynamics. However, it is unclear whether this is an advantage or a disadvantage. There are strong arguments for the propositions that sympatric speciation is rare, that genetic mechanisms play a very important role in speciation (Coyne 1992), and that distinct invading species are likely to have a different fitness function than that of the resident. All of these arguments imply that the decisions of whether to add an additional species at a branching point, and whether that new species should have a fitness function identical to the resident, are beyond the purview of the simplified phenotypic evolution models under discussion.

In asexual species, each mutant type represents a new lineage, and the assumption that sympatric speciation occurs whenever appropriate AD models predict that it is possible, is quite reasonable. However, most theoretical and empirical work on speciation has involved diploid sexual species. It is certainly not true that sympatric speciation will always occur when there is disruptive selection in a sexual lineage (Felsenstein 1979). Recent arguments in favour of sympatric speciation have investigated a limited range of models. For example, analyses by Doebeli (1996b) and Dieckmann & Doebeli (1999) have assumed that there is no cost to assortative mating, and that assortment can be very effective. It is not clear whether these assumptions are frequently met, and

the consequences of violating the assumptions have yet to be explored in detail. If sympatric speciation could occur whenever a branching point arose, it would imply that history, which determines the regional species pool, should have very little effect on species diversity. Ecologically similar communities in ecologically similar environmental circumstances in different locations should contain similar numbers of species. In contrast, recent work suggests that history or the regional pool is very often a more important determinant of species diversity than are local ecological interactions (Ricklefs & Schluter 1993). Certainly, one does not commonly observe approximate equality of species number in ecologically similar circumstances in different parts of the world (Abrams 1981; Ricklefs & Schluter 1993). In addition, one would not expect to often observe disruptive selection if sympatric speciation was rampant, but Endler's (1986) survey showed disruptive selection to be very common.

The case of the three-spined stickleback (*Gasterosteus aculeatus*) in British Columbia is very suggestive of strong limitations on the process of sympatric speciation. Even though selection on the ancestral generalized (marine) phenotype in lakes appears to be disruptive, favouring benthic and pelagic morphs (Schluter 1994), apparent speciation has only been observed in four lakes (out of thousands containing this species). These four lakes are unique in that their proximity to the sea makes it likely that a second invasion occurred a significant time after the initial invasion (Schluter & McPhail 1992; Schluter 2000). This would have led to two lineages that probably had significant reproductive isolation at the outset of their interaction, allowing independent evolutionary trajectories. Given the existence (Doebeli 1996b) or possible evolution (Dieckmann & Doebeli 1999) of assortative mating, speciation of sexual species undergoing frequency-dependent disruptive selection might occur. However, the empirical observations reviewed above suggest that these preconditions may not be common.

A second major difference between the three techniques discussed here is their flexibility with regard to the time-scale of ecological and evolutionary processes. Recent work (reviewed by Thompson 1998) suggests that there is no clear distinction between ecological and evolutionary time-scales in many systems. QG allows for essentially any speed of evolutionary change, and can potentially be used to model behavioural or other nongenetic processes of adaptation (Abrams *et al.* 1993b). AD can allow a range of evolutionary rates, by changing mutation rates or the effect sizes of mutant alleles. Nevertheless, for most realistic assumptions about both of these quantities, evolutionary change is likely to be substantially slower than changes in population densities. Finally, Vincent and Brown's ESS methods explicitly assume that population

densities always have the values specified by current trait values (Cohen *et al.* 1999). This represents an extreme and inflexible assumption about the relative time scales of evolutionary and ecological processes.

The three methods also differ in their ability to model systems that lack a stable equilibrium point. Having this ability is important for two reasons. Ecological systems are seldom stable, and often show evidence of self-generating cycles (Ellner & Turchin 1995; Kendall *et al.* 1998). Even the simplest predator–prey or parasite–host models are often characterized by limit cycles or more complex dynamics. Even when ecological dynamics alone would result in a stable system, the interaction of traits in two species or the interaction of ecological and evolutionary dynamics can drive cycles in both traits and population densities (Abrams & Matsuda 1996, 1997). QG and AD methods make no assumptions about stability. On the other hand, published ESS analyses assume that the interacting species have a locally stable ecological equilibrium (Cohen *et al.* 1999) and that population densities are located near that equilibrium. The ability to deal with nonequilibrium population dynamics is important, because the mean trait values in systems with ecologically or evolutionarily driven cycles can be very different from what is predicted by the equilibrium points of those systems (Abrams 1997). The assumption of stable population dynamics in ESS approaches is inconsistent with the lack of stability constraints on the evolving traits under that method; cycles in these traits will generally drive cycles in population dynamics (Abrams & Matsuda 1996, 1997; Marrow *et al.* 1996).

Differences between the predictions of the three models usually mean that it is necessary to know some details about the actual genetic system before making predictions about the species or community under study. For example, Maynard Smith & Brown (1986) studied models of asymmetrical competition, where quantitative genetic inheritance resulted in a stable large phenotype. The fitness of the stable phenotype was less than the fitness of a very small phenotype in that population, but small phenotypes could not arise and breed true, given the trait determination by many loci with small individual effects. Asexual or haploid models using the same fitness function, but assuming a wide spectrum of mutant phenotypes, produced evolutionary cycles. Here small individuals were able to invade and replace large ones after the mean size had increased to a value close to the locally evolutionarily stable point. There are without doubt many more scenarios where the range of potential mutants or invaders influences the predicted evolutionary outcome. In these cases, a single phenotypic approach to modelling is not likely to be sufficient to understand the system.

## CONCLUSIONS

Given the preceding discussion, what approach should be used to understand evolutionary problems? If the species of interest are sexually reproducing, and especially if the traits are known to be quantitative, then QG models appear to be a logical starting point. Because independent species can be added to account for invasion or sympatric speciation, it is easy to investigate the consequences of these two processes. Whether such additions are appropriate depends on the genetic and behavioural details of the species or the nature of the pool of potential invading species. Neither of these details is, or should be, part of a simplified phenotypic approach to evolution. Regional control of species diversity appears to be common (Ricklefs & Schluter 1993), and sympatric speciation has rarely been demonstrated. Populations located at branching points are susceptible to invasion by other species having somewhat different fitness functions. These facts make investigator control over the number and nature of new lineages or species a desirable property for theoretical investigations. On the other hand, if an asexual species is the object of study, then AD models would seem to be the most appropriate method for studying the evolution of traits involved in interactions. The actual simulation models used in AD analyses are explicit genetic models of asexual populations. In this case, having the model generate new lineages is an advantage. By allowing mutations with large phenotypic effects, AD models can be extended to cover situations in which essentially instantaneous speciation is possible. This summary is not meant to imply that AD approaches cannot also provide some insights into possible evolutionary trajectories in sexual populations. However, it is usually necessary to construct a more detailed population genetic model to determine to what extent phenomena from AD models, such as branching, are likely to occur in sexual populations. This was the approach of Dieckmann & Doebeli (1999), who used additive multilocus population genetic models to determine whether branching would occur in assortatively mating sexual populations. In practice, if dynamics are determined by versions of equation (2), rather than the simulation of asexual lineages, there will be no qualitative difference between QG and AD approaches.

ESS approaches originated without any explicit dynamics of traits, and the methods have still not completely incorporated trait dynamics. The current limitation (Cohen *et al.* 1999) of the ESS approach to ecologically stable scenarios, and its assumption that evolutionary processes are much slower than population dynamics (Cohen *et al.* 1999), represent rather restrictive assumptions. It is important to be able to make predictions about evolution when the system does not come to a stable

equilibrium point, because of either environmental fluctuations or intrinsically unstable dynamics. Because evolutionary dynamics may produce rapid phenotypic changes (Thompson 1998), it is also important not to make general assumptions about separation of evolutionary and ecological time-scales. QG allows any rate of adaptive change, and AD allows some flexibility by changing mutation rates and the variance of mutational effects on the character. To the extent that the ESS approach abandons these assumptions and uses equation (2) to describe trait dynamics, then it reduces to the QG approach with some additional assumptions about an abundance of potential invading species sharing the same fitness function as the resident.

Because all of the approaches discussed here are simplifications of the real population genetic mechanism of evolution, it is important to be able to determine whether the mathematical simplifications affect the qualitative predictions. Because of the clearer connection to genetics of QG and AD than ESS methods, it is clearer how the former types of models should be modified to deal in a biologically justifiable way with cases with multiple characters per species (Iwasa *et al.* 1991) or cases in which the phenotypic variance is large (Abrams *et al.* 1993b; Case & Taper 2000).

One of the important differences in predictions of the QG and AD models is whether one can expect to observe evolutionary equilibria where the mean fitness of species is minimized, and the trait undergoes disruptive selection. AD models predict that such branching point equilibria will generally be transient in single species systems (and often in multispecies systems as well). Sexual models of continuous traits predict that fitness-minimizing equilibria in a single species can be permanent, although they are susceptible to invasion by other similar species (Abrams *et al.* 1993b), and may split, given the right type of assortative mating (Dieckmann & Doebeli 1999). Introduction of new alleles or evolution of modifier alleles can also produce branching in sexual populations (Kisdi & Geritz 1999). However, it is not yet clear whether conditions allowing branching in sexual populations occur frequently, and it would be surprising if branching always occurred rapidly at fitness-minimizing evolutionary attractors. It would be very informative to examine previous studies of natural selection that have identified disruptive selection, to determine if the type of frequency dependence required of fitness minimizing attractors is the source of this pattern.

Greater understanding of the realms of applicability of the three methods reviewed here will allow greater progress in using some or all of the methods to understand differences in the structure of biological communities. The previous work referred to in this

review has only begun to investigate the population and evolutionary dynamics of one- and two-species systems under relatively simple assumptions. Multi-species and multitrait systems have received relatively little attention (but see Leimar 2000). Because of the potential importance of understanding coevolution in predicting the outcome of species additions and deletions (Abrams 1996), phenotypic methods of studying coevolution should be important in answering most applied questions that are potentially affected by interspecific interactions.

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#### BIOSKETCH

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