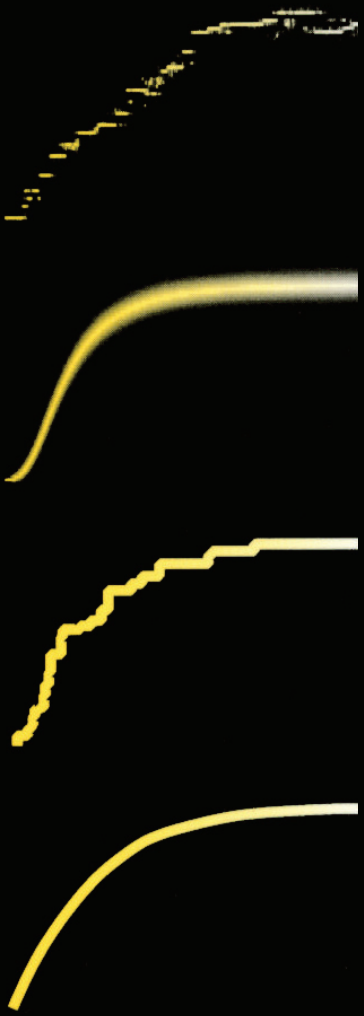
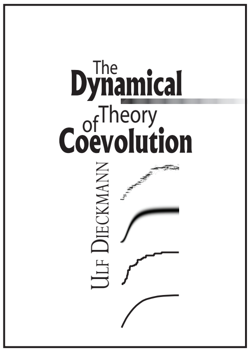
The Dynamical Theory of Coevolution

Ulf Dieckmann





Stellingen

1. Derivations from individual-based models are a necessary antidote against hidden assumptions and vague concepts in models for higher levels of biological complexity.

2. Ecological theory needs to give attention to predictions and conclusions that are both explicitly conditional and qualitative.

3. When bridging mathematical models to ecological applications, convergence to limit arguments ought to be analysed by perturbation expansions.

4. The adaptive dynamics framework contains classical evolutionary game theory as a special, structurally unstable case.

5. The canonical equation of adaptive dynamics only applies under restrictive conditions, higher-order terms are ignored and the phenomenon of evolutionary slowing down is missed.

6. Standard diffusion models of phenotypic mutation-selection processes disregard the discreteness of individuals and lead to qualitatively misleading predictions.

7. Focusing attention on evolutionary equilibria is deceiving: evolutionary cycling and other types of non-equilibrium attractors of coevolutionary dynamics must be considered.

8. Evolution under asymmetric competition leads to rich coevolutionary patterns which are not foreseen by the simple supposition of character divergence.

9. Constructing evolutionary dynamics on variable adaptive topographies is meaningless unless fitness functions are derived mechanistically.

10. Evolutionary stability crucially depends on underlying mutation structures: in general selection alone is not enough to understand evolutionary outcomes.

Ulf Dieckmann
January 23rd, 1997

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Introduction

Long-term evolution is due to the invasion and establishment of mutational innovations. The establishment changes the parameters and structure of the very population-dynamical systems the innovation took place in. By closing this feedback loop in the evolutionary explanation, a new mathematical theory of the evolution of complex adaptive systems arises. The dynamical theory of coevolution provides a rigorous and coherent framework that links the interactions of individuals through the dynamics of populations (made up of individuals) to the evolution of communities (made up of populations). To encompass the effects of evolutionary innovations it allows, for the first time, for the simultaneous analysis of changes in population sizes and population traits. The approach thus captures the process of self-organization that enables complex systems to adapt to their environment.

It is generally agreed that minimal conditions exist for a process of self-organization to be enacted by natural selection. A characterization of such features is provided by the replicator concept, originally proposed by Dawkins (1976). Dawkins argues that units, called replicators, inevitably will undergo evolution by natural selection if the following four conditions are met.

1. The units are capable to reproduce or multiply.
2. In the course of the reproduction some traits are inherited from parent to offspring.
3. Reproduction is not entirely faithful: a process of variation can introduce differences between parent and offspring trait values.
4. The units interact with each other causing rates of fecundity or survival to be trait-dependent.

Similar conditions have been given, for example, by Eigen and Schuster (1979) and by Ebeling and Feistel (1982), who emphasize in addition that evolutionary units physically are realized as systems open to fluxes of energy and matter (Schrödinger 1944). Replicators therefore are the abstract entities on which to base an encompassing theory of adaptation and the evolutionary process.

Only on short time scales biological populations can be envisaged as adapting to environments constant in time. In contrast, ecological communities of interacting populations will adapt in a coevolutionary manner. We will use the term coevolution to indicate adaptation to environments that in turn are adaptive. In other words, the environment that stimulates adaptation in one population, as a result of the environmental feedback, is itself responsive to that adaptation. The technical notion of coevolution was introduced by Ehrlich and Raven (1964) when analyzing mutual evolutionary influences of plants and herbivorous insects. Janzen (1980) defines coevolution, more restrictively than we do, to indicate that a trait in one species has evolved in response to a trait in another species, which trait itself has evolved in response to the trait in the first. Futuyma and Slatkin (1983) point out that this definition requires not only reciprocal change (both traits must evolve) but also specificity (the evolution in each trait is due to the evolution of the other). Like Janzen's definition suggests, coevolutionary phenomena are most easily observed in a single pair of tightly associated species. However, since most species interact with a variety of other species, we do not restrict attention to the adaptation of pairwise interactions.

Broadening the focus from evolutionary to coevolutionary processes changes our expectations concerning evolutionary outcomes. When considering adaptation separately in only one population, natural selection is expected to take the population towards a state where it has met whatever environmental challenges it originally had faced. Such stationary endpoints of evolution are unrealistic on a larger evolutionary time scale. In contrast, if two or more species are adapting in response to each other, continued evolutionary progress may take place.

The traditional fields for investigating evolutionary phenomena are population genetics and quantitative genetics (see e.g. Bulmer 1980; Falconer 1989). However, to assess coevolutionary dynamics at the level of genes appears to be virtually impossible (Levin 1983). Numerous simplifying assumptions have to be made before feasible equations are obtained (Lande 1979). Moreover, how to relate the fitness functions employed in genetic models to interactions among individuals is not always obvious. These circumstances have fostered the development of simpler models of coevolutionary dynamics at the phenotypic level. Most prominently, evolutionary game theory reduces the intricacies of ecological interactions to a matrix description of payoffs, resulting from encounters between phenotypes (Maynard Smith and Price 1973; Maynard Smith

1982). Unfortunately, individual-based derivations of payoff matrices typically are not given, and evolutionary game theory cannot make dynamical predictions about the actual pathways of evolutionary or coevolutionary change.

The dynamical theory of coevolution tries to bridge the gap between genetic and game-theoretic models of adaptation. Coevolutionary change in communities of replicator populations is derived from the underlying ecological interactions. The theory is individual-based, thus allowing for the meaningful interpretation of ecological parameters, and it explicitly accounts for the stochastic components of evolutionary change. A hierarchy of increasingly tractable models of coevolutionary dynamics is constructed by mathematical limit arguments. Particular attention is given to invasibility conditions. These act as a powerful tool for analyzing the long-term effects of the interactions between ecological and evolutionary processes, as observed by Diekmann et al. (1996).

> Approaches to the analysis of biological evolution have taken somewhat divergent paths. [...] These approaches have led to different definitions and descriptions of equilibrium, stability and dynamics in the context of evolution. More and more it becomes clear, however, that invasibility (of a resident type by a variant) serves as a unifying principle.

Nevertheless, the dynamical theory of coevolution goes beyond invasibility conditions. Where the latter reach their limitations, dynamical analyses of coevolutionary change become essential. For adaptive systems with more than one phenotypic dimension, stability of evolutionary attractors (and hence the outcome of adaptive change) generally is unknown when ignoring the dynamics of evolution. Only a fully dynamical account of coevolutionary processes reveals phenomena like evolutionary cycling or Red Queen coevolution, evolutionary slowing down, evolution to extinction and the crucial importance of mutation structures.

The dynamical theory of coevolution, at its present stage, is concerned with replicators possessing internal degrees of freedom that reflect adaptive traits under evolutionary change. As a future development it will be interesting systematically to investigate the impact other internal degrees of freedom can have on the process of evolution.

1. Replicators can carry diploid genotypic information and can undergo sexual reproduction. Recent studies in this direction are e.g. Eshel (1996), Hammerstein (1996), Matessi and Di Pasquale (1996), and Weissing (1996).
2. Populations of replicators may be structured according to age or stage. Here an evolutionary perspective could be integrated into the conceptual framework of Metz and Diekmann (1986).
3. Replicators can be explicitly located in physical space and may possess specific patterns of movement. The importance of spatial structure for predicting the

outcome of selection has been demonstrated e.g. by Boerlijst and Hogeweg (1991) and by Rand et al. (1995).

All three dimensions for extensions are bound to bring about novel evolutionary phenomena which then can be studied in their own right. The additional amount of structure available in these models will help to construct increasingly realistic descriptions of the evolutionary process. For these extensions the coevolutionary theory of basic replicators advanced here may serve as a backbone and guideline.

The structure of subsequent chapters is as follows. *Chapter 1* provides an introduction to basic adaptive dynamics theory. Fundamental concepts are explained, recent research in the field is discussed and prospects for the future are assessed. *Chapter 2* advances some of the main derivations within the dynamical theory of coevolution. From an individual-based account of intra- and interspecific ecological interactions, combined with a process of mutation, stochastic and deterministic models of coevolutionary change are extracted. In particular, the canonical equation of adaptive dynamics is recovered and identified as a special case. For this equation higher-order corrections are established and are shown to give rise to novel evolutionary effects including shifting evolutionary isoclines and evolutionary slowing down. Extensions to more general ecological settings like multi-trait coevolution and coevolution under nonequilibrium population dynamics are developed. *Chapter 3* places the dynamical theory of coevolution into a broader context and discusses its relation with results from quantitative genetics. Special attention is given to the distinction between classical evolutionary stability, convergence stability and the asymptotic stability of coevolutionary attractors. In systems with more than one phenotypic dimension the relations between these notions become weak and only the asymptotic stability of coevolutionary attractors carries sufficient information to predict evolutionary outcomes. The crucial dependence of asymptotic stability on assumptions regarding mutation structures is illustrated. *Chapter 4* analyzes the coevolutionary dynamics in predator-prey communities. The new phenomenon of evolutionary cycling is encountered and the conditions for such continuous coevolutionary change to occur in the absence of external forcing are discussed. *Chapter 5* investigates patterns of coevolutionary change under asymmetric competition. A rich set of evolutionary attractors is observed and the dependences on the intra- and interspecific competition structures are analyzed. The applications in Chapters 4 and 5 illustrate a particular capacity of the dynamical theory of coevolution: to infer evolutionary predictions at the community level from ecological assumptions at the level of individuals.

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1

Can Adaptive Dynamics Invade?

Trends Ecol. Evol. (in press)

Slightly modified version.

Trends Ecol. Evol. (in press)

Can Adaptive Dynamics Invade?

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An international group of scientists gathered in August 1996 for a workshop in the Matrahaza mountains of Hungary to report and assess recent developments and open research topics in the new field of adaptive dynamics. This paper provides a brief overview of basic adaptive dynamics theory, outlines recent work within the field and evaluates the prospects for the future.

1 Introduction

The emerging field of adaptive dynamics sets out to provide additional insights into the long-term dynamics of evolutionary and coevolutionary processes.

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

Now population genetics' detailed knowledge, which reflects the chromosomal mechanisms of evolutionary change, can be complemented by a new framework for understanding the dynamics 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 research topics: an extended classification scheme for evolutionarily stable strategies (Figure 1) and a network of evolutionary models linking classical evolutionary game theory to replicator dynamics and individual-based ecological models (Figure 2).

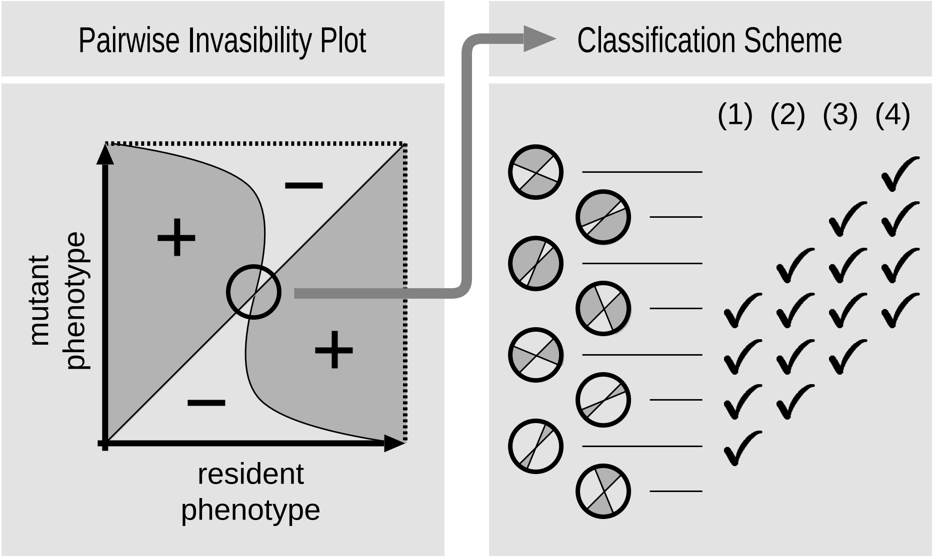

Figure 1 Pairwise invasibility plots and the classification of evolutionarily singular points. The adaptive dynamics invasion function of a particular ecological system defines a pairwise invasibility plot for resident and mutant phenotypes. When the invasion function is positive for a particular pair 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. Knowing the slope of the countour line at these singular points suffices to answer four separate questions: (1) Is a singular phenotype immune to invasions by neighboring phenotypes? (2) When starting from neighboring phenotypes, do successful invaders lie closer to the singular one? (3) Is the singular phenotype capable of invading into all its neighboring types? (4) When considering a pair of neighboring phenotypes to both sides of a singular one, can they invade into each other?

2 From Mutant Invasions to Adaptive Dynamics

Interactions between individuals are bound to change the environments 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 into which mutant phenotypes must succeed to invade for long-term evolution to proceed. Whether or not such an event may occur can be decided by adaptive dynamics' invasion functions: if the initial exponential growth rate of a small mutant population in an established resident population (a rate which one obtains as a Lyapunov exponent) is positive, the mutant phenotype has a chance to replace the former resident phenotype (Metz et al. 1992; Rand et al. 1994; Ferrière and Gatto 1995).

Once the invasion function of the evolving system is known, pairwise invasibility plots can be constructed (van Tienderen and de Jong 1986; Taylor 1989; Metz et al. 1996). 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 Figure 1. This line separates regions of potential invasion success from those of invasion failure and its shape carries important information about the evolutionary process (Metz et al. 1996). 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 theory 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 one? 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? Only if so, the phenotype at the singular point can be reached in a single mutation step.
4. When considering a pair of neighboring phenotypes to both sides of a singular one, 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 (Metz et al. 1996), see Figure 1.

3 Models of Phenotypic Evolution Unified

A large variety of phenotypic models has been used in the past 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 (Dieckmann et al. 1995; Dieckmann and Law 1996). 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 (Figure 2a). This generalized replicator dynamics can 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

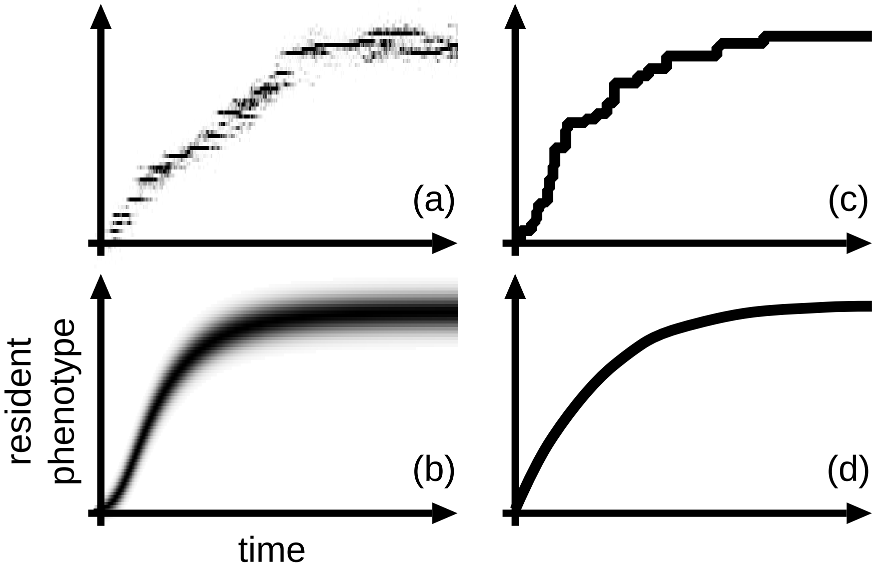

Figure 2 Generalized replicator dynamics. Four traditional types of models for phenotypic evolution are unified into a single network of linked descriptions: (a) individual-based birth-death-mutation process (polymorphic and stochastic), (b) reaction-diffusion model (polymorphic and deterministic), (c) evolutionary random walk (monomorphic and stochastic), (d) gradient ascent on an adaptive topography (monomorphic and deterministic).

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 (Schuster and Sigmund 1983) to nonlinear stochastic population dynamics with mutations, simplified models are derived. First, a reaction-diffusion approximation can be obtained for sufficiently large populations (Figure 2b). Second, if the conventional separation between the ecological and the evolutionary time scale is accepted, the evolutionary dynamics become mutation-limited and phenotypic distributions are monomorphic at most points in time (Figure 2c). The occurring phenotypic substitutions (although not their expected rates) can then 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 (Figure 2d). This dynamic provides an underpinning for a class of models in the literature that are based on time-variable adaptive topographies (Hofbauer and Sigmund 1990; Abrams et al. 1993; Vincent et al. 1993).

4 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 (Metz et al. 1996). Stefan Geritz and Hans Metz from the 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, actually can 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 (Metz et al. 1996). However, only when going beyond a merely phenotypic description of the evolutionary process by incorporating genetic mechanisms, two critical questions can be evaluated.

1. Does the phenomenon of evolutionary branching persist when diploid genetics and sexual reproduction are introduced?
2. 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 Döbeli from the University of Basel, Switzerland, and Ulf Dieckmann, IIASA Laxenburg, Austria, demonstrated that an evolving degree of assortative mating in a multi-locus genetic model is sufficient to allow for evolutionary branching at those phenotypes predicted by adaptive dynamics theory.

Other talks also were concerned with integrating phenotypic and genetic understanding of evolutionary dynamics. Carlo Matessi, IGBE-CNR Pavia, Italy, talked about the role of genetic canalization for selection in fluctuating environments. Tom van Dooren from the University of Antwerp, Belgium, and Stefan Geritz presented methods for extending the analyses of pairwise invasibility plots to systems with diploid inheritance.

5 Evolving Ecologies

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

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

6 Adaptive Dynamics in the Wild

Several participants of the workshop reported on interpreting empirically observed patterns in terms of adaptive processes.

Paul Marrow, University of Cambridge, U.K., showed experimental data on the distribution of offspring numbers in Soey sheep and studied whether its 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 to what extent 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.

7 Remaining Challenges

Much progress has been made in setting up the adaptive dynamics framework over the past five years. Nevertheless, many interesting directions for future research remain widely open. Three examples illustrate this assertion.

Mikko Heino, University of Helsinki, Finland, and Géza Meszéna, Eötvös University Budapest, Hungary, independently reported findings which 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, and Sido Mylius, Leiden University, both in the Netherlands, have analyzed the evolution of reproductive timing in salmons. Their model seems to show that adaptive dynamics' invasion functions can not always be obtained from the growth rates of mutants when these are rare. Under which conditions can attention remain focused on initial invasion dynamics when predicting phenotypic substitutions? The invasion-oriented approach to phenotypic evolution already has succeeded in advancing our understanding substantially (Diekmann et al. 1996), but its limitations still have to be evaluated in more detail.

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

With problems of this calibre 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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2

The Dynamical Theory of Coevolution: A Derivation from Stochastic Ecological Processes

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The Dynamical Theory of Coevolution: A Derivation from Stochastic Ecological Processes

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In this paper we develop a dynamical theory of coevolution in ecological communities. The derivation explicitly accounts for the stochastic components of evolutionary change and is based on ecological processes at the level of the individual. We show that the coevolutionary dynamic can be envisaged as a directed random walk in the community's trait space. A quantitative description of this stochastic process in terms of a master equation is derived. By determining the first jump moment of this process we abstract the dynamic of the mean evolutionary path. To first order the resulting equation coincides with a dynamic that has frequently been assumed in evolutionary game theory. Apart from recovering this canonical equation we systematically establish the underlying assumptions. We provide higher order corrections and show that these can give rise to new, unexpected evolutionary effects including shifting evolutionary isoclines and evolutionary slowing down of mean paths as they approach evolutionary equilibria. Extensions of the derivation to more general ecological settings are discussed. In particular we allow for multi-trait coevolution and analyze coevolution under nonequilibrium population dynamics.

1 Introduction

The self-organisation of systems of living organisms is elucidated most successfully by the concept of Darwinian evolution. The processes of multiplication, variation, inheritance and interaction are sufficient to enable organisms to adapt to their environments by means of natural selection (see e.g. Dawkins 1976). Yet, the development of a general and coherent mathematical theory of Darwinian evolution built from the underlying ecological processes is far from complete. Progress on these ecological aspects of evolution will critically depend on properly addressing at least the following four requirements.

1. *The evolutionary process needs to be considered in a coevolutionary context.* This amounts to allowing feedbacks to occur between the evolutionary dynamics of

a species and the dynamics of its environment (Lewontin 1983). In particular, the biotic environment of a species can be affected by adaptive change in other species (Futuyma and Slatkin 1983). Evolution in constant or externally driven environments thus are special cases within the broader coevolutionary perspective. Maximization concepts, already debatable in the former context, are insufficient in the context of coevolution (Emlen 1987; Lewontin 1979, 1987).

2. *A proper mathematical theory of evolution should be dynamical.* Although some insights can be gained by identifying the evolutionarily stable states or strategies (Maynard Smith 1982), there is an important distinction between non-invadability and dynamical attainability (Eshel and Motro 1981; Eshel 1983; Taylor 1989). It can be shown that in a coevolutionary community comprising more than a single species even the evolutionary attractors generally cannot be predicted without explicit knowledge of the dynamics (Marrow et al. 1996). Consequently, if the mutation structure has an impact on the evolutionary dynamics, it must not be ignored when determining evolutionary attractors. Furthermore, a dynamical perspective is required in order to deal with evolutionary transients or evolutionary attractors which are not simply fixed points.
3. *The coevolutionary dynamics ought to be underpinned by a microscopic theory.* Rather than postulating measures of fitness and assuming plausible adaptive dynamics, these should be rigorously derived. Only by accounting for the ecological foundations of the evolutionary process in terms of the underlying population dynamics, is it possible to incorporate properly both density and frequency dependent selection into the mathematical framework (Brown and Vincent 1987a; Abrams et al. 1989, 1993; Saloniemi 1993). Yet, there remain further problems to overcome. First, analyses of evolutionary change usually can not cope with nonequilibrium population dynamics (but see Metz et al. 1992; Rand et al. 1993). Second, most investigations are aimed at the level of population dynamics rather than at the level of individuals within the populations at which natural selection takes place; in consequence, the ecological details between the two levels are bypassed.
4. *The evolutionary process has important stochastic elements.* The process of mutation, which introduces new phenotypic trait values at random into the population, acts as a first stochastic cause. Second, individuals are discrete entities and consequently mutants that arise initially as a single individual are liable to accidental extinction (Fisher 1958). A third factor would be demographic stochasticity of resident populations; however, in this paper we assume resident populations to be large, so that the effects of finite population size of the *residents* do not have to be considered (Wissel and Stöcker 1989). The importance of these stochastic impacts on the evolutionary process has been stressed by Kimura (1983) and Ebeling and Feistel (1982).

Only some of the issues above can be tackled within the mathematical framework of evolutionary game dynamics. This field of research focuses attention on change in phenotypic adaptive traits and serves as an extension of traditional evolutionary game theory. The latter identifies a game's payoff with some measure of fitness and is based on the concept of the evolutionarily stable strategy (Maynard Smith and Price 1973). Several shortcomings of the traditional evolutionary game theory made the extension to game dynamics necessary. First, evolutionary game theory assumes the simultaneous availability of all possible trait values. Though one might theoretically envisage processes of immigration having this feature, the process of mutation typically will only yield variation that is localized around the current mean trait value (Mackay 1990). Second, it has been shown that the non-invadability of a trait value does not imply that trait values in the vicinity will converge to the former (Taylor 1989; Christiansen 1991; Takada and Kigami 1991). In consequence, there can occur evolutionarily stable strategies that are not dynamically attainable, these have been called 'Garden of Eden' configurations (Hofbauer and Sigmund 1990). Third, the concept of maximization, underlying traditional game theory, is essentially confined to single species adaptation. Vincent et al. (1993) have shown that a similar maximization principle also holds for ecological settings where several species can be assigned a single fitness generating function. However, this is too restrictive a requirement for general coevolutionary scenarios, so in this context the dynamical perspective turns out to be the sole reliable method of analysis.

We summarize the results of several investigations of coevolutionary processes based on evolutionary game dynamics by means of the following *canonical equation*

$$\frac{d}{dt} s_i = k_i(s) \cdot \frac{\partial}{\partial s_i'} W_i(s_i', s) \Big|_{s_i' = s_i} . \tag{1.1}$$

Here, the s_i with $i = 1, \ldots, N$ denote adaptive trait values in a community comprising N species. The $W_i(s_i', s)$ are measures of fitness of individuals with trait value s_i' in the environment determined by the resident trait values s, whereas the $k_i(s)$ are non-negative coefficients, possibly distinct for each species, that scale the rate of evolutionary change. Adaptive dynamics of the kind (1.1) have frequently been postulated, based either on the notion of a hill-climbing process on an adaptive landscape or on some other sort of plausibility argument (Brown and Vincent 1987a, 1987b, 1992; Rosenzweig et al. 1987; Hofbauer and Sigmund 1988, 1990; Takada and Kigami 1991; Vincent 1991; Abrams 1992; Marrow and Cannings 1993; Abrams et al. 1993). The notion of the adaptive landscape or topography goes back to Wright (1931). A more restricted version of equation (1.1), not yet allowing for intraspecific frequency dependence, has been used by Roughgarden (1983). It has also been shown that one can obtain an equation similar to the dynamics (1.1) as a limiting case of results from quantitative genetics (Lande 1979; Iwasa et al. 1991; Taper and Case 1992; Vincent et al. 1993; Abrams et al. 1993).

In this paper we present a derivation of the canonical equation that accounts for all four of the above requirements. In doing this we recover the dynamics (1.1) and go beyond them by providing higher order corrections to this dynamical equation; in passing, we deduce explicit expressions for the measures of fitness W_i and the coefficients k_i. The analysis is concerned with the simultaneous evolution of an arbitrary number of species and is appropriate both for pairwise or tight coevolution and for diffuse coevolution (Futuyma and Slatkin 1983). We base the adaptive dynamics of the coevolutionary community on the birth and death processes of individuals. The evolutionary dynamics are described as a stochastic process, explicitly accounting for random mutational steps and the risk of extinction of rare mutants. From this we extract a deterministic approximation of the stochastic process, describing the dynamics of the mean evolutionary path. The resulting system of ordinary differential equations covers both the asymptotics and transients of the adaptive dynamics, given equilibrium population dynamics; we also discuss an extension to nonequilibrium population dynamics.

The outline of the paper is as follows. *Section 2* provides a general framework for the analysis of coevolutionary dynamics. The relationship of population dynamics to adaptive dynamics is discussed in a coevolutionary context and we describe the basic quantities specifying a coevolutionary community. For the purpose of illustration we introduce a coevolutionary predator-prey system that serves as a running example to demonstrate most of the ideas in this paper. In *Section 3* we derive the stochastic representation of the coevolutionary process, explaining the notion of a trait substitution sequence and giving a dynamical description of these processes in terms of a master equation. In *Section 4* we utilize this representation in combination with the stochastic concept of the mean evolutionary path in order to construct a deterministic approximation of the coevolutionary process. From this the canonical equation (1.1) is recovered and we demonstrate its validity up to first order. This result is refined in *Section 5* by means of higher order corrections, where a general expression for the adaptive dynamics is deduced allowing for increased accuracy. The higher order corrections give rise to new, unexpected effects which are discussed in detail. We also provide the conditions that must be satisfied for making the canonical equation exact and explain in what sense it can be understood as the limiting case of our more general process. In *Section 6* we extend our theoretical approach to a wider class of coevolutionary dynamics by discussing several generalizations such as multiple-trait coevolution and coevolution under nonequilibrium population dynamics.

2 Formal Framework

Here we introduce the basic concepts underlying our analyses of coevolutionary dynamics. Notation and assumptions are discussed, and the running example of predator-prey coevolution is outlined.

2.1 Conceptual Background

The coevolutionary community under analysis is allowed to comprise an arbitrary number N of species, the species are characterized by an index $i = 1, \ldots, N$. We denote the number of individuals in these species by n_i, with $n = (n_1, \ldots, n_N)$. The individuals within each species can be distinct with respect to adaptive trait values s_i, taken from sets $\widehat{S}_i$ and being either continuous or discrete. For convenience we scale the adaptive trait values such that $\widehat{S}_i \subset (0, 1)$. The restriction to one trait per species will be relaxed in Section 6.2, but obtains until then to keep notation reasonably simple.

The development of the coevolutionary community is caused by the process of mutation, introducing new mutant trait values s_i', and the process of selection, determining survival or extinction of these mutants. A formal description will be given in Sections 2.2 and 3.2; here we clarify the concepts involved. The change of the population sizes n_i constitutes the *population dynamics*, that of the adaptive trait values s_i is called *adaptive dynamics*. Together these make up the *coevolutionary dynamics* of the community. We follow the convention widely used in evolutionary theory that population dynamics occurs on an ecological time scale that is much faster than the evolutionary time scale of adaptive dynamics (Roughgarden 1983). Two important inferences can be drawn from this separation.

First, the time scale argument can be used in combination with a principle of mutual exclusion to cast the coevolutionary dynamics in a *quasi-monomorphic framework*. The principle of mutual exclusion states that no two adaptive trait values s_i and s_i' can coexist indefinitely in the populations of species $i = 1, \ldots, N$ when not renewed by mutations; of the two trait values eventually only the single more advantageous one survives. For the moment we keep this statement as an assumption; in Section 6.1 we will have built up the necessary background to clarify its premisses. Together with the time scale argument we conclude that there will be one trait value prevailing in each species at almost any point in time. This is not to say that coexistence of several mutants cannot occur at all: we will regard an evolving population as quasi-monomorphic, if the periods of coexistence are negligible compared to the total time of evolution (Kimura 1983). The adaptive state of the coevolutionary community is then aptly characterized by the vector $s = (s_1, \ldots, s_N)$ of prevailing or resident trait values and the state space of the coevolutionary dynamics is the Cartesian product of the *monomorphic trait* *space* $\widehat{S} = \times_{i=1}^{N} \widehat{S}_i \subset R^N$ and the *population size space* $\widehat{N} = \times_{i=1}^{N} \widehat{N}_i = Z_+^N$. When considering large population sizes we may effectively replace $\widehat{N}_i = Z_+$ by $\widehat{N}_i = R_+$.

Second, we apply the time scale argument together with an assumption of monostable population dynamics to achieve a *decoupling* of the population dynamics from the adaptive dynamics. In general, the population dynamics could be multistable, i.e. different attractors are attained depending on initial conditions in population size space. It will then be necessary to trace the population dynamics $\frac{d}{dt}n$ in size space $\widehat{N}$ simultaneously with the adaptive dynamics $\frac{d}{dt}s$ in trait space $\widehat{S}$. This is no problem in principle but it makes the mathematical formulation more complicated; for simplicity we hence assume *monostability*. Due to the different time scales, the system of simultaneous equations can then be readily decomposed. The trait values s or functions thereof can be assumed constant as far as the population dynamics $\frac{d}{dt}n$ are concerned. The population sizes n or functions F thereof can be taken averaged when the adaptive dynamics $\frac{d}{dt}s$ are considered, i.e.

$$\overline{F}(s) = \lim_{T\to\infty} \frac{1}{T} \cdot \int_0^T F(s, n(s,t))\, dt \tag{2.1}$$

where $n(s,t)$ is the solution of the population dynamics $\frac{d}{dt}n$ with initial conditions $n(s,0)$ which are arbitrary because of monostability. With the help of these solutions $n(s,t)$ we can also define the *region of coexistence* $\widehat{S}_c$ as that subset of trait space $\widehat{S}$ that allows for sustained coexistence of all species

$$\widehat{S}_c = \left\{ s \in \widehat{S} \mid \lim_{t\to\infty} n_i(s,t) > 0 \quad \text{for all} \quad i = 1, \dots, N \right\} . \tag{2.2}$$

If the boundary $\partial\widehat{S}_c$ of this region of coexistence is attained by the adaptive dynamics, the coevolutionary community collapses from N species to a smaller number of N' species. The further coevolutionary process then has to be considered in the corresponding N'-dimensional trait space. There can also exist processes that lead to an increase in the dimension of the trait space, see e.g. Section 6.1.

2.2 SPECIFICATION OF THE COEVOLUTIONARY COMMUNITY

We now have to define those features of the coevolutionary community that are relevant for our analysis in terms of ecologically meaningful quantities.

We first consider the process of selection. In an ecological community the environment e_i of a species i is affected by influences that can be either internal or external with respect to the community considered. The former effects are functions of the adaptive trait values s and population sizes n in the community; the latter may moreover be subject to external effects like seasonal forcing which render the system non-autonomous. We thus write

$$e_i = e_i(s, n, t) \, . \tag{2.3}$$

The quantities $\widetilde{b}_i$ and $\widetilde{d}_i$ are introduced to denote the *per capita birth and death rates* of an individual in species i. These rates are interpreted stochastically as probabilities per unit time and can be combined to yield the per capita growth rate $\widetilde{f}_i = \widetilde{b}_i - \widetilde{d}_i$ of the individual. They are affected by the trait value s_i' of the individual as well as by its environment e_i, thus with equation (2.3) we have

$$\widetilde{b}_i = \widetilde{b}_i\big(s_i', s, n, t\big) \quad \text{and} \quad \widetilde{d}_i = \widetilde{d}_i\big(s_i', s, n, t\big) \, . \tag{2.4}$$

Since we are mainly interested in the phenomenon of coevolution – an effect internal to the community – in the present paper we will not consider the extra time-dependence in equations (2.4) which may be imposed on the environment by external effects.

We now turn to the process of mutation. In order to describe its properties we introduce the quantities μ_i and M_i. The former denote the *fraction of births that give rise to a mutation* in the trait value s_i. Again, these fractions are interpreted stochastically as probabilities for a birth event to produce an offspring with an altered adaptive trait value. These quantities may depend on the phenotype of the individual itself,

$$\mu_i = \mu_i(s_i) \, , \tag{2.5}$$

although in the present paper we will not dwell on this complication. The quantities

$$M_i = M_i\big(s_i, s_i' - s_i\big) \tag{2.6}$$

determine the *probability distribution of mutant trait values* s_i' around the original trait value s_i. If the functions M_i and μ_i are independent of their first argument, the mutation process is called *homogeneous*; if M_i is invariant under a sign change of its second argument, the mutation process is called *symmetric*.

With equilibrium population sizes $\hat{n}(s)$ satisfying $\widetilde{f}_i(s_i, s, \hat{n}(s)) = 0$ for all $i = 1, \ldots, N$, the time average in equation (2.1) is simply given by $\overline{F}(s) = F(s, \hat{n}(s))$. In particular we thus can define

$$\overline{f}_i\big(s_i', s\big) = \widetilde{f}_i\big(s_i', s, \hat{n}(s)\big) \tag{2.7}$$

and analogously for $\overline{b}_i$ and $\overline{d}_i$. We come back to the general case of nonequilibrium population dynamics in Section 6.3.

We conclude that for the purpose of our analysis the coevolutionary community of N species is completely defined by specifying the ecological rates $\widetilde{b}_i$, $\widetilde{d}_i$ and the mutation properties μ_i, M_i. An explicit example is introduced for illustration in Section 2.3. We will see that our formal framework allows us to deal both with density dependent selection as well as with interspecific and intraspecific frequency dependent selection.

2.3 APPLICATION

To illustrate the formal framework developed above, here we specify a coevolutionary community starting from a purely ecological one. The example describes coevolution in a predator-prey system.

First, we choose the population dynamics of prey (index 1) and predator (index 2) to be described by a Lotka-Volterra system with self-limitation in the prey

$$\begin{aligned} \frac{d}{dt}n_1 &= n_1 \cdot (r_1 - \alpha \cdot n_1 - \beta \cdot n_2) \, , \\ \frac{d}{dt}n_2 &= n_2 \cdot (-r_2 + \gamma \cdot n_1) \end{aligned} \tag{2.8}$$

where all parameters r_1, r_2, α, β and γ are positive. These control parameters of the system are determined by the species' intraspecific and interspecific interactions as well as by those with the external environment.

Second, we specify the dependence of the control parameters on the adaptive trait values $s = (s_1, s_2)$

$$\begin{aligned} \gamma(s_1, s_2)/u &= c_1 \cdot \beta(s_1, s_2) \\ \beta(s_1, s_2)/u &= \exp\left(-\delta_1^2 + 2c_2 \cdot \delta_1 \cdot \delta_2 - \delta_2^2\right) \, , \\ \alpha(s_1)/u &= c_7 - c_8 \cdot s_1 + c_9 \cdot s_1^2 \end{aligned} \tag{2.9}$$

with $\delta_1 = (s_1 - c_3)/c_4$ and $\delta_2 = (s_2 - c_5)/c_6$; r_1 and r_2 are independent of s_1 and s_2. The constant u can be used to scale population sizes in the community. For the sake of concreteness s_1 and s_2 may be thought of as representing the body sizes of prey and predator respectively. According to the Gaussian functions β and γ, the predator's harvesting of the prey is most efficient at $(s_1 = c_3, s_2 = c_5)$ and, since $c_2 > 0$, remains particularly efficient along the line $(s_1, s_2 = s_1)$, i.e. for predators having a body size similar to their prey. According to the parabolic function α, the prey's self-limitation is minimal at $s_1 = c_8/2c_9$. Details of the biological underpinning of these choices are discussed in Marrow et al. (1992).

Third, we provide the per capita birth and death rates for a rare mutant trait value s_1' or s_2' respectively,

$$\begin{aligned} \widetilde{b}_1(s_1', s, n) &= r_1 \, , \\ \widetilde{d}_1(s_1', s, n) &= \alpha(s_1') \cdot n_1 + \beta(s_1', s_2) \cdot n_2 \, , \\ \widetilde{b}_2(s_2', s, n) &= \gamma(s_1, s_2') \cdot n_1 \, , \\ \widetilde{d}_2(s_2', s, n) &= r_2 \, . \end{aligned} \tag{2.10}$$

These functions are the simplest choice in agreement with equations (2.8) and can be inferred by taking into account that mutants are rare when entering the community.

<table>
<tr><td colspan="11">parameters affecting selection</td></tr>
<tr><td>r_1</td><td>r_2</td><td>c_1</td><td>c_2</td><td>c_3</td><td>c_4</td><td>c_5</td><td>c_6</td><td>c_7</td><td>c_8</td><td>c_9</td></tr>
<tr><td>0.5</td><td>0.05</td><td>0.2</td><td>0.6</td><td>0.5</td><td>0.22</td><td>0.5</td><td>0.25</td><td>2.0</td><td>8.0</td><td>10.0</td></tr>
<tr><td colspan="11">parameters affecting mutation</td></tr>
<tr><td colspan="2">σ_1</td><td colspan="2">μ_1</td><td colspan="2">σ_2</td><td colspan="2">μ_2</td><td colspan="2">u</td><td rowspan="2"></td></tr>
<tr><td colspan="2">$5 \cdot 10^{-3}$</td><td colspan="2">10^{-4}</td><td colspan="2">$5 \cdot 10^{-3}$</td><td colspan="2">10^{-3}</td><td colspan="2">10^{-3}</td></tr>
</table>

TABLE 1 The default parameter values for the coevolutionary predator-prey community.

Fourth, we complete the definition of our coevolutionary community by the properties of the mutation process,

$$\begin{aligned} &\mu_1 \ , \\ &M_1(s_1, \Delta s_1) = \frac{1}{\sqrt{2\pi} \cdot \sigma_1} \cdot \exp\left(-\frac{1}{2} \Delta s_1^2 / \sigma_1^2\right) \ , \\ &\mu_2 \ , \\ &M_2(s_2, \Delta s_2) = \frac{1}{\sqrt{2\pi} \cdot \sigma_2} \cdot \exp\left(-\frac{1}{2} \Delta s_2^2 / \sigma_2^2\right) \ . \end{aligned} \tag{2.11}$$

The standard numerical values for all parameters used in subsequent simulations are given in Table 1.

Although the coevolutionary community defined by (2.10) and (2.11) captures some features of predator-prey coevolution, other choices for the same purpose or for entirely different ecological scenarios could readily be made within the scope of our approach. Many features of the model presented will be analyzed in the course of this paper; additional discussion is provided in Marrow et al. (1992, 1996) and Dieckmann et al. (1995).

3 Stochastic Representation

In this section we establish the stochastic description of the coevolutionary dynamics. The central idea is to envisage a sequence of trait substitutions as a *directed random walk in trait space* determined by the processes of mutation and selection.

3.1 Stochastic Description of Trait Substitution Sequences

The notion of the directed random walk is appropriate for three reasons. First, the current adaptive state of the coevolutionary community is represented by the vector $s = (s_1, \ldots, s_N)$ composed of the trait values prevalent in each species. This is due to the assumption of quasi-monomorphic evolution discussed in the last section. So a *trait substitution sequence* is given by the dynamics of the point s in N-dimensional trait space (Metz et al. 1992). Second, these dynamics incorporate stochastic change. As already noted in the Introduction, the two sources for this randomness are (i) the process of mutation and (ii) the impact of demographic stochasticity on rare mutants. Third, the coevolutionary dynamics possess no memory, for mutation and selection depend only on the present state of the community. The trait substitution sequence thus will be Markovian, provided that s determines the state of the coevolutionary system. To meet this requirement for realistic systems, a sufficient number of traits may need to be considered, see Section 6.2.

By virtue of the Markov property the dynamics of the vector s is described by the following equation

$$\frac{d}{dt} P(s,t) = \int \Big[\, w(s|s') \cdot P(s',t) - w(s'|s) \cdot P(s,t) \, \Big] \, ds' . \tag{3.1}$$

Here $P(s,t)$ denotes the probability that the trait values in the coevolutionary system are given by s at time t. Note that $P(s,t)$ is only defined on the region of coexistence $\widehat{S}_c$. The $w(s'|s)$ represent the transition probabilities per unit time for the trait substitution $s \to s'$. The stochastic equation above is an instance of a master equation (see e.g. van Kampen 1981) and simply reflects the fact that the probability $P(s,t)$ is increased by all transitions to s (first term) and decreased by all those from s (second term).

3.2 Transition Probabilities per Unit Time

We now turn to the definition of the transition probabilities per unit time. Since the change dP in the probability $P(s,t)$ is only considered during the infinitesimal evolutionary time interval dt, it is understood that only transitions corresponding to a trait substitution in a single species have a nonvanishing probability per unit time. This is denoted by

$$w(s'|s) = \sum_{i=1}^{N} w_i(s_i', s) \cdot \prod_{\substack{j=1 \\ j \neq i}}^{N} \delta(s_j' - s_j) \tag{3.2}$$

where δ is Dirac's delta function. For a given s the ith component of this sum can be envisaged in the space of all $s' - s$ as a singular probability distribution that is only nonvanishing on the ith axis. The derivation of $w_i(s_i', s)$, the transition probability per unit time for the trait substitution $s_i \to s_i'$, comes in three parts.

1. Mutation and selection are statistically uncorrelated. For this reason the probability per unit time w_i for a specific trait substitution is given by the probability per unit time $\mathcal{M}_i$ that the mutant enters the population times the probability $\mathcal{S}_i$ that it successfully escapes accidental extinction

$$w_i(s_i', s) = \mathcal{M}_i(s_i', s) \cdot \mathcal{S}_i(s_i', s) \, . \tag{3.3}$$

2. The processes of mutation in distinct individuals are statistically uncorrelated. Thus the probability per unit time $\mathcal{M}_i$ that the mutant enters the population is given by the product of the following three terms.
   a. The per capita mutation rate $\mu_i(s_i) \cdot \bar{b}_i(s_i, s)$ for the trait value s_i. The term $\bar{b}_i(s_i, s)$ is the per capita birth rate of the ith species in the community determined by the resident trait values s, and $\mu_i(s_i)$ denotes the fraction of births that give rise to mutations in the species i.
   b. The equilibrium population size $\hat{n}_i(s)$ of the ith species.
   c. The probability distribution $M_i(s_i, s_i' - s_i)$ for the mutation process in the trait s_i.

   Collecting the results above we obtain

$$\mathcal{M}_i(s_i', s) = \mu_i(s_i) \cdot \bar{b}_i(s_i, s) \cdot \hat{n}_i(s) \cdot M_i(s_i, s_i' - s_i) \tag{3.4}$$

   for the probability per unit time that the mutant enters the population.

3. The process of selection determines the mutant's probability $\mathcal{S}_i$ of escaping initial extinction. Since mutants enter as single individuals, the impact of demographic stochasticity on their population dynamics must not be neglected (Fisher 1958). We assume, however, that the equilibrium population sizes $\hat{n}_i$ are large enough for there to be negligible risk of accidental extinction of the established resident populations. Two consequences stem from this.
   a. Frequency-dependent effects on the population dynamics of the mutant can be ignored when the mutant is rare relative to the resident.
   b. The actual equilibrium size of the mutant after fixation is not important as long as it is large enough to exceed a certain threshold. Above this threshold the effect of demographic stochasticity is negligible (Wissel and Stöcker 1991).

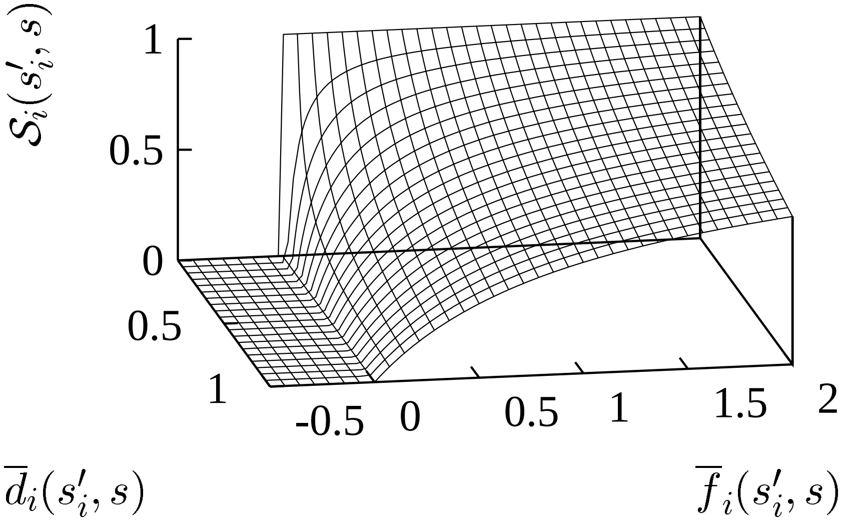


FIGURE 1 Invasion success of a rare mutant. The probability $\mathcal{S}_i(s_i', s)$ of a mutant population initially of size 1 with adaptive trait value s_i' in a community of monomorphic resident populations with adaptive trait values s to grow in size such as to eventually overcome the threshold of accidental extinction is dependent on the per capita growth and death rates, $\overline{f}_i(s_i', s)$ and $\overline{d}_i(s_i', s)$, of individuals in the mutant population. Deleterious mutants with $\overline{f}_i(s_i', s) < 0$ go extinct with probability 1 but even advantageous mutants with $\overline{f}_i(s_i', s) > 0$ have a survival probability less than 1. Large per capita deaths rates hinder invasion success while large per capita growth rates of the mutant favor it.

The probability that the mutant population reaches size n starting from size 1 depends on its per capita birth and death rates, b and d. Based on the stochastic population dynamics of the mutant (Dieckmann 1994) and statement (a) above, this probability can be calculated analytically. The result is given by $[1 - (d/b)]/[1 - (d/b)^n]$ (Bailey 1964; Goel and Richter-Dyn 1974). We exploit statement (b) above by taking the limit $n \to \infty$. The probability $\mathcal{S}_i$ of escaping extinction is then given by

$$\begin{aligned} \mathcal{S}_i(s_i', s) &= \begin{cases} 1 - \overline{d}_i(s_i', s)/\overline{b}_i(s_i', s) & \text{for} \quad \overline{d}_i(s_i', s)/\overline{b}_i(s_i', s) < 1 \\ 0 & \text{for} \quad \overline{d}_i(s_i', s)/\overline{b}_i(s_i', s) \geq 1 \end{cases} \\ &= \overline{b}_i^{\,-1}(s_i', s) \cdot \left(\overline{f}_i(s_i', s)\right)_+ \end{aligned} \tag{3.5}$$

where the function $(\ldots)_+ \, : \, x \to x \cdot \Theta(x)$, the product of the identity and the Heaviside function, leaves positive arguments unchanged and maps negative ones to zero. It follows from equation (3.5) that deleterious mutants (with a per capita growth rate smaller than that of the resident type) have no chance of survival but even advantageous mutants (with a greater per capita growth rate) experience some risk of extinction, see Figure 1.

We conclude that the transition probabilities per unit time for the trait substitutions $s_i \rightarrow s_i'$ are

$$\begin{aligned} &w_i(s_i', s) = \\ &\mu_i(s_i) \cdot \overline{b}_i(s_i, s) \cdot \hat{n}_i(s) \cdot M_i(s_i, s_i' - s_i) \cdot \overline{b_i}^{-1}(s_i', s) \cdot (\overline{f}_i(s_i', s))_+ \,. \end{aligned} \tag{3.6}$$

This expression completes the stochastic representation of the mutation-selection process in terms of the master equation.

3.3 Applications

The information contained in the stochastic representation of the coevolutionary dynamics can be used in several respects.

First, we can employ the *minimal process method* (Gillespie 1976) to obtain actual realizations of the stochastic mutation-selection process. We illustrate this method by means of our example of predator-prey coevolution. The two-dimensional trait space $\widehat{S}$ of this system is depicted in Figure 2a. The dashed line surrounds the region of coexistence $\widehat{S}_c$. Within this region different trait substitution sequences $(s_1(t), s_2(t))$ are displayed by continuous lines. Note that trait substitution sequences starting from the same initial states (indicated by asterisks) are not identical. This underlines the unique, historical nature of any evolutionary process. But, although these paths are driven apart by the process of mutation, they are kept together by the directional impact of selection.

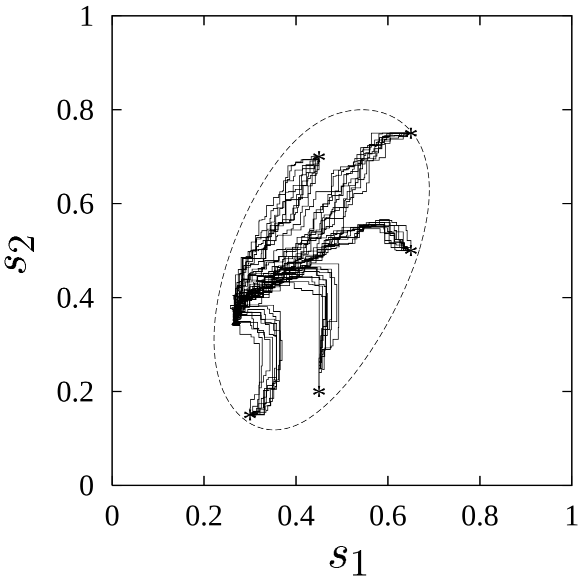


FIGURE 2A Stochastic representation of the adaptive dynamics: trait substitution sequences as defined by equations (3.1), (3.2) and (3.6). Ten directed random walks in trait space for each of five different initial conditions (indicated by asterisks) are depicted by continuous lines. The discontinuous oval curve is the boundary of the region of coexistence. The coevolution of both species drives the trait values towards a common equilibrium $\hat{s}$. The parameters of the coevolutionary predator-prey community are given in Table 1.

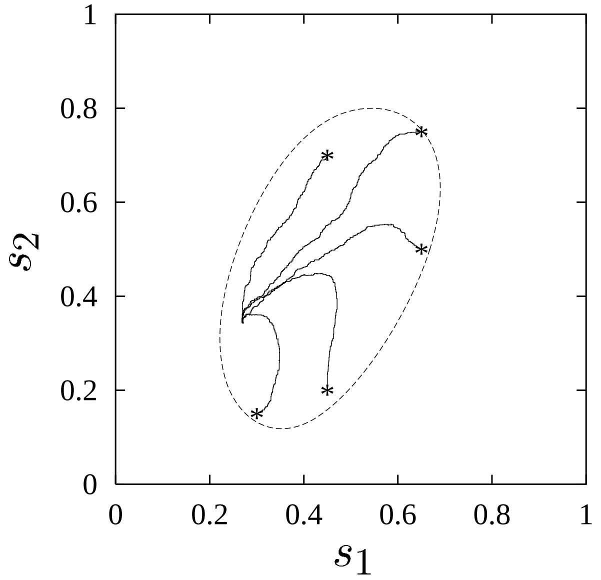


FIGURE 2B Stochastic representation of the adaptive dynamics: mean paths as defined by equation (3.7). Ten trait substitution sequences for each of the five different initial conditions (indicated by asterisks) are combined to obtain estimates for the mean paths, depicted by continuous lines. The jaggedness of the lines is caused by the finite number of ten trait substitution sequences. The discontinuous oval curve is the boundary of the region of coexistence. The parameters of the coevolutionary predator-prey community are as in Figure 2a.

Second, the latter observation underpins the introduction of a further concept from stochastic process theory. By imagining a large number r of trait substitution sequences $s^k(t) = \big(s_1^k(t), \ldots, s_N^k(t)\big)$, with $k = 1, \ldots, r$, starting from the same initial state, it is straightforward to apply an averaging process in order to obtain the *mean path* $\langle s \rangle(t)$ by

$$\langle s \rangle(t) = \lim_{r \to \infty} \frac{1}{r} \cdot \sum_{k=1}^{r} s^k(t) \,. \tag{3.7}$$

The construction of these mean paths is illustrated in Figure 2b. Since the mean path obviously summarizes the essential features of the coevolutionary process, it is desirable to obtain an explicit expression for its dynamics. This issue will be addressed in the next two sections.

4 Deterministic Approximation: First Order

We now derive an approximate equation for the mean path of the coevolutionary dynamics. In this section we obtain a preliminary result and illustrate it by application to predator-prey coevolution. The argument in this section will be completed by the results of Section 5.

4.1 Determining the Mean Path

The mean path has been defined above as the average over an infinite number of realizations of the stochastic process. Equivalently, we can employ the probability distribution $P(s,t)$ considered in the last section to define the mean of an arbitrary function $F(s)$ by $\langle F(s) \rangle(t) = \int F(s) \cdot P(s,t)\, ds$. In particular we thereby obtain for the mean path

$$\langle s \rangle(t) = \int s \cdot P(s,t)\, ds \,. \tag{4.1}$$

The different states s thus are weighted at time t according to the probability $P(s,t)$ of their realization by the stochastic process at that time. In order to describe the dynamics of the mean path we start with the expression

$$\frac{d}{dt} \langle s \rangle(t) = \int s \cdot \frac{d}{dt} P(s,t)\, ds \,. \tag{4.2}$$

and utilize the master equation to replace $\frac{d}{dt}P(s,t)$. One then finds with some algebra

$$\frac{d}{dt} \langle s \rangle(t) = \int \int (s' - s) \cdot w(s'|s) \cdot P(s,t)\, ds'\, ds \,. \tag{4.3}$$

By exploiting the delta function property of $w(s'|s)$, see equation (3.2), and introducing the so called *kth jump moment of the ith species*

$$a_{ki}(s) = \int \big(s_i' - s_i\big)^k \cdot w_i(s_i', s)\, ds_i' \tag{4.4}$$

with $a_k = (a_{k1}, \ldots, a_{kN})$ we obtain

$$\frac{d}{dt}\langle s\rangle(t) = \langle a_1(s)\rangle(t)\,. \tag{4.5}$$

If the first jump moment $a_1(s)$ were a linear function of s, we could make use of the relation $\langle a_1(s)\rangle = a_1(\langle s\rangle)$ giving a self-contained equation for the mean path

$$\frac{d}{dt}\langle s\rangle(t) = a_1(\langle s\rangle(t))\,. \tag{4.6}$$

However, the coevolutionary dynamics typically are nonlinear so that the relation $\langle a_1(s)\rangle = a_1(\langle s\rangle)$ does not hold. Nevertheless, as long as the deviations of the stochastic realizations from the mean path are relatively small or, alternatively, the nonlinearity is weak, the equation above provides a very good approximation to the dynamics of the mean path. A quantitative discussion of this argument is provided in van Kampen (1962) and Kubo et al. (1973). To distinguish between the mean path itself and that actually described by equation (4.6), the latter is called the *deterministic path* (Serra et al. 1986).

4.2 DETERMINISTIC APPROXIMATION IN FIRST ORDER

We can now calculate the deterministic path of the coevolutionary dynamics by substituting (3.6) into (4.4) and the result into (4.6). Since from now on we concentrate on this deterministic approximation we will cease denoting it by angle brackets $\langle\ldots\rangle$. So we obtain

$$\begin{aligned}\frac{d}{dt}s_i =&\mu_i(s_i)\cdot \overline{b}_i(s_i,s)\cdot \hat{n}_i(s)\cdot\\ &\int_{R_i(s)} (s_i'-s_i)\cdot M_i(s_i,s_i'-s_i)\cdot \overline{b}_i^{-1}(s_i',s)\cdot \overline{f}_i(s_i',s)\,ds_i'\,,\end{aligned} \tag{4.7}$$

where, as an alternative to employing the function $(\ldots)_+$ in the integrand, we have restricted the range of integration in (4.7) to $s_i' \in R_i(s)$ with

$$R_i(s) = \left\{ s_i' \in \widehat{S}_i \mid \overline{f}_i(s_i',s) > 0 \right\}. \tag{4.8}$$

Note that the process of mutation causes the evolutionary rate of s_i to be dependent on the per capita growth and birth rates of all possible mutant trait values s_i'. This dependence is manifested both by the integrand of (4.7) and in the range of integration (4.8). In order to transform the global coupling into a local one we apply a Taylor expansion to $\overline{f}_i(s_i',s)$ and $\overline{b}_i^{-1}(s_i',s)\cdot\overline{f}_i(s_i',s)$ about $s_i' = s_i$. Higher orders in these expansions are discussed in Section 5; in this section we will use the results only up to first order

$$\overline{f}_i(s_i',s) = \partial_i'\overline{f}_i(s_i,s)\cdot(s_i'-s_i) + \mathcal{O}[(s_i'-s_i)^2] \tag{4.9}$$

and

$$\overline{b}_i^{-1}(s_i', s) \cdot \overline{f}_i(s_i', s) = \overline{b}_i^{-1}(s_i, s) \cdot \partial_i' \overline{f}_i(s_i, s) \cdot (s_i' - s_i) + \mathcal{O}[(s_i' - s_i)^2] \tag{4.10}$$

We have exploited the condition $\overline{f}_i(s_i, s) = 0$ above, for the population dynamics of the resident species are assumed to be at equilibrium. Since derivatives of the ecological rate functions will be used throughout this paper, we apply the abbreviated notations

$$\partial_i' \overline{f}_i = \frac{\partial}{\partial s_i'} \overline{f}_i \, , \qquad \partial_i \overline{f}_i = \frac{\partial}{\partial s_i} \overline{f}_i \tag{4.11}$$

and analogously for all functions taking the arguments (s_i', s). From (4.8) and (4.9) we can infer that the range $R_i(s)$ of integration in this first order result is either $(s_i, +\infty)$ or $(-\infty, s_i)$, depending only on the sign of $\partial_i' \overline{f}_i(s_i, s)$. If we assume the mutation process to be symmetric, we obtain the same result in both cases by substituting (4.10) into (4.7)

$$\boxed{\frac{d}{dt} s_i = \frac{1}{2} \cdot \mu_i(s_i) \cdot \sigma_i^2(s_i) \cdot \hat{n}_i(s) \cdot \partial_i' \overline{f}_i(s_i, s) \qquad (4.12)}$$

where

$$\sigma_i^2(s_i) = \int \Delta s_i^2 \cdot M_i(s_i, \Delta s_i) \, d\Delta s_i \, . \tag{4.13}$$

denotes the second moment of the mutation distribution M_i. Since the first moment of M_i vanishes due to symmetry, the second moment of this distribution equals its variance.

The set of equations (4.12) provides a first order, deterministic approximation of the coevolutionary dynamics. The rate of evolution in the trait s_i is determined by two factors.

1. The first terms in equation (4.12) represent the influence of mutation. This product is affected by the fraction $\mu_i(s_i)$ of mutations per birth and by the variance $\sigma_i^2(s_i)$ of the mutation distribution M_i. For homogeneous mutation processes these terms are constant. The third factor $\hat{n}_i(s)$ is the equilibrium population size. All these three terms make up the *evolutionary rate coefficient* which is non-negative and serves to scale the rate of evolutionary change.
2. The last factor accounts for the impact of selection. The function

$$\begin{aligned} \partial_i' \overline{f}_i(s_i, s) &= \frac{\partial}{\partial s_i'} f_i(s_i', s) \Big|_{s_i' = s_i} \\ &= \lim_{\Delta s_i \to 0} \frac{1}{\Delta s_i} \cdot \left[\overline{f}_i(s_i + \Delta s_i, s) - \overline{f}_i(s_i, s) \right] \\ &= \lim_{\Delta s_i \to 0} \frac{1}{\Delta s_i} \cdot \overline{f}_i(s_i + \Delta s_i, s) \end{aligned} \tag{4.14}$$

> which we call the *selection derivative* (Marrow et al. 1992), indicates the sensitivity of the per capita growth rate of a species to a change in the trait value s_i. It is a measure of the selection pressure generated by the environment through the ecological interactions. Consequently, this factor determines the direction of adaptive change. When the selection derivative of $\overline{f}_i$ is positive (negative), an increase (a decrease) of the trait value s_i will be advantageous in the vicinity of the resident trait value.

The sign of the selection derivative evidently carries important information on the dynamical structure of the mutation-selection process; yet, in Marrow et al. (1996) we demonstrate that this information in general is not sufficient to predict evolutionary attractors.

By means of equation (4.12) we have recovered the canonical equation (1.1) from the stochastic ecological processes underlying the adaptive dynamics. For the evolutionary rate coefficients we obtain $k_i(s) = \frac{1}{2} \cdot \mu_i(s_i) \cdot \sigma_i^2(s_i) \cdot \hat{n}_i(s)$. In addition, we have shown the appropriate measure of fitness to be given by the per capita growth rate of a rare mutant evaluated while resident population sizes are at equilibrium, $W_i(s_i', s) = \overline{f}_i(s_i', s)$.

4.3 APPLICATIONS

The deterministic approximation (4.12) readily allows us to calculate *phase portraits* of the adaptive dynamics. The application to predator-prey coevolution is depicted in Figure 2c. The evolutionary trajectories given by the deterministic paths coincide with the mean paths calculated from the stochastic process itself, see Figure 2b. In Figure 3 phase portraits of the predator-prey system are displayed that correspond to other choices of parameters. We see that the coevolutionary dynamics can either lead to extinction of one species (Figure 3a), approach one of several coevolutionarily stable states (Figure 3b), or it can give rise to continuous, in particular cyclic, coevolutionary change (Figure 3c); see Dawkins and Krebs (1979) for a discussion of the ecological and evolutionary implications and Dieckmann et al. (1995) for a detailed investigation of the cyclic regime.

However, some caveats are necessary for understanding the validity of any deterministic approximation of a stochastic process. First, if the adaptive dynamics turn out to be multistable (as in Figure 3b), it will be possible for trait substitution sequences to exhibit jumps between the existing basins of attraction. This must be kept in mind while applying the deterministic approximation to initial states very close to the basin boundary. Figure 4a illustrates this point. In principle, large fluctuations between the multiple stable states themselves can happen. However, the latter will typically be associated with extremely small probabilities per unit time, which are negligible

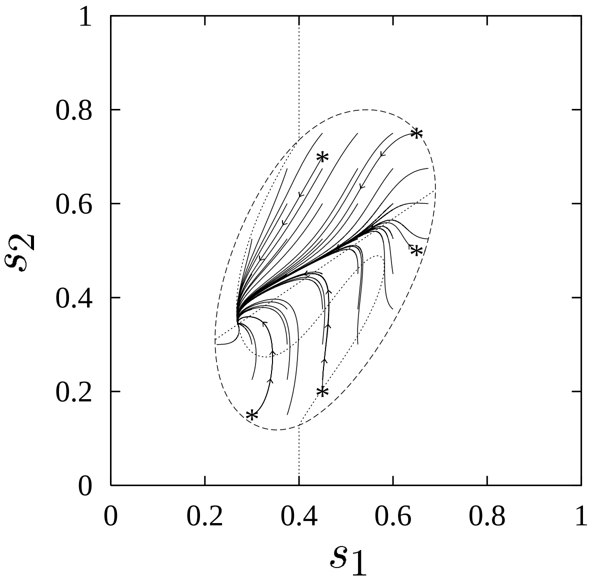
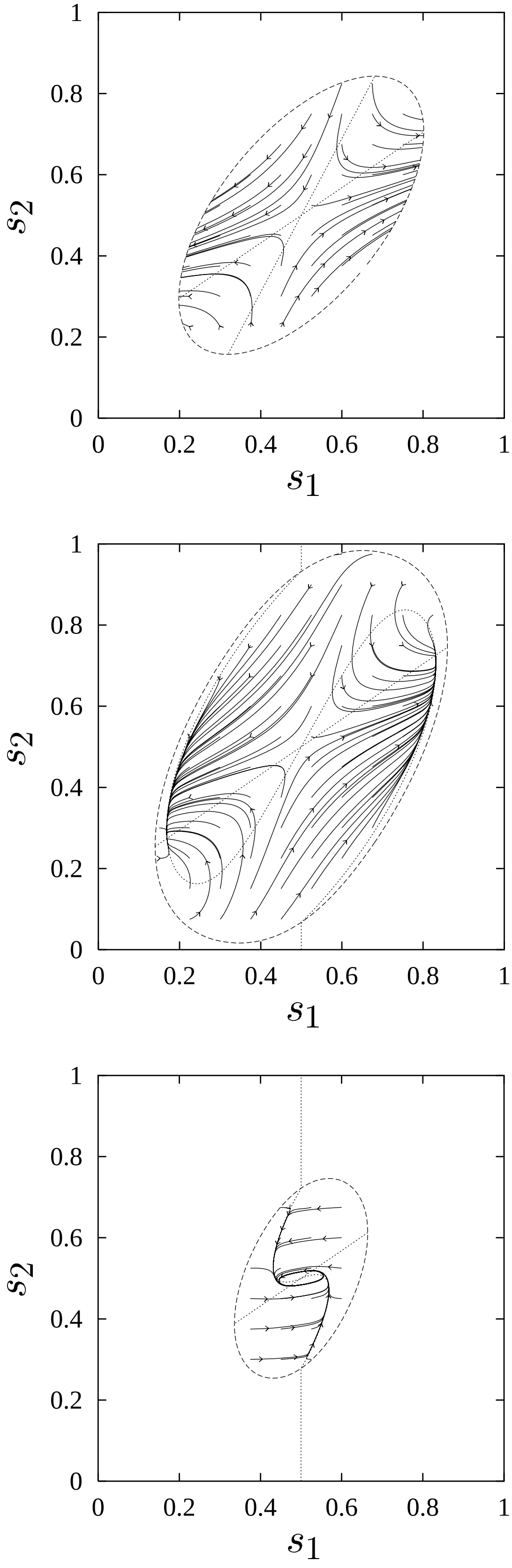


Figure 2c Deterministic approximation of the adaptive dynamics: phase portrait as defined by equations (4.12). The deterministic trajectories which correspond to the trait substitution sequences in Figure 2a and to the mean paths in Figure 2b are depicted by continuous lines (initial conditions are indicated by asterisks). Other trajectories have been added to supplement the phase portrait. The structure of the evolutionary flow in trait space thereby becomes visible. The discontinuous oval curve is the boundary of the region of coexistence. The dotted curves are the inner evolutionary isoclines of the two species (straight line: predator, curved line: prey). The parameters of the coevolutionary predator-prey community are as in Figure 2a.

on ecological and even on evolutionary time scales; moreover, when the mutation distributions are bounded, such large jumps become impossible altogether. Second, if the flow of the dynamical system describing the deterministic path is expanding, i.e. trajectories are diverging (as in some regions of Figure 3b), the deviations of the stochastic realizations from the mean path can grow too fast for the identification of the deterministic path with the mean path to be reliable (see Figure 4b). Note that the construction of phase portraits based on the deterministic path is useful in any case, since these allow qualitative predictions of the stochastic dynamics by considering the combined process of movement along the trajectories accompanied by jumps between them. For illustration compare Figure 2a and 2c, see also Figure 4b. Third, if the attractors of the adaptive dynamics turn out to have dimensions other than 0 (as in Figure 3c), the deterministic approximation in principle cannot predict aspects of the asymptotic mean dynamics of the stochastic process tangential to the attractor. The reason is that the tangential fluctuations are not balanced by counteracting forces. In consequence, for example, the asymptotic mean phase of stochastic limit cycle dynamics is not defined, though the asymptotic mean period is accurately described (Dieckmann et al. 1995).


1
0.8
0.6
0.4
0.2
0
s_2
0
0.2
0.4
0.6
0.8
1
s_1
1
0.8
0.6
0.4
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s_2
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0.2
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1
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1
0.8
0.6
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0.2
0
s_2
0
0.2
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0.8
1
s_1

Figure 3a,b,c

In addition to investigating the coevolutionary dynamics by means of phase portraits, much insight is gained by applying techniques from *bifurcation analysis* to the deterministic approximation (4.12). The effects of varying different ecological parameters, which have an impact on the adaptive dynamics, can then be systematically explored (Dieckmann et al. 1995).

5 Deterministic Approximation: Higher Orders

The first order result that we have obtained in Section 4 for the adaptive dynamics is not always sufficient. In this section we will enhance the deterministic approximation by accounting for the higher order corrections. In particular, two interesting consequences, the shifting of evolutionary isoclines and the phenomenon of evolutionary slowing down will be discussed.

5.1 DETERMINISTIC APPROXIMATION IN HIGHER ORDERS

The process of mutation has induced a global coupling in the adaptive dynamics (4.7). To substitute it precisely by a local one, an infinite number of orders in the Taylor expansions of $\overline{f}_i(s_i', s)$ and $\overline{b}_i^{-1}(s_i', s) \cdot \overline{f}_i(s_i', s)$ about $s_i' = s_i$ is required. The jth order results are given by

$$\overline{f}_i(s_i', s) = \sum_{k=1}^{j} (s_i' - s_i)^k \cdot \frac{1}{k!} \cdot \partial_i'^k \overline{f}_i(s_i, s) + \mathcal{O}[(s_i' - s_i)^{j+1}] \tag{5.1}$$

and

$$\begin{aligned} &\overline{b}_i^{-1}(s_i', s) \cdot \overline{f}_i(s_i', s) = \\ &\sum_{k=1}^{j} (s_i' - s_i)^k \cdot \frac{1}{k!} \cdot \sum_{l=1}^{k} \binom{k}{l} \cdot \partial_i'^l \overline{f}_i(s_i, s) \cdot \partial_i'^{k-l} \overline{b}_i^{-1}(s_i, s) \\ &+ \mathcal{O}[(s_i' - s_i)^{j+1}] \, . \end{aligned} \tag{5.2}$$

FIGURE 3A,B,C (CONTINUED) Deterministic approximation of the adaptive dynamics: phase portraits. The deterministic trajectories are depicted by continuous lines. Three qualitatively distinct outcomes of two-species coevolution are illustrated. Figure 3a: Evolutionary extinction (the coevolution of both species drives the trait values towards a boundary isocline where the predator becomes extinct). Figure 3b: Evolutionary multistability (depending on initial condition the coevolution of both species drives the trait values towards one of two equilibria which are separated by a saddle). Figure 3c: Evolutionary cycling (the coevolution of both species eventually forces the trait values to undergo sustained oscillatory change). The discontinuous oval curve in each figure is the boundary of the region of coexistence. The dotted curves are the inner evolutionary isoclines of the two species (straight lines: predator, curved lines: prey). The parameters of the coevolutionary predator-prey community are as in Table 1, except for: $c_1 = 1$, $c_7 = 3$, $c_8 = 0$, $c_9 = 0$ and $\mu_1 = 10^{-3}$ (Figure 3a); $c_1 = 1$, $c_7 = 3$, $c_8 = 10$ and $\mu_1 = 10^{-3}$ (Figure 3b); $c_1 = 0.11$, $c_7 = 3$, $c_8 = 10$ and $\mu_1 = 10^{-3}$ (Figure 3c).

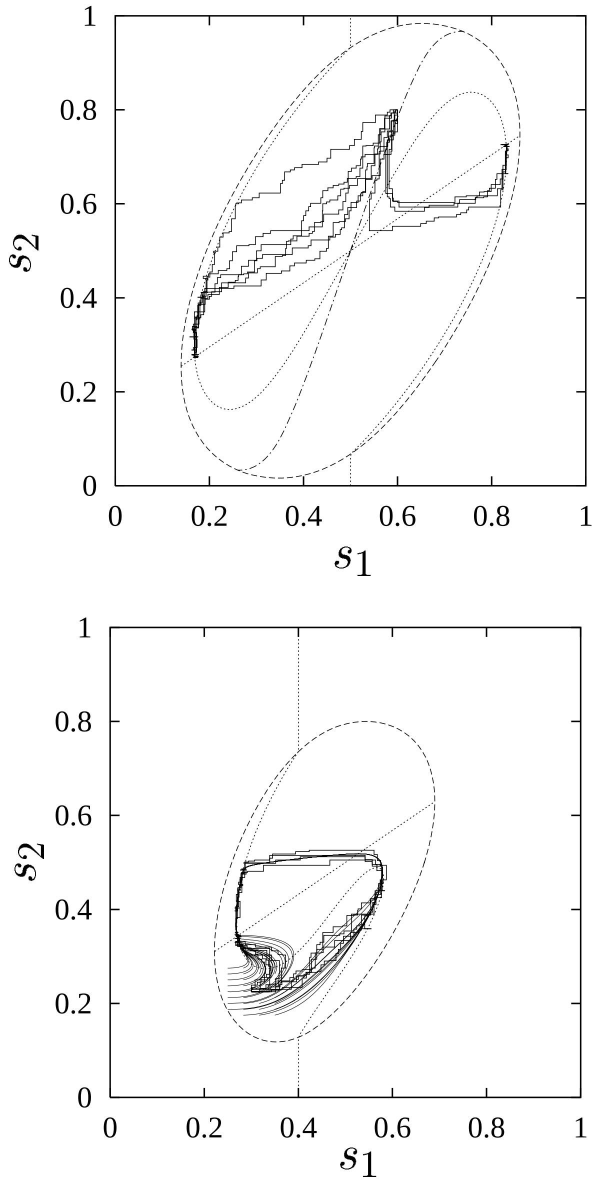

Figure 4a,b Descriptive capacity of the stochastic representation. Ten directed random walks in trait space with a common initial condition are depicted in each figure by continuous lines. Figure 4a: The set of trait substitution sequences splits permanently into two separate bundles as the initial condition is close to an existing basin boundary (depicted as a curve of dots and dashes). Figure 4b: The splitting of the set of trait substitution sequences into two separate bundles is only temporary and is caused by the existence of an expanding flow (shown as gray curves) in a region that contains the initial condition. Deterministic descriptions of the dynamics of the mean path cannot capture these features. The discontinuous oval curve in each figure is the boundary of the region of coexistence. The parameters of the coevolutionary predator-prey community for Figure 4a are as in Figure 3b, and for Figure 4b as in Figure 2c except for $\mu_1 = 10^{-3}$.

Again we have already accounted for $\overline{f}_i(s_i, s) = 0$. Substituting (5.2) into (4.7) yields the result for the deterministic approximation of the coevolutionary dynamics in jth order

$$\boxed{\begin{aligned} &\frac{d}{dt}s_i = \mu_i(s_i) \cdot \hat{n}_i(s) \cdot \\ &\sum_{k=1}^{j} m_{k+1,i}(s) \cdot \frac{1}{k!} \cdot \sum_{l=1}^{k} \binom{k}{l} \cdot \partial_i'^{l} \overline{f}_i(s_i, s) \cdot \partial_i'^{k-l} \overline{b}_i^{-1}(s_i, s) \end{aligned}} \tag{5.3}$$

with

$$m_{ki}(s) = \int_{R_i(s)} \left(s_i' - s_i\right)^k \cdot M_i(s_i, s_i' - s_i)\, ds_i' \,. \tag{5.4}$$

The range of integration in (5.4) is given by substituting (5.1) into (4.8)

$$R_i(s) = \{s_i' \in \widehat{S}_i \mid \sum_{k=1}^{j} \left(s_i' - s_i\right)^k \cdot \frac{1}{k!} \cdot \partial_i'^{k} \overline{f}_i(s_i, s) > 0\} \,. \tag{5.5}$$

The interpretation of the adaptive dynamics (5.3) is analogous to that given for (4.12) in Section 4.2. The $m_{ki}(s)$ are called the *kth mutation moments of the ith species*. They actually coincide with the kth moments of the mutation distribution M_i only if the range of integration $R_i(s)$ is $(-\infty, +\infty)$. However, as (5.5) indicates, this is generically not the case. Even in the first order result the range of integration was restricted to either $(s_i, +\infty)$ or $(-\infty, s_i)$ and the situation gets more complicated now that higher orders are considered. Notice that in the derivation above we did not require any symmetry properties of the mutation process so the result (5.3) is independent of this assumption.

The corrections arising from the higher order result (5.3) in comparison to the first order result (4.12) can be small for two reasons.

1. The ratios of the per capita growth and birth rates, $\overline{f}_i(s_i', s)$ and $\overline{b}_i(s_i', s)$, can be almost linear, i.e. they can possess only weak nonlinearities in s_i' around s_i. In this case the ith derivatives $\partial_i'\left(b_i^{-1} f_i\right)(s_i, s)$ with $i \geq 2$ are small compared to the first order derivative.
2. Moreover, the mutation distributions M_i can be narrow, i.e. they may have only small variances. Then the higher order mutation moments $m_{ki}(s)$ are negligible compared to the second order moment.

We conclude that in either limit – that of vanishing nonlinearity or that of vanishing variance – the first order result (4.12) of the adaptive dynamics becomes an exact representation of the deterministic path. The virtue of the dynamics (4.12) is its simplicity combined with good accuracy as long as one of the two conditions above is met. The virtue of the dynamics (5.3) is its generality, as it covers the coevolutionary dynamics of mutation-selection systems allowing both for nonlinearities in the ecological rates and for finite mutational steps as well as for asymmetric mutation processes. However, it should be kept in mind that both results describe the dynamics of the deterministic path; conditions for it to coincide with the mean path have been discussed in Section 4.1. To illustrate the importance of the higher order corrections in specific circumstances we now investigate two consequences. Both effects, the shifting of evolutionary isoclines and the phenomenon of evolutionary slowing down, only become visible in the deterministic dynamics when second and higher order correction terms are considered.

5.2 SHIFTING OF EVOLUTIONARY ISOCLINES

Given expression (5.3) which describes the coevolutionary dynamics beyond the first order result, we can now analyze the conditions under which evolution in single traits or in the whole community comes to a halt.

The evolutionary s_i-isoclines are defined as those manifolds in trait space $\widehat{S}$ on which $\frac{d}{dt}s_i = 0$ holds. The intersection of all isoclines coincides with the set of fixed points of the adaptive dynamics. In a first step we analyze the location of the evolutionary isoclines considering only infinitesimal mutational steps, in accordance with assumptions usually made in the literature (see e.g. Reed and Stenseth 1984; Taylor 1989). The result (4.12) is then exact, and we infer that the evolutionary s_i-isoclines are given by the union of manifolds on which either the selection derivative $\partial_i' \overline{f}_i(s_i, s)$ or the population size $\hat{n}_i(s)$ vanishes. We refer to the former as *inner isoclines* (these are subsets of $\widehat{S}_c$) and call the latter *boundary isoclines* (as they are subsets of $\partial\widehat{S}_c$). Since extinction of one species terminates the coevolutionary process of the N-species system, we concentrate on the inner isoclines. These can be classified as below (Metz et al. 1994).

1. Inner isoclines on which $\partial_i'^2 \overline{f}_i(s_i, s) < 0$ holds are called δ-stable or *non-invadable*.
2. Inner isoclines whose points satisfy $\partial_i'^2 \overline{f}_i(s_i, s) - \partial_i^2 \overline{f}_i(s_i, s) < 0$ are called m-stable or *convergent*.
3. Inner isoclines characterized by $\partial_i'^2 \overline{f}_i(s_i, s) + \partial_i^2 \overline{f}_i(s_i, s) < 0$ are said to be *not mutually invadable*.

The notions of δ- and m-stability are due to Taylor (1989) the other names have been used by Metz et al. (1994). For illustration, the evolutionary isoclines of the predator-prey system are given in Figures 2c, 3 and 4, the dotted curve corresponding to the prey, the dotted straight line to the predator. The conditions above can be slightly generalized in order to account also for those cases where the right hand side of the inequalities vanishes; for brevity this issue will not be covered here.

Now we consider the second order result. According to equation (5.5) the range of integration here is given by $R_i(s) = \{s_i' \in \widehat{S}_i \mid (s_i' - s_i) \cdot \partial_i' \overline{f}_i(s_i, s) + (s_i' - s_i)^2 \cdot \frac{1}{2} \cdot \partial_i'^2 \overline{f}_i(s_i, s) > 0\}$. For $\partial_i' \overline{f}_i(s_i, s) = 0$ this range either vanishes or extends to $(-\infty, +\infty)$, depending on the sign of $\partial_i'^2 \overline{f}_i(s_i, s)$. Thus if an inner s_i-isocline is non-invadable, the mutation moment $m_{3i}(s)$, see equation (5.4), and in consequence the second order correction in equation (5.3) drops out owing to the vanishing integration range. If the inner s_i-isocline is invadable, the same conclusion holds true for symmetric mutation distributions since $m_{3i}(s)$ now coincides with the vanishing third moment of those distributions. For asymmetric mutation distribution we already in second order get a shifting of invadable inner evolutionary isoclines. For symmetric mutation distributions, however, the evolutionary isoclines of the second order result match those already established by the first order result. In both cases the inner isoclines are determined by the vanishing of the selection derivative, $\partial_i' \overline{f}_i(s_i, s) = 0$.

This simple picture changes when we consider the adaptive dynamics in terms of the third and higher order results. We first examine the case of invadable evolutionary s_i-isoclines. Since in general the integration range is now no longer symmetric, the odd mutation moments do not vanish, and neither do the even mutation moments. Further, the second and higher order derivatives $\partial_i'^l \overline{f}_i(s_i, s)$ and the first and higher order derivatives $\partial_i'^{k-l} \overline{b}_i^{-1}(s_i, s)$ in equation (5.3) usually contribute. The third and higher order corrections therefore cause a displacement of the invadable inner evolutionary isoclines. These displacements are quantitative deviations from the first order result. But the higher order corrections can give rise even to qualitative discrepancies. Consider a manifold in trait space on which $\partial_i' \overline{f}_i(s_i, s) = \partial_i'^2 \overline{f}_i(s_i, s) = 0$ but $\partial_i'^3 \overline{f}_i(s_i, s) \neq 0$ hold. In terms of the first order result (4.12) this manifold would be called an evolutionary s_i-isocline. In terms of the more general higher order result (5.3) we notice that this manifold is not an isocline at all, for the evolutionary rate $\frac{d}{dt} s_i$, though probably being small, does not vanish here. The deviations are not so dramatic for non-invadable s_i-isoclines. Here the range of integration cannot contain the resident trait value s_i. The displacement of the isocline thus will only be significant, if the mutation distribution $M_i(s_i, s_i' - s_i)$ extends considerably beyond that zero s_i' of $\overline{f}_i(s_i', s)$ which is closest to the zero at s_i itself. In general however, inner evolutionary isoclines are no longer determined by the vanishing of the selection derivative.

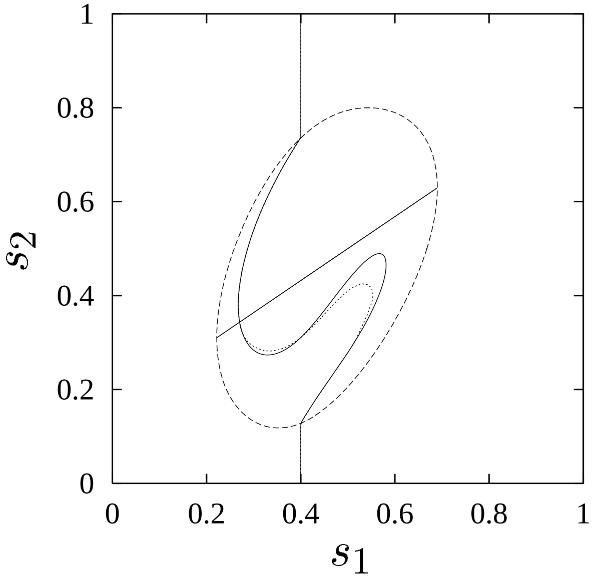

Figure 5a Shifting of evolutionary isoclines: the effect of finite mutation variance. The discontinuous oval curve is the boundary of the region of coexistence. The continuous curves are the inner evolutionary isoclines of the two species (straight line: predator, curved line: prey) for infinitesimal mutation variances, $\sigma_1 \to 0$ and $\sigma_2 \to 0$. The dotted curve is the inner evolutionary isoclines of the predator for finite mutation variances, $\sigma_1 = 5 \cdot 10^{-2}$ and $\sigma_2 = 5 \cdot 10^{-2}$. The other parameters of the coevolutionary predator-prey community are as in Table 1.

We summarize that the shift of inner evolutionary isoclines owing to the finiteness of mutational steps is a second or third order effect, depending on the symmetry of the mutation distribution. This shift is illustrated for the case of predator-prey coevolution by the dotted curve in Figure 5a. Note that not only the isoclines can be displaced, but in consequence also the fixed points themselves. Thus the shifting discussed here may affect the asymptotic stationary states of the coevolutionary system.

5.3 Conditions for Evolutionary Slowing Down

For illustration, we consider the two dynamical systems $\frac{d}{dt}x_1 = -x_1$ and $\frac{d}{dt}x_2 = -x_2^3$. Both examples possess a locally stable fixed point at the origin. The time evolution of these systems is described by $x_1(t) = x_1(0) \cdot e^{-t}$ and $x_2(t) = \pm\left[x_2^{-2}(0) + 2t\right]^{-1/2}$. Note that for $t \to \infty$ the first system approaches the fixed point *exponentially*, $x_1(t) \propto e^{-t}$, while in the second case the approach is only *algebraic*, $x_2(t) \propto t^{-1/2}$, and therefore much slower. The latter effect is called slowing down. It can occur at fixed points that are not only characterized by the vanishing of the rate of the dynamical system, $\frac{d}{dt}x = 0$, but also by a vanishing of the rate's slope, $\frac{d}{dx}\frac{d}{dt}x = 0$.

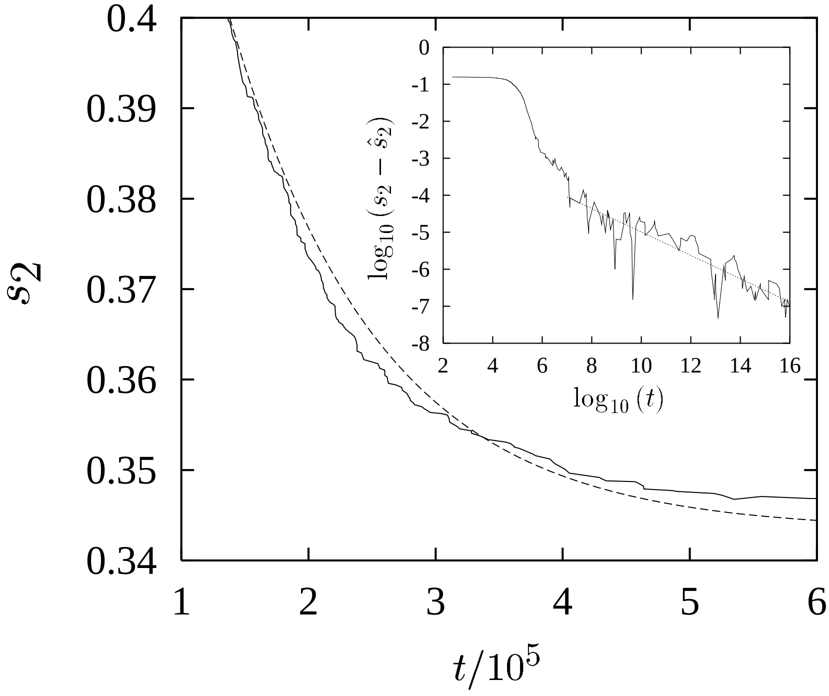

Figure 5b Evolutionary slowing down: algebraic approach towards a fixed point. The continuous curve shows the mean path dynamics of the predator's trait value close to the evolutionary equilibrium $\hat{s}$ in Figure 2 (constructed from 20 trait substitution sequences). The fixed point $\hat{s}$ lies on a non-invadable predator isocline. In the figure the actual algebraically slow approach to $\hat{s}$ is compared to the exponentially fast one, depicted by the discontinuous curve, that is obtained from the first order result which cannot account for evolutionary slowing down. The inset confirms the derived power law $s_2(t) - \hat{s}_2 \propto t^{-1/3}$ by means of a double logarithmic plot, the jaggedness of the continuous curve stems from the extreme amplification of single trait substitutions due to the logarithmic scale. The dotted straight line resulting from a linear least square fit to the time series turns out to have a slope of -0.3154, close to the predicted value of $-1/3$. The parameters of the coevolutionary predator-prey community are as in Table 1.

In general, a dynamical system $\frac{d}{dt}x = F(x)$ is said to exhibit jth order slowing down at a fixed point $\hat{x}$ if $F(x) = \sum_{k=j}^{\infty} a_{k\pm} \cdot (x - \hat{x})^k$ around $x = \hat{x}$ with (i) $j > 1$ and with (ii) $\pm a_{j\pm} < 0$ for j even and $a_{j\pm} < 0$ for j odd. The distinction ± refers to the two cases $\pm(x - \hat{x}) > 0$ and is necessary to account for slowing down of even order. Condition (ii) only ensures the local stability of the fixed point $x = \hat{x}$, whereas condition (i) implies the vanishing of the rate's slope at $x = \hat{x}$. The algebraically slow approach towards the fixed point is described by $x(t) - \hat{x} \propto \pm(a_{j\pm} \cdot t)^{1/(1-j)}$.

The phenomenon of slowing down does arise in the context of coevolutionary dynamics. Before turning to the general case, for intuition we first utilize the second order result. We consider a locally stable fixed point of the adaptive dynamics which is situated on a non-invadable inner evolutionary s_i-isocline such that $\partial_i'^2 \overline{f}_i(s_i, s) < 0$ holds in the vicinity of this isocline. Thus the range of integration is given according to (5.5) by $R_i(s) = \big(s_i, s_i - 2 \cdot \partial_i' \overline{f}_i(s_i, s)/\partial_i'^2 \overline{f}_i(s_i, s)\big)$ for $\partial_i' \overline{f}_i(s_i, s) > 0$ and by $R_i(s) = \big(s_i - 2 \cdot \partial_i'\overline{f}_i(s_i, s)/\partial_i'^2\overline{f}_i(s_i, s), s_i\big)$ for the other side of the isocline. Evidently, the range of integration in second order vanishes on the isocline itself. The ecological interpretation of this statement is intuitive: fewer and fewer mutants s_i' are advantageous while approaching the fixed point, until finally all possible mutants are deleterious. In order to prove formally that this process gives rise to evolutionary slowing down, we examine the coefficients $a_{j\pm}$ defined above in the case of the adaptive dynamics described by equation (4.7). For adaptation in a single species the results obtained are $a_{0\pm} = a_{1\pm} = a_{2\pm} = a_{3\pm} = 0$ whereas $a_{4+} = -a_{4-} < 0$. Thus we are confronted with slowing down of fourth order.

We conclude that evolutionarily stable fixed points of the adaptive dynamics are attained at a rate that is algebraically slow in those traits s_i whose isoclines are non-invadable at the fixed point. In principle, the evolutionary slowing down thus can drastically increase the length of evolutionary transients. Let us now briefly consider invadable isoclines. Here, the evolutionary rate $\frac{d}{dt}s_i$ in the vicinity of the isoclines actually is increased by a factor 2, since here the integration range is doubling rather than vanishing. Compared to the first order result, this amounts only to a quantitative but not to a qualitative change.

The phenomenon of evolutionary slowing down can be exemplified in the coevolutionary predator-prey system. Figure 5b shows the algebraically slow dynamics taking place in lieu of an exponentially fast approach towards a stable fixed point of the adaptive dynamics. A double logarithmic plot in the inset confirms the predicted power law $s_2(t) - \hat{s}_2 \propto \pm t^{-1/3}$ and thus the fourth order of the evolutionary slowing down.

6 Extensions and Open Problems

In this section we discuss generalizations and limitations of our approach. We point out how to extend the theoretical framework presented, in order to cover more complicated ecological and evolutionary scenarios.

6.1 Polymorphic Coevolution

We have assumed in Section 2.1 that without mutations two or more trait values s_i within a species cannot coexist indefinitely, only the single more advantageous trait value surviving. This *principle of mutual exclusion* can be proved for the case of Lotka-Volterra population dynamics (Dieckmann 1994).

The theorem is as follows. Consider the population sizes n_i and n_i' of a resident trait value s_i and a sufficiently close mutant trait value s_i' respectively in an environment defined by trait values s_j and population sizes n_j with $j = 1, \ldots, N \neq i$. The dynamics of the population sizes are assumed to be of Lotka-Volterra type. When the mutant is absent we call the remaining dynamical system for the population sizes the *resident* *system*, when the resident is absent the *mutant system*, and when both are present the *combined system*. Provided that, first, the selection derivative $\partial_i' \overline{f}_i(s_i, s)$ does not vanish, and that, second, the Lotka-Volterra interaction matrix is regular and varies smoothly with s_i', there exists no fixed point of the combined system in R_+^{N+1}. It can then be shown that the mutant will either go to fixation or to extinction. To our knowledge there exists no proof of the principle of mutual exclusion for coevolutionary communities not of Lotka-Volterra type, although even in such cases the principle has been tacitly assumed (e.g. Rand et al. 1993).

We pointed out in Section 2.1 that the quasi-monomorphic feature of the populations rests on two requirements, the principle of mutual exclusion and a time scale separation. We can now investigate the conditions for and the consequences of a violation of these requirements.

1. The principle of mutual exclusion may fail to hold for species i in the vicinity of an inner evolutionary s_i-isocline, since this isocline is close or identical to the manifold given by $\partial_i' \overline{f}_i(s_i, s) = 0$. Whether this failure actually happens, depends on the class of the isocline as defined in Section 5.2. In particular, the population will remain quasi-monomorphic, if the isocline is not mutually invadable. Metz et al. (1994) have suggested that otherwise the population can become polymorphic via a process of evolutionary branching.
2. As a second possibility, the time scale separation may be violated. Again, this can occur for species i in the vicinity of an inner evolutionary s_i-isocline, since here the per capita growth rates of a resident trait value and a close mutant trait value will differ only slightly. For this reason it may take a relatively long time until the mutant replaces the former resident.

Both cases can best be treated within a polymorphic framework that allows for phenotypic distributions $p_i(s_i)$ describing the density distribution of trait values s_i in each species' population (Dieckmann 1994, Dieckmann et al. 1995).

6.2 Multi-trait Coevolution

So far we have restricted attention to the case that each species i possesses only a single adaptive trait s_i. To understand the significance of coevolutionary phenomena on the adaptive dynamics this was sufficient.

However, in real ecosystems adaptive change not only simultaneously happens with respect to multiple species but also with respect to multiple traits within species. For instance, life-history traits like rates of reproduction and growth at given ages typically undergo concurrent evolution (Stearns 1992). We allow multiple traits within species by turning s_i into a vector $s_i = (s_{il})$ with a species index $i = 1, \ldots, N$ and a trait index $l = 1, \ldots, \nu_i$.

Moreover, allowing for multiple adaptive traits per species can be a prerequisite for the reliability of the Markov assumption, introduced in Section 5.2; knowledge of all the trait values at present ought to be sufficient to determine the potential of further adaptive change in the immediate future.

A third reason for considering multiple traits in phenotypic coevolution is that the path of evolution can be constrained. In addition to natural bounds on certain trait values – e.g. fecundities or weights necessarily must be non-negative – which already ought to be accounted for when considering only one trait per species, the set of accessible trait values is further restricted by *constraints* on the combinations of different trait values. These constraints may depend on simple matters of physics – e.g. surface to volume ratios cannot decrease beyond a certain threshold. Alternatively, the constraints may be an outcome of developmental pathways of the organism – e.g. an organism that matures at a small size has only a small amount of resources to give to reproduction. Constraints may also follow from the mapping from genotype to phenotype – e.g. if the same gene influences two traits, the trait values that result are not independent; this effect is called pleiotropy (Falconer 1989). For a more detailed discussion of constraints see Maynard Smith et al. (1985), Loeschcke (1987) or Stearns (1992). We allow for such constraints as follows.

1. Constraints restrict the set of trait values accessible within each species to a subset of $\widehat{S}_i$ which we denote by $\widehat{S}_{i,c'}$. The Cartesian product of all these sets is called $\widehat{S}_{c'} = \times_{i=1}^{N} \widehat{S}_{i,c'}$. The adaptive dynamics of the N-species community are then confined to the subset $\widehat{S}_C$ of $\widehat{S}$ with $\widehat{S}_C = \widehat{S}_c \cap \widehat{S}_{c'}$ where $\widehat{S}_c$ denotes the region of coexistence as defined in equation (2.2).
2. Due to pleiotropy the effects of mutations on different traits can be correlated. For this reason we write the probability distribution for a change Δs_i from a given trait value s_i due to mutation as a single multivariate distribution$M_i(s_i, \Delta s_i)$ rather than as a product of ν_i separate distributions $M_{il}(s_i, \Delta s_{il})$.

Here we generalize the results obtained in the previous sections to match the extended framework of multiple-trait coevolution. The results for the stochastic representation in Section 3, in particular equations (3.1), (3.2) and (3.6), carry over without alteration. Notice first that the delta functions in equation (3.2) now take vectors as arguments such that the usual definition $\delta(s_i) = \prod_{l=1}^{\nu_i} \delta(s_{il})$ applies, and second that the mutation distribution in equation (3.6) now is multivariate. In addition, the principle of mutual exclusion is more likely to be violated in mult-trait coevolution, but resulting polymorphisms will usually be of a transient type. The results for the deterministic approximation in Section 4 generalize as below. No modifications are required in equations (4.7) and (4.8). However, the integral in equation (4.7) now is multi-dimensional with $ds_i = \prod_{l=1}^{\nu_i} ds_{il}$, and consequently the range $R_i(s)$ of integration in (4.8) now becomes a subspace of dimension ν_i instead of an interval. In generalizing equations (4.12) and (4.13) we obtain

$$\frac{d}{dt} s_i = \frac{1}{2} \cdot \mu_i(s_i) \cdot \sigma_i^2(s_i) \cdot \hat{n}_i(s) \cdot \nabla_i' \overline{f}_i(s_i, s) \tag{6.1}$$

as the first order result for the deterministic approximation of the multi-trait coevolutionary dynamics in S_C. Here $\nabla_i' \overline{f}_i(s_i, s)$ with $\nabla_i' = \left(\partial_{i1}', \ldots, \partial_{i\nu_i}'\right)$ denotes the *selection gradient* for species i, a vector being composed of simple selection derivatives $\partial_{il}' \overline{f}_i(s_i, s)$ with $\partial_{il}' = \partial / \partial s_{il}'$ for the traits $l = 1, \ldots, \nu_i$ of species i. In the case of multi-trait coevolution σ_i^2 is the *variance-covariance matrix* of the multivariate mutation distribution M_i. The elements of this square matrix $\sigma_i^2 = \left(\sigma_{i,ll'}^2\right)$ are given by

$$\sigma_{i,ll'}^2(s_i) = \int \Delta s_{il} \cdot \Delta s_{il'} \cdot M_i(s_i, \Delta s_i) \, d\Delta s_i \tag{6.2}$$

with $l, l' = 1, \ldots, \nu_i$.

Notice that finite off-diagonal elements in σ_i^2 (non-vanishing covariances) cause the adaptive dynamics to take a suboptimal path, i.e. the direction of adaptive change is not parallel to the selection gradient. Notice also that up to first order the inner evolutionary isoclines of the adaptive system (6.1) for species i are now given by those manifolds in S_C where the selection gradient $\nabla_i' \overline{f}_i(s_i, s)$ either vanishes or lies in the null space of the variance-covariance matrix σ_i^2. The location and type of boundary isoclines on ∂S_C is less easy to settle and phase portraits of the system (6.1) will prove useful in this circumstance.

6.3 COEVOLUTION UNDER NONEQUILIBRIUM POPULATION DYNAMICS

In this section we discuss the issue of coevolution under nonequilibrium population dynamics. In relaxing the assumption of a fixed point attractor in population size space made at the end of section 2.1 we now allow for arbitrary attractors A that give rise to periodic, quasi-periodic or chaotic population dynamics. We first outline some mathematical concepts that have been considered in this context and then investigate how these relate to the stochastic formalism developed in this paper.

To decide upon the initial increase of a rare mutant s_i' in an environment given by the residents s the following constructs have been suggested

$$\begin{aligned} E_1(s_i', s) &= \lim_{T\to\infty} \frac{1}{T} \cdot \int_0^T \widetilde{f}_i(s_i', s, n(t))\, dt\,, \\ E_2(s_i', s) &= \lim_{T\to\infty} \frac{1}{T} \cdot \log \frac{|\Delta n(T)|}{|\Delta n(0)|}\,, \\ E_3(s_i', s) &= \int_{A(s)} \widetilde{f}_i(s_i', s, n)\, d\nu(n)\,. \end{aligned} \tag{6.3}$$

The first quantity E_1 is the *time average of the per capita growth rate* of the rare mutant along a trajectory $n(t)$ that starts on the attractor $A(s)$ of the resident system. This construct immediately follows from our formal framework set out in Section 2.1; in generalization of equation (2.7) we thus write $\overline{f}_i(s_i', s) = E_1(s_i', s)$. The second quantity E_2 (Metz et al. 1992) is the *Lyapunov exponent* of the combined system along the direction of the mutant's population size for a point on the attractor $A(s)$ of the resident system. It is given by the average logarithmic growth rate of the distance between two specific trajectories. The first trajectory $n(t)$ starts from $n(0)$ on the attractor $A(s)$ itself, the second trajectory $\widetilde{n}(t)$ has initial conditions $\widetilde{n}(0) = n(0)+\Delta n(0)$ where $\Delta n(0)$ denotes an initial displacement in the direction of the mutant's population size. The distance between these two trajectories is given by $|\Delta n(t)|$ with $\Delta n(t) = \widetilde{n}(t) - n(t)$, where the particular choice of the distance function $|\ldots|$ does not affect the result. Note that the mathematical definition of a Lyapunov exponent requires the time development of $\widetilde{n}(t)$ to be evaluated according to the linearization of the dynamics of the combined system along the attractor $A(s)$ (Eckmann and Ruelle 1985). As a convenient alternative for numerical estimations of Lyapunov exponents one might utilize the combined system directly but then choose a small $\Delta n(0)$ and extend the average only over a finite time interval $(0, T)$; nonetheless in order to cover the attractor $A(s)$ sufficiently, several repetitions of this procedure usually are necessary where each single repetition is followed by a rescaling $\alpha \cdot \Delta n(T) \to \Delta n(0)$ with $\alpha \ll 1$ (Baker and Gollub 1990). The third quantity E_3 (Rand et al. 1993) is called *invasion exponent* and in our case is simply the phase average of the per capita growth rate of the mutant on the attractor $A(s)$ of the resident system weighted by the natural measure $d\nu(n)$ of this attractor. Taking the natural measure rather than an arbitrary invariant measure is important when the attractor $A(s)$ is chaotic (Ott 1993). For practical applications this caveat however is immaterial due to the noise inevitably associated with any numerical estimation (Schuster 1989).

In the literature, the condition for initial increase of the rare mutant is taken to be $E_k > 0$ with $k = 1, 2, 3$ (e.g. Metz et al. 1992, Rand et al. 1993). The equivalence of the three criteria can readily be established. First, the time average E_1 coincides with the phase average E_3 (Ott 1993) – there can be exceptional initial conditions

$n(0)$ that do not satisfy this identity, but since the set of these has Lebesque measure zero they are irrelevant for realistic systems. Second, the time average E_1 equals the Lyapunov exponent E_2. To show this we linearize the dynamics of the combined system about the trajectory $n(t)$ and obtain $\frac{d}{dt}\Delta n(t) = J(n(t)) \cdot \Delta n(t)$ where $J(n)$ denotes the Jacobian matrix of the dynamics of the combined system evaluated at n. From the population dynamics of the combined system we get $\Delta n_i(0) = 0 \Rightarrow \Delta n_i(t) = 0$ (the left hand side holds since the initial displacement between $n(0)$ and $\widetilde{n}(0)$ is only affecting the mutant's population size n_i') as well as $n_i'(0) = 0 \Rightarrow n_i'(t) = 0$ (the left hand side holds for the trajectory $n(t)$ since it starts on the attractor of the resident system where the mutant is absent). From the first implication we obtain $|\Delta n(t)| = |\Delta n_i'(t)|$ and applying the second implication to the linearized dynamics yields $\frac{d}{dt}\Delta n_i'(t) = \widetilde{f}_i(s_i', s, n)|_{n=n(t)} \cdot \Delta n_i'(t)$. From these equations we conclude $|\Delta n(T)|/|\Delta n(0)| = \exp \int_0^T \widetilde{f}_i(s_i', s, n(t))\, dt$ which completes the proof of $E_1 = E_2$.

We investigate whether or not we recover the condition $E_1 > 0$ for the initial increase of a rare mutant in the light of our stochastic approach. Already in the case of a fixed point attractor in population size space we had to distinguish between the time scale τ_a of adaptive change and the time scale $\tau_f \ll \tau_a$ on which a mutant either goes extinct or reaches fixation while the population dynamics of the combined system attain its attractor. With population dynamics settling to a nonequilibrium attractor $A(s)$, an additional time scale τ_p for the motion on this attractor is introduced. We assume $\tau_a \gg \tau_f \gg \tau_p$. In this case the invasion of a successful mutant happens slowly compared to the dynamics on the attractor $A(s)$; this is typical for mutants whose trait values s_i' are sufficiently close to the resident trait value s_i. In generalizing equations (3.6) and (4.12) we obtain for the probabilities per unit time in the stochastic representation

$$\begin{aligned} & w_i\big(s_i', s\big) = \\ & \mu_i(s_i) \cdot \overline{b_i(s_i, s) \cdot n_i(s)} \cdot M_i\big(s_i, s_i' - s_i\big) \cdot \overline{b}_i^{-1}\big(s_i', s\big) \cdot \big(\overline{f}_i\big(s_i', s\big)\big)_+ \end{aligned} \tag{6.4}$$

and for the adaptive dynamics the deterministic approximation in first order yields

$$\frac{d}{dt}s_i = \frac{1}{2} \cdot \mu_i(s_i) \cdot \sigma_i^2(s_i) \cdot \overline{b}_i^{-1}(s_i, s) \cdot \overline{b_i(s_i, s) \cdot n_i(s)} \cdot \partial_i' \overline{f}_i(s_i, s)\,. \tag{6.5}$$

The construction of the higher order deterministic approximations for the adaptive dynamics follows the same scheme as in Section 5.1 and is not repeated here. Note that in result (6.5) the term $\overline{b}_i^{-1}(s_i, s) \cdot \overline{b_i(s_i, s) \cdot n_i(s)}$ will differ more from $\overline{n}_i(s)$ the larger the variation in the resident population size of species i is along the attractor $A(s)$.

We now turn to the invasion criteria. A rare mutant s_i' can successfully invade a community given by the resident trait values s provided that there is a positive transition probability per unit time for the trait substitution $s_i \to s_i'$, i.e. $w_i(s_i', s) > 0$. We easily draw the conclusion that our stochastic approach yields the criterion $E_1 > 0$

which is equivalent to those proposed previously. To see this, consider equation (6.4) together with the definitions of $(\ldots)_+$ and that of $\overline{f}_i(s_i', s) = E_1(s_i', s)$ in equation (6.3). However, our analysis not only yields these criteria for the initial increase of a rare mutant but provides us also with a full dynamical description of the adaptive process. We emphasize that the results above readily generalize to cover the issue of coevolution in slowly varying environments where the additional time dependence stems from external influences rather than from internal interactions.

7 Conclusions

In this paper we have established the canonical equation (1.1) of adaptive dynamics from the underlying stochastic ecological processes. In the course of this derivation we revealed the implicit assumptions, on which this result is based. Moreover, our approach allowed us to relax many of these assumptions and thus to provide generalized descriptions of coevolutionary dynamics.

To conclude, we briefly summarize these generalizations.

1. To obtain a dynamics like equation (1.1) from a mutation-selection process certain symmetry properties of the mutation distributions are needed, see Section 4.2. Both our deterministic approximation in higher orders, see Section 5.1, and the stochastic representation in general remove this assumption.
2. Being a deterministic description of the coevolutionary dynamics, the canonical equation describes the mean path and thus does not cover the full richness of dynamical effects that can occur in stochastic mutation-selection systems, see e.g. the discussion in Section 4.3. We have provided a stochastic representation in Sections 3.1 and 3.2 that accounts for these features. Two examples illustrating the difference are given in Figures 4a and 4b.
3. We have recovered the canonical equation as an exact description of the coevolutionary deterministic path, provided that the mutational steps are considered to be infinitesimal. Although the canonical equation gives a good approximation for small finite mutation variance, the approximation becomes inaccurate as the variance increases and consideration of higher order correction terms is recommended, see the derivation in Section 5.1.
4. The canonical equation does not permit interdependencies between several traits within one species. In Section 6.2 we could show how the stochastic approach to the coevolutionary mutation-selection process in this case naturally leads to the introduction of the variance-covariance matrix for the mutation distributions. The latter can give rise to less direct pathways towards evolutionary attractors.
5. The scope of the canonical equation is confined to coevolutionary systems with equilibrium population dynamics and a constant external environment. We have

demonstrated in Section 6.3 that this limitation can be overcome such that more general ecological scenarios may be tackled.

Such relaxation of the restrictions of the canonical equation are variations on a single theme: In modelling complex systems, like those exhibiting coevolutionary dynamics, one can always trade descriptive capacity for mathematical simplicity. The canonical equation may indeed be sufficient for specific goals, but this depends on what assumptions can reasonably be made. We have shown in this paper that new and distinct evolutionary phenomena emerge by removing any of these assumptions. Conversely, if the generalizations summarized above are not to be made, it is important to be aware of the evolutionary phenomena that are then sacrificed.

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3

Evolutionary Dynamics of Predator-Prey Systems: An Ecological Perspective

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Evolutionary Dynamics of Predator-Prey Systems: An Ecological Perspective

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Evolution takes place in an ecological setting that typically involves interactions with other organisms. To describe such evolution, a structure is needed which incorporates the simultaneous evolution of interacting species. Here a formal framework for this purpose is suggested, extending from the microscopic interactions between individuals — the immediate cause of natural selection, through the mesoscopic population dynamics responsible for driving the replacement of one mutant phenotype by another, to the macroscopic process of phenotypic evolution arising from many such substitutions. The process of coevolution that results from this is illustrated in the context of predator-prey systems. With no more than qualitative information about the evolutionary dynamics, some basic properties of predator-prey coevolution become evident. More detailed understanding requires specification of an evolutionary dynamic; two models for this purpose are outlined, one from our own research on a stochastic process of mutaton and selection and the other from quantitative genetics. Much of the interest in coevolution has been to characterize the properties of fixed points at which there is no further phenotypic evolution. Stability analysis of the fixed points of evolutionary dynamical systems is reviewed and leads to conclusions about the asymptotic states of evolution rather different from those of game-theoretic methods. These differences become especially important when evolution involves more than one species.

1 Introduction

It is a central problem in evolutionary theory that the evolution of a lineage needs to be considered in the context of ecological conditions experienced by the lineage. Natural selection, the source of much biotic evolution, is driven by differences among organisms in survival and reproduction as they live out their lives in an ecological setting, and the relationship between evolution and ecology is aptly summed up in Hutchinson's (1967) metaphor 'The ecological theater and the evolutionary play'. The birth and death processes of individuals are a common object of study of both subjects, and there is a wide recognition that a synthesis of the relevant areas of population ecology and evolutionary genetics is needed to inject an ecological basis into evolutionary theory; see for instance comments by Lewontin (1979).

The ecological setting of evolution can take many different forms, involving abiotic as well as biotic factors. In this paper we focus on the ecological process of predation, and consider how to model the evolutionary dynamics generated by an interaction between a prey and predator species. We do this to provide some background to the subject for theoreticians interested in entering the subject area, and also to illustrate and place in context some mathematical methods developed by Marrow et al. (1992) and Dieckmann and Law (1996). Although we concentrate on predation, the main ideas can be applied to a variety of biotic interactions falling within the scope of *coevolution*, a term coined by Ehrlich and Raven (1964) to describe the evolutionary process caused by the coupled evolution of all of the lineages concerned. Slatkin and Maynard Smith (1979) and Futuyma and Slatkin (1983) give introductions to coevolution. In a coevolving system, the evolution of the component species needs to be considered simultaneously, because evolutionary changes in one species can be the cause of evolutionary changes in the other(s).

A number of biological issues are raised by the coevolution of predators and prey. Most important is an instability inherent in their coevolution, since natural selection by the prey on the predator favours predator phenotypes best able to consume the prey, whereas selection by the predator on the prey favours prey phenotypes least likely to be killed. This may lead to an escalation in traits affecting attack and defence, referred to as an evolutionary ’rat race’ by Rosenzweig (1973) and an ’arms race’ by Dawkins and Krebs (1979). Abrams (1986) argued that an arms race does not exhaust the possibilities; for example, continuing evolution in one species may occur even if the other remains constant. Although evidence is hard to find, Bakker (1983) documented changes in mammalian herbivores and carnivores during the Paleocene to Mid Eocene that could be of the kind suggested by Dawkins and Krebs (1979). Those taxa characteristic of open habitats, where pursuit and flight are critical features of predation, show similar speed-enhancing changes in limb morphology; during this time the prey appear to have evolved faster than predators. Dawkins and Krebs (1979) argued that an asymmetry in the selection pressures would be expected, on the grounds that the prey is running for its life whereas the predator ’is only running for his dinner’. Notice that, if the predator evolves faster than the prey, it could gain such a great advantage that it destroys its prey altogether and brings about its own extinction. This led for example Slobodkin (1968, 1974) and Michod (1979) to consider how the apparent ’prudence’ in exploitation of prey by natural predators could come about by selection operating at the level of the individual. One likely cause is that the predator selects for prey life histories in which the effects of predation on the prey's reproductive success are reduced, a process experimentally confirmed in the water flea *Daphnia magna* by Edley and Law (1988).

To investigate these and other issues arising in the coevolution of predators and prey it helps to have a formal structure for modelling the process. Such models might be cast in terms of population genetics, evolutionary game theory, or quantitative genetics. Population genetics deals with how the frequency of a gene in each species with some effect on the interaction changes over the course of time, as discussed by Jayakar and Zonta (1990). This approach is to focus on the detailed dynamics of single genes. Evolutionary game theory in contrast sacrifices genetics to focus on the details of ecological, frequency-dependent interactions among organisms. Each species is assumed to comprise a set of phenotypes influencing the interaction, and a search is made for fixed points at which the phenotypes present are uninvadable by others; see for instance Parker (1983, 1985). The focus in this case is on an endpoint of evolution and, implicit in this, is an assumption that a sequence of gene substitutions, the stuff of population genetics, can bring the system to the fixed point in the first place. With these two approaches in mind, evolution has been likened to the motion of a streetcar, with many stops and starts as one gene is substituted for another, before eventually reaching the terminus; population genetics deals with the path between one stop and the next, and evolutionary game theory searches for the terminus. (We will see below, however, that a terminus does not necessarily exist.) The third approach, quantitative genetics, focuses on statistical properties of traits with continuous variation caused by the environment and a large (unspecified) number of genes with small effects; see for example Saloniemi (1993). This has the advantage that many of the traits important in coevolution are continuous variables, and the disadvantage that, like much of evolutionary game theory, it lacks an explicit mechanistic basis in genetics.

The approach used here is motivated by the ecology of interactions between predators and prey-the proximate cause of natural selection. The evolutionary variables are therefore phenotypic traits (properties such as body weight or height) rather than gene frequencies. But we wish to go beyond the game theoretic study of fixed points to investigate a dynamical system of evolution within which the properties of fixed points can be seen in their proper context. This could be done either through quantitative genetics or as a development of evolutionary game theory; we have chosen the latter path to keep a close connection with game theory. Casting the dynamics in these terms entails some compromise over the genetic system; the methods we describe apply explicitly to a system of pure-breeding clones, but it will be seen that a model used in quantitative genetics has many of the same features. Our approach also departs from single-species evolutionary game theory in being based on density in addition to frequency of different phenotypes. This is an important ecological feature when dealing with games between species because, as Pimentel (1968) pointed out, the whole game achieves more or less significance in the evolution of each species as the abundance of the other species becomes respectively greater or lower.

2 A Structure for Modelling Coevolution

We seek a formal description for the process of coevolution that works from the details of phenotype-dependent interactions of individuals (the cause of natural selection) to the large-scale phenotypic evolution of the system. One would like the process to be ’self-referencing’ in the sense that the path of evolution is driven internally by the population dynamics of the interacting species. We focus on one prey and one predator species, but note that the structure could readily be extended to systems with greater numbers of species and involving other kinds of interactions, as described by Dieckmann (1994) and Dieckmann and Law (1996). The following argument rests on a hierarchy of three time scales: microscopic interactions among individuals, mesoscopic population dynamics, and macroscopic phenotypic evolution.

2.1 INTERACTIONS AMONG INDIVIDUALS

Suppose that coevolution is taking place in one trait in each species, the value of the trait in an individual (i.e. its phenotype) being s_1 in the prey and s_2 in the predator; the traits might for instance be adult body sizes. The trait values are taken to be continuous and are elements of the sets S_1 and S_2 in the prey and predator respectively. The phenotypes of a prey individual and a predator individual, which are denoted $s = (s_1, s_2)$ and taken from the set $S = S_1 \times S_2$, determine what happens when they encounter one another. One must specify the effect of the encounter on the birth and death rates of the individuals concerned. In qualitative terms the encounter will most likely lead to an increased risk of mortality in the prey; the predator on the other hand most likely experiences a reduced rate of mortality or, in the longer term, an increased rate of reproduction, or both. How great the effect on the vital rates is, depends on the phenotypes of the individuals; any difference in vital rates between co-occuring conspecific individuals with different phenotypes causes natural selection. For instance, a large prey individual is more likely than a small one to defend itself successfully from a predator of intermediate size and, as a result, to gain a selective advantage through a lower risk of death in the encounter. Some specific choices for the effect of encounters on vital rates are given in an example in Section 3.

2.2 POPULATION DYNAMICS OF RESIDENT PHENOTYPES

The population dynamics described below will drive the replacement of one phenotype by another. Suppose first, as a preliminary, that each species comprises only one phenotype, the pair of phenotypes being given by s. To consider the population dynamics, we introduce state variables $x = (x_1, x_2)$ for the densities of prey and predator respectively. The population dynamics of the two species may then be written as a pair of differential equations

$$\dot{x}_i = x_i f_i(s, x) \qquad \text{for} \qquad i = 1, 2 \tag{1}$$

where f_i is the per capita rate of increase of species i, and depends on s through a set of control parameters the values of which depend on the current phenotypes. These control parameters indicate how the birth and death rates caused by s influence population dynamics; for example in the familiar Lotka-Volterra equations, $\dot{x}_i = x_i\Big(r_i + \sum_j \alpha_{ij} x_j\Big)$, they are the r_i's and α_{ij}'s. The control parameters would be taken as constants in a pure ecological model, but in the presence of coevolution they may change as the phenotypic state changes, as discussed by Lewontin (1979) and Stenseth (1986). Clearly we are only concerned with systems in which the densities are bounded; moreover, the issue of coevolution only arises if the population dynamics allow coexistence of the species over a subset of S, denoted by S_c.

2.3 POPULATION DYNAMICS OF RESIDENT AND MUTANT PHENOTYPES

To examine how the system evolves, we start by allowing a mutant to arise and determine what happens to its population density x_i'. Suppose a mutation occurs in species i, causing a phenotypic change δs_i in a system currently composed of individuals of phenotypes s; such a mutant is denoted $s_i' = s_i + \delta s_i$. Two factors are crucial in determining whether the mutant replaces the resident. First it should increase when rare and second it should then tend to fixation.

To determine the initial behaviour of a mutant when rare, the initial per capita rate of increase must be written in such a way that it distinguishes the phenotype of the individual under consideration from those in the environment in which it occurs. Thus we write $\widetilde{f}_i(s_i', s, x)$, where the first argument s_i' defines the phenotype of this individual, and the latter arguments s, x can be regarded as defining the biotic environment, see below. The dynamics of the system augmented by the rare mutant are therefore written

$$\begin{aligned} \dot{x}_j &= x_j \widetilde{f}_j\big(s_j', s, x\big) \qquad \text{for} \qquad j = 1, 2\,, \\ \dot{x}_i' &= x_i' \widetilde{f}_i\big(s_i', s, x\big)\,. \end{aligned} \tag{2}$$

The first two equations describe the dynamics of the resident phenotypes, and the last gives the dynamics of the mutant. Since the mutant is rare initially, its effect on the biotic environment at this stage is negligible and the environment is determined by the resident phenotypes. For simplicity we assume that, before arrival of a mutant, the densities of resident populations with phenotypes s have come to equilibrium given by

$$\hat{x}_j(s): \qquad \widetilde{f}_j(s'_j, s, \hat{x}) = 0 \quad \text{for} \quad j = 1, 2\,; \tag{3}$$

in this case of a system at equilibrium the environment is fully specified by s, so the third argument of $\widetilde{f}_i$ is no longer needed, and we write the initial per capita rate of increase of the mutant as $\overline{f}_i(s'_i, s)$. The conditions under which the assumption of equilibrium population dynamics can be removed are considered in Dieckmann and Law (1996). A necessary condition then for the mutant to increase when rare is that it should have a positive per capita rate of increase in the environment of the resident phenotypes at their equilibrium densities, i.e.

$$\overline{f}_i(s'_i, s) > 0\,. \tag{4}$$

The eventual fate of an initially successful mutant is less easy to settle. Either it goes to fixation, thereby replacing the former resident, or both the mutant and the resident stay in the system at finite densities. For population dynamics (2) of Lotka-Volterra type (i.e. $f_i = r_i + \sum_j \alpha_{ij} x_j$), the latter outcome can typically be excluded; this is principle of mutual exclusion is proven in Dieckmann (1994). In this case, invasion implies fixation, and the phenotype of species i has made a step from s_i to s'_i. The idea here is to allow the dynamical system of population densities explicitly to drive the replacement of one mutant by another.

2.4 PHENOTYPIC EVOLUTION

Once a method is in place to determine whether a mutant phenotype replaces the resident phenotype, it is straightforward to consider a sequence of mutants each one replacing the phenotype that was previously present. Such a sequence, called a trait-substitution sequence by Metz et al. (1994), indicates the long-term evolutionary path of the system. The aim now is to find a system of equations describing this macroscopic evolution, in which the phenotypic traits are themselves the state variables.

As a preliminary, we make two assumptions. These are that the principle of mutual exclusion applies and that successful mutants occur rarely enough for evolution to be modelled to a good approximation by a monomorphic dynamic within species. These assumptions apply below unless otherwise stated. We caution that the assumption of monomorphism would not apply if the mutant and resident phenotypes come to persist in a protected polymorphism; Metz et al. (1994) and Dieckmann (1994) consider ways to deal with this problem.

A *selection derivative*, measuring the sensitivity of the mutant's initial rate of increase to changes in its phenotype, is central to the evolutionary dynamic. This is defined as2

$$\frac{\partial}{\partial s_i'}\overline{f}_i(s_i', s)_{s_i'=s_i} = \lim_{s_i' \to s_i} \frac{\overline{f}_i(s_i', s) - \overline{f}_i(s_i, s)}{s_i' - s_i} \tag{5}$$

where $\overline{f}_i(s_i, s) = 0$, because the resident phenotype is at equilibrium with respect to population density. Notice that the derivative is evaluated while holding the environment (defined by the equilibrium densities) constant, since it refers to a rare mutant invading at $\hat{x}(s)$. The selection derivative is important because it indicates whether phenotypic evolution takes place in the direction of greater or smaller phenotypic values; if $\partial\overline{f}_i/\partial s_i' > 0$ (respectively $\partial\overline{f}_i/\partial s_i' < 0$), then the system is vulnerable to invasions by mutants with $s_i' > s_i$ (respectively $s_i' < s_i$) with s_i' sufficiently close to s_i. One would expect, then, the macroscopic evolutionary dynamics to have a property

$$\dot{s}_i \quad \begin{cases} > 0 & \text{when} \quad \partial\overline{f}_i/\partial s_i' > 0 \\ = 0 & \text{when} \quad \partial\overline{f}_i/\partial s_i' = 0 \\ < 0 & \text{when} \quad \partial\overline{f}_i/\partial s_i' < 0 \end{cases} \quad \text{for} \quad i = 1, 2\,. \tag{6}$$

These conditions do not, of course, yet specify an evolutionary dynamic; this would entail the introduction of a scaling factor which can be dependent on the process of mutation. We will give in Section 4 such a dynamic from Dieckmann and Law (1996) that is derived from the assumption of infinitesimal mutational steps and as such applies as a close approximation for mutations of small finite size. Nonetheless, without specifying the mutation process, it is still possible to get some qualitative insights into predator-prey evolution and other kinds of coevolving systems. Notice, in particular that isoclines of zero evolution according to (6) are defined by

$$\phi_i(s): \qquad \frac{\partial}{\partial s_i'}\overline{f}_i(s_i', s)_{s_i'=s_i} = 0\,; \tag{7}$$

the fixed points in phenotypic evolution are thus given by the intersections of ϕ_1 and ϕ_2. These qualitative properties are illustrated in the next section.

3 An Example

We show how the structure above may be used in the context of a specific model investigated by Marrow et al. (1992), in which the traits s undergoing evolution are interpreted as body sizes of the prey and predator. The per capita rates of increase of phenotypes s at densities x are given by

$$\begin{aligned} \text{prey:} \quad & f_1(s, x) = r_1 - \alpha(s)x_1 - \beta(s)x_2 \\ \text{predator:} \quad & f_2(s, x) = -r_2 + \gamma(s)x_1 \end{aligned} \tag{8}$$

where r_1, r_2, α, β and γ are positive control parameters. The benefit to a predator of a prey item, $\gamma(s)$, is taken to be at its maximum for some intermediate body size of both the predator and the prey. It is assumed that a bell-shaped function describes the relationship:

$$\gamma(s) = c_1 \exp\left(-\delta_1^2 + 2c_2\delta_1\delta_2 - \delta_2^2\right)$$

where $\delta_1 = (s_1 - c_3)/c_4$ and $\delta_2 = (s_2 - c_5)/c_6$, and c_1 to c_6 are positive parameters. On the basis that what is good for the predator is bad for the prey, the loss to the prey, $\beta(s)$, is taken to be proportional to $\gamma(s)$

$$\beta(s) = \exp\left(-\delta_1^2 + 2c_2\delta_1\delta_2 - \delta_2^2\right)$$

The term $\alpha(s)$ represents self-limitation in the prey and therefore depends only on s_1, and a quadratic function is assumed such that the prey would evolve to an intermediate body size in the absence of predation

$$\alpha(s_1) = c_7 - c_8 s_1 + c_9 s_1^2$$

where c_7 , c_8 and c_9 are positive parameters.

For certain ranges of the parameters in the functions α, β and γ, there are body sizes that permit both species to have positive equilibrium densities $\hat{x}$; the set of body sizes with this property, S_c, is delimited by the oval curve in Figure 1. As Harrison (1979) for example showed, $\hat{x}$ has global asymptotic stability given Equations (1) and (8), and this ensures that the system comes to equilibrium for a given s. Suppose that a mutation occurs causing small changes in body size to the predator or prey. A prey mutant (respectively predator mutant) increases when rare if it satisfies respectively:

$$\begin{aligned}\overline{f}_1(s_1', s) &= r_1 - \alpha(s_1')\hat{x}_1(s) - \beta(s_1', s_2)\hat{x}_2(s) > 0\\ \overline{f}_2(s_2', s) &= -r_2 + \gamma(s_1, s_2')\hat{x}_1(s) > 0\ .\end{aligned}$$

Since these dynamics are of Lotka-Volterra type, invasion typically implies fixation. Exceptions to this principle of mutual exclusion can occur close to the isoclines $\phi_i(s)$, as discussed in Dieckmann (1994), in which case both resident and mutant may remain causing the population to become polymorphic. Usually this behaviour does not persist because evolution in the other species takes the system away from the isocline, and the system reverts to monomorphism. But it is possible for evolution to lead to a fixed point with this polymorphic property (see Section 5), in which case the monomorphic assumption underpinning the model breaks down, as discussed by Metz et al. (1994). With these caveats, conditions (6) can be used to partition Sc into regions in which evolution towards larger ($\partial\overline{f}_i/\partial s_i' > 0$), or smaller ($\partial\overline{f}_i/\partial s_i' < 0$), body size occurs for each species, separated by the isocline $\phi_i(s)$ on which there is no selection. An example is given in Figure 1, the qualitative direction of evolution being shown by the arrows.

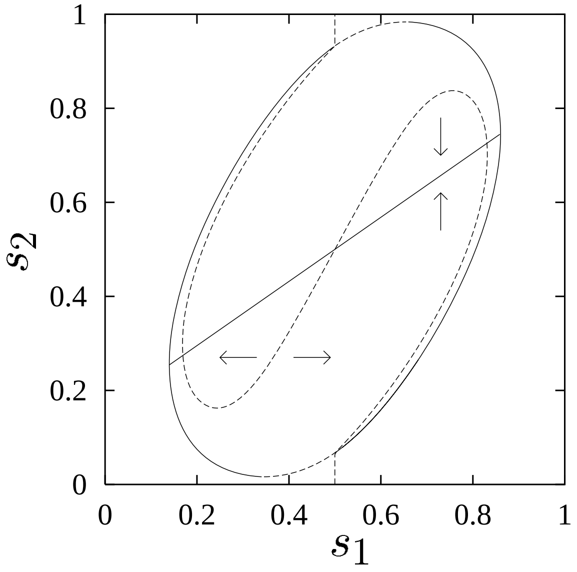

FIGURE 1 Some qualitative properties of evolutionary dynamics of prey (s_1) and predator (s_2) body size. S_c is the interior of the oval region. The line ϕ_1 is shown as discontinuous; the straight line ϕ_2 is shown as continuous. Fixed points of the system occur at the intersections of ϕ_1 and ϕ_2. Arrows indicate the direction in which body size evolves in each species, horizontal arrows for prey and vertical arrows for predators. Discontinuous part of the boundary of the oval region indicates where a prey mutant could cause predator extinction. From Marrow et al. (1992: Figure 2a), with parameters: $r_1 = 0.5$, $r_2 = -0.05$, $c_1 = 1.0$, $c_2 = 0.6$, $c_3 = 0.5$, $c_4 = 0.22$, $c_5 = 0.5$, $c_6 = 0.25$, $c_7 = 3.0$, $c_8 = 10.0$, $c_9 = 10.0$.

Simple though this approach is, it illustrates some features of a coevolving predator-prey system. First, it shows the tension typical of predator-prey coevolution. In the example given, the predator gains its greatest benefit from the prey at $s_1 = 0.5$, $s_2 = 0.5$, but the prey suffers its greatest loss here and the system does not tend to this point. Second, there is continuing evolution across the phenotype space, only terminated if the system reaches a fixed point. We should emphasize that, although evolution in this example leads to a fixed point, this is by no means an inevitable outcome, and an example is given later (Figure 2) in which the ω-limit set of the evolving system is a limit cycle — the species driving each other to continue evolving as long as the system remains in existence. Third, if one species tended to its isocline, continuing evolution would require mutations in the other species to shift it along the isocline; such evolution can be envisaged as an arms race because there would be no further change without the 'escalation' due to these mutations. Fourth, the geometry of fixed points of the system is exposed, that is, the points at which the lines ϕ_1 and ϕ_2 intersect. There can be several such points, and the properties of these fixed points are of interest in their own right (see Section 5). It can be seen that, in the case of the outer pair of fixed points, each species is evolving towards its isocline; but, in the case of the intermediate fixed point, the predator converges while the prey diverges. Fifth, the shape of S_c indicates that there is only a limited range of body sizes enabling coexistence of the species; it is

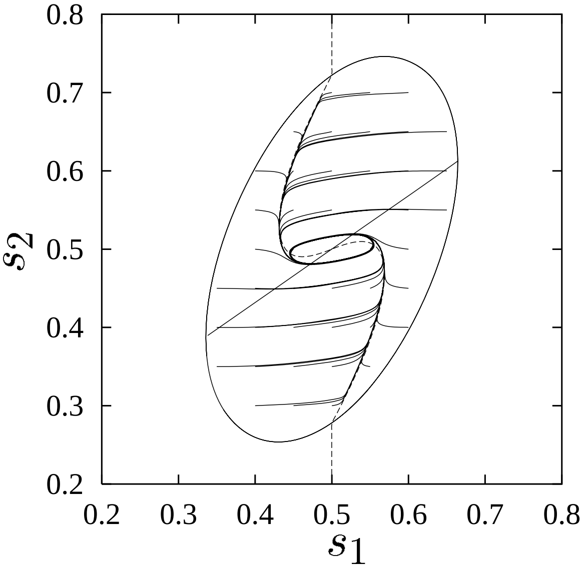

FIGURE 2 Phase portrait of a system with an evolutionary limit cycle. S_c is the interior of the oval region. The discontinuous line is ϕ_1 and the straight continuous line is ϕ_2. A fixed point of the system occurs at the intersection of ϕ_1 and ϕ_2. Curved continuous lines within S_c are orbits, all of which tend to the limit cycle around the fixed point. The dynamical system (9) is set such that $(\mu_1\sigma_1^2)/(\mu_2\sigma_2^2) = 1$; other parameters are as in Figure 1 except for $c_1 = 0.11$ (Marrow et al. 1992: Figure 2g).

possible for a sequence of mutant substitutions in the prey to lead to extinction of the predator, if they take a path across the part of the boundary shown as discontinuous. On the other hand there is no region of phenotype space in which both species have an equilibrium population density of zero, and thus there is in this example no evolutionary path in which the predator can gain such an advantage over the prey that it destroys the prey and brings about its own extinction.

4 Evolutionary Dynamics

To take the investigation of coevolution further, an explicit dynamic for the process is needed. This can be done in several ways; here we mention a stochastic trait-substitution model and one from quantitative genetics.

4.1 STOCHASTIC TRAIT-SUBSTITUTION MODEL

This models evolutionary trait-substitution sequences as directed random walks in phenotype space arising from mutation and selection. Stochasticity is induced in the evolutionary dynamics first by making the occurrence and size δs_i of mutations a random variable. Second, it comes about from the chance extinction that even advantageous mutants experience after their first appearance in a single individual, due to the effects of demographic stochasticity as discussed by Fisher (1958: 80 et seq.). These random effects are countered by natural selection arising from the biotic environment and this imposes directionality on the random walks. A master equation for this process is derived in Dieckmann and Law (1996), and it is shown that, by taking the first jump moments of the equation (van Kampen 1981), this yields a system of ordinary differential equations

$$\langle \dot{s}_i \rangle = k_i(s) \frac{\partial}{\partial s_i'} \overline{f}_i(s_i', s)_{s_i'=s_i} \qquad \text{for} \qquad i = 1, 2 \, , \tag{9}$$

where

$$k_i(s) = \frac{1}{2} \mu_i \sigma_i^2 \frac{\hat{x}_i(s)}{x_u} \qquad \geq 0 \, .$$

Here $\langle s_i \rangle$ is the expected phenotypic value, μ_i is the probability that a given birth is a mutant, x_u is the unit density scaling $\hat{x}_i$ to numbers, and σ_i^2 is the variance of the mutation distribution. The factor $k_i(s)$ scales the rate of evolution in species i and comprises two parts, the evolutionary rate constant $\frac{1}{2}\mu_i\sigma_i^2$ and the equilibrium population size. Notice the dependence of this system on the selection derivative (5); as a consequence the qualitative properties of the dynamics (6) remain in place, and system (9) specifies a full dynamic for the process of coevolution developed earlier. The system (9) is a first order result which is exact for mutational steps of infinitesimal size, and gives a good approximation for mutational steps of small size. The system can be refined by consideration of higher-order corrections, as derived and discussed in Dieckmann and Law (1996).

Figure 2 illustrates some evolutionary orbits of a coevolving system of predator and prey based on equations (9), having the feature that the ω-limit set is a limit cycle rather than a fixed point. This is of some biological interest because it shows that the interaction between the predator and prey is sufficient to keep the system evolving indefinitely; as discussed by Marrow et al. (1992), changes in the physical environment are not a prerequisite for continuing evolution.

4.2 QUANTITATIVE GENETICS MODEL

In the literature, an evolutionary dynamic from quantitative genetics has most often been used. Quantitative genetics at its simplest distinguishes between two components of the phenotypic value s_i: an additive genetic part a_i and a non-genetic part e_i statistically independent of a_i. The distinction between s_i and a_i is made because selection operates on phenotypic values but only the additive genetic components are inherited, as discussed by Falconer (1989). The standard formulation of a quantitative-genetic dynamic given by Lande (1979) does not allow the per capita rate of increase (fitness) associated with phenotype s_i to depend on the environment. But Iwasa et al. (1991), Taper and Case (1992) and Abrams et al. (1993) have suggested ways of removing this limitation. By assuming that the phenotypic distributions are narrow and that the time scale of population dynamics can be separated from that of evolution, a dynamic resembling closely that of equations (9) can be obtained:

$$\dot{\bar{s}}_i = k_i \frac{\partial}{\partial s'_i} \bar{f}_i(s'_i, \bar{s})_{s'_i = \bar{s}_i} \quad \text{for} \quad i = 1, 2\,, \tag{10}$$

where

$$k_i = \sigma^2_{a_i} \qquad > 0$$

where $\bar{s}_i$ is the expected mean phenotypic value and $\sigma^2_{a_i}$ the variance of the additive genetic values, often assumed to be constant. Although not usually explicitly derived from quantitative genetics, dynamics of this kind have been used on a number of occasions; see for instance Brown and Vincent (1987a), Rosenzweig et al. (1987), Hofbauer and Sigmund (1990), Vincent (1990) and Marrow and Cannings (1993).

In view of the models' radically different starting points, the similarity of dynamics (9) and (10) is notable. They do however differ in the source of variation on which selection operates. Dynamics (10) depend on phenotypic variation due to many genes with small additive phenotypic effects placed together in different combinations; evolution is then a process of selection on these combinations as they are reshuffled through segregation and recombination. Dynamics (9) on the other hand depend on variation generated by mutation. The quantitative genetic model is well-founded empirically, whereas the mutation-driven dynamic (9) is based on a somewhat simplified notion of phenotypic variation. On the other hand dynamics (9) are derived explicitly from a stochastic process of mutation and initial increase of advantageous mutants in Dieckmann and Law (1996), and represent a natural dynamical extension to evolutionary game theory.

5 Fixed Point Properties

Much of the interest in models of coevolution has been to characterize properties of fixed points in phenotype space at which the selection pressures generated by interacting species are balanced, so that there is no further phenotypic evolution of the system. Such work has usually been developed in the context of evolutionary game theory, and a dynamic is often not made explicit in this context. Here we mention some of the literature on the application of evolutionary game theory to questions of coevolution. We then point out that the introduction of an evolutionary dynamic is necessary to determine the asymptotic stability of fixed points (in contrast to the assertions of game theory). It should be kept in mind, however, that these fixed point properties cannot tell us all we need to understand the evolutionary process for, as we have already seen, the ω-limit set of an evolutionary dynamic need not be a fixed point (Figure 2).

5.1 EVOLUTIONARILY STABLE STRATEGY (ESS)

The notion of an ESS, defined by Maynard Smith and Price (1973), has been widely used to identify fixed points in phenotypic evolution, as discussed by Maynard Smith (1982). An ESS is a phenotype which, if adopted by almost all individuals in a population, cannot be invaded by a rare mutant of any other phenotype. The notion has been applied to multispecies coevolution by Brown and Vincent (1987a, 1987b) amongst others. In the context of two-species coevolution used in this paper, a sufficient condition for the phenotypes s to be an ESS is that, for individuals of phenotypes $s_i' \neq s_i$,

$$\widetilde{f}_i\big(s_i', s_i, s_j, \hat{x}(s)\big)_{s_i'=s_i} > \widetilde{f}_i\big(s_i', s_i, s_j, \hat{x}(s)\big) \quad \text{for} \quad i,j = 1,2 \quad \text{and} \quad j \neq i\,,$$

recalling from (2) that the first argument of $\widetilde{f}_i$ defines the individual's phenotype, and the other arguments define its biotic environment. The set from which s_i' is drawn is discussed below. The argument s is written out in full above to distinguish the condition for an ESS from another notion given earlier by Roughgarden (1979, 1983), that of a coevolutionarily stable community (CSC); this has the property (in our notation)

$$\widetilde{f}_i\big(s_i', s_j, \hat{x}(s)\big)_{s_i'=s_i} > \widetilde{f}_i\big(s_i', s_j, \hat{x}(s)\big) \quad \text{for} \quad i,j = 1,2 \quad \text{and} \quad j \neq i\,,$$

where the phenotype of the conspecific resident is not allowed to affect the per capita rate of increase of the mutant other than by the equilibrium densities, and is thus not specified. This means that the mutant's $\widetilde{f}_i$ depends on the phenotype of the conspecific resident only through the effect of the latter on the equilibrium densities. Consequently intraspecific frequency-dependent selection is excluded, and the circumstances under which the notion of a CSC applies are rather more restricted than those for the ESS, as discussed by Abrams (1989) and Taper and Case (1992). Notice that these game-theoretic properties of fixed points do not consider evolutionary dynamics, and such points may or may not be attractors in phenotypic evolution. An ESS as defined above might be better called an evolutionarily *steady* state, as this makes no reference to the dynamical notion of stability.

To add to the problems of terminology, the term ESS has also been used to refer to local asymptotic stability of equilibria of population densities in coevolutionary theory by Reed and Stenseth (1984). They envisaged a vector x of densities for resident phenotypes s, and a vector x' of densities for mutant phenotypes s', the set of phenotypes s being an ESS if the equilibrium point at which $x \neq 0$ and $x' = 0$ has local asymptotic stability for all $s' \neq s$, given that s' lies in the neighbourhood of s. This definition explicitly extends the notion of an ESS to account for population dynamics but, like the definitions above, makes no reference to evolutionary dynamics.

In these arguments and those below it is important to be clear about what set of mutant phenotypes is tested against the fixed-point phenotypes. Typically in evolutionary game theory, it is assumed that all phenotypes in S_i are tested (Maynard Smith 1982). How useful it is to test the fixed point against all possible phenotypes in coevolutionary models is debatable, because the range of phenotypes created by mutation and recombination around the current mean value is typically a small subset of S_i. As Roughgarden (1987) pointed out, one would not expect all the phenotypic variation apparent in different breeds of dogs to arise in a natural population of *Canis lupus*. To restrict phenotypic variation to a small region in the neighbourhood of the current mean is in keeping with Darwin's (1859) notion that evolution typically occurs by the accumulation of small phenotypic changes. It therefore seems more natural to use a local test, comparing the fixed point against phenotypes involving small deviations from it, as in the definition of an ESS above by Reed and Stenseth (1984); we adopt the local test below. We also restrict attention to a fixed point that lies in S_c. An interior fixed point of this kind, denoted $\hat{s}$ below, has the property that the selection derivatives $\partial \overline{f}_i / \partial s'_i$ vanish at $\hat{s}$ for both species.

5.2 Asymptotic Stability of Fixed Points

Here we review and develop some results concerning the asymptotic stability of fixed points given dynamics (9) to contrast with those from evolutionary game theory. We assume throughout that $\overline{f}_i(s'_i, s)$ is continuous, twice differentiable in s'_i and s_i, and has non-zero second derivatives. The function $\overline{f}_i(s'_i, s)$ then is saddle-like in s'_i and s_i around the isoclines $\phi_i(s)$; on the line $s'_i = s_i$, we have $\overline{f}_i(s'_i, s) = 0$. As a preliminary, we note two properties of the isoclines. The first is *non-invasibility* such that, on $\phi_i(s)$, mutants in species i with phenotypes close to $\phi_i(s)$ are not able to invade:

$$\frac{\partial^2}{\partial s'^2_i} \overline{f}_i(s'_i, s)_{s'_i = s_i} < 0 \; ; \tag{11}$$

the converse of this we refer to as *invasibility*. The notion of non-invasibility is familiar from ESS theory (Parker and Maynard Smith 1990) and the arguments of Roughgarden (1983) and Brown and Vincent (1987a, 1987b). Second is the property of *convergence* that successive mutations in species i cause evolution towards $\phi_i(s)$:

$$\frac{\partial^2}{\partial s'^2_i} \overline{f}_i(s'_i, s)_{s'_i = s_i} + \frac{\partial^2}{\partial s_i \partial s'_i} \overline{f}_i(s'_i, s)_{s'_i = s_i} < 0 \; ; \tag{12}$$

with the converse property of *divergence*. Attention was first drawn to the distinction between convergence and non-invasibility by Eshel and Motro (1981) and Eshel (1983), and was discussed in more detail by Taylor (1989). It is, for instance, conceivable that the isocline is non-invasible, but that starting from other points in its neighbourhood species i evolves away from it; such a configuration has aptly been called a 'Garden of Eden' configuration by Hofbauer and Sigmund (1990).

As shown by Abrams et al. (1993), the relationship between these isoclinic properties and asymptotic stability is trivial if the dynamical system comprises only one species. If we take just one of equations (9), the Jacobian at the fixed point $\hat{s}_1$ is:

$$J = k_1(s)\left(\frac{\partial^2 \overline{f}_1(s_1', s)}{\partial s_1'^2} + \frac{\partial^2 \overline{f}_1(s_1', s)}{\partial s_1 \partial s_1'}\right)_{s_i'=s_1=\hat{s}_1} .$$

The condition for dynamical stability of a fixed point $J < 0$ thus coincides with the condition for convergence (inequality 12). Clearly, dynamical stability of the fixed point is not equivalent to non-invasibility of the fixed point.

For 2-dimensional systems as given in equations (9), the fixed points are given by the intersection of the isoclines $\phi_1(s)$ and $\phi_2(s)$, and the Jacobian at a fixed point $\hat{s}$ is

$$J = \begin{bmatrix} k_1(s)\left(\frac{\partial^2 \overline{f}_1(s_1',s)}{\partial s_1'^2} + \frac{\partial^2 \overline{f}_1(s_1',s)}{\partial s_1 \partial s_1'}\right) & k_1(s)\frac{\partial^2 \overline{f}_1(s_1',s)}{\partial s_1' \partial s_2} \\ k_2(s)\frac{\partial^2 \overline{f}_2(s_2',s)}{\partial s_2' \partial s_1} & k_2(s)\left(\frac{\partial^2 \overline{f}_2(s_2',s)}{\partial s_2'^2} + \frac{\partial^2 \overline{f}_2(s_2',s)}{\partial s_2 \partial s_2'}\right) \end{bmatrix}_{s'=s=\hat{s}}$$

As in the 1-dimensional case, the bracketed terms on the diagonal are the same as the expressions given in inequality (12), and are therefore the isoclinic conditions for convergence of each species. But there is a much more indirect relationship between these convergence conditions and dynamical stability. Abrams et al. (1993) consider the necessary and sufficient condition for local stability of a fixed point, that tr $J < 0$ and $\det J > 0$. From this and our own work we collect together the following results for 2-dimensional systems. (i) Convergence of each species (i.e. bracketed terms in J negative) is neither necessary nor sufficient for local asymptotic stability of the fixed point. Convergence is not sufficient because, although convergence implies tr $J < 0$, the sign of $\det J$ depends on the off-diagonal mixed partial derivatives. Convergence is not necessary because it is possible to have tr $J < 0$ and $\det J > 0$ when one species is convergent and the other divergent. (ii) If each species is divergent, i.e. both bracketed terms of J are positive, we have tr $J > 0$ and hence the fixed point is unstable. Thus certain classes of fixed point are definitely evolutionary repellors, but others could be either repellors or attractors. However, by allowing for conditions on the signs of the off-diagonal elements of J, three further results about these remaining fixed points can be given. (iii) If each species is convergent and the off-diagonal elements are of opposite sign, the fixed point is an evolutionary attractor. (iv) If one species is convergent, the other divergent and the off-diagonal elements have the same sign, the fixed point is an evolutionary repellor. (v) In all cases not covered by (ii), (iii) or (iv) local stability of the fixed point can be tuned just by varying the evolutionary rate constants. We conclude from these results that the simple identity of the condition for convergence

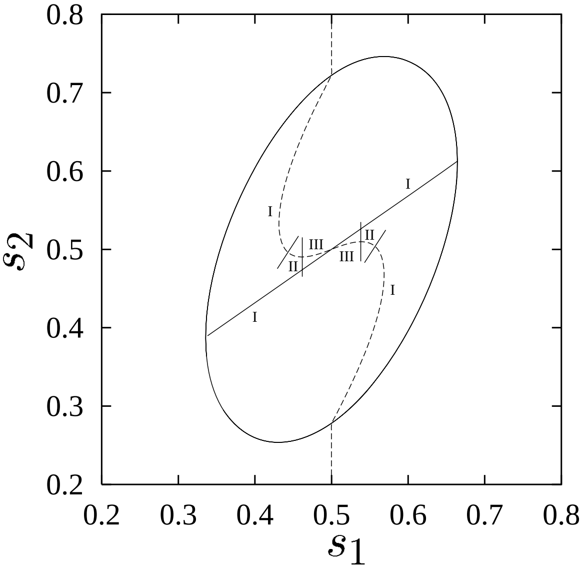

Figure 3 A system with isoclines such that the predator is convergent and the prey is divergent at the fixed point. S_c is the interior of the oval region. The discontinuous line is ϕ_1 and the straight continuous line is ϕ_2. A fixed point of the system occurs at the intersection of ϕ_1 and ϕ_2. The parameters defining the isoclines are as in Figure 2. Sections of the isoclines are labelled as follows. I: satisfies both inequality (11) and (12); II: satisfies (12) but not (11); III: satisfies neither (11) nor (12).

with that for local asymptotic stability, which holds for single-species evolution, has no counterpart in multispecies coevolution. In the latter case, the stability of a fixed point can depend critically on the details of the dynamical features of the coevolving system.

5.3 Example

Figure 3 is an example which illustrates some of the results described above. At the point of intersection of the isoclines, the prey phenotype $\hat{s}_1$ has the properties of invasibility and divergence, whereas the predator phenotype $\hat{s}_2$ has the properties of non-invasibility and convergence. This example is interesting for several reasons. First, the fixed point is an example of case (v) above, i.e. its dynamical stability depends on the evolutionary rate constants. If the rate constants of the prey and predator are chosen in the ratio 1:1, the fixed point is unstable and the attractor is given by a limit cycle (Figure 2). On the other hand, if the rate constants are chosen in the ratio 1:10, allowing faster predator evolution, the fixed point becomes stable and serves as an attractor for the evolutionary dynamics (Figure 4). Second, the example illustrates how dynamical stability is independent of non-invasibility of the fixed point. It can be seen that $\hat{s}$ is an attractor in Figure 4 notwithstanding the fact that coevolution leads to a local fitness minimum for the prey. Takada and Kigami (1991) and Abrams et al. (1993) have also noted that a system of coevolving species may be driven to a fixed point where one species is at a local fitness minimum. Third, the fixed point has a

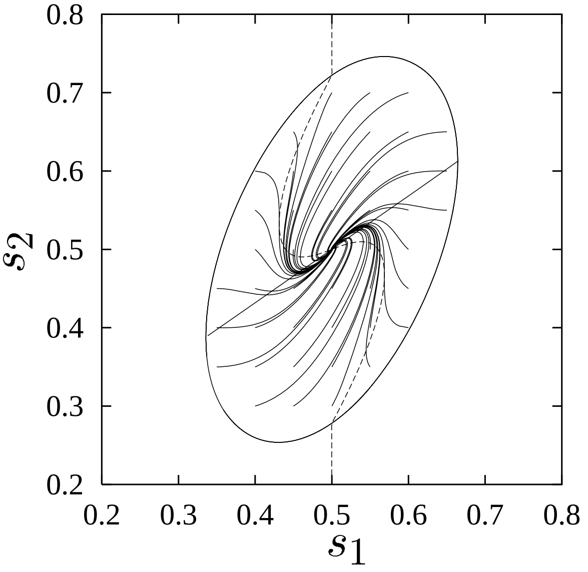

Figure 4 Phase portrait of a system based on the isoclines given in Figure 3. S_c is the interior of the oval region. The discontinuous line is ϕ_1 and the straight continuous line is ϕ_2. A fixed point of the system occurs at the intersection of ϕ_1 and ϕ_2. Curved continuous lines within S_c are orbits, all of which tend to the fixed point. The dynamical system is the same as that in Figure 2, except that parameters of dynamical system (9) are set to relatively slow down prey evolution: $(\mu_1\sigma_1^2)/(\mu_2\sigma_2^2) = 0.1$.

property that there is disruptive selection in the prey population and, as a result of this, two phenotypes can coexist on opposite sides of the fixed point. This can lead to evolutionary branching in the prey species, and the monomorphic evolutionary dynamic (9) ceases to be appropriate when the system reaches the fixed point, a phenomenon noted by Christiansen (1991) and discussed in depth by Metz et al. (1994). Fourth, in the system illustrated in Figure 4, the three basic kinds of selection discussed by Mather (1973: 90) are all present: selection is *directional* for both species away from the isoclines, *stabilizing* for the predator around its isocline and *disruptive* for the prey around its isocline in the neighbourhood of the fixed point.

6 Discussion

6.1 Evolutionary Game Theory and Dynamical Systems

A distinction between game theoretic methods, concerned primarily with non-invasibility of fixed points (ESSs), and more general considerations of dynamics runs rather deep through evolutionary theory. In evaluating these methods, the following points should be stressed. First, even in the evolution of a single species, non-invasibility does not guarantee dynamical stability of the fixed point. Second, in the coevolution of interacting species, neither non-invasibility nor convergence is sufficient to ensure dynamical stability of the fixed point. One needs further knowledge of the mixed partial derivatives arising from interactions between species and on the rates at which evolutionary processes take place within species to determine whether a fixed point is an attractor. Notice in particular that the evolutionary rates and thus the evolutionary stability can depend on specific features of the mutation process, see equations (9), which therefore must not be excluded from the discussion of evolutionary phenomena.

Third and perhaps most important, there are no a priori grounds in the first place to suppose that an evolving system should tend to a fixed point; other ω-limit sets such as limit cycles or even chaotic orbits in phenotype space seem just as plausible. In fact Van Valen (1973) proposed, on the basis of palaeontological evidence, that interactions among organisms could be sufficient to cause continuing evolutionary change. As pointed out by Fisher (1958: 45), such biotic processes could be responsible for a continual deterioration in the environment experienced by a species, and Van Valen (1973) used the metaphor of the Red Queen's hypothesis 'it takes all the running you can do, to stay in the same place' from Carroll (1871) to describe the resulting evolutionary process. Such ω-limit sets are referred to as *Red Queen* dynamics in the literature by authors such as Rosenzweig et al. (1987) and Marrow et al. (1992), and an example of such a system was given in Figure 2.

Knowledge of non-invasibility and of other fixed point properties is nonetheless a helpful guide to understanding certain features of the dynamics. In particular we note that a system tending to a fixed point at which there is disruptive selection for at least one species will violate the assumption of monomorphic dynamics on which equations (9) depend. See Dieckmann and Law (1996) for suggestions as to how this problem may be overcome.

6.2 EMPIRICAL BACKGROUND

To the theorist interested in entering the field of coevolution, we ought to point out that the empirical base of the subject is not strong. Although many features of living organisms are best interpreted as the outcome of a process of coevolution, rather little is known about the dynamics of the process. There is, for instance, some evidence for coevolution of predators and their prey from the fossil record of hard-bodied organisms; see for example Vermeij and Covitch (1978), Kitchell et al. (1981), Vermeij (1982,1983, 1987), Bakker (1983), Stanley et al. (1983), West et al. (1991). But in such examples one sees only an outcome of the evolutionary dynamics, and the dynamics themselves are not readily reconstructed. A rare exception in the case of host-pathogen evolution is myxomatosis in Australia documented by Fenner and Ratcliffe (1965) where, following the release of the myxoma virus in 1950, the virulence of the myxoma virus declined as did the susceptibility of the rabbit; from the information available, some inferences about the evolution of virulence can be made from the data, as discussed by Anderson and May (1982) and Dwyer et al. (1990). There is unfortunately no experimental basis in coevolution to match, for instance, the experiments of single-species quantitative genetics where selection differentials can be applied to specific traits and responses to selection measured, as described by Falconer (1989). This is not altogether surprising, because the experimental problems of getting two or more interacting species to live together while each generates selection differentials on the other(s) are, to say the least, substantial. Yet experiments along these lines are needed to set the evolutionary dynamics of coevolution on a firm empirical base and to guide development of theory.

We end with three suggestions about possible directions for future research.

6.3 COMMUNITY COEVOLUTION

We have considered a simple case of coevolution involving two species, it being straightforward in this case to visualise the geometry of evolutionary dynamics. In reality matters are more complicated since it is rare for a predator and prey species to live in isolation of other interactions; as reviewed by Pimm et al. (1991), typically they would be embedded in a food web with other species. Unless the interactions between a particular pair of species are much stronger than those with others, one needs to think of the traits evolving as a result of an ensemble of the selection pressures of all the species present, a process referred to as diffuse coevolution by Janzen (1980). The issue of how these larger communities evolve is of interest in its own right, and there is much to be done to develop a mathematical framework for such investigations. Some steps in this direction are the lag-load model of Maynard Smith (1976) and Stenseth and Maynard Smith (1984), the plant-herbivore model of Levin et al. (1990), the rugged fitness landscape models of Kauffman and Johnsen (1991) and Kauffman (1993), and the predator-prey community model of Brown and Vincent (1992).

6.4 EVOLUTION OF POPULATION DYNAMICS

As phenotypic evolution takes place, the control parameters of population dynamics will typically change and this may lead to qualitative changes in the population dynamics, for instance a change from an equilibrium to a non-equilibrium ω-limit set for population densities. There have been few attempts to document this experimentally, although Stokes et al. (1988) have suggested that changes observed in the population dynamics of a laboratory population of blowflies were consistent with evolution from oscillatory to equilibrium population dynamics. Data from natural populations such as those collated by Hassell et al. (1976) have suggested that chaotic dynamics are rather rare; on the other hand recent research by Rand and Wilson (1991) and Turchin and Taylor (1992) suggests that such dynamics do occur. A question that arises from the feedback from evolution to population dyanamics is whether there could be a tendency for equilibrium attractors for population density to come to prevail in natural systems. Work by Hansen (1992), Metz et al. (1992), Gatto (1993) and Godfray et al. (1993) argues for this. But whether there is a general mechanism (based on individual selection) for evolution to do so is open to debate, and needs further investigation.

6.5 ADAPTIVE LANDSCAPES

One might ask if some property of the species increases during their coevolution, that is, whether in some sense the species are 'improving' on an absolute scale. The metaphor of an adaptive topography, which envisages that phenotypic values of a species can be mapped on to a scale of mean population fitness to produce a hilly landscape, has been widely used in evolutionary theory. Evolution is then seen as a process of hill climbing until a local maximum in mean fitness is reached. But it is not at all clear that this metaphor is appropriate if selection is generated by interactions within the system as opposed to factors set externally (e.g. abiotic factors such as temperature and humidity). Let us consider two interpretations of this metaphor. We will examine evolution in one of the species, and assume that the system is at some point s in a phenotype space prior to a mutation in this species, with population dynamics that have settled to equilibrium. Suppose an advantageous mutant starts to spread. (i) A first obvious interpretation of mean fitness would be the population's mean per capita rate of increase. But this measure is not appropriate because the total population density may decline as the mutant starts to spread; from a starting height of zero, the mean per capita rate of increase would then become negative and the path of evolution would be down a surface defined by this measure. (ii) An alternative interpretation would be to use a surface defined by the initial per capita rate of increase of mutants in the environment s, the slope of which is given locally by the selection derivative (5) indicating the correct direction of evolution. Yet, by the time the mutant reaches fixation, it has a per capita rate of increase of zero. Thus, based on this second measure, there is no overall gain arising from the evolution, and we conclude that it remains debatable as to how appropriate a hill-climbing metaphor is in the context of coevolution. This leads us to ask what, if any, metaphor would be appropriate to describe a process of coevolution, and under what circumstances there exists a function that is maximized during the course of evolution.

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4

Evolutionary Cycling in Predator-Prey Interactions: Population Dynamics and the Red Queen

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Evolutionary Cycling in Predator-Prey Interactions: Population Dynamics and the Red Queen

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This paper describes the coevolution of phenotypes in a community comprising a population of predators and of prey. It is shown that evolutionary cycling is a likely outcome of the process. The dynamical systems on which this description is based are constructed from microscopic stochastic birth and death events, together with a process of random mutation. Births and deaths are caused in part by phenotype-dependent interactions between predator and prey individuals and therefore generate natural selection. Three outcomes of evolution are demonstrated. A community may evolve to a state at which the predator becomes extinct, or to one at which the species coexist with constant phenotypic values, or the species may coexist with cyclic changes in phenotypic values. The last outcome corresponds to a Red Queen dynamic, in which the selection pressures arising from the predator-prey interaction cause the species to evolve without ever reaching an equilibrium phenotypic state. The Red Queen dynamic requires an intermediate harvesting efficiency of the prey by the predator and sufficiently high evolutionary rate constant of the prey, and is robust when the model is made stochastic and phenotypically polymorphic. A cyclic outcome lies outside the contemporary focus on evolutionary equilibria, and argues for an extension to a dynamical framework for describing the asymptotic states of evolution.

1 Introduction

Predator-prey interactions are ubiquitous in nature (Crawley 1992). The ecological interactions between predator and prey species can sometimes be strong enough for the predator to have a major effect on the environment in which the prey is evolving and vice versa. Such interactions have therefore motivated a variety of theoretical models of phenotypic coevolution in predator-prey communities (e.g. Rosenzweig 1973; Parker 1985; Abrams 1986; Brown and Vincent 1992). Of some interest has been the question as to whether the phenotypes of the predator and prey evolve to an equilibrium asymptotic state such as an evolutionarily stable strategy (Maynard Smith and Price 1973). An alternative could be that their interaction prevents attainment of an equilibrium point and that there is continuous evolutionary change of their phenotypes. Following Van Valen's (1973) Red Queen's hypothesis, the latter behaviour has become known as Red Queen dynamics (Stenseth and Maynard Smith 1984; Rosenzweig et al. 1987; Marrow et al. 1992). To make this notion precise, we refer here to a Red Queen dynamic as any phenotypic dynamic that, in the absence of external forcing, does not tend to an equilibrium state.

In the literature, it has been argued that a Red Queen dynamic would require the set of feasible phenotypes to be unbounded, so that the phenotypes could evolve to ever more extreme states. Rosenzweig et al. (1987) concluded that "the Red Queen depends on the existence of special phenotypic features, i.e. those which are independent, boundless, and about which it may be said, the larger (or smaller, or denser, or furrier, or ...), the better". This requirement is unlikely to be met in reality, and calls into question whether Red Queen dynamics could occur at all. To investigate whether Red Queen dynamics are possible, we have developed models of the evolutionary dynamics of predator and prey phenotypes (Marrow et al. 1992; Marrow and Cannings 1993). These models suggested that, over the course of evolution, the phenotypes could either tend to equilibrium or to non-equilibrium asymptotic states. The models did not incorporate time explicitly, and for this reason could give only qualitative information on the direction of evolution. To determine the asymptotic states of coevolving systems, it is necessary to build the time-dependent processes into the framework of a dynamical system (Dieckmann and Law 1996; Marrow et al. 1996).

In this paper we utilize a hierarchy of three dynamical models to investigate the phenotypic states to which coevolving predators and prey could tend. These models represent different balances between descriptive capacity and corresponding analytic tractability. Mathematical details are given in the Appendix. Section 2 introduces the ecological interactions which define the predator-prey community, and Section 3 briefly explains the distinctive features of the three models used. In Section 4 we demonstrate that the system eventually attains one of three different evolutionary states: (a) the predator goes extinct, (b) coevolution leads to constant phenotypes in predator and prey, and (c) the phenotypes in both species undergo coupled and sustained oscillations on a limit cycle corresponding to Red Queen dynamics. Section 5 analyzes the requirements for this evolutionary cycling. The dependence of cycling on the interaction and mutation structure of the predator and prey is revealed, and we show that the phenomenon is robust under changes in the modelling approach. We conclude that the conceptual framework of evolutionary theory, with its current focus on fixed points (like evolutionarily stable strategies) as the endpoints of evolution, needs to be expanded to encompass more complex evolutionary attractors such as the limit cycles presented here.

2 The Coevolutionary Community

Our models of phenotypic evolution are underpinned by ecological processes describing the dynamics of predator and prey populations. This ensures that the process of natural selection directing evolution is driven explicitly by the ecology of predator-prey interactions, rather than by an external ad hoc notion of relative fitness of different phenotypes. For simplicity, we focus on a single phenotypic trait in each species; in view of the importance of body size in determining interactions between predator and prey (Cohen et al. 1993), one might think of these traits as body sizes s_1 and s_2 of prey and predator respectively.

To describe the population dynamics in our community, it is necessary to define the ecological processes that affect the population sizes of the two species (Table 1). Table 1a describes the birth and death events that are dependent on phenotype, these being the events that arise from encounters with other individuals, as opposed to the constant birth and death events given in Table 1b.

Evolutionary processes in the community require a mechanism for generating phenotypic variation on which natural selection caused by the interaction between predator and prey can operate. We assume that variation is created by a simple mutation process; in order to keep the analysis tractable we envisage that the genetic systems of the species are clonal. Table 1c shows that each birth event gives rise with probabilities μ_1 and μ_2 to a mutant offspring in the phenotypic traits s_1 and s_2 of prey and predator respectively. The new phenotypes are chosen according to the mutation distributions M_1 and M_2 of prey and predator respectively.

Natural selection arises from the dependence of the birth and death probabilities per unit time α, β, and γ on the phenotypes of the interacting individuals. Various functions could be used for this purpose; we use functions as described in Figure 1. Thus the function α, which characterizes the ecological processes responsible for self-limitation in the prey's population size, is taken to be parabolic such that intermediate phenotypes are favored in the absence of the predator (Figure 1a). The function β describing the effect of a predator on the probability of death of the prey is taken to be bivariate Gaussian (Figure 1b), on the grounds that the predator is likely to show some degree of specialization in the size of prey it chooses relative to its own size (Cohen et al. 1993). On the basis that what is bad for the prey is good for the predator, the function γ is related to β by a constant of proportionality, $\gamma = h \cdot \beta$. We call h the harvesting efficiency.

<table>
<tr><td colspan="4">(a) Birth and death processes affected by phenotype</td></tr>
<tr><td>Target individual</td><td>Encountered individual</td><td>Birth/death event</td><td>Probability of event per encounter per unit time</td></tr>
<tr><td>prey s_1</td><td>prey $\tilde{s}_1$</td><td>death of prey s_1</td><td>$\alpha(s_1)$ †</td></tr>
<tr><td>prey s_1</td><td>predator s_2</td><td>death of prey s_1</td><td>$\beta(s_1, s_2)$</td></tr>
<tr><td>predator s_2</td><td>prey s_1</td><td>birth predator s_2</td><td>$\gamma(s_1, s_2)$</td></tr>
<tr><td colspan="4">(b) Birth and death processes independent of phenotype</td></tr>
<tr><td colspan="2">Target individual</td><td>Birth/death event</td><td>Probability of event per capita per unit time</td></tr>
<tr><td colspan="2">prey s_1</td><td>birth of prey s_1</td><td>r_1</td></tr>
<tr><td colspan="2">predator s_2</td><td>death of predator s_2</td><td>r_2</td></tr>
<tr><td colspan="4">(c) Mutation processes</td></tr>
<tr><td colspan="2">Birth event</td><td>Mutation event</td><td>Probability distribution of event ‡</td></tr>
<tr><td colspan="2">birth of prey s_1</td><td>prey $s_1 \to s_1'$</td><td>$(1-\mu_1) \cdot \delta(s_1' - s_1) + \mu_1 \cdot M_1(s_1' - s_1)$</td></tr>
<tr><td colspan="2">birth of predator s_2</td><td>predator $s_2 \to s_2'$</td><td>$(1-\mu_2) \cdot \delta(s_2' - s_2) + \mu_2 \cdot M_2(s_2' - s_2)$</td></tr>
</table>

TABLE 1 Definition of birth, death and mutation processes for a prey individual of size s_1 and predator of size s_2.

† This death event is taken to be dependent only on the phenotype s_1 of the target individual, not on that of the encountered individual $\tilde{s}_1$.

‡ μ_i is the probability that the birth event in species i is a mutant; δ is the Dirac δ-function; M_i is the mutation distribution.

The ecological community presented here extends the model of Marrow et al. (1992) by providing a full dynamical description of the birth, death and mutation processes. It generalizes the former account in the sense that (a) it allows stochastic population dynamics arising from individual-based encounters, and (b) it permits the populations to have polymorphic phenotypic distributions since multiple phenotypic trait values may be present simultaneously in each species. From Table 1 we recover as a special case the well-known Lotka-Volterra equations

$$\begin{aligned} \dot{n}_1 &= n_1(+r_1 - \alpha(s_1)n_1 - \beta(s_1, s_2)n_2) \,, \\ \dot{n}_2 &= n_2(-r_2 + \gamma(s_1, s_2)n_1) \end{aligned} \tag{1}$$

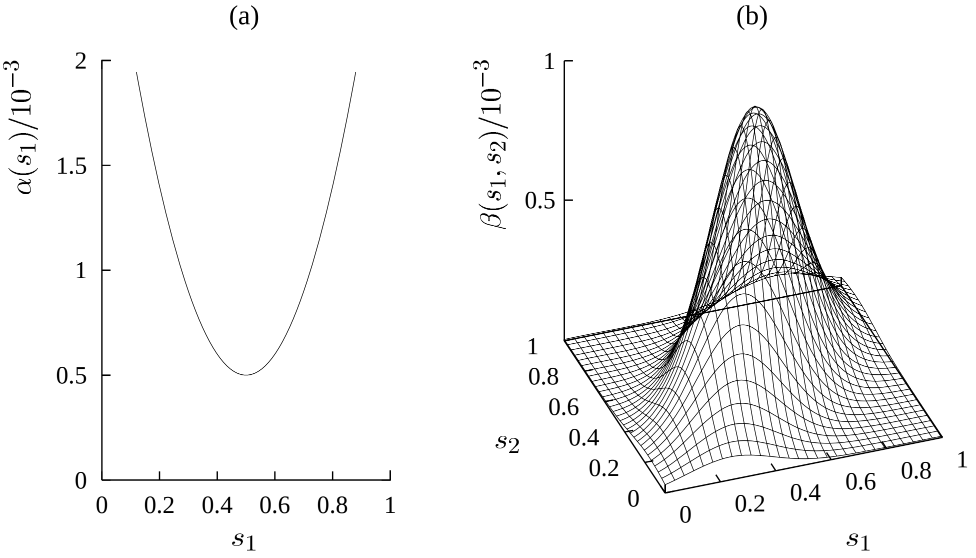

Figure 1 Specification of the coevolutionary community given in Table 1. The functions used to describe the effect of phenotype (s_1, s_2) on the birth and death probabilities arising from encounters between individuals are: (a) prey self-limitation $\alpha(s_1)/u = c_1 - c_2 s_1 + c_3 s_1^2$, (b) effect of predator on prey $\beta(s_1, s_2)/u = \exp\left(-\delta_1^2 + 2c_4\delta_1\delta_2 - \delta_2^2\right)$, where $\delta_1 = (s_1 - c_5)/c_6$ and $\delta_2 = (s_2 - c_7)/c_8$, and u is a constant that scales population sizes. Parameters take the values: $c_1 = 3.0$, $c_2 = 10.0$, $c_3 = 10.0$, $c_4 = 0.6$, $c_5 = 0.5$, $c_6 = 0.22$, $c_7 = 0.5$, $c_8 = 0.25$. The function $\gamma(s_1, s_2)$ is not shown since it is related to $\beta(s_1, s_2)$ by the constant of proportionality h. The constant birth and death terms are: $r_1 = 0.5$, $r_2 = 0.05$. Mutation parameters used in the paper are: $\mu_1 = 10^{-3}$, $\mu_2 = 10^{-3}$; M_1 and M_2 are normal distributions with mean 0 and $\sqrt{\mathrm{var} M_1} = 2 \cdot 10^{-3}$, $\sqrt{\mathrm{var} M_2} = 2 \cdot 10^{-3}$, except where otherwise stated. The quantity $u = 10^{-3}$ is constant throughout.

for the population sizes n_1 and n_2 of prey and predator respectively, by assuming no mutations, random encounters, deterministic population dynamics (the population sizes of the species are large), and monomorphic phenotypic distributions (only one phenotype present within each species).

3 Three Dynamical Models of Coevolution

Equations 1 illustrate how the general coevolutionary process defined in Table 1 can be reduced by making appropriate simplifying assumptions. In a similar spirit, three dynamical models are derived in the Appendix for the change in phenotypic traits s_1 and s_2 of the prey and predator respectively.

1. *Polymorphic stochastic model.* This provides a full description of the dynamics defined in Table 1. It can be given as a multivariate functional master equation, and depends only on the assumption of random encounters, thus allowing both for polymorphism and for stochasticity.

2. *Monomorphic stochastic model.* This retains the stochasticity arising from mutation in the coevolutionary process, but assumes that variation in the phenotypic distributions is small enough for an assumption of monomorphism to provide a good approximation. The coevolutionary process can then be described as a directed random walk in the phenotype space spanned by s_1 and s_2. Stochastic steps occur when a resident phenotype is replaced by an advantageous mutant, e.g. $s_1 \rightarrow s_1'$; a sequence of such substitutions is called a trait substitution sequence (Metz et al. 1992). The model is framed as a multivariate master equation.
3. *Monomorphic deterministic model.* This is a deterministic approximation to the monomorphic stochastic model above. It is given in terms of a system of ordinary differential equations describing the expected evolutionary paths in the phenotype space.

Further information as to the relation between the three models is given in the Appendix and in Dieckmann (1994). The full derivation of the monomorphic models is given in Dieckmann and Law (1996), and a discussion of the third model can be found in Marrow et al. (1996).

4 Evolutionary Outcomes

Here we describe the variety of possible evolutionary outcomes in a predator-prey community, using the monomorphic deterministic model. Deterministic dynamics of this kind have been used elsewhere in the literature (e.g. Hofbauer and Sigmund 1990; Vincent 1991; Abrams et al. 1993), but have not previously been underpinned by a formal derivation.

In the case of the monomorphic dynamics we can immediately infer from equations (1) that there is a region in the phenotype space where both species can coexist with positive population densities. The boundary of this region is depicted by the oval discontinuous curves in Figure 2. Only within this region can the predator population harvest the prey sufficiently to survive; given a pair of phenotypes (s_1, s_2) outside this region, the predator population is driven to extinction by the population dynamics (1). Accordingly, coevolution of the predator and prey can only be observed within this region of coexistence.

For a coevolving predator-prey community starting with phenotypes in the region of coexistence, there are eventually three possible outcomes.

1. *Evolution to a fixed point.* In Figure 2a, the phenotypic values tend to an equilibrium point; once this is reached, no further evolution occurs. There are in fact three fixed points at the intersection of the isoclines (i.e. at $\dot{s}_1 = 0$, $\dot{s}_2 = 0$, see Appendix) in this example, as can be seen from the accompanying phase portrait (Figure 2b); two of

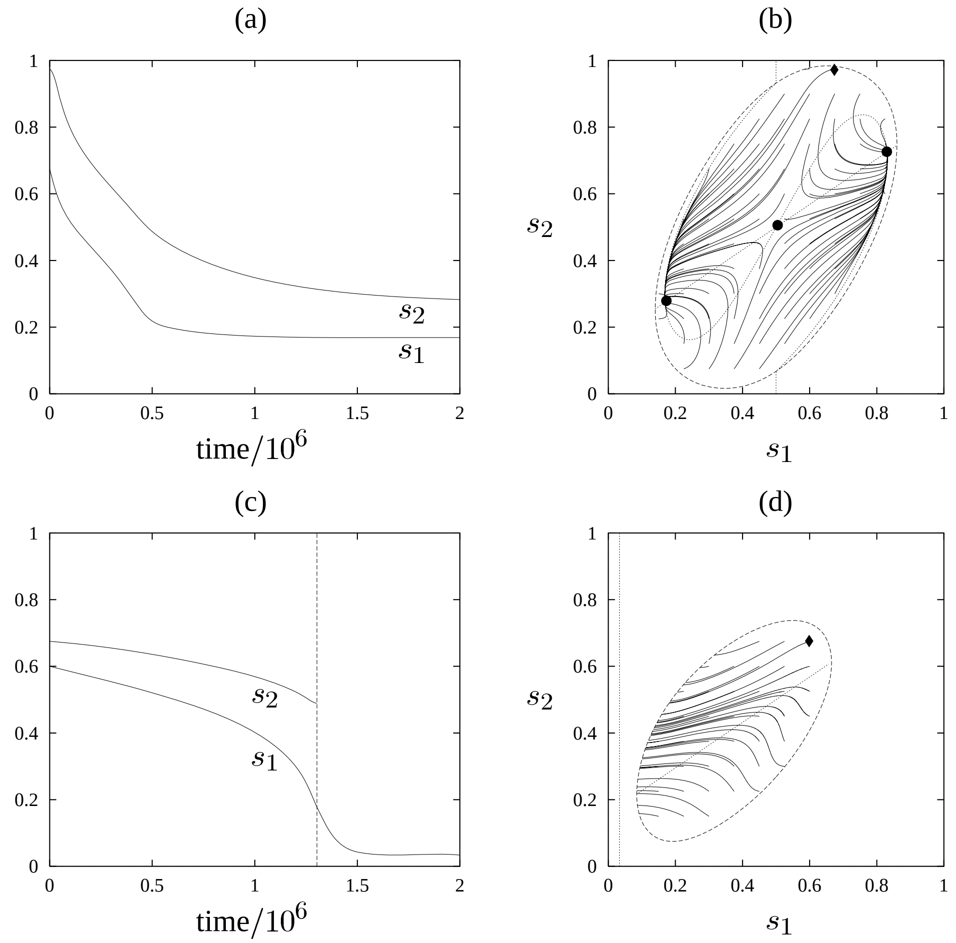

Figure 2 Patterns of evolution of prey (s_1) and predator (s_2) phenotypes obtained from the monomorphic deterministic model. (a) Solution that tends to an equilibrium point over the course of time obtained using the parameter values in Figure 1 with $h = 1$. (b) Phase portrait of the phenotype space from which (a) is drawn with orbits shown as continuous lines; the starting point of the orbit corresponding to the solution in (a) is shown as the diamond. The boundary of the region of coexistence of the predator and prey is given as the discontinuous oval line. Isoclines are shown as dotted lines (straight line: predator; curved line: prey); equilibrium points occur at the intersection of the isoclines and are indicated by the filled circles. (c) Solution for a community that evolves to predator extinction at time = $1.30 \cdot 10^6$. After this time, the prey continues to evolve in the absence of the predator. Parameter values as in Figure 1, except $c_1 = 1.0$, $c_2 = 1.0$, $c_3 = 15.0$, and with $h = 1$. (d) Phase portrait of the phenotype space from which solution (c) is drawn; the starting point of the orbit corresponding to the solution in (c) is shown as the diamond. The prey isocline lies outside the region of coexistence and orbits touch the boundary of the region of coexistence at which point the predator goes extinct.

these are attractors and they are separated by the stable manifold of the third which is a saddle point. Notice that the coevolutionary process here is multistable with two attractors having disjunct domains of attraction; thus there may be no more reason for a particular observed asymptotic state than the more or less arbitrary initial conditions.

2. *Evolution to extinction.* In Figure 2c the coevolutionary process drives the phenotypic values towards the boundary of the region of coexistence (see Figure 2d). There the predator population goes extinct and the predator phenotype is no longer defined. The phenotype space of the community collapses from (s_1, s_2) to the one dimensional space s_1, where the prey phenotype continues to evolve to its own equilibrium point. Note here that the extinction of the predator is driven by the evolutionary dynamics in (s_1, s_2) and not merely by the population dynamics in (n_1, n_2).
3. *Evolutionary cycling.* In Figure 3a, the coevolutionary process in the predator-prey community continues indefinitely; mutants replace residents in a cyclic manner such that the phenotypes eventually return to their original values and do not reach an equilibrium point. As can be seen from Figure 3b, the attractor is a limit cycle, confirming the conjecture made by Marrow et al. (1992) that Red Queen coevolution can occur in this predator-prey community.

These three outcomes of coevolution correspond to the endpoints of evolutionary arms races discussed qualitatively by Dawkins and Krebs (1979), namely: (i) equilibrium endpoints, (ii) one side wins, and (iii) cyclic endings.

5 Requirements for Cycling

Here, we investigate the robustness of the phenomenon of evolutionary cycling. We do this in two ways. First a bifurcation analysis of the monomorphic deterministic model is given; this allows one to establish the range of parameters in the model that permit evolutionary cycling to occur. Second, we examine the monomorphic stochastic model and finally the polymorphic stochastic model to see how robust the phenomenon of evolutionary cycling is when the simplifying assumptions of the monomorphic deterministic model are removed.

5.1 BIFURCATION ANALYSIS OF THE MONOMORPHIC DETERMINISTIC MODEL

We focus attention on the effect of two quantities of particular interest from an ecological viewpoint. These are firstly the predator's efficiency in harvesting the prey as given by the ratio $h = \gamma/\beta$, and secondly the ratio of the evolutionary rate constants $r = (\mu_1 \mathrm{var} M_1)/(\mu_2 \mathrm{var} M_2)$ (see Appendix). The results of the bifurcation analysis are presented in Figure 4a. Four distinct regions within the parameter space can be seen:

1. For $h < 5\%$ the two species cannot coexist, and therefore no coevolution can occur.
2. For $5\% < h < 9.8\%$ there exists only one fixed point for the monomorphic deterministic model. This fixed point is an attractor; the system evolves to this point and there is no further coevolution once it is reached.

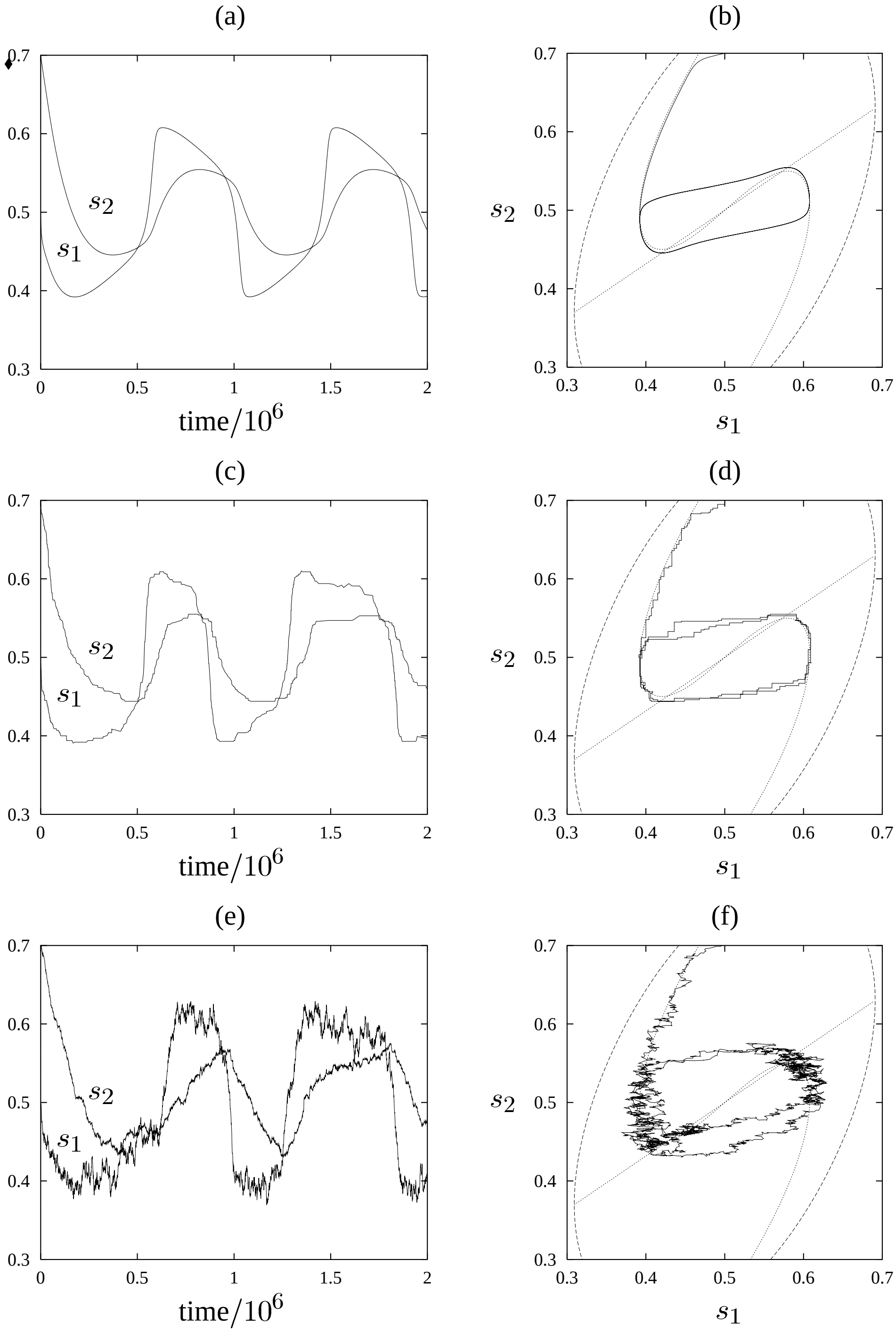

Figure 3 Example of evolutionary cycling using the monomorphic deterministic model in (a) and (b), the monomorphic stochastic model in (c) and (d), and the polymorphic stochastic model in (e) and (f). Graphs (a), (c) and (e) show the values of the prey (s_1) and predator (s_2) phenotypes as functions of time (mean values in the case of the polymorphic model). The corresponding orbits are shown as continuous lines in the phase spaces given in graphs (b), (d) and (f). See Figure 2 for an explanation of the phase portrait. Parameter values for these simulations are identical and are set as given in Figure 1, except $\mu_1 = 10^{-2}$, $\mu_2 = 10^{-2}$and with $h = 0.14$.

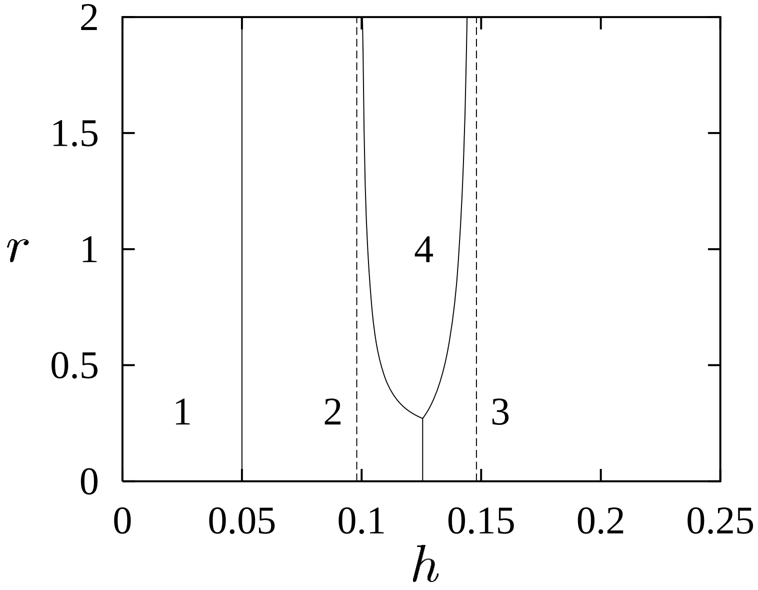

Figure 4 Results of bifurcation analysis, showing the effect of the harvesting efficiency h, and the ratio of the evolutionary rate constants r on the dynamics of the monomorphic deterministic model. Regions are: (1) predator absent, (2) one fixed point present, which is an attractor, (3) three fixed points, two of which are attractors, (4) limit cycle attractor.

3. For $h > 14.8\%$ there exist three fixed points of the dynamics. The two outer points are stable, and which of these is reached depends on the phenotypes initially present.
4. For $9.8\% < h < 14.8\%$ and sufficiently high values of r (Figure 4a), the attractor turns into a limit cycle, giving rise to Red Queen dynamics. On the other hand, for low values of r, the limit cycle breaks down and we recover the dynamical behavior of cases 2 and 3 with the switch occurring at $h = 12.6\%$.

The boundary of region 4 is in fact slightly more complicated than the description above suggests because two further kinds of dynamics can occur here: (i) a limit-cycle attractor around each of the outer fixed points, and (ii) a limit-cycle attractor around all three fixed points with each of the outer fixed points also being an attractor. But the parameter space permitting these dynamics is very small compared to the others and they are therefore of less biological interest. We conclude that evolutionary cycling requires an intermediate harvesting efficiency plus prey evolution to occur sufficiently fast compared to predator evolution.

The results from the bifurcation analysis are intuitive in that evolutionary cycling requires: (i) the effect of selection by the predator on the prey to be great enough to drive the prey from the phenotypic equilibrium it would have in the absence of the predator (h not too low), (ii) sufficient need for the predator to track the prey's phenotypic change (h not too high), and (iii) in the resulting evolutionary race the prey must be fast enough not to be 'caught up' by the predator (r not too low). In view of the respiratory costs that the predators have to meet from consumption of prey simply to stay alive, one would expect h to be substantially less than 1 and evolutionary cycling to occur in a range of h likely to be observed in reality.

5.2 Monomorphic Stochastic Model

A realization of the monomorphic stochastic dynamics is given in Figures 3c and 3d. The parameter values used are the same as those in Figures 3a and 3b, and we see that the cyclic behaviour is still maintained. In addition two major new effects should be noted. First, it can be seen that the oscillations in phenotypic values do not all have the same period. This phenomenon, which is well known in the theory of stochastic processes (phase diffusion, Tomita et al. 1974), comes about because stochastic perturbations along the limit cycle are not balanced by a counteracting force, whereas those orthogonal to the limit cycle are. Second, limit cycles whose extension in phenotype space is small relative to the typical mutational step sizes (given by $\sqrt{\mathrm{var} M_1}$ and $\sqrt{\mathrm{var} M_2}$) will be obscured by the stochastic noise. The boundaries of region 4 (Figure 4a) will then be less sharp than those in the monomorphic deterministic model, as illustrated in Figure 4b. Thus, if the evolutionary cycling is to be visible, the mutational steps must not be too large.

5.3 Polymorphic Stochastic Model

A realization of the polymorphic stochastic model is shown in Figures 3e and 3f, using as before the parameter values of Figures 3a and 3b. The phenomenon of evolutionary cycling still persists despite the phenotypic distributions now being polymorphic. In addition, this model allows for the effects of demographic stochasticity also of the resident phenotypes (see Appendix). Although this superimposes more random variation to the solution, cycling is maintained. Provided that phenotypic variance is not too large and population sizes are not too small, we thus can conclude that evolutionary cycling is robust to relaxation of the simplifying assumptions of the monomorphic deterministic model, and that it can actually occur in predator-prey communities like the one defined in Section 2.

6 Discussion

The main result of this analysis is that evolutionary limit cycles, in which the predator and prey phenotypes continue to change indefinitely, are a natural outcome in a coevolutionary community. The cyclic behaviour is not an artefact of determinism or monomorphism, because the phenomenon can be observed both in the stochastic monomorphic simulations and in the stochastic polymorphic ones. Clearly there is no general rule in nature to say that phenotypic evolution would lead to an equilibrium point in the absence of external changes in the environment.

A simple classification of the outcomes of phenotypic evolution can be constructed from two dichotomies. The first depends on whether an attractor exists, and the second on whether the attractor is a fixed point. This gives three classes of dynamics:

(i) evolution to a fixed-point attractor with stationary phenotypes,
(ii) evolution to an attractor that is not a fixed point on which the phenotypes continue to change indefinitely, and
(iii) evolution without an attractor, such that the phenotypes take more and more extreme values.

According to the definition in the Introduction, Red Queen dynamics would encompass both class (ii) and class (iii). Class (iii) is unrealistic for most kinds of phenotypes and, if the Red Queen were to depend on the existence of such dynamics in nature, one could reasonably conclude that Red Queen dynamics would be very unusual (Rosenzweig et al. 1987). But this would be to miss class (ii), and dynamics of this kind we have shown here to be feasible. In fact the limit cycle is but one of a number of non-equilibrium attractors; for instance in systems with more than two coevolving species, chaotic evolutionary attractors could be found.

Cyclic phenotype dynamics can occur in coevolution as is well known from theoretical studies of genetic polymorphisms under frequency-dependent selection (e.g. Akin 1981; Seger 1992), and research into the dynamics of strategy frequencies (Nowak and Sigmund 1989). The system considered here is different in two respects. First, the trait values are continuous, whereas cyclic dynamics have typically been observed in polymorphic systems with large qualitative differences between a small number of coexisting phenotypes. Second, and more important, the underlying genetic process here would be a sequence of gene substitutions in which mutants keep replacing the resident types rather than one in which the genes always coexist and undergo oscillations in frequency. Thus we are here looking at a process operating on an altogether larger evolutionary scale, such that the populations can undergo drastic changes in their phenotypic state, and still return to some earlier value.

The monomorphic deterministic dynamic described here in fact turns out to be canonical (Dieckmann and Law 1996), and can be derived from other starting points such as quantitative genetics (Abrams et al. 1993). It seems therefore that there is a large class of models of phenotypic coevolution with the potential for non-equilibrium asymptotic states. This needs to be emphasized because the assumption that asymptotic states of evolution are fixed points underlies much contemporary evolutionary thought. This assumption and the techniques that go with it (in particular evolutionarily stable strategies) are clearly not appropriate for dealing with non-equilibrium asymptotic states. The prevailing view among evolutionary biologists, centred on equilibrium points, needs to be extended to a dynamical framework to assimilate the Red Queen.

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Appendix

In this appendix we provide a brief derivation of the three dynamical models describing the process of coevolution for the reader interested in the more technical details. The theory outlined here is general in so far as it applies to a large variety of N-species coevolutionary communities of which the predator-prey system analyzed in this paper is just a particular instance.

THE POLYMORPHIC STOCHASTIC MODEL

At time t there are n_i individuals in species i with $i = 1, \ldots, N$. These have phenotypes s_{ij} with $j = 1, \ldots, n_i$ such that the phenotypic distribution $p_i(s_i)$ in species i is given by

$$p_i = \sum_{j=1}^{n_i} \delta_{s_{ij}} \tag{A.1}$$

with $\delta_x(y) = \delta(x - y)$ where δ denotes Dirac's δ-function. These distributions change in time due to stochastic birth, death and mutation processes like those specified in Table 1.

The dynamics of the phenotypic distributions can be described by a functional master equation for $P(p, t)$, the probability density of $p = (p_1, \ldots, p_N)$ to be realized at time t (Dieckmann 1994). The algorithm derived from this equation is the following.

1. Initialize the phenotypic distributions p_i with $i = 1, \ldots, N$ at time $t = 0$ and specify the time T when to stop the dynamics.
2. Calculate the birth and death probabilities $b_i(s_{ij}, p)$ and $d_i(s_{ij}, p)$ for each individual $i = 1, \ldots, N$, $j = 1, \ldots, n_i$ with phenotype s_{ij} in the environment given by p.

   Remark. According to Table 1 we have for the predator-prey community $b_1(s_1, p) = r_1$, $d_1(s_1, p) = \int \alpha(s_1)p_1(\tilde{s}_1)\, d\tilde{s}_1 + \int \beta(s_1, s_2)p_2(s_2)\, ds_2$, $b_2(s_2, p) = \int \gamma(s_1, s_2)p_1(s_1)\, ds_1$, and $d_2(s_2, p) = r_2$.
3. Construct the sums $w_{ij} = b_i(s_{ij}, p) + d_i(s_{ij}, p)$, $w_i = \sum_{j=1}^{n_i} w_{ij}$ and $w = \sum_{i=1}^{N} w_i$ with $i = 1, \ldots, N$, $j = 1, \ldots, n_i$.
4. Choose the waiting time Δt for the next event to occur according to $\Delta t = -\frac{1}{w} \ln r$ where $0 < r \leq 1$ is a uniformly distributed random number.
5. Choose species i with probability $\frac{1}{w} w_i$. Choose individual j in species i with probability $\frac{1}{w_i} w_{ij}$. Choose then a birth or death event with probability $\frac{1}{w_{ij}} b_i(s_{ij}, p)$ and $\frac{1}{w_{ij}} d_i(s_{ij}, p)$ respectively.
6. If a birth event occurs for an individual with phenotype s_{ij}, choose a new phenotype s'_{ij} with probability density $(1 - \mu_i)\delta(s'_{ij} - s_{ij}) + \mu_i M_i(s'_{ij} - s_{ij})$.
7. Update time and phenotypic distributions according to $t \to t + \Delta t$ and $p_i \to p_i + \delta_{s'_{ij}}$ or $p_i \to p_i - \delta_{s_{ij}}$ for a birth or death event in species i respectively.
8. Continue from Step 2 until $t \geq T$.

The protocol above utilizes the minimal process method (Gillespie 1976) to simulate the functional master equation. Note in particular that according to Step 4 the waiting times follow an exponential distribution, the standard result for stochastic processes described by homogeneous master equations.

The Monomorphic Stochastic Model

If μ_i is sufficiently small for all $i = 1, \ldots, N$ the phenotypic distributions in each species will be sharply concentrated around a single phenotype, the resident phenotype. The distributions then are called monomorphic (precisely one should refer to them as quasi-monomorphic since still more than one phenotype may be present in the population) and can well be approximated by $p_i = n_i \delta_{s_i}$ with resident phenotype s_i and population size n_i. In this case phenotypic change occurs via a sequence of trait substitutions where a resident phenotype s_i is replaced by a mutant phenotype s_i' (Dieckmann 1994).

The resulting directed random walk in the phenotype space is described by the master equation

$$\frac{d}{dt} P(s,t) = \int \Big[\, w(s|s') P(s',t) - w(s'|s) P(s,t) \, \Big] \, ds' \tag{A.2}$$

where $P(s,t)$ denotes the probability density of the resident phenotypes to be given by $s = (s_1, \ldots, s_N)$ at time t. Equation (A.2) only holds if the stochastic dynamics of s are a Markov process; to guarantee this it can be necessary to consider more than one trait per species. This more general case is analyzed in Dieckmann and Law (1996). In the infinitesimal time interval dt a trait substitution in only a single trait can occur and thus the probability per unit time $w(s'|s)$ for the transition $s \rightarrow s'$ can be decomposed according to

$$w(s'|s) = \sum_{i=1}^{n} w_i(s_i', s) \prod_{\substack{j=1 \\ j \neq i}}^{n} \delta(s_j' - s_j) \ . \tag{A.3}$$

Here $w_i(s_i', s)$ denotes the probability per unit time for a trait substitution $s_i \rightarrow s_i'$ to occur in species i given an environment of phenotypes s.

A trait substitution requires that, first, a specific mutant phenotype s_i' enters the population of species i and, second, that it succeeds in replacing the resident phenotype s_i. Since these two processes are statistically independent, their probabilities multiply and $w_i(s_i', s)$ is given by the product

$$w_i(s_i', s) = \underbrace{\overbrace{\mu_i b_i(s_i, s) n_i(s)}^{\text{a}} \ \overbrace{M_i(s_i' - s_i)}^{\text{b}}}_{\text{term I}} \ \underbrace{b_i^{-1}(s_i', s) \big(f_i(s_i', s)\big)_+}_{\text{term II}} \ . \tag{A.4}$$

The functions $b_i(s_i', s)$, $d_i(s_i', s)$ and $f_i(s_i', s) = b_i(s_i', s) - d_i(s_i', s)$ denote the per capita birth, death and growth probabilities per unit time (or rates) of a phenotype s_i' in an environment given by the phenotypes s. They are defined in terms of the analogous quantities of the polymorphic stochastic model by e.g. $b_i(s_i', s) = b_i(s_i', p)$

with $p = (n_1(s)\delta_{s_1}, \ldots, n_N(s)\delta_{s_N})$. Here the population sizes $n_i(s)$ are determined as the equilibrium solutions of the resident's population dynamics $\frac{d}{dt} n_i = n_i f_i(s_i, s)$. The general case of nonequilibrium population dynamics is treated in Dieckmann and Law (1996). A more formal analysis is given in Rand et al. (1993)

Remark. For the predator-prey community we obtain $b_1(s_1', s) = r_1$, $d_1(s_1', s) = \alpha(s_1')n_1(s) + \beta(s_1', s_2)n_2(s)$, $b_2(s_2', s) = \gamma(s_1, s_2')n_1(s)$, and $d_2(s_2', s) = r_2$.

We now explain the different terms in equation (A.4).

1. Term I represents the impact of the mutation process and is given by weighting (a) the probability per unit time for any mutant to occur in the resident population of phenotype s_i by (b) the probability density for the mutant phenotype to be given by s_i'. Since mutations in distinct individuals are statistically uncorrelated, term Ia is composed of three factors. The per capita birth rate $b_i(s_i, s)$ of the resident phenotype is multiplied by μ_i, the mutation probability for each birth event, giving the per capita mutation rate of the resident phenotype. This is multiplied by the resident's population size n_i to yield the mutation rate of the resident population. Term Ib simply is the mutation distribution $M_i(s_i' - s_i)$ for mutant phenotypes s_i' given the resident phenotype s_i.
2. Term II stands for the process of selection. In the monomorphic stochastic model it is assumed that the resident populations are sufficiently large not to be subject to accidental extinction due to stochastic fluctuations of their population sizes. In contrast, the mutant population starts with population size 1 such that the impact of demographic stochasticity on its dynamics ought to be considered. Since the function $()_+$ returns its argument if the argument is positive and 0 otherwise, deleterious mutants, with $f_i(s_i', s) < 0$, have no chance to survive in the resident population. But even advantageous mutants, with $f_i(s_i', s) > 0$, experience some risk of accidental extinction due to random sampling when initially rare (Fisher 1958). Term II also shows that for large initial per capita growth rates of the mutant the probability for it to succeed in replacing the resident saturates at 1. The exact form of term II is derived in Dieckmann and Law (1996).

Combining equations (A.2), (A.3) and (A.4) yields a complete description of the stochastic coevolutionary dynamics provided that phenotypic distributions are sufficiently concentrated and that population sizes are sufficiently large. The algorithm for this model again follows the minimal process method.

The Monomorphic Deterministic Model

To capture the representative features of the monomorphic coevolutionary dynamics directly, rather than having to consider a large number of different realizations of the monomorphic stochastic model, a deterministic approximation of the latter is devised. The deterministic path $\langle s \rangle$ associated with a stochastic process is described by the equation (Serra et al. 1986)

$$\frac{d}{dt}\langle s \rangle = a(\langle s \rangle) \tag{A.5}$$

where the function a is the first jump moment of the stochastic process whose components in our case are given by

$$a_i(s) = \int (s_i' - s_i) w_i(s_i', s)\, ds_i' \tag{A.6}$$

with $i = 1, \ldots, N$. If the different realizations of the stochastic process do not spread too far apart, i.e. if the variance of the probability density $P(s,t)$ in equation (A.2) stays small, the deterministic path $\langle s \rangle$ provides a good approximation of the mean path $\int sP(s,t)\, ds$ (van Kampen 1981).

We obtain the deterministic monomorphic model by introducing equation (A.4) into (A.6). To simplify the result, we expand the functions $f_i(s_i', s)$ and $b_i^{-1}(s_i', s)$ in the mutant phenotype s_i' about the resident phenotype s_i. Here we only present the first order result for symmetric mutation distributions, the derivation of higher order correction terms and for arbitrary mutation distributions is given in Dieckmann and Law (1996). By introducing the result into equation (A.5) we obtain the deterministic path of the monomorphic stochastic model

$$\frac{d}{dt}\langle s_i \rangle = \underbrace{\left(\frac{1}{2}\mu_i \mathrm{var} M_i\right) n_i(\langle s \rangle)}_{\text{term I}} \; \underbrace{\frac{\partial}{\partial s_i'} f_i(s_i', \langle s \rangle)\, \Big|_{s_i' = \langle s_i \rangle}}_{\text{term II}} \tag{A.7}$$

for $i = 1, \ldots, N$. The deterministic path thus is described by a simple, though typically nonlinear, dynamical system composed of N coupled first order differential equations. The terms on the right hand side of equation (A.7) have the following meanings.

1. Term I again captures the influence of mutation on the coevolutionary dynamics. The factor $\frac{1}{2}\mu_i \mathrm{var} M_i$, called the evolutionary rate constant, is affected by the proportion μ_i of births that produce mutants and by the variance $\mathrm{var} M_i$ of the mutation distribution in the trait s_i. Together with the population size n_i all these terms are non-negative, so term I as a whole serves to scale the rate of evolutionary change.

2. Term II accounts for the impact of selection as it determines the direction of evolutionary change. When this derivative of the per capita growth rate f_i is positive (respectively negative), mutants with increased (respectively decreased) phenotypic values s_i will be advantageous in the environment given by $\langle s \rangle$. The lines on which the terms II are zero are the isoclines of the monomorphic deterministic dynamics.

The Runge-Kutta method can be employed to construct an algorithm for the monomorphic deterministic model. Equations (A.7) have features in common with other models of adaptive dynamics (Hofbauer and Sigmund 1990; Vincent 1991; Abrams et al. 1993) but are here explicitly derived from the underlying stochastic ecological processes.

5

On Evolution under Asymmetric Competition

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On Evolution under Asymmetric Competition

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The evolutionary consequences of asymmetric competition between species are poorly understood in comparison with symmetric competition. A model for evolution of body size under asymmetric competition within and between species is described. The model links processes operating at the scale of the individual to that of macroscopic evolution through a stochastic mutation-selection process. Phase portraits of evolution in a phenotype space characteristically show character convergence and parallel character shifts, with character divergence being relatively uncommon. The asymptotic states of evolution depend very much on the properties of asymmetric competition. Given relatively weak asymmetries between species, a single equilibrium point exists; this is a local attractor, and its position is determined by the intra- and interspecific asymmetries. When the asymmetries are made stronger, several fixed points may come about, creating further equilibrium points which are local attractors. It is also possible for periodic attractors to occur; such attractors comprise Red Queen dynamics with phenotype values that continue to change without ever settling down to constant values. From certain initial conditions, evolution leading to extinction of one of the species is also a likely outcome.

1 Introduction

Asymmetric competition arises when, during an encounter between two or more individuals for some limited resource, these resources are divided up unequally. The larger individual wins the contest (Clutton-Brock et al., 1979), the territory holder keeps the territory (Davies, 1978), the taller plant gets more light (Weiner, 1990). Such asymmetries are known to be a common phenomenon in nature (Lawton and Hassell, 1981; Connell, 1983; Schoener, 1983; Weiner, 1990), and are therefore likely to be an important force of natural selection. Asymmetric competition has a special interest because it does not necessarily cause evolution of weak interactions among species, as one might expect through divergent character displacement (the ’ghost of competition past’: Connell, 1980). Thus natural selection generated by asymmetric competition is likely to be a persistent and continuing phenomenon in communities.

In view of the importance of asymmetric competition between species, it is surprising how little understanding there is of its evolutionary effects both empirically and theoretically. Interest has focussed more on interactions within species and how these contribute to arms races and cyclic changes in phenotype (Maynard Smith, 1982: 94 et seq.; Parker, 1983; Maynard Smith and Brown, 1986; Abrams and Matsuda, 1994; Matsuda and Abrams, 1994). There has however been some study of the role of asymmetries in the taxon cycles of Anolis lizards (Rummell and Roughgarden, 1983, 1985; Taper and Case, 1992a), and some more general discussion of the evolutionary consequences of asymmetric competition (Abrams, 1987; Abrams et al., 1993a; Abrams and Matsuda, 1994).

Studies of asymmetric competition in the empirical literature are of three main kinds, distinguished by the temporal scale at which the process is studied. Those at the smallest, microscopic scale deal with encounters between individuals which depend on behavioural mechanisms of competition between animals (Perfecto, 1994; Robinson and Terborgh, 1995), and on short-term effects of neighbours on growth in plants (Goldberg, 1987). Those at the intermediate, mesoscopic scale are concerned with population dynamics, often involving the manipulation of densities of pairs of species in a reciprocal manner. Asymmetries are commonly found in these studies, one species being much more affected by the manipulations than the other (Lawton and Hassell, 1981; Morin and Johnson, 1988; Thompson and Fox, 1993). Studies at the largest temporal scale, the macroscopic scale of phenotype evolution, attempt to account for phenotype patterns across species as an outcome of evolution driven by asymmetric competition. Such patterns include the differences in body size of lizard species when they coexist on islands, in contrast to their intermediate sizes on islands where only one species occurs (Case and Bolger, 1991). The Anolis lizards of the Lesser Antilles have been studied in greatest detail, and there is fossil evidence suggesting that coexisting Anolis species gradually decline in body size. The larger Anolis species is thought to do so at a faster rate, leading to extinction of the smaller species, the taxon cycle eventually repeating itself by invasion of a new species of large body size from the mainland (Roughgarden and Pacala, 1989).

In this paper we link together these three time scales in a formal model of phenotypic evolution of two interacting species. The idea is to apply a single theoretical framework across the time scales to retain explicitly the individual-based ecological processes ultimately responsible for natural selection (Marrow et al., 1992; Dieckmann, 1994; Dieckmann and Law, 1996; Marrow et al., 1996). This entails deriving a model of macroscopic phenotype dynamics as an approximation to a stochastic mutation-selection process (Dieckmann and Law, 1996), where individuals with different phenotypic values arise by mutation and replace one another in a trait substitution sequence (Metz et al., 1992). Our intention is to complement earlier research, which was based on quantitative genetics, by making explicit the randomness associated with mutation and survival of mutants when rare. Our approach also differs from previous theory on taxon cycles (Rummell and Roughgarden, 1983, 1985; Brown and Vincent, 1987; Taper and Case, 1992a) in that asymmetric competition becomes monotonically greater the larger the phenotypic difference between individuals. This earlier work, motivated by resource utilization functions, assumed that, if the phenotypic difference was large enough, there would be no interaction. We want to add to this, because some kinds of interspecific competition are intrinsically asymmetric however great the phenotypic difference. Such asymmetries include for instance that between tall and short plants in competition for light, and the asymmetry between large and small individuals in aggressive interactions.

We give our results in the form of phase portraits of the evolutionary dynamics in a two-dimensional phenotype space. These portraits show that modifications to the properties of asymmetric competition can cause a diverse range of evolutionary outcomes, with multiple local attractors leading to extinction of one species or coexistence of both species. (Multiple local attractors should not be confused with single equilibrium points that allow multiple strategies within species at an ESS (Vincent and Brown, 1988).) In cases where the species coexist, the attractors may be fixed points or cyclic orbits. The fixed points have the property that only one of the species is uninvadable to mutants (i.e. at an ESS); the other is at a fitness minimum. The cyclic orbits can be thought of as ’Red Queen’ dynamics, from Van Valen’s (1973) Red Queen’s hypothesis, as phenotype dynamics that do not tend to a fixed point in the absence of external forcing (Dieckmann et al., 1995).

2 Theory

In the theory developed below, we assume that the evolving community comprises two species. Individuals are distinguished by the value of some phenotypic trait, denoted s_i for an individual of species i (where $i = 1, 2$). The phenotype values are continuous and drawn from the sets S_i, scaled so that $S_i \subset (0, 1)$. It is convenient, but by no means essential, to think of the traits as body size in view of the well-documented effect this has on asymmetric competition (Clutton-Brock et al., 1979; Weiner, 1990). The intention is to describe how these traits evolve under natural selection due to asymmetric competition between and within species. We investigate this by constructing a model for macroscopic phenotypic evolution from microscopic encounters between individuals and mesoscopic population dynamics.

The ecological assumptions made below are needed simply to specify a model system, and can readily be altered to match the behaviour of particular ecological interactions.

On the other hand the evolutionary assumptions, labelled (A1) to (A3), are structural and needed in the derivation of the macroscopic evolutionary dynamic.

2.1 ENCOUNTERS BETWEEN INDIVIDUALS (MICROSCOPIC SCALE)

The essence of asymmetric competition is that, when two individuals encounter one another as they search for resources, the effect on them is unequal. We assume that eventually this is transformed into different probabilities of death, α_{ij}, (per encounter per unit time) of the two individuals, and describe the asymmetry as

$$\alpha_{ij}(s_i, s_j)/\gamma = c_{ij}\left(1 - \frac{1}{1 + u_{ij}(s_i, s_j)}\right) \tag{1}$$

where $u_{ij}(s_i, s_j) = \exp\left(-k_{ij}(s_i - s_j)\right)$. The first argument s_i is the body size of the individual whose mortality risk we wish to determine and the second s_j is the body size of the other individual. Parameters c_{ij} and k_{ij} are positive and non-negative respectively. The parameter γ has dimensions time^{-1} and scales the population sizes. Body size can be thought of as log-transformed when the asymmetry depends on body-size ratios rather than differences (Schwinning and Fox, 1995); the scaling $s_i \in (0, 1)$ can be achieved by the transformation

$$s_i = \log\left(\frac{l_i}{l_{i,min}}\right) / \log\left(\frac{l_{i,max}}{l_{i,min}}\right) \tag{2}$$

where the untransformed trait value is $l_i \in (l_{i,min}, l_{i,max})$.

Although Equations (1) are rather simple, they are readily tailored to different kinds of encounters (Figure 1). This includes encounters with conspecifics ($i = j$) and individuals of the other species ($i \neq j$). The parameter c_{ij} sets the overall mortality risk. When the other individual is of the same size, $\alpha_{ij} = c_{ij}/2$; mortality increases to a maximum value c_{ij} if the other individual is much larger, and to a minimum of zero if the other individual is much smaller. The term k_{ij} measures the sensitivity of α_{ij} to changes in s_i when $s_i \approx s_j$. The limit as $k_{ij} \to \infty$ describes a version of the opponent-independent costs game (Parker, 1983) in which the costs arising from an encounter are set prior to the encounter and the larger individual gets all the reward; the costs here would take the form of increased mortality risks inherent from having a larger body size, and the rewards would be reduced mortality risks associated with encounters.

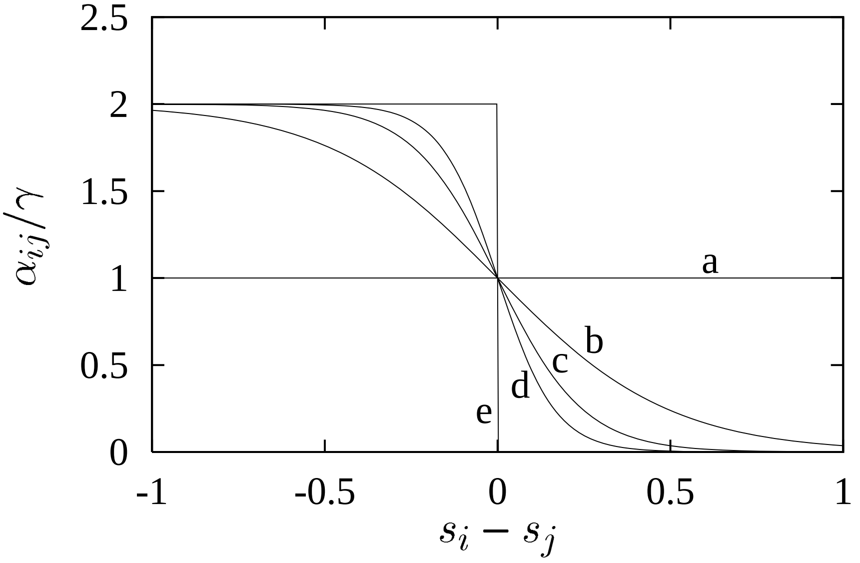

Figure 1 Asymmetric competition functions $\alpha_{ij}(s_i, s_j)$, with $c_{ij} = 2$. (a) No asymmetry: $k_{ij} = 0$; (b) weak asymmetric competition: $k_{ij} = 4$; (c) intermediate asymmetric competition: $k_{ij} = 8$; (d) strong asymmetric competition: $k_{ij} = 12$; (e) the limit as $k_{ij} \to \infty$.

2.2 Population Dynamics (Mesoscopic Scale)

We define a model of population dynamics which describes how the number of individuals in each population is affected by competitive encounters and the fate of mutant individuals with body sizes that differ from those of the residents. By doing this the need for an external measure of fitness is eliminated; natural selection is described internally by the population dynamics of mutant phenotypes. We start by defining the dynamics of a community without phenotypic variation within species, and then determine the fate of mutants as they are added to it.

Call $s = (s_1, s_2)$ the pair of body sizes in the resident community. Let $n = (n_1, n_2)$ be the number of individuals with each body size at some point in time. With large numbers and the simplest assumption that individuals encounter one another at random, the dynamics are given by

$$\dot{n}_i = n_i \cdot f_i(s, n) = n_i \cdot \left(\beta_i - \delta_i(s_i) - \sum_{j=1,2} \alpha_{ij}(s_i, s_j) \cdot n_j \right) \tag{3}$$

Here the per capita rate of increase $f_i(s, n)$ is partitioned into the following birth and death components. The first, β_i, is a birth rate; this is taken to be independent of encounters and body size. The second component is a basal rate of mortality δ_i. The dependence of δ_i on s_i is introduced because an intrinsic cost to large body size is to be expected; we use a linear function

$$\delta_i(s_i) = a_i + b_i s_i \tag{4}$$

to describe this, where a_i and b_i are non-negative parameters. This mortality is augmented by the third component caused by asymmetric competition from Equations (1).

2.3 PHENOTYPE EVOLUTION (MACROSCOPIC SCALE)

A dynamic for phenotype evolution can be constructed as the mean of a stochastic process, the randomness entering both through mutation and through selection. First we deal with mutation, writing the probability of a mutation per unit time as

$$\mathcal{M}_i(s_i', s) = \mu_i \cdot \beta_i \cdot \hat{n}_i(s) \cdot M_i(s_i' - s_i) \tag{5}$$

(Dieckmann and Law, 1996). Here $s_i' = s_i + \delta s_i$ is a mutant phenotype. The term μ_i is the probability that a newborn individual is a mutant. This mutant has a phenotype value drawn from a probability distribution M_i symmetric around s_i and with constant variance σ_i^2. (Departures from symmetry will have little effect on the deterministic dynamics below as these are based on the assumption of small mutational steps. A constant variance is most likely when body sizes are log-transformed.) The probability per unit time of a birth is given by the product of the per capita birth probability per unit time, β_i, and the equilibrium population size of the resident phenotypes, $\hat{n}_i(s)$. Equilibrium populations $\hat{n}_i(s)$. are obtained from Equations (3) with $\dot{n}_i = 0$ for $i = 1, 2$. We have made an assumption (A1) in Equation (5) that mutations occur rarely enough for the population sizes to reach equilibrium values between mutation events. This separation of ecological and evolutionary time scales is widely used in theoretical work, in view of the difficulties in making any generalizations about evolution on the transients of ecological dynamics (e.g. Lande, 1982; Roughgarden, 1983a).

Stochasticity arises during natural selection because mutations occur first in single individuals and are liable to extinction irrespective of how advantageous they are (Fisher, 1958: 80 et seq.). We now make a second assumption (A2) that populations of residents are large. This has two consequences. First mutants will initially be rare enough for their effect on the population dynamics of the residents to be ignored. The initial per capita rate of increase of the mutant $\overline{f}_i(s_i', s)$ can then be written as a function of the mutant phenotype s_i' and the environment in which it arises, the latter being fully specified by the resident trait values s. Thus

$$\overline{f}_i(s_i', s) = \beta_i - \delta_i(s_i') - \sum_{j=1,2} \alpha_{ij}(s_i', s) \cdot \hat{n}_j(s) \,. \tag{6}$$

This function is related to the fitness generating function (G-function) $G_i(u_i, u, p, N)$, which has been used to characterize evolutionary games in the context of ESS theory, where $u_i = s'_i$, $u = s$, $p = (1, 1)$, and $N = \hat{n}$ (Vincent and Brown, 1988; Brown and Vincent, 1992). Rosenzweig and McCord (1991) suggest that the G-function defines a ’bauplan’ within which microevolution takes place.

The second consequence of assumption (A2) is that the effect of demographic stochasticity on the residents will be negligible. The probability that mutant numbers become large enough to escape extinction due to demographic stochasticity can then be written as

$$\mathcal{S}_i(s'_i, s) = \begin{cases} \overline{f}_i(s'_i, s)/\beta_i & \text{for } \overline{f}_i(s'_i, s) > 0 \\ 0 & \text{for } \overline{f}_i(s'_i, s) \leq 0 \end{cases} \tag{7}$$

(Goel and Richter-Dyn, 1974: 79). With a third assumption (A3) that no two trait values s'_i and s_i can coexist, a mutant which escapes accidental extinction when rare must go to fixation. Under Lotka-Volterra dynamics such as those in Equations (3), it can be shown that this assumption typically holds (Dieckmann, 1994: 96 et seq.).

Assumptions (A1) and (A3) specify a regime which is phenotypically monomorphic except for those times when a mutant is replacing a resident phenotypic value. Under these conditions the probability per unit time of the transition from s_i to s'_i is given by the product $\mathcal{M}_i(s'_i, s) \cdot \mathcal{S}_i(s'_i, s)$. This is a stochastic mutation-selection process in which, from time to time, new trait values replace old ones in a trait substitution sequence (Metz et al., 1992). A large number of realizations of this process can be averaged to give a mean path. As long as the deviations from the mean path are small, the mean path can be replaced by the following deterministic dynamics

$$\dot{s}_i = \kappa_i(s) \cdot \frac{\partial}{\partial s'_i} \overline{f}_i(s'_i, s) \Big|_{s'_i = s_i} \tag{8}$$

where

$$\kappa_i(s) = \frac{1}{2} \cdot \mu_i \cdot \sigma_i^2 \cdot \hat{n}_i(s)$$

(van Kampen, 1992: 122 et seq.; Dieckmann and Law, 1996). These dynamics describe the process of phenotypic evolution in a trait space S which is the Cartesian product $S_1 \times S_2$. The dynamics are exact if the mutational steps are infinitesimal and apply as a close approximation if the steps are small, i.e. σ_i^2 is small. Evolution is driven essentially by two factors according to Equations (8). The first is a coefficient $\kappa_i(s)$ that scales the rate of evolution, its value depending on how often mutations occur and the size of the mutational steps. The second is a selection derivative (an evolutionary rate) which depends on the underlying ecological processes responsible for natural selection, i.e. what happens when individuals encounter one another and what effect these encounters have on population dynamics. The dynamics are canonical, in that they can alternatively be derived from a starting point in quantitative genetics, although the meaning of the evolutionary rate coefficient is then different (Iwasa et al., 1991; Taper and Case, 1992a; Abrams et al., 1993a; Marrow et al., 1996).

2.4 Selection Derivative

This measures how sensitive the initial per capita rate of increase of a mutant is to changes in its body size s_i' close to s_i, when the mutant arises in a community with trait values s. It is given by

$$\frac{\partial}{\partial s_i'}\overline{f}_i(s_i', s)\Big|_{s_i'=s_i} = \lim_{s_i'-s_i\to 0}\frac{\overline{f}_i(s_i', s)-\overline{f}_i(s_i, s)}{s_i'-s_i} \tag{9}$$

(Marrow et al., 1992), where $\overline{f}_i(s_i, s) = 0$ since it is assumed that the populations of resident phenotypes have come to equilibrium. The selection derivative is important because it indicates the direction in which evolution is taking place; if it is positive (negative), then mutants of greater (smaller) body size invade. From Equations (1), (4) and (6), it can be written as

$$\begin{aligned}&\frac{\partial}{\partial s_i'}\overline{f}_i(s_i', s)\Big|_{s_i'=s_i} = \\ &\underbrace{-b_i}_{(I)} \quad \underbrace{+\tfrac{\gamma\cdot c_{ii}\cdot k_{ii}}{4}\cdot\hat{n}_i(s)}_{(II)} \quad \underbrace{+\tfrac{\gamma\cdot c_{ij}\cdot k_{ij}\cdot u_{ij}(s_i,s_j)}{(1+u_{ij}(s_i,s_j))^2}\cdot\hat{n}_j(s)}_{(III)}\end{aligned} \tag{10}$$

where is as given in Equations (1). This expression comes in three parts. (I) is a constant negative term due to the intrinsic advantage of smaller body size. (II) is a positive term proportional to the number of conspecifics, due to the advantage of larger body size in encounters with these individuals. (III) is also a positive term, in this case due to encounters with individuals of the other species, and proportional to the population size of the other species.

2.5 Inner Evolutionary Isoclines

The isoclines are lines in the trait space S on which $\dot{s}_i = 0$, and are given by the union of the manifolds on which either the resident population or the selection derivative vanishes (Equations (8)). We are concerned primarily with the isocline

$$\frac{\partial}{\partial s_i'}\overline{f}_i(s_i', s)\Big|_{s_i'=s_i} = 0\,, \tag{11}$$

because this allows both species to be present and as a result coevolution can occur; we call this the inner isocline. The following properties of the inner isoclines, which we refer to as non-invasibility and convergence, help in understanding the phenotype dynamics.

Non-invasibility is familiar from the concept of an evolutionarily stable strategy (ESS) as the property that mutants s_i', with phenotypes close to the isoclinic values s_i satisfying Equation (11), cannot invade (Parker and Maynard Smith, 1990), and is given by the condition

$$0 > \frac{\partial^2}{\partial s_i'^2} \overline{f}_i(s_i', s) \Big|_{s_i'=s_i} . \tag{12}$$

From Equation (10) this condition is

$$0 > -\gamma \cdot c_{ij} \cdot k_{ij}^2 \cdot \hat{n}_j(s) \cdot u_{ij}(s_i, s_j) \cdot \frac{1 - u_{ij}(s_i, s_j)}{(1 + u_{ij}(s_i, s_j))^3} \tag{13}$$

where $u_{ij}(s_i, s_j)$ is as given in Equations (1). Notice that Inequality (13) holds only for the larger species, which means that there is no point in the trait space satisfying it simultaneously for both species.

Convergence was introduced in the context of phenotype dynamics in one dimension and refers to the property of successive mutations in the vicinity of a fixed point to cause evolution towards this point (Taylor, 1989; Abrams et al. 1993a; Metz, et al. 1994). This is distinct from the property of non-invasibility, and is given by

$$0 > \frac{\partial^2}{\partial s_i \partial s_i'} \overline{f}_i(s_i', s) \Big|_{s_i'=s_i} \tag{14}$$

on the inner isocline of this two-dimensional system. Convergence means that, in the vicinity of the isocline, a sequence of successful mutants tends to the isocline, provided that the body size in the other species is held constant.

The fixed points $\hat{s}$ at which both species coexist are the points in the trait space at which the inner isoclines intersect, i.e.

$$\frac{\partial}{\partial s_i'} \overline{f}_i(s_i', s) \Big|_{s_i'=s_i} = 0 \quad \text{for} \quad i = 1, 2 . \tag{15}$$

These are of special interest because they are contenders as attractors of evolutionary trajectories; over the course of time phenotypes may evolve towards them. It is clear from Inequality (13) that, at all fixed points satisfying $\hat{s}_1 \neq \hat{s}_2$, the species with smaller body size is at a fitness minimum, and the one with a greater body size is at a maximum. Nevertheless, it will be seen below that evolution readily leads towards such a point, notwithstanding the fact that it is not an ESS for the species with smaller body size. This is of interest because it shows that the ESS criterion cannot serve as a necessary condition for identifying evolutionary attractors (Brown and Pavlovic, 1992; Abrams et al., 1993a; Marrow et al., 1996). Neither does it qualify as a sufficient condition (Hofbauer and Sigmund, 1990; Takada and Kigami, 1991; Abrams et al., 1993a; Marrow et al., 1996); use of the ESS criterion is inadequate for delimiting the outcome of these evolutionary processes.

3 Results

The evolutionary dynamics (8) can be represented in terms of a two dimensional phase portrait in the trait space S. This gives a clear picture of the geometry of evolution, indicating the orientation of the isoclines, the positions of fixed points and the flow of evolutionary trajectories. In this section we illustrate the varied evolutionary behaviour which stems from modifications in asymmetric competition in Equations (1) using these phase portraits. Throughout we hold $\gamma = 5 \cdot 10^{-4}$, $\beta_i = 1$, $a_i = 0$, and $b_i = 1$ for $i = 1, 2$ in Equations (1), (3) and (4), as this makes it possible to focus simply on the effects of changes to asymmetric competition. The coefficients of the evolutionary rates of the species in Equations (8) are kept the same unless otherwise stated.

It is important to appreciate that, on the time scale of population dynamics, the species may not coexist, i.e. the asymptotic state to which the population size of one species tends may be zero for constant s. To make this precise, we define a subspace S_c of S for which both species have positive equilibrium populations asymptotically:

$$S_c = \{s \in S \mid \hat{n}_i(s) > 0 \text{ for } i = 1, 2\} . \tag{16}$$

It may often be the case that S_c is an empty set, and questions about coevolution obviously do not then arise. We deal here only with those systems for which S_c is not empty, so that there is some region in which coevolution takes place. For this to be the case, we require that there should be some region in S with the properties

$$\frac{\beta_i - \delta_i(s_i)}{\alpha_{ii}(s_i, s_i)} < \frac{\beta_j - \delta_j(s_j)}{\alpha_{ji}(s_j, s_i)} \quad \text{for} \quad i = 1, 2 \quad \text{and} \quad j \neq i . \tag{17}$$

These conditions ensure that there is an equilibrium point satisfying $\hat{n}_i(s) > 0$ for $i = 1, 2$, and that the equilibrium point is a global attractor. With the values β_i, a_i and b_i given above, there are values of s satisfying Inequalities (17) when $c_{ii} > c_{ji}$ for $i = 1, 2$ and $j \neq i$. This is no more than saying that there is a region in S where intraspecific competition is stronger than interspecific competition. To ensure that there is a substantial region of coexistence, we set $c_{ii} = 2$ and $c_{ij} = 1$ for $i = 1, 2$ and $j \neq i$ in the examples below.

Notice that, once evolution of body size has been introduced, it is entirely feasible for the body sizes to evolve to the boundary of the subspace of coexistence S_c, i.e. to a point where the equilibrium population size of one of the species is zero. In such cases the dynamics subsequently lie in one of the one-dimensional subspaces S_1 or S_2. We indicate such parts of the S_c boundary by discontinuous lines in Figure 2, in contrast to those which repel the evolutionary trajectories. It should be borne in mind that the deterministic population dynamics in Equations (3) do not allow for accidental extinction of a species close to the S_c boundary that results from the small size of the resident population there.

3.1 Asymmetry Absent

This is the null case, indicating what would happen if competition was present but there were no asymmetries in the encounters ($c_{ij} > 0$, $k_{ij} = 0$ for $i = 1, 2$). The path of evolution is very simple (Figure 2a): body sizes just evolve to the smallest values in S. This is because the intrinsic costs associated with large size (Equation (4)) are not countered by any advantage in encounters with other individuals. Notice that, in certain regions of the trait space S, coexistence is not possible; body size, if large enough, causes an intrinsic mortality rate too great to maintain a population under competition. Moreover, evolution can lead to the boundary of S_c, and there the larger species becomes extinct. Evolution then continues in one of the subspaces S_1, S_2 until the smallest body size is reached.

3.2 Asymmetric Competition within Species

A first step towards a more realistic system would be to suppose that asymmetric encounters occur only among conspecifics ($k_{ii} > 0$, $k_{ij} = 0$ for $i = 1, 2$ and $i \neq j$). This would be expected if asymmetries were a special feature of intraspecific interactions such as the ability to hold territories against conspecifics (Davies, 1978). Figure 2b shows that the intrinsic advantage of small size is now opposed by an advantage of larger body size in encounters with conspecifics. Just how great the overall advantage stemming from asymmetric encounters is depends on the number of conspecifics (Equation (10)). When conspecifics are scarce, as they will be when body size is large, encounters occur infrequently and the advantage is not great enough to counter that of small body size. This is reversed when body size is small and, as a result, inner evolutionary isoclines exist for both species. The isoclines intersect at a single point $\hat{s}$ which satisfies the condition for convergence for both species and the second order condition for non-invasibility for neither of them (see Inequalities (13) and (14)); nonetheless it is an attractor for evolutionary trajectories in its neighbourhood. As before evolution leads to the boundary of S_c from certain starting points, although this can now happen only over a subset of the boundary.

3.3 Moderate Asymmetric Competition between Species

Asymmetric competition between species in addition to that within species is likely to occur when all individuals must compete for a common resource, irrespective of their identity. This changes some important features of the phase portrait. We consider first a case in which the degree of asymmetry is equal for both species, ($k_{12} = k_{21}$) and moderate in size (Figure 2c). The inner isoclines and the boundary of S_c are now non-linear. In the example shown, the single fixed point, now shifted to larger body sizes, still remains in existence and is still an attractor for evolutionary trajectories in

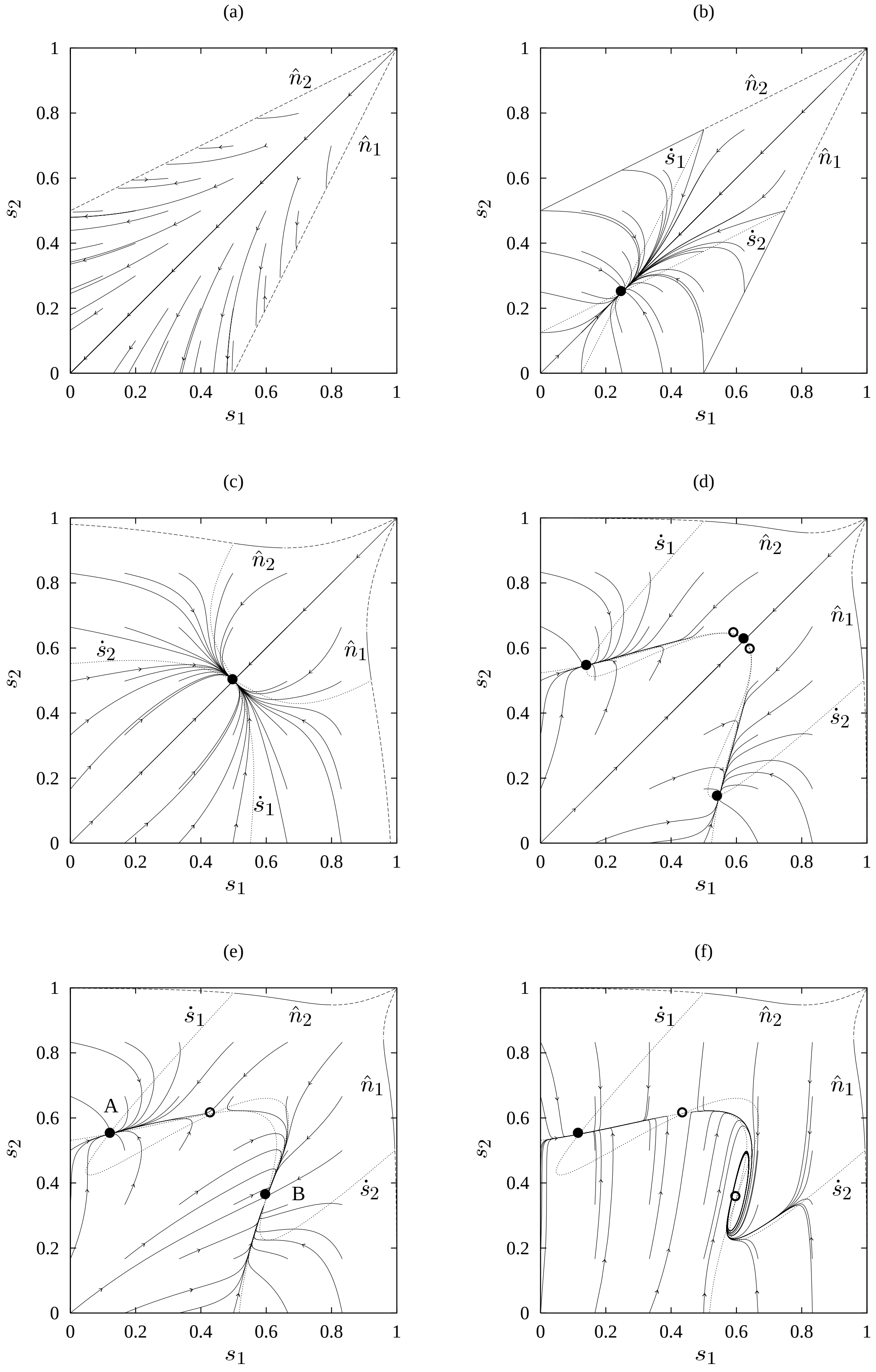

Figure 2

its neighbourhood. It is notable that the asymmetry in interspecific encounters expands the region S_c over which the species coexist. This may seem counterintuitive until it is understood that individuals of large body size are now less adversely affected in their encounters with small individuals of the other species and that their populations are correspondingly larger. A substantial part of the non-linear boundary of S_c permits evolution on to the boundary, leading to extinction of the larger species.

3.4 Strong Asymmetric Competition between Species

As the asymmetry between species is made stronger, the non-linearities of the inner isoclines become greater, generating more fixed points. This is because, where individuals of the two species are similar in size, the advantage of being the larger one becomes greater; this distorts the inner isoclines, pulling them towards the upper right corner, $s = (1, 1)$. In Figure 2d for example, the single fixed point has been replaced by five fixed points. The one in the middle at which the species have the same body size still exists and has a small basin of attraction. But two new attracting fixed points have arisen at which the body sizes of the two species are quite different; these are attractors even though the species with smaller body size is at a fitness minimum (see Inequality (13)). Evidently, as the degree of asymmetry increases, alternative outcomes to coevolution become possible; which outcome is realized depends on the body sizes at the start of the evolutionary process.

Figure 2 (continued) Phase portraits of the trait space S, showing contrasting dynamics as asymmetric competition is altered. Evolutionary trajectories within the region of coexistence shown as continuous lines. Inner evolutionary isoclines $\dot{s}_i = 0$ shown as dotted lines: $\dot{s}_1$ species 1, $\dot{s}_2$ species 2. Isoclines marking the boundary of coexistence $\hat{n}_i = 0$ shown as: $\hat{n}_1$ species 1, $\hat{n}_2$ species 2; the isocline is given as continuous (discontinuous) if it repels (attracts) orbits from the interior of the coexistence region. Fixed points are shown as circles, and filled if the fixed point is an attractor. Parameters are set as follows unless otherwise specified. Equations (1): $\gamma = 5 \cdot 10^{-4}$, $c_{ii} = 2$, $c_{ij} = 1$, $k_{ii} = 4$, for $i = 1, 2$ and $j \neq i$; Equations (3): $\beta_i = 1$, for $i = 1, 2$; Equations (4): $a_i = 0$, $b_i = 1$, for $i = 1, 2$; Equations (8): $\mu_i = 10^{-4}$, $\sigma_i^2 = 10^{-6}$, for $i = 1, 2$. (a) No asymmetric competition within and between species: $k_{ij} = 0$, for $i, j = 1, 2$. (b) Asymmetric competition present within species and absent between species: $k_{12} = 0$, $k_{21} = 0$. (c) Moderate asymmetric competition between species: $k_{12} = 4$, $k_{21} = 4$. (d) Strong asymmetric competition between species: $k_{12} = 8$, $k_{21} = 8$. (e) Differences between species in interspecific asymmetric competition functions: $k_{12} = 9$, $k_{21} = 7$. (f) Differences between species in interspecific asymmetric competition functions together with fast evolutionary rate for species 2: $k_{12} = 9$, $k_{21} = 7$ $\sigma_2^2 = 10^{-5}$.

3.5 Differences in Interspecific Asymmetric Competition

In general the advantage gained by a large individual of species 1 over a small one of species 2 does not have to be the same as the advantage to an individual of species 2 when the sizes are reversed, ($k_{12} \neq k_{21}$). For instance, one might well expect the canopy architecture of two plant species to differ; the one with the more open canopy then has a less adverse effect on its smaller neighbours than the species with the more closed canopy when there is competition for light. Such differences between species seem particularly likely when the species in competition are not closely related (Englund et al., 1992).

Differences in the degree of asymmetry between species can add further complexities to the dynamics, because the phase portrait is no longer symmetric about the line $s_1 = s_2$. Figure 2e gives an example in which the inner isoclines intersect at three points, the outer two points (A) and (B) both being attractors. Fixed point (A) satisfies the condition for convergence for both species and the condition for non-invasibility for species 2 (Inequalities (13), (14)). Point (B) satisfies the conditions for non-invasibility and convergence for species 1 only. This illustrates the fact that convergence by both species is not necessary for the fixed point to be an attractor, just as non-invasibility is not (Abrams et al., 1993a; Marrow et al., 1996).

In fact the stability properties of fixed point (B) depend on the coefficients that scale the evolutionary rates in Equations (8), in addition to the properties of the inner isoclines. This is shown in Figure 2f, where the coefficient of species 2 is increased by a factor of ten. As can be seen from the orientation of the trajectories, evolution in the vertical direction (species 2) is now faster than in the horizontal direction (species 1), and this prevents point (B) from being an attractor. The evolutionary trajectories are nonetheless confined to a region around the fixed point, and consequently the asymptotic state is now a periodic orbit.

The periodic asymptotic state constitutes a Red Queen dynamic, the sequence of trait substitutions continuing for as long as the system remains in existence (Figure 3a) (Marrow et al., 1992, 1996; Dieckmann et al. 1995). Depending on where the species are on the periodic orbit, invasions are sometimes by larger mutants, and sometimes by smaller mutants. The oscillations in body size of the two species are nearly in phase, but the larger evolutionary rate constant of species 2 causes it to have oscillations of greater amplitude. The cycle cannot be driven by changes in the relative abundance of the two species (cf. Pimentel, 1968; Pease, 1984), since their equilibrium numbers are approximately in phase, being high when body size is relatively small (Figure 3b). Selection follows these changes in population size, the component due to intraspecific encounters being at its peak when numbers are greatest as measured by Equation (10)

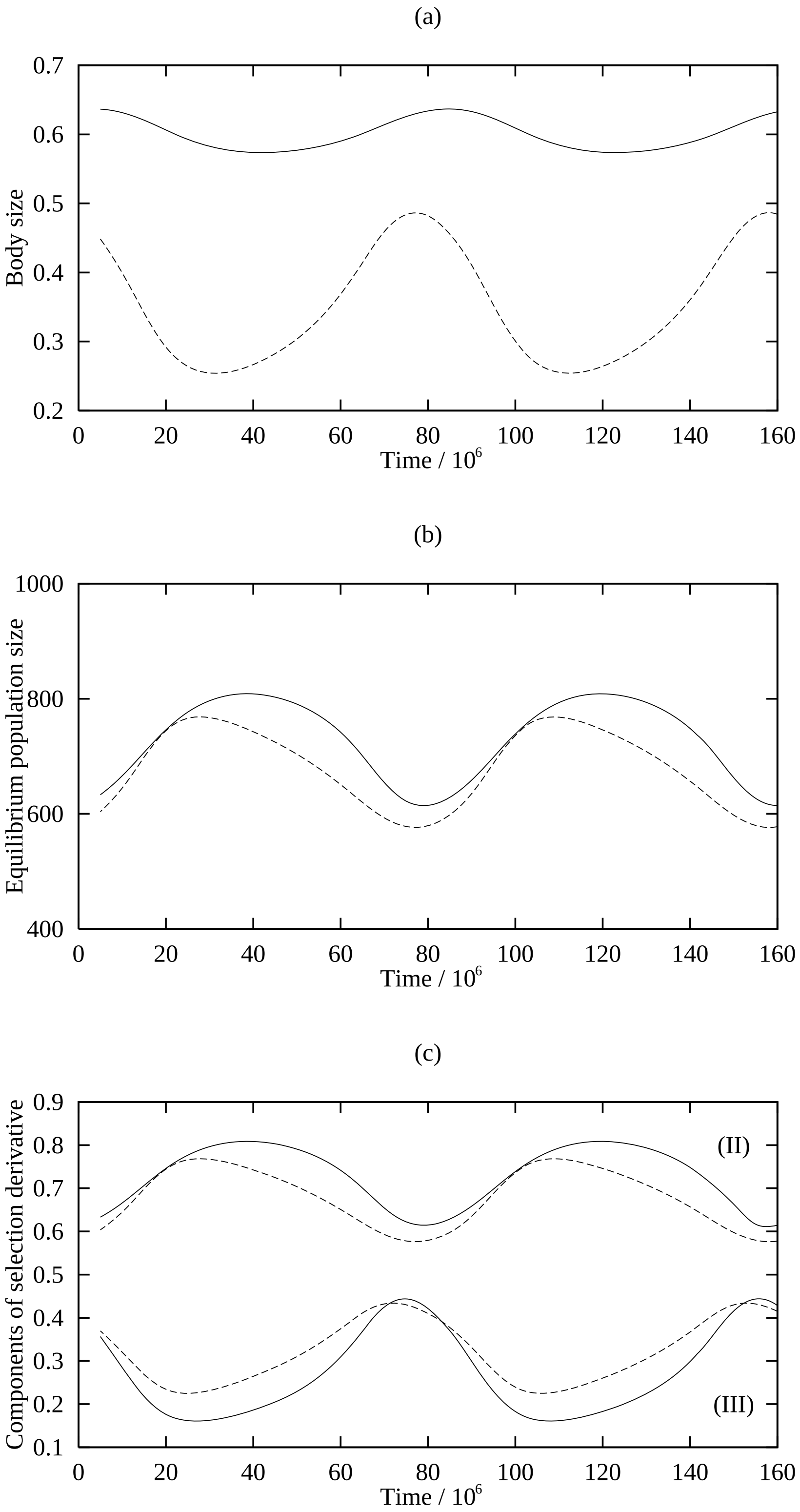

Figure 3 Properties of the periodic attractor of Figure 2f, variables being given as functions of time: (a) body size; (b) equilibrium population size / $2 \cdot 10^{-3}$; (c) the intraspecific component of the selection derivative (Equation (9,II)) shown as II, and the interspecific component of the selection derivative (Equation (9,III)) shown as III. Continuous lines: species 1; discontinuous lines: species 2. Parameter values as in Figure 2f.

part (II) (Figure 3c). Conversely, the component due to interspecific encounters is at its peak when the numbers are lowest as measured by Equation (10) part (III).

4 Discussion

The results above show that asymmetric competition between species can, in principle, have the following evolutionary effects. First, the non-linearities in the inner isoclines created by asymmetric competition (a) cause evolutionary fixed points to be shifted to larger body sizes, and (b) can give rise to multiple fixed points. Second, the asymptotic states can be periodic orbits (Red Queen dynamics), rather than fixed points. Third, because large individuals suffer less disadvantage when competition is asymmetric, coexistence of the species occurs over a larger part of the phenotype space. Fourth, evolution to the boundary of the coexistence region remains possible, and the smaller species then drives the larger one to extinction, as Taper and Case (1992a) found in their analysis. Much of this rich behaviour arises from modelling evolution in a manner that links it directly to the underlying population dynamics. Such population processes are important for ecologically-significant traits, because the selection pressures one species generates upon another depend on the abundance of the species concerned, as is clear from Equation (10) (see also Pimentel, 1968; Abrams and Matsuda, 1994).

4.1 Quasi-Monomorphism

To lay bare the links from individual encounters, through population dynamics, to a macroscopic model of coevolution, we have deliberately kept the processes operating at each scale rather simple. As a result, some warnings about the limitations of the phenotype dynamics in Equations (8) are needed. The most critical assumption is that the populations can be treated, to a good approximation, as monomorphic with respect to the evolving traits. Clearly one would wish to remove this; a model which tracks phenotype distributions through time would be preferable. The quantitative-genetic recursion used by Slatkin (1980) and Taper and Case (1985, 1992a) does retain the phenotype distribution, but does not deal with the mutation process and is much less tractable analytically. What we know from our stochastic simulations is that the model remains a good approximation to the mean of a stochastic birth/death process in which different phenotypes occur with a low probability through mutation, generating a phenotype distribution with a small variance (Dieckmann, 1994; Dieckmann et al., 1995).

The assumption of almost complete monomorphism is widely made in modelling coevolution, through the use of the first order term of a Taylor's expansion of the fitness function (i.e. a selection derivative of the form used in Equations (8)). In models motivated by quantitative genetics, the argument of the function is the additive genetic value, in which case monomorphism applies to this rather than the phenotypic value (Iwasa et al., 1991; Taper and Case, 1992a; Abrams et al., 1993a; Marrow et al., 1996). One might alternatively require that terms in the fitness function of order greater than two are negligible (Abrams et al., 1993b), but this would not be generic for coevolving systems. Dynamics like those of Equations (8) have been used heuristically on a number of occasions in evolutionary biology (e.g. Brown and Vincent, 1987; Hofbauer and Sigmund, 1990); these approaches also have an assumption of monomorphism although this is not made explicit.

4.2 Dynamical Systems and Evolutionary Game Theory

The model illustrates how dynamical and game-theoretic approaches to study of evolution differ. Game theoretic approaches use isoclinic properties of non-invasibility (the ESS condition). But it is clear from the phase portraits that this isoclinic property is not enough to indicate whether the fixed point is an attractor of the evolutionary trajectories (Takada and Kigami, 1991; Abrams et al., 1993a; Marrow et al., 1996). In addition, they can provide no information on periodic attractors, where the trajectories do not tend to a fixed point at all. There appears to be no short cut possible; direct investigation of the dynamical system is needed.

Nevertheless, the isoclinic properties do provide some useful insights. For instance, in the coevolutionary system considered here, at any fixed point with the property $\hat{s}_1 \neq \hat{s}_2$, the species with smaller body size is at a fitness minimum. Although selection on the larger species is stabilizing, it is disruptive for the smaller one and this may lead to a polymorphism developing (Christiansen, 1991; Metz et al., 1994). In this event, evolutionary branching takes place, and the quasi-monomorphic evolutionary dynamic we have used is no longer appropriate. In principle, it is possible to follow the evolution further, by increasing the dimensionality of Equations (8) to three, and treating the two phenotypes of the smaller species separately. We have not done this because it has not yet been possible to observe such branching in our stochastic simulations of the underlying birth-death processes; the robustness of branching remains to be demonstrated.

4.3 Genetic Systems

Strictly speaking, the model we have described applies only to phenotypes with an asexual or haploid genetic system. We suggest that, with few modifications, the dynamics would also apply over much of the trait space to a diploid genetic system if there is an ordering of the phenotypic effects of the genes. The ordering is either that $s_i < s_i' < s_i''$ or that $s_i > s_i' > s_i''$, where s_i' and s_i'' are the phenotypes of the mutant heterozygote and homozygote respectively; additivity of the phenotypic effects is a special case of this. The probability that a mutant replaces a resident allele depends first of all on the probability that it escapes extinction when rare; this is still given by Equations (6) and (7), the per capita rate of increase now being that of the rare heterozygote. Replacement subsequently depends on whether the mutant goes to fixation. As long as s_i' and s_i'' do not straddle the inner s_i-isocline, this ordering should lead to fixation of mutants which have escaped extinction when rare. Moreover, polymorphisms straddling the isocline would not normally be maintained, because evolution in the other species usually moves the system away from the vicinity of the isocline. Exceptions to this are the evolutionary fixed points themselves; here the larger species may go into a sustained polymorphic state, in which case the assumption of quasi-monomorphism no longer applies. Notice that the evolutionary rate coefficient in Equation (8) has to be multiplied by a factor of two if a switch from haploidy to diploidy is involved.

4.4 Transients of Evolutionary Dynamics

The focus of most early work on evolution of competing species was the divergence of characters, in view of the potential importance of niche differentiation in structuring ecological communities (Hutchinson, 1959; Roughgarden, 1983b). The trajectories in Figure 2 illustrate how minor a role character divergence can play once asymmetric competition is introduced (see also Abrams, 1987; Taper and Case, 1992a). Character divergence would require a region in the phase space where the species with larger body size evolves still larger sizes and the smaller species evolves still smaller sizes. Although such regions do exist, the dynamics over most of the phase space comprise either character convergence or parallel character shifts (Taper and Case, 1992b). Convergence occurs when the larger species is evolving to a smaller size and the smaller one to a larger size, as in the top left and bottom right regions of the phase space. Parallel character shifts occur when both species change in the same direction, as in most of the rest of the phase space. The parallel character shifts may themselves be convergent, getting closer to the line $s_1 = s_2$, but it is also common in our examples to observe divergent shifts, getting further from the line $s_1 = s_2$. Notice that, if there had already been single-species evolution to a fixed point before the two species met, the starting point for coevolution would be the body size at the fixed point that applies in the absence of interspecific competition.

4.5 Red Queen Dynamics

The results show that evolution can lead to a cyclic asymptotic state, although our exploration of the parameter space suggests that such behaviour is relatively infrequent. The existence of a Red Queen dynamic is important for several reasons. First, it warns that the current preoccupation of evolutionary theory with fixed-point asymptotic states of evolution, in particular ESSs, misses other possible outcomes (Dieckmann et al., 1995); these are likely to require more consideration as theorists turn to problems of higher dimensionality such as those of coevolution. Second, it demonstrates that continuing evolution is not dependent on changes in the abiotic environment (although normally this obviously plays a major part); all that is needed is a system of interacting and mutating species to prevent evolution from coming to a halt.

Cyclic solutions are well known from previous studies of evolution under asymmetric competition within species. What happens is that mutants with body sizes greater than those prevailing in the population gain an advantage and body size increases; but eventually mutants of small size can invade because they gain an advantage so great from the low costs of small size that this outweighs the defeat they experience in every encounter (Maynard Smith and Brown, 1986). Such models have the properties that: (a) mutants can cause large changes in phenotype, and (b) the payoffs are discontinuous functions of phenotype. Parker (1985) suggested that cyclic systems will typically revert to fixed point behaviour if the payoffs are made continuous; if in addition mutational steps are made small, cyclic dynamics ought to become still less likely. That Red Queen dynamics can still occur in our model, under a small mutation variance and a continuous fitness function, suggests that cyclic asymptotic states to phenotypic evolution are more robust than has previously been thought.

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Summary

The Dynamical Theory of Coevolution

A unifying framework is presented for describing the phenotypic coevolutionary dynamics of a general ecological community. We start from an individual-based approach allowing for the interaction of an arbitrary number of species. The adaptive dynamics of species' trait values are derived from the underlying population dynamics within the community; in consequence, the evolutionary process is driven by ecological change.

We present a hierarchy of dynamical models for the investigation of coevolutionary systems. The necessity of stochastic treatment is demonstrated and deterministic approximations are derived where appropriate. The mathematical framework advanced here to our knowledge is the first one to combine the individual-based, stochastic perspective with a fully dynamical analysis of the phenotypic coevolutionary process.

The hierarchy of models presented is particularly geared to infer evolutionary predictions from ecological assumptions. Applications to evolutionary dynamics both in predator-prey systems and under asymmetric competition demonstrate the versatility of our approach. Rich coevolutionary patterns are obtained and novel evolutionary phenomena are revealed.

Deductions are given to derive various well-known equations from the literature of evolutionary modelling. Consequently the different domains of validity for these models are delineated and several ad-hoc assumptions are removed. In particular, equations central to the fields of evolutionary game theory, adaptive dynamics, replicator dynamics and reaction-diffusion models of phenotypic evolution are recovered and are identified as special cases within a dynamical theory of coevolution.

Curriculum Vitae

Ulf Dieckmann was born on November 11th, 1966, in Hattingen, Germany. After obtaining his Abitur from Gymnasium Waldstraße, Hattingen, Germany, in 1986, and serving in the German social service from 1986 to 1988, he took up his studies in physics at the Rheinisch-Westfälische Technische Hochschule at Aachen, Germany, in 1988.

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Ulf Dieckmann has worked at Stanford University and the Xerox Palo Alto Research Center, California, USA, the Research Center Jülich, Germany, the University of York, U.K., Leiden University, the Netherlands, and has been a Research Fellow at the Institute for Advanced Study, Wissenschaftskolleg zu Berlin, Germany. He is working on the mathematical foundations of coevolutionary dynamics, on selection in spatially extended systems, the adaptational design of neural networks, and on the evolutionary origin of hierarchical organization.

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