Coevolutionary Dynamics of Stochastic Replicator Systems

Ulf Dieckmann

This material has first appeared in 1994 as
Volume 3018 of the Reports of the Research Center Jülich
(Jül-3018, ISSN 0944–2952)

Abstract

In this thesis we establish a theory of evolutionary dynamics that accounts for the following requirements.

1. The evolutionary process is considered in a coevolutionary context.
2. The theory describes the full dynamics of the coevolutionary process.
3. The coevolutionary dynamics are derived from the underlying population dynamics.
4. The theory accounts for the stochastic aspects of the evolutionary process.

To our knowledge the mathematical framework advanced here is the first to simultaneously combine these four key features of evolution.

We present a hierarchy of three dynamical models for the investigation of coevolutionary systems; each of these models stands for a different balance between descriptive capacity and corresponding analytic tractability. Deductions are given to clarify the interconnections between the models; from the assumptions necessary for these derivations we infer their domains of validity. Equations central to the fields of evolutionary game theory, replicator dynamics and adaptive dynamics are recovered as specialized cases from our mathematical framework. In particular, the canonical equation of adaptive dynamics, which so far has been used on the grounds of plausibility arguments, is underpinned by a formal derivation.

Table of Contents

Introduction

Fluctuations are caused by the discrete nature of matter.

N.G. van Kampen (1981)

The self-organisation of systems of living organisms is elucidated most successfully by the concept of Darwinian evolution. The processes of reproduction, variation, inheritance and interaction are sufficient to enable organisms to adapt to their environments by means of natural selection. 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 of evolutionary states (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. 1994). Consequently, if the mutation structure affects the evolutionary dynamics, it must not be ignored when investigating evolutionary outcomes. Furthermore, a dynamical perspective is required in order to deal with evolutionary transients and nonequilibrium evolutionary attractors.
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 can be demographic stochasticity of resident populations, this can only be ignored provided that population sizes are sufficiently large (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).

In this thesis we establish a theory of evolutionary dynamics that accounts for the above requirements. To our knowledge the mathematical framework advanced here is the first to simultaneously combine these four key features of evolution. We present a hierarchy of three dynamical models for the investigation of coevolutionary systems; each of these models stands for a different balance between descriptive capacity and corresponding analytic tractability. Deductions are given to clarify the interconnections between the models; from the assumptions necessary for these derivations we infer their domains of validity. Equations central to the fields of evolutionary game theory, replicator dynamics and adaptive dynamics can be recovered as specialized cases from our mathematical framework. In particular, the canonical equation of adaptive dynamics, which so far has been used on the grounds of plausibility arguments, is underpinned by a formal derivation.

The thesis is devided into three parts. In *Part A* we outline definitions, empirical evidence and mathematical descriptions of coevolutionary dynamics. In the main *Part B* the hierarchy of our three models of coevolutionary dynamics is established and analyzed. In *Part C* we give an application of the derived framework to a specific type of coevolutionary community.

After a brief introduction to the biological background of evolutionary and coevolutionary processes in *Chapter 1*, *Chapter 2* sketches the models that have been employed in the mathematical literature to describe such processes. In *Chapter 3* we summarize some limitations of these approaches and conclude a profile of desiderata that has served to shape the present work.

Based on the minimal conditions for the incidence of evolution by means of natural selection, *Chapter 4* presents a general framework for describing the simultaneous evolution of an arbitrary number of species in terms of individual birth, death and mutation processes. The resulting generalized replicator equation defines our first model of coevolutionary dynamics, the polymorphic stochastic model. After introducing the monomorphic regime in *Chapter 5* we employ the generalized replicator equation to derive as a limiting case the reduced description of adaptive dynamics which we call the monomorphic stochastic model. This second model of coevolutionary dynamics still retains the important stochastic features of the adaptive process and explicitly accounts for random mutational steps and the risk of extinction of rare mutants. From this, our third model of coevolutionary dynamics, the monomorphic deterministic model, is obtained as a deterministic approximation in *Chapter 6*. The canonical equation of adaptive dynamics is recovered and we demonstrate its validity up to first order. We refine this result by means of higher order correction terms allowing for increased accuracy. Algorithms for implementing our three models of coevolution are provided throughout Chapters 4 to 6 and the richness of resulting coevolutionary phenomena is illustrated by means of examples. In *Chapter 7* the two monomorphic models are analyzed in more detail. Stability conditions for the adaptive dynamics are established, and the higher orders of the monomorphic deterministic model are shown to give rise to new, unexpected evolutionary effects. Moreover, the complicated principle of mutual exclusion is proved for a special case, and a method for constructing variable adaptive landscapes for the dynamics of adaptation is presented. In *Chapter 8* we further extend our mathematical framework such as to encompass more complex evolutionary scenarios.

Chapter 9 is concerned with predator-prey coevolution. We employ the hierarchy of coevolutionary models derived so far to investigate a prototypic community of such species. Possible evolutionary outcomes are classified and the conditions for their occurrence analyzed. In particular, we focus on the phenomenon of evolutionary cycling and show that so called Red Queen dynamics are a likely outcome of coevolutionary processes.

Parts of the work described here have been reported in the following papers

1. Dieckmann, U., Law, R.: *The dynamical theory of coevolution: A derivation from stochastic ecological processes.* Accepted for publication by the Journal of Mathematical Biology.
2. Marrow, P., Dieckmann, U., Law, R.: *Evolutionary dynamics of predator-prey systems: an ecological perspective.* Accepted for publication by the Journal of Mathematical Biology.
3. Dieckmann, U., Marrow, P., Law, R.: *Evolutionary cycling in predator-prey interactions.* Submitted for publication.

and were presented in talks at the University of Warwick, the University of Utrecht, the Humboldt-Universität Berlin and as an invited lecture at the “Symposium Adaptive Dynamics” of the European Science Foundation.

List of Symbols

Basic Notation

i	Species index.
k	Individual index.
l	Trait index.
N	Number of species making up the coevolutionary community.
n_i	Number of individuals in species i. $n = (n_1, \dots, n_N)$.
ν_i	Number of adaptive traits in species i.
s_i	Adaptive trait value(s) or phenotype in species i. $s = (s_1, \dots, s_N)$.
$p_i(s_i)$	Distribution of adaptive trait values in species i. $p = (p_1, \dots, p_N)$.
$n_i(s_i, p_i)$	Number of individuals with adaptive trait value s_i in species i as given by the distribution p_i.

Time and Timescales

t	Process time.
T	Average waiting time between two subsequent events in the stochastic models.
τ	Typical timescale of a particular dynamic (specified by an index).

Ecological Rates

$f_i(s_i', p)$	Per capita growth rate of an individual of species i with adaptive trait value s_i' in an environment determined by the phenotypic distributions p. When a dependence of the environment on external influences is considered, this is indicated by an extra argument t.
$\widetilde{f}_i^j(s_i', s, n)$	Per capita growth rate of individuals in species i with adaptive trait values s_i' in an environment determined by the phenotypic distributions $p = \big(n_1 \cdot \delta_{s_1}, \ldots, n_j \cdot \delta_{s_j} + n_0 \cdot \delta_{s_0}, \ldots, n_N \cdot \delta_{s_N}\big)$. Resident populations are assumed to be monomorphic and a single mutant population, formally taking the index $i = 0$, is considered in species j. When a dependence of the environment on external influences is considered, this is indicated by an extra argument t.
$\overline{f}_i(s_i', s)$	Time-averaged per capita growth rate of rare mutant individuals in species i with adaptive trait values s_i' in an environment determined by the monomorphic resident populations with adaptive trait values s. The time average is trivial for resident population dynamics attaining equilibria but is essential for coevolution under nonequilibrium population dynamics. When a dependence of the environment on external influences is considered, this is indicated by an extra argument t.
b_i, $\widetilde{b}_i^j$, $\overline{b}_i$	Per capita birth rates of individuals. Definitions are equivalent to those of $f_i(s_i, p)$, $\widetilde{f}_i^j(s_i', s, n)$ and $\overline{f}_i(s_i', s)$ above.
d_i, $\widetilde{d}_i^j$, $\overline{d}_i$	Per capita death rates of individuals. Definitions are equivalent to those of $f_i(s_i, p)$, $\widetilde{f}_i^j(s_i', s, n)$ and $\overline{f}_i(s_i', s)$ above.

Mutation Properties

$M_i(s_i, s_i' - s_i)$	Mutation distribution in species i for mutations in individuals with adaptive trait values s_i giving rise to others with adaptive trait values s_i'. When only homogeneous mutation distributions are considered, this is indicated by dropping the then superfluous first argument s_i.
$m_{ji}(s_i)$	jth mutation moment of the mutation distribution M_i at the adaptive trait value s_i. When only homogeneous mutation distributions are considered, this is indicated by dropping the then superfluous argument s_i.
$\sigma_i^2(s_i)$	Variance of the mutation distribution M_i at the adaptive trait value s_i. When only homogeneous mutation distributions are considered, this is indicated by dropping the then superfluous argument s_i.
$\mu_i(s_i)$	Mutation ratio in species i at the adaptive trait value s_i. When only homogeneous mutation ratios are considered, this is indicated by dropping the then superfluous argument s_i.
$B_i(s_i, s_i' - s_i)$	Probability distribution in species i of offspring adaptive trait values s_i' arising from adaptive trait values s_i. When only homogeneous mutation processes are considered, this is indicated by dropping the then superfluous first argument s_i. $B_i(s_i, s_i' - s_i) = (1 - \mu_i(s_i)) \cdot \delta(s_i' - s_i) + \mu_i(s_i) \cdot M_i(s_i, s_i' - s_i)$.

Probabilities

P	Probability density distribution. Examples: $P(p, t)$, $P(n, t)$ and $P(s, t)$.
$w(p'\|p)$	Transition probability per unit time from the phenotypic distributions p to p'. When a dependence of the environment on external influences is considered, this is indicated by an extra argument t.
$w_i(p_i', p)$	Transition probability per unit time for a change of the phenotypic distribution in species i from p_i to p_i' in an environment determined by p. When a dependence of the environment on external influences is considered, this is indicated by an extra argument t.

$w_i^-(s_i', p)$	Transition probability per unit time for the removal of an individual with adaptive trait value s_i' from the phenotypic distribution in species i in an environment determined by p. When a dependence of the environment on external influences is considered, this is indicated by an extra argument t.
$w_i^+(s_i', p)$	Transition probability per unit time for the insertion of an individual with adaptive trait value s_i' into the phenotypic distribution in species i in an environment determined by p. When a dependence of the environment on external influences is considered, this is indicated by an extra argument t.
$w(s' \vert s)$	Transition probability per unit time from the adaptive trait values s to s'. When a dependence of the environment on external influences is considered, this is indicated by an extra argument t.
$w_i(s_i', s)$	Transition probability per unit time for a trait substitution in species i from the adaptive trait value s_i to s_i' in an environment determined by the monomorphic resident populations with adaptive trait values s. When a dependence of the environment on external influences is considered, this is indicated by an extra argument t.
$\mathcal{M}_i(s_i', s)$	Probability density per unit time for a mutation within the population of species i from s_i to s_i' in an environment determined by the monomorphic resident populations with adaptive trait values s. When a dependence of the environment on external influences is considered, this is indicated by an extra argument t.
$\mathcal{S}_i(s_i', s)$	Probability of a mutant s_i' within the population of species i to successfully escape extinction in an environment determined by the monomorphic resident populations with adaptive trait values s. When a dependence of the environment on external influences is considered, this is indicated by an extra argument t.

Spaces and Subspaces

$\widehat{P}_i$	Polymorphic trait space of species i. $\widehat{P} = \times_{i=1}^{N} \widehat{P}_i$.
$\widehat{N}_i$	Population size space of species i. $\widehat{N} = \times_{i=1}^{N} \widehat{N}_i$.
$\widehat{S}_i$	Monomorphic trait space of species i. $\widehat{S} = \times_{i=1}^{N} \widehat{S}_i$.
$\widehat{S}_c$	Region of coexistence. Subspace of $\widehat{S}$ allowing for positive population sizes in all N species. $\widehat{S}_c = \{ s \in \widehat{S} \mid \hat{n}_i(s) > 0 \quad \text{for all} \quad i = 1, \ldots, N \}$.
$\widehat{S}_{i,c'}$	Subspace of the monomorphic trait space $\widehat{S}_i$ not excluded by constraints on trait values or on combinations therof. $\widehat{S}_{c'} = \times_{i=1}^{N} \widehat{S}_{i,c'}$.
$\widehat{S}_C$	Subspace of the monomorphic trait space $\widehat{S}$ accessible to the adaptive dynamics of the N-species coevolutionary community. $\widehat{S}_C = \widehat{S}_c \cap \widehat{S}_{c'}$.

Mappings

$\lvert \ldots \rvert$	Absolute value function. $\lvert x \rvert = \sqrt{\sum_i x_i^2}$.
$\langle \ldots \rangle$	Expectation value function. $\langle f(x) \rangle = \int f(x) \cdot P(x)\, dx$.
$(\ldots)_+$	Product of Heaviside function and identical function. $(x)_+ = x \cdot \Theta(x)$.
∂_i', ∂_i	Abbreviations for derivatives. $\partial_i' f = \frac{\partial}{\partial s_i'} f$ and $\partial_i f = \frac{\partial}{\partial s_i} f$. Convention: When evaluating a function which is obtained as a derivative and takes particular arguments, the derivation precedes the substitution of the arguments.
δ_{ij}	Kronecker symbol. $\delta_{ij} = 1$ for $i = j$, $\delta_{ij} = 0$ for $i \neq j$.
δ, δ_y	Dirac's δ-function. $\int f(x) \cdot \delta(x)\, dx = f(0)$ and $\int f(x) \cdot \delta_y(x)\, dx = \int f(x) \cdot \delta(x - y)\, dx = f(y)$.
Δ	Δ-functional in function space. Used only in combination with a functional integration indicated by $\mathcal{D}$. $\int F(f) \cdot \Delta(f - g)\, \mathcal{D}f = F(g)$.
$\mathcal{D}$	Differentiation symbol employed instead of d to denote a functional integration. Used only in combination with the functional Δ. $\int F(f) \cdot \Delta(f - g)\, \mathcal{D}f = F(g)$.

Miscellaneous Constructs

$\hat{n}$	Population sizes at fixed points of the population dynamics.
$\hat{s}$	Adaptive trait values either located on isoclines or at fixed points of the adaptive dynamics.
$\alpha_i(\hat{s})$	Invasion angle of $\hat{s}$. $\alpha_i(\hat{s}) = \arctan\big(\partial_i'^2 \overline{f}_i(\hat{s}_i, \hat{s}), \partial_i^2 \overline{f}_i(\hat{s}_i, \hat{s})\big)$.
$R_i(s)$	Range of adaptive trait values s_i' that have a positive per capita growth rate when being rare in an environment determined by the monomorphic resident populations with adaptive trait values s. $R_i(s) = \big\{s_i' \in \widehat{S}_i \mid \overline{f}_i(s_i', s) > 0\big\}$.
$e_i(p, t)$	Environment of species i at time t given the phenotypic distributions p.
$a_{ji}(s)$	jth jump moment of species i for resident adaptive trait values s.
$m^{ij}(A)$	Minor of the matrix A where the ith row and the jth column have been deleted.
$z^{ij}(A)$	The matrices $z^{ij}(A)$ are derived from the matrix A by replacing the elements of the ith row and the jth column by 0, except the element A_{ij} itself which is replaced by 1; successive mappings of this sort are denoted by $z^{ij,kl}(A) = z^{ij}\big(z^{kl}(A)\big)$. Similarly, the vector $z^i(a)$ is obtained from a vector a by setting a_i to 0.
1^i	Vector with components $1_j^i = \delta_{ij}$.
$k_i(s)$	Evolutionary rate coefficient of species i for resident adaptive trait values s.
W	Adaptive landscape or “fitness” function. Examples: $W_i(s_i', s)$, variable adaptive landscape for species i (extented in s_i' and parameterized by s), and $W(s', s)$, variable adaptive landscape for the entire coevolutionary community (extented in s' and parameterized by s).

Part A
Background and Previous Work

The process of evolution by means of natural selection is fundamental to our understanding of nature. It underpins many of the phenomena of self-organization encountered at all sorts of levels in the complex hierarchy of being.

Evolution taking place in a constant environment is an abstraction. This simplified view sometimes is justified to facilitate the analysis of single adaptive features observed in the world of living organisms; yet, in its idealized form it is seldom met in reality. The real world is coevolving: adaptive systems are situated in environments which in turn are adaptable.

In this part we give a brief introduction to evolutionary and coevolutionary thought and indicate some of the major empirical evidence for coevolution in nature (Chapter 1). We then sketch the key concepts that have been advanced in the past to promote mathematical analyses of coevolutionary dynamics (Chapter 2). From a discussion of these ideas we conclude a profile for a dynamical theory of coevolution (Chapter 3) contributions to which are presented in the next part.

Chapter 1
The Concept of Coevolution

1.1 Origin of Coevolutionary Thought

In the following we introduce definitions for evolutionary and coevolutionary processes and outline the evidence for the occurrence of the latter.

Evolution

The theory of *evolution by natural selection* has been developed independently by Darwin and Wallace (Figure 1.1). In constructing his theory, Darwin combined insight gained both from observing the abundance of offspring in numerous species, which he had noticed during his voyage on the H.M.S. ”Beagle”, and from studying Malthus' work on a principle of competition in the “Essay on the Principle of Population” (1798). Darwin's seminal book “The Origin of Species by Means of Natural Selection, or The Preservation of Favoured Races in the Struggle for Life” was published in 1859 and advanced two major hypotheses: that all organisms have descended with modifications from common ancestors, and that the chief agent of modification is the process of natural selection acting on individual variation.

It is generally agreed that there exist *minimal conditions* for a process of self-organization in living organisms to be enacted by natural selection. A general and abstract characterization of such features is the *replicator concept* proposed by Dawkins (1976). He

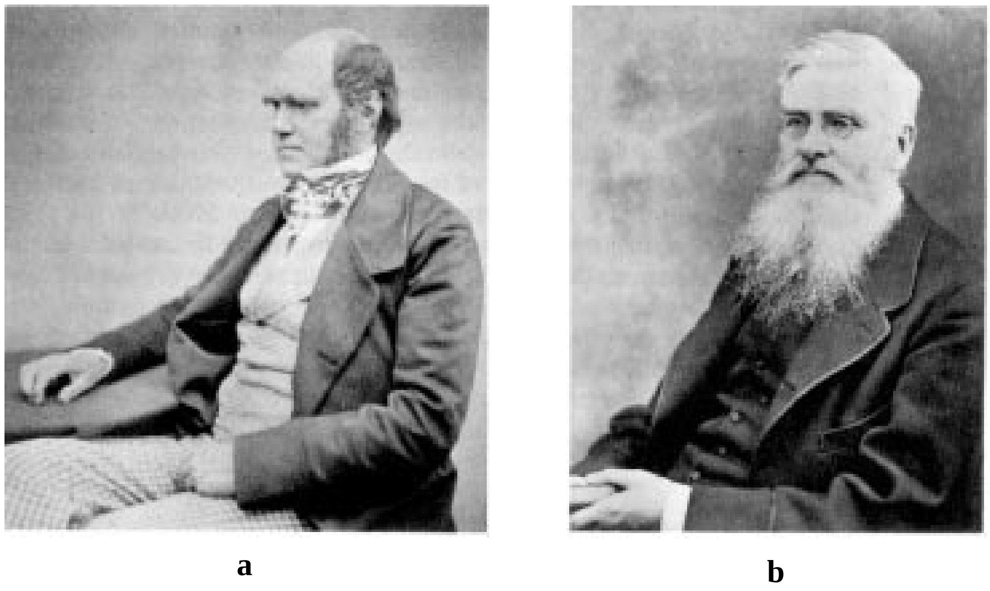

Figure 1.1 Fathers of evolutionary thought. (a) Charles Robert Darwin (1809–1882), (b) Alfred Russel Wallace (1823–1913). Their theory of evolution by means of natural selection was presented at the Linnaean Society of London in 1858.

argues that units, called replicators, which are capable of (i) reproduction, (ii) inheritance of traits allowing for (iii) variability, and (iv) interaction causing reproduction or survival of replicators to be trait-dependent, inevitably will undergo evolution by natural selection. Similar conditions have been given 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). In Chapter 4 we will translate Dawkins' replicator concept into mathematical language by establishing what we call the *generalized replicator equation*.

Coevolution

We will use the term *coevolution* to indicate adaptation to an environment that in turn is adaptive. In other words, the selective factor that stimulates adaptation in a species is itself responsive to that adaptation. By *adaptation* we refer to the process of evolution by natural selection described above.

The idea of coevolution is already implicit in Darwin's original work. When discussing pollination of flowers by insects he remarks "Thus I can understand how a flower and a bee might slowly become, either simultaneously or one after the other, modified and adapted in the most perfect manner to each other" (Darwin 1959). The explicit 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 mean 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 conceived in terms of a single pair of species. However, since most species interact with a variety of other species, we do not restrict the meaning of coevolution to the adaptation of pairwise relations. The reciprocal evolutionary change of interactions among classes of species is called *diffuse coevolution*.

The concept of coevolution overcomes the conceptual limitations of traditional biological fields like population genetics. Due to the formidable asperities inherit in a detailed description of the genetic background of evolutionary change, here each species is considered in isolation, with the environment and associated species relegated to the background which is assumed to be unchanged (Futuyma and Slatkin 1983). Coevolutionary dynamics explicitly encompass the feedback loop between a species and its environment (Lewontin 1983) when analyzing evolutionary phenomena. In consequence, the study of coevolutionary processes also spawns a more elaborate view of the time course of evolution. When considering only one species, this would be expected to evolve by means of natural selection towards a state where it has met whatever challenges it faced in terms of its environment. Such endpoints of evolution are clearly unrealistic on a larger evolutionary timescale. In contrast, if two or more species are adapting in response to each other, continued evolutionary progress can take place.

Evidence for Coevolution

The existence of coevolutionarily evolved interactions between species is underpinned by observations from a variety of fields. From observation of genetic change, over indications from the fossil record, the evidence ranges to taxonomic considerations and results from morphology and ethology. Details are given in Futuyma and Slatkin (1983).

The challenge in any potential instance of coevolution is, however, to show explicitly that traits have evolved in response to particular interactions; the decision between such a coevolutionary explanation and the assertion of the interaction being established only after the traits considered had evolved, is sometimes debatable. The examples given in the next section illustrate these considerations.

1.2 Classical Examples of Coevolutionary Dynamics

In this section we briefly review three classical cases giving empirical evidence for coevolutionary dynamics. In passing, we introduce ecological scenarios that have fostered the incidence of coevolution.

Mimetic Coevolution

The observation of mimicry is probably the earliest instance of adaptation suggesting coevolutionary processes to have occurred in nature. Fisher called mimicry theory “the greatest post-Darwinian application of natural selection” (Gilbert 1983).

Mimicry, defined generally as “resemblance of birds, animals and insects to their natural surroundings, giving some protection from enemies” (Hornby 1977), in a coevolutionary context means the phenotypic convergence in the outer appearance of a model species and a mimetic species owing to common selective pressure by the biotic environment. Even more specific, Wickler (1968) defines mimicry as the sending of fake signals by a mimetic species; the signals are fake or deceptive relative to those sent by a model species to a third species such as a predator. From this it is clear that mimicry is expected to evolve only on the basis of well-established communication systems. In consequence the incidence of mimicry is more likely under circumstances of tight ecological association between species and has therefore been suggested as a rough index to the degree of specificity and long-term stability of behavioural interactions in an ecosystem (Gilbert 1983).

There are two specific kinds of mimicry, *Batesian* and *Müllerian*. Bates (1862) suggested edible species of butterflies to have acquired a resemblance to warningly colored and noxious or distasteful species. With birds acting as selective agents, effective communication has evolved between the birds and the unpalatable butterflies (model species), protecting the latter from predation and the former from wasting time and energy in pursuit of unsuitable prey. The edible butterflies (mimetic species) take

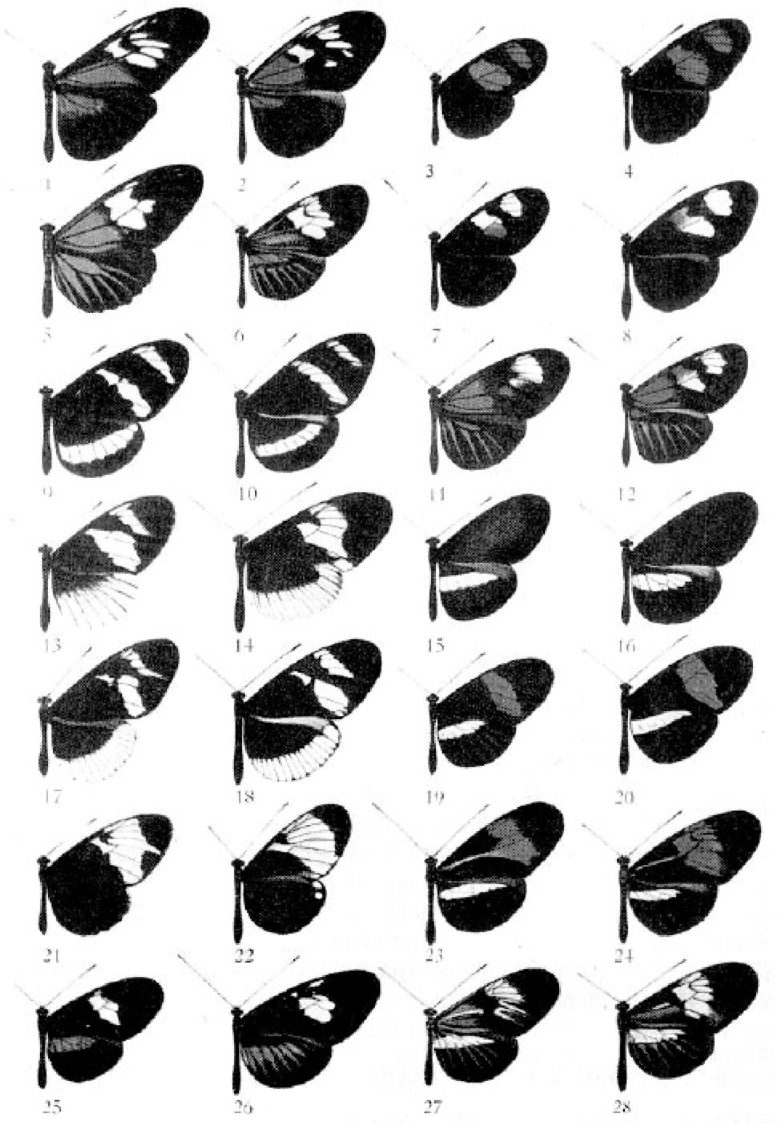

Figure 1.2 Coevolutionary outcomes in parallel races of two butterfly species. Odd numbers refer to races of Heliconius erato, the immediately following even numbers to the corresponding races of Heliconius melpomene from the same geographical area. Each pair of corresponding races has developed a closely resembling color pattern. (after Eltringham 1916)

advantage of this established signalling by imitating the model species' color pattern and in consequence benefit from the same protection from predation. In contrast, Müller (1879) explained phenotypic convergence of color patterns in two species of butterflies that both are distasteful. Due to cooperative education of predators, two species in a common area should benefit by employing the same signalling. Although in this case both species mutually act as model and mimic, the less abundant species will essentially converge to the more frequent one. The Batesian-Müllerian distinction, however, is often considered to characterize the limits of a continuum (Sbordoni et al. 1979).

Figure 1.2 shows one of the best-documented example of Müllerian convergence. The two species of butterflies, Heliconius erato and Heliconius melpomene, have several parallel races showing some strong phenotypic affinities despite the fact that the two species represent distinctive radiations within the genus Heliconius. These parallel races are correlated spatially but not genetically – as far as genes not involved in determining color pattern are concerned (Turner 1971; Turner et al. 1979). It has been shown explicitly that Heliconius melpomene has influenced the evolution of Heliconius erato and vice versa (Gilbert 1983), thus this system is an example of mimetic coevolution.

Predator-Prey Coevolution

As an effect of individual selection on the ecological interactions among predator and prey species the latter should evolve protective characteristics against predation whereas the former is expected to become more efficient in harvesting the prey.

Simple though this prediction is, several complications can arise. First, the simultaneous evolution in the prey and predator species can lead to an *arms race* in the traits affecting their interactions (Dawkins and Krebs 1979). The resulting potential for so called *Red Queen evolution* (Van Valen 1973) is discussed in more detail in Chapter 9. Furthermore, predator-prey coevolution can be diffuse rather than tight. In this case coevolution is likely to be slower and less refined as each species can be involved in a multiplicity of predator-prey interactions, and the coevolutionary process of the entire predator-prey community (then containing numerous species) will often include the extinction of one group of species and its replacement by another (Futuyma 1986).

Figure 1.3 illustrates these aspects. Considered as phenotypic trait for prey and predator is a morphological index that has been shown to be positively correlated with running speed (Bakker 1983). The index measures the depth of the astragular groove relative to the width of the trochlea; it determines the degree to which the limb is constrained to move in a single plane. Low values of the index correspond to ankle joints that enable rotation, a feature that facilitates motions which are useful for climbing or moving over uneven ground. High values indicate that flexibility has been sacrificed to minimize the danger of dislocation in high-speed runs. From the fossil record the temporal evolution

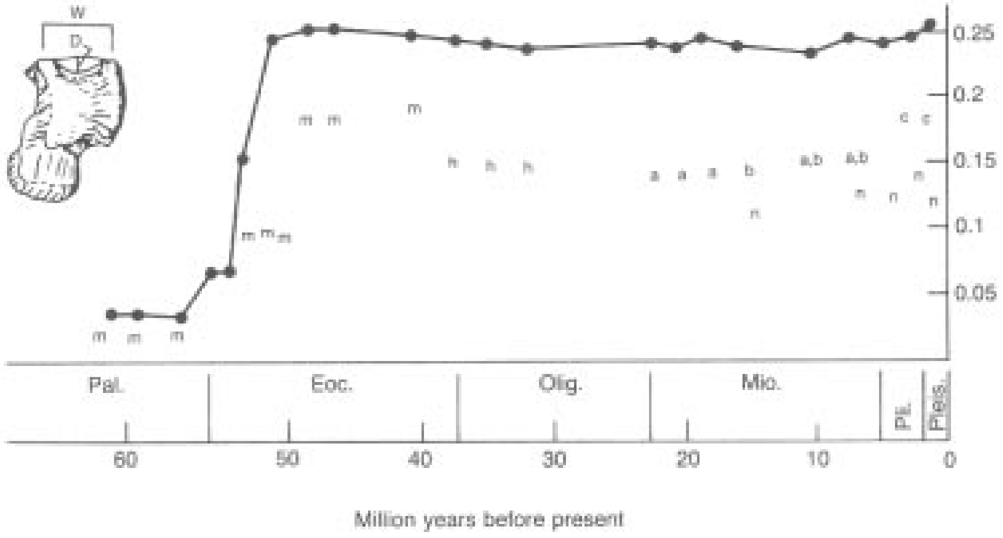

Figure 1.3 Coevolutionary dynamics in North American ungulates and several of their carnivory predators. Plotted is the temporal evolution of a speed index over the past 60 million years. As speed index serves the ratio of astragular groove depth and trochlea width, two features of the ankle joint. Dots connected by solid lines refer to the group of prey species (ungulates, i.e. hoofed mammals), letters to different groups of predator species (mesonychid, hyaenodontid, amphicyonid, borophagine, neofelid, canine). Each index value shown was computed by averaging within the particular group of species. The temporal increase in prey speed index appears to be accompanied by a simultaneous increase in some of the predator speed indices. (after Bakker 1983)

of this index is evaluated over the past 60 million years for a group of prey species and several groups of predator species (see figure legend). The data provides evidence for coevolution by an increase in the prey speed index accompanied by a simultaneous increase in the speed index of some of the predators. Nevertheless, the adaptation in the predator phenotypes is less pronounced than in the prey phenotypes; this can either be interpreted as an effect of diffuse coevolution (Futuyma 1986), attributed to a smaller diversity of predator species compared to prey species (Bakker 1983), or explained by the fact that predator species typically have evolved additional morphological features to increase running speed, like a flexible backbone, that have not been considered in the above analysis (Maynard Smith 1989).

Parasite-Host Coevolution

Despite various similarities to predator-prey coevolution the evolutionary relationships among parasites and their hosts have some singular features.

Though hosts will – like prey species – benefit from more effective defence mechanisms, the extent to which a parasite weakens or kills its host is – in contrast to the case of predation – often correlated with the reproductive rate of the parasite (Futuyma 1986). If this correlation is positive, the evolution in the parasites will tend to maximize their virulence. If, however, the parasites are mainly exchanged between live hosts, the death of the host will hinder the parasites from being transmitted. Consequently, the virulence of the parasite may evolve towards intermediate values.

Notice that within one host strains of the virus possessing a large rate of reproduction and thus a high virulence will be advantageous in terms of individual selection. Nevertheless, between hosts those virus populations are favored that have a large effective transmission rate. This is a seldom case of *group selection* counteracting individual selection; it is based on the existence of temporarily isolated trait groups of parasites within hosts (Wilson 1983).

An example of parasite-host coevolution with a negative correlation between virulence and transmission is provided by the spread of the myxoma virus in the wild rabbit population of Australia after its release in 1950. The myxoma virus is the causative agent of myxomatosis, a disease that is mild in South American rabbits, from which it originated, but usually is fatal in European and Australian rabbits that have not yet been in contact with the virus (Fenner and Ratcliffe 1965). While the disease successfully was reducing the Australian rabbit population size, which had grown to become a serious pest of sheep and cattle grazing land, both virus and host were undergoing evolutionary changes. The coevolutionary dynamics of this case are summarized in Figure 1.4. The vector (transmitting species) of this epidemic is a mosquito that feeds on rabbits only when they are alive; therefore the chance of transmission of the parasite from rabbits that carry a high load of viruses is reduced as such rabbits are likely to be the first to die. This explains the shift in the frequency distribution of the virus population towards more benign strains (Figure 1.4a) and thus the decrease in the virulence of the parasite (Figure 1.4b). Simultaneously, the rabbit population has built up an increased resistance against the myxoma virus (Figure 1.4d) such that the symptomatology of the disease

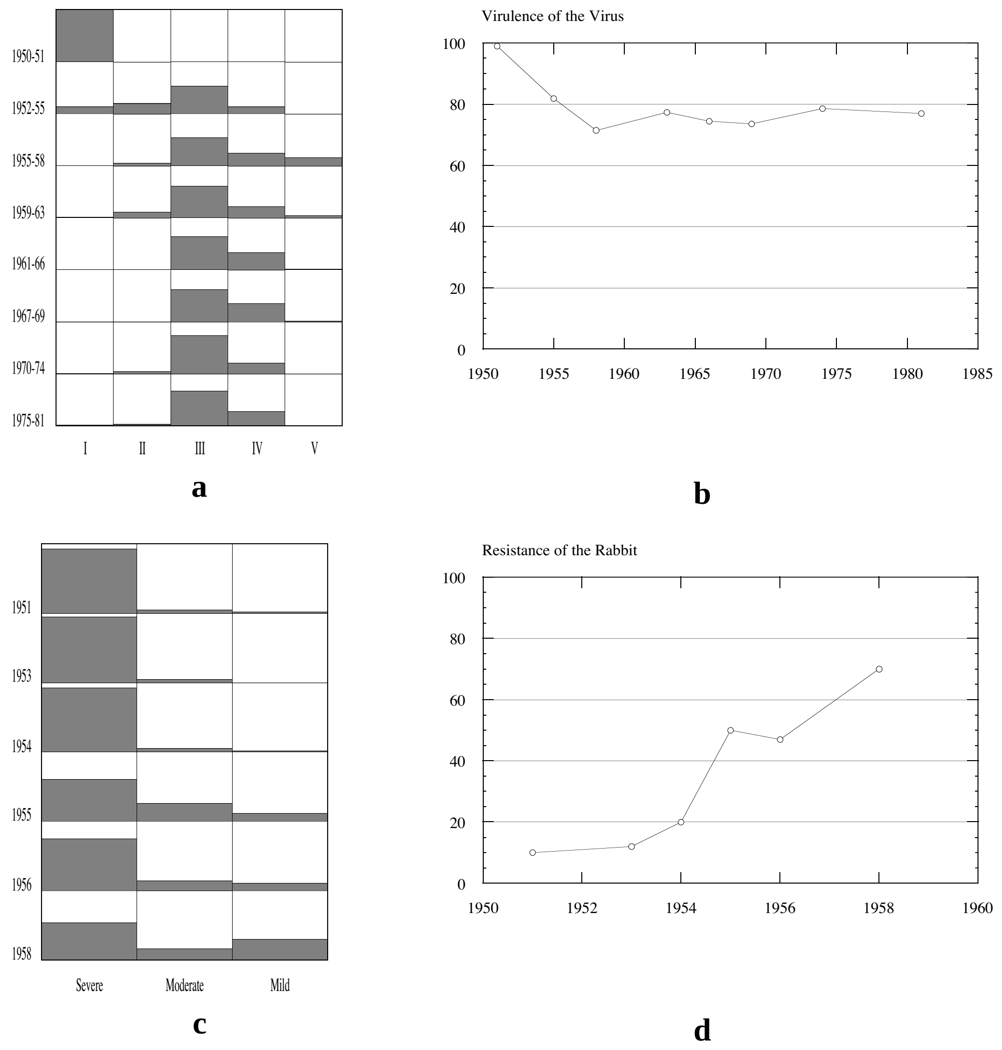

Figure 1.4 Coevolutionary dynamics in the Australian wild rabbit and the myxoma virus. One trait in each species is considered: the virulence of the virus (measured as mortality probability of a standard rabbit strain infected by the virus) and the resistance of the rabbit (measured as survival probability of the rabbit infected by a standard virus strain). Plots (b) and (d) show the temporal evolution of these traits after the introduction of the myxoma virus to Australia in 1950. In addition, plots (a) and (c) illustrate the change in the frequency distributions of virus and rabbit populations; on the horizontal axes standard classifications of virus virulence and rabbit resistance have been used. Initially the myxoma virus has been introduced as a highly virulent strain (belonging to class I) while the resistance of the rabbit was very low (corresponding to severe symptomatology of the infection). In the following decade virus and rabbit populations have coevolved towards more benign virulence and increased resistance. (data from Fenner and Ross 1994)

became more and more moderate (Figure 1.4c). It is interesting to observe that during the past decades the virulence of the myxoma strains has shown signs of slight increase (right part of Figure 1.4b); this might be interpreted as a counteraction to the acquired resistance of the rabbits.

Due to the relatively fast evolutionary changes and the detailed monitoring of the populations, the Australian myxoma disease is one of the best-documented instances of coevolutionary dynamics.

Chapter 2
Models of Coevolution

The traditional fields for the mathematical investigation of evolutionary phenomena are *population genetics* and *quantitative genetics* (Bulmer 1980; Falconer 1989). To assess coevolutionary dynamics at the level of genes appears to be virtually impossible (Levin 1983). Numerous simplifying assumptions have to be employed before feasible equations are obtained (Lande 1979), for two recent approaches see e.g. Iwasa et al. (1991) and Saloniemi (1993). We only briefly mention that in the resulting models the evolutionary process is treated deterministically and that usually “fitness” functions are employed whose relations to the interactions among individuals are not always obvious.

These circumstances have fostered the development of various simpler mathematical models of coevolutionary dynamics. Below we sketch research from *evolutionary game theory* as well as from the areas of *replicator dynamics* and *adaptive dynamics*.

2.1 Invasion Criteria

Central Idea

Evolutionary game theory envisages individuals to adopt different strategies. With these strategies, members of populations are pictured to play games against each other. As a result of such contests, individuals receive payoffs according to their success in these games. A strategy can invade a population of other strategies if its payoff exceeds that of the other strategies. When a strategy is non-invadable by any other strategy it is said to be evolutionarily stable.

Mathematical Description

The condition for an *evolutionarily stable strategy* (ESS) is given by (Maynard Smith and Price 1973; Maynard Smith 1982; Parker and Maynard Smith 1990)

$$W_{ss} > W_{s's} \,. \tag{2.1}$$

Here, $W_{s's}$ denotes the payoff of strategy s' received in a game against strategy s. When inequality (2.1) holds for a population mainly of strategy s against all possible strategies s' then s is an evolutionarily stable strategy.

In contrast, if inequality (2.1) does not hold for a population mainly of strategy s and a particular strategy s' then s is vulnerable to invasion by s'.

In the case $W_{ss} = W_{s's}$ inequality (2.1) has to be replaced by the condition $W_{ss'} > W_{s's'}$; Rand et al. (1993) show that this amounts to a second order condition which is generally not needed when payoffs are nonlinear.

Traditionally, evolutionary game theory is concerned with the frequency of strategies, not with their total density in the population. When dealing with games between species this restriction needs to be overcome 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. In evolutionary game theory different species are only distinguished by the sets of strategies they can adopt.

In Section 5.3 we will recover the condition (2.1) for “evolutionary stability” from the stochastic framework established in Part B for the description of coevolutionary processes.

Conditions similar to inequality (2.1) can be derived when instead of payoffs population dynamics are considered (Reed and Stenseth 1984; Metz et al. 1992; Rand et al. 1993). We will tackle these more sophisticated invasion criteria in Section 8.2.

2.2 Replicator Dynamics

Central Idea

The central assumption common to the various instances of replicator dynamics is that the per capita growth rate of individuals is proportional to the difference between their own "fitness" and the "average fitness" of the entire community.

Mathematical Description

When denoting the densities of different "species" by x_i with $i = 1, \ldots, N$ and their "fitness" by $W_i(x)$ the assumption above is equivalent to

$$\frac{d}{dt}x_i = x_i \cdot \left[W_i(x) - \frac{1}{c} \cdot \sum_{j=1}^{N} W_j(x) \cdot x_j\right] \tag{2.2}$$

with $c = \sum_{j=1}^{N} x_j$.

In the replicator equation no distinction is made between populations of different species and populations of the same species with different trait values.

Mathematical structures analogous to equation (2.2) have been used in population genetics (Fisher 1958), in the study of hypercycle dynamics (Eigen and Schuster 1979) and in the extension of evolutionary game theory to a dynamical framework (Taylor and Jonker 1978). The name *replicator equation* has been suggested by Schuster and Sigmund (1983) in resemblance of Dawkins' replicator concept (Dawkins 1976).

2.3 Adaptive Dynamics

Central Idea

The concept underlying the model of adaptive dynamics given below is that the different species in a coevolutionary community change their adaptive trait values according to a hill-climbing process on adaptive landscapes defined by "fitness" functions.

Mathematical Description

We summarize the results of numerous investigations of adaptive dynamics by means of the following *canonical equation*

$$\frac{d}{dt} s_i = k_i(s) \cdot \frac{\partial}{\partial s_i'} W_i(s_i', s) \Big|_{s_i' = s_i} \ . \tag{2.3}$$

Here, the s_i with $i = 1, \ldots, N$ denote adaptive traits 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 (2.3) 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; Marrow et al. 1994). The notion of the adaptive landscape or topography goes back to Wright (1931). A more restricted version of equation (2.3), 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 (2.3) 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 Section 6.2 we will recover the canonical equation (2.3) of adaptive dynamics from the stochastic framework established in Part B for the description of coevolutionary processes. The assumptions underlying this equation thus will be revealed and the functions k_i and W_i will be determined.

Chapter 3
Resulting Desiderata

3.1 Discussion of Previous Work

Here we briefly review some restrictions of the established models of evolution. These limitations will provide us with directions for devising a more general theory of coevolutionary dynamics.

Invasion Criteria

Investigating coevolutionary processes by means of the invasion condition, inequality (2.1), can be misleading for several reasons.

1. Recognition has grown that the question of “evolutionary stability” of strategies, based on the notion of non-invadability, is independent of the attainability of these strategies. Strategies that are characterized by continuous trait values and that maximize individual payoff can be unstable in the sense that evolution tends away from these strategies (Eshel and Motro 1981).
2. When restricting attention to “evolutionarily stable strategies”, evolutionary transients and nonequilibrium evolutionary attractors are excluded from consideration.
3. In a coevolutionary context, the relative magnitude of evolutionary rates can be essential for determining evolutionary outcomes, see Section 7.2. As invasion criteria lack a notion of dynamics, in such cases even the prediction of evolutionary endpoints is beyond their scope.

Determining payoffs in evolutionary game theory is usually not underpinned by a population dynamic (Maynard Smith 1982). We have noted in Section 2.1 attempts to derive invasion criteria based on population dynamics (Reed and Stenseth 1984; Metz et al. 1992; Rand et al. 1993); yet, the three limitations outlined above still apply.

Replicator Dynamics

Replicator dynamics, see equation (2.2), have been shown to provide a common framework for various evolutionary models (Schuster and Sigmund 1983). Consequently, these models share a common set of drawbacks.

1. There is no mechanism provided to generate variation in the considered community. Only those species or trait values that are present initially undergo concurrent population dynamics corresponding to a process of selection.
2. The population dynamics in the system are considered to be deterministic and continuous, thus the replicators are not treated as individual entities. This requires population sizes to be large.
3. The per capita growth rates in equation (2.2) are assumed to be of a special type, constrained by the condition of constant organization (Eigen and Schuster 1979).

A stochastic replicator dynamic incorporating a mutation process has been suggested by Ebeling and Feistel (1982); however, only a discrete set of species or trait values is allowed here.

Adaptive Dynamics

The canonical equation (2.3) of adaptive dynamics might be unsatisfactory for the following reasons.

1. The idea of modelling evolution as a hill-climbing process on an adaptive landscape amounts to an ad-hoc approach. In the context of coevolution this type of dynamics is not underpinned by a formal derivation. For this reason it is not clear how to define the functions k_i and W_i in equation (2.3) independent of the dynamics (2.3) itself.
2. It can be shown that an arbitrary dynamical system can be cast in the form of equation (2.3) when appropriate choices for k_i and W_i are made, see Section 7.5. The significance of equation (2.3) thus is debatable unless specific assignments are made to the functions k_i and W_i.

3. The canonical equation describes the adaptive process as a deterministic process. The stochasticity arising from random mutations and from the impact of demographic stochasticity of small populations thus is ignored.

Resume

We conclude that the reviewed approaches to evolutionary processes lack one or more features which may be regarded as essential. We summarize these key features in the next section, thus providing a basis for the construction of the extended perspective on evolutionary processes offered in Part B.

3.2 Conclusions for Present Work

From the discussion in Sections 2.1, 2.2, 2.3 and 3.1 we extract the following four desiderata for a mathematical theory of adaptive change. These requirements define a profile serving to shape our approach to evolutionary processes in Part B.

Coevolution

The evolutionary process needs to be considered in a coevolutionary context.

Evolution taking place in a constant environment is an abstraction. It is necessary to allow for feedbacks to occur between the evolutionary dynamics of a species and the dynamics of its environment (Lewontin 1983). We have seen in Chapter 1 that 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 are special cases within the broader coevolutionary perspective.

Dynamics

A proper mathematical theory of evolution should be dynamical.

Due to the discrepancy between non-invadability and dynamical attainability (Eshel and Motro 1981; Eshel 1983; Taylor 1989; Christiansen 1991; Takada and Kigami 1991) invasion criteria are insufficient to determine evolutionary stability in a coevolutionary context. A dynamical perspective is moreover required to account for evolutionary transients, nonequilibrium evolutionary attractors, evolution under nonequilibrium population dynamics or in a varying environment.

Individuals

The coevolutionary dynamics ought to be based at the level of individuals.

Rather than postulating measures of “fitness” and assuming plausible adaptive dynamics, these should be rigorously derived. For this purpose we need to consider the interaction between individuals in the coevolutionary community. Only by accounting for the population dynamics underlying the evolutionary process, is it possible to incorporate properly both density and frequency dependent selection into the mathematical framework. Yet, the process of natural selection takes place at the level of individuals. Hence it is important not to restrict attention to the level of population dynamics, otherwise the ecological details between these two levels are bypassed.

Stochasticity

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 thus mutants arise initially as a single individual. In consequence they are liable to accidental extinction (Fisher 1958). Also resident populations are subject to this demographic stochasticity, although this third effect might be ignored provided that population sizes are sufficiently large (Wissel and Stöcker 1989).

Part B
The Dynamical Theory of Coevolution

For a proper mathematical theory of evolutionary processes we suggest four criteria. First, it should allow for coevolutionary interdependencies within the considered system. Second, the theory needs to encompass the dynamics of evolution rather than predicting only evolutionary outcomes. Third, it ought to be derived from those processes underlying the adaptive change and should be based on interactions between individuals. Fourth, the theory needs to be a stochastic one to account for the randomness of mutations and the impact of demographic stochasticity.

Several areas of research have traditionally been concerned with the theoretical analysis of evolutionary processes. As explained in the last section neither the fields of population genetics and quantitative genetics nor those of evolutionary game theory, replicator dynamics and adaptive dynamics can simultaneously meet the criteria above. For this reason we rely on the replicator concept, as incorporating the minimal conditions for the incidence of evolution by means of natural selection, for building up a dynamical theory of coevolution.

In this part we present and analyze a hierarchy of three evolutionary models. We begin by deriving the polymorphic stochastic model which is represented in form of the generalized replicator equation and which serves as a fundamental description of coevolutionary dynamics (Chapter 4). From this we deduce the monomorphic stochastic model (Chapter 5) and the monomorphic deterministic model (Chapter 6) in order to obtain reduced descriptions of the coevolutionary process while retaining its essentials. The latter models are investigated in detail (Chapter 7) and extensions to all three models are provided (Chapter 8).

To illustrate the theoretical considerations of this part we will occasionally employ the coevolutionary predator-prey community presented in the next part. A synopsis of all assumptions needed for the deductions given is provided in Figure 1 of the Chapter “Summary and Conclusions”.

Chapter 4
The Polymorphic Stochastic Model

In this chapter we present a fundamental representation of the coevolutionary processes in ecological communities. We call the resulting mathematical description the *generalized replicator equation*. When excluding the effects of space, age structure and genetics from consideration, this representation is as general as possible. It is from here that the more reduced descriptions of coevolutionary dynamics are derived, which we analyze in later chapters.

4.1 Characterization of Coevolutionary Communities

In this section notation and key concepts underlying our analysis of coevolutionary dynamics are introduced.

Replicators

In Section 1.1 we already have mentioned the replicator concept, an attempt due to Dawkins (1976) to capture the minimal conditions for evolution to occur by natural selection. In other words, replicators are the smallest units capable of this type of self-organization. They possess properties as below.

1. *Reproduction.* The replicator units can multiply by producing replicas.
2. *Inheritance.* The units have certain distinctive features that are basically inherited in the process of replication.

3. *Variability.* There exists some variation in the features of replicas with respect to the original unit, not all replicas are true.
4. *Interaction.* The replicators exhibit some kind of interaction causing a dependence of their reproduction or survival on the inherited features.

The following mathematical description of individuals in a community closely matches these characteristics of Dawkins' replicators. To allow not only for evolutionary but for coevolutionary dynamics we consider communities comprising several species of replicators.

Individuals, Populations and Species

The coevolutionary community under analysis is allowed to be made up of an arbitrary *number N of species*, the species are characterized by an index $i = 1, \ldots, N$. At time t there are n_i *individuals in the population of species* i. These individuals are identified by an index $k = 1, \ldots, n_i$.

The individuals within each species can be distinct with respect to *adaptive traits* 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 8.1, it only obtains until then to keep the derivation conceivable and the notation reasonably simple. Individuals have adaptive trait values or phenotypes s_{ik} with $k = 1, \ldots, n_i$ such that the *phenotypic distribution* $p_i(s_i)$ in species i is given by

$$p_i = \sum_{k=1}^{n_i} \delta_{s_{ik}} \tag{4.1}$$

with $\delta_y(x) = \delta(x - y)$ where δ denotes Dirac's δ-function which in turn is defined by $\int f(x) \cdot \delta(x - y)\, dx = f(y)$ for an arbitrary test-function f. A population made up of individuals with many different adaptive trait values is called *polymorphic*.

The development of the coevolutionary community is caused by the process of mutation, introducing new mutants, and the process of selection, determining survival or extinction of these mutants. 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.

Selection

We first consider the process of selection. In an ecological community the environment e_{ik} of an individual k in species i is affected by influences that can be either internal or external with respect to the considered community. The former effects are functions of the phenotypic distributions $p = (p_1, \ldots, p_N)$ in the community, the latter may moreover be subject to external effects like seasonal forcing which render the system non-autonomous. We thus write

$$e_{ik} = e_{ik}(p, t) \ . \tag{4.2}$$

The quantities b_{ik} and d_{ik} are introduced to denote the *per capita birth and death rates* of an individual k in species i. These rates are interpreted stochastically as probabilities per unit time and can be combined to yield the per capita growth rate

$$f_{ik} = b_{ik} - d_{ik} \tag{4.3}$$

of the individual. They are affected by the trait value s_{ik} of the individual as well as by its environment e_{ik}, thus with equation (4.2) we have

$$b_{ik} = b_i(s_{ik}, p, t) \quad \text{and} \quad d_{ik} = d_i(s_{ik}, p, t) \ . \tag{4.4}$$

Notice that the functions b_i and d_i are in fact functionals as they take the vector of phenotypic distributions p as an argument. By assuming in equation (4.4) these functions not to depend on the particular individual k of species i we take the environment to be spatially homogeneous. Since we are mainly interested in the phenomenon of coevolution – an effect internal to the community – we will not always consider the extra time-dependence in equations (4.4) which may be induced by external effects on the environment.

Mutation

We now consider the process of mutation. In order to describe its properties we introduce the quantities μ_{ik} and M_{ik}.

The former denote the *fraction of births that give rise to a mutation* in the trait value s_{ik}. 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 considered individual itself,

$$\mu_{ik} = \mu_i(s_{ik}) \,, \tag{4.5}$$

although this complication is not frequently considered.

The quantities

$$M_{ik} = M_i\big(s_{ik}, s'_{ik} - s_{ik}\big) \tag{4.6}$$

determine the *probability distribution of mutant trait values* s'_{ik} around the original trait value s_{ik}. The functions M_i are not dependent on the index k of an individual other than via its adaptive trait value s_{ik}. 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*.

In the next two sections we show that the above functions b_i, d_i, μ_i and M_i suffice to construct a formal representation of the coevolutionary dynamics.

4.2 Stochastic Description of Coevolutionary Community Dynamics

In this section the fundamental equation describing the polymorphic stochastic dynamics of coevolutionary communities is introduced. When combined with the transition probabilities per unit time derived in the next section we call the resulting representation the *generalized replicator equation*.

Markov Property

The dynamics of the coevolutionary community are taking place in the *polymorphic trait space* $\widehat{P}$ of phenotypic distributions p. The events of birth, death and mutation of individuals constitute a stochastic process on $\widehat{P}$.

The coevolutionary dynamics possess no memory, for mutation and selection depend only on the present state of the community. The corresponding stochastic process in p thus will be *Markovian*, provided that the knowledge of p suffices to determine the potential for coevolutionary change in the immediate future. To meet this requirement for real biological systems, a sufficient number of adaptive traits may need to be considered, see Section 8.1.

Master Equation

The coevolutionary dynamics of the community thus is described by a functional master equation

$$\frac{d}{dt}P(p,t) = \int \Big[\, w(p|p',t) \cdot P(p',t) - w(p'|p,t) \cdot P(p,t) \,\Big]\, \mathcal{D}p' \tag{4.7}$$

for $P(p,t)$, the probability density in $\widehat{P}$ of phenotypic distributions $p = (p_1, \ldots, p_N)$ to be realized at time t. The probabilities per unit time for the transition $p \to p'$ at time t are denoted by $w(p'|p,t)$. The functional integration over $\widehat{P}$ is indicated by the symbol $\mathcal{D}$.

The equation (4.7) for the stochastic dynamics in p is an instance of a master equation (see e.g. van Kampen 1981) and simply reflects the fact that the probability $P(p,t)$ is increased by all transitions to p (first term) and decreased by all those from p (second term).

4.3 Transition Probabilities per Unit Time

The probabilities per unit time $w(p'|p,t)$ for the transition $p \to p'$ at time t can be constructed as below.

Preliminary Considerations

We start be introducing three helpful constructs.

1. The *number of individuals with adaptive trait value* s_i in the population of species i is obtained by

$$n_i(s_i,p_i) = \int_{s_i-\varepsilon}^{s_i+\varepsilon} p_i\big(s_i'\big)\, ds_i' \tag{4.8}$$

   for an arbitrarily small $\varepsilon > 0$.
2. The *probability distributions of offspring adaptive trait values* s_i' arising from a birth event in an individual with trait s_i is given by

$$\begin{aligned} B_i\big(s_i, s_i' - s_i\big) = (1 - \mu_i(s_i)) \cdot \delta\big(s_i' - s_i\big) + \\ \mu_i(s_i) \cdot M_i\big(s_i, s_i' - s_i\big) \;, \end{aligned} \tag{4.9}$$

   where the first term on the right hand side corresponds to birth events without mutation and the second to those events with mutation.

3. We define a *functional* Δ in the spaces $\widehat{P}_i$ by means of the identity

$$\int F(p_i') \cdot \Delta(p_i' - p_i)\, \mathcal{D}p_i' = F(p_i) \tag{4.10}$$

holding for an arbitrary test functional F.

From General Events to Events in a Single Species

Due to the nature of the master equation (4.7) it is only necessary to consider a single stochastic event to cause a change dP of the probability distribution $P(p,t)$ during the infinitesimal time interval dt (van Kampen 1981). Therefore the probabilities per unit time $w(p'|p,t)$ for the transition $p \to p'$ at time t can be decomposed according to

$$w(p'|p,t) = \sum_{i=1}^{N} w_i(p_i', p, t) \cdot \prod_{\substack{j=1 \\ j \neq i}}^{N} \Delta(p_j' - p_j)\ . \tag{4.11}$$

Equation (4.11) can be read as guaranteeing that $w(p'|p,t)$ does not contribute to the right hand side of equation (4.7) if $p_i' \neq p_i$ happens to hold for more than one $i = 1, \ldots, N$.

From Events in a Single Species to Single Birth or Death Events

Let the considered stochastic event happen in species i. This event can remove or insert a single individual to the population of species i. When we denote this individual's trait value by s_i', the stochastic event is described by either $p_i' = p_i - \delta_{s_i'}$ or $p_i' = p_i + \delta_{s_i'}$. Since the stochastic event in species i can occur at any adaptive trait value s_i' we have

$$\begin{aligned} w_i(p_i', p, t) = \int \Big[\, & w_i^-(s_i', p, t) \cdot \Delta\Big(p_i' - \Big(p_i - \delta_{s_i'}\Big)\Big) + \\ & w_i^+(s_i', p, t) \cdot \Delta\Big(p_i' - \Big(p_i + \delta_{s_i'}\Big)\Big) \,\Big]\, ds_i'\ . \end{aligned} \tag{4.12}$$

Single Birth or Death Events

The removal of an individual can only be due to a death event, thus $w_i^-(s_i', p, t)$ is given by

$$w_i^-(s_i', p, t) = d_i(s_i', p, t) \cdot p_i(s_i', p_i)\ , \tag{4.13}$$

as multiplying the per capita death probability per unit time $d_i(s_i', p, t)$ of an individual with trait s_i' by the density $p_i(s_i', p_i)$ of individuals with that trait value yields the transition probability density per unit time for a death event at that particular trait value.

The insertion of an individual is due to a birth event either without a mutation or accompanied by a mutation. By the same argument as above we obtain for $w_i^+(s_i', p, t)$

$$\begin{aligned} w_i^+(s_i', p, t) &= b_i(s_i', p, t) \cdot p_i(s_i', p_i) + \\ &\quad \int b_i(s_i, p, t) \cdot p_i(s_i, p_i) \cdot M_i(s_i, s_i' - s_i)\, ds_i \\ &= \int b_i(s_i, p, t) \cdot p_i(s_i, p_i) \cdot B_i(s_i, s_i' - s_i)\, ds_i \,. \end{aligned} \tag{4.14}$$

The term in the first line corresponds to a birth event without mutation, that in the second line to a birth event giving rise to a mutation from s_i to s_i'. In the third line the construct B_i has been used to condense the result.

Conclusion

By collecting the results above we arrive at

$$\begin{aligned} w(p'|p, t) = \sum_{i=1}^{N} \int \Big[& d_i(s_i', p, t) \cdot p_i(s_i', p_i) \cdot \\ & \Delta\Big(p_i' - p_i + \delta_{s_i'}\Big) \cdot \prod_{\substack{j=1 \\ j \neq i}}^{N} \Delta(p_j' - p_j) + \\ & \int b_i(s_i, p, t) \cdot p_i(s_i, p_i) \cdot B_i(s_i, s_i' - s_i)\, ds_i \cdot \\ & \Delta\Big(p_i' - p_i - \delta_{s_i'}\Big) \cdot \prod_{\substack{j=1 \\ j \neq i}}^{N} \Delta(p_j' - p_j) \Big]\, ds_i' \,. \end{aligned} \tag{4.15}$$

Notice that after introducing the transition probabilities per unit time (4.15) into the master equation (4.7) each functional $\Delta(\ldots\, p_i' \,\ldots)$ defined in the function spaces $\widehat{P}_i$ can be collapsed by a functional integration $\int \ldots\, \mathcal{D}p_i'$ over $\widehat{P}_i$. This demonstrates that neither the functional integration in equation (4.7) nor the occurrence of the Δ-functionals in equation (4.15) causes problems in delineating the dynamics in terms of the master equation; evaluated according to equation (4.10) they guarantee a well-defined description of the function-valued stochastic process. In consequence, problems of the sort having urged van Kampen to develop his *method of compounding moments* (van Kampen 1981) do not arise in our mathematical framework.

The above equation completes the specification of the coevolutionary process of the community. By combining equations (4.7) and (4.15) we obtain our first and fundamental model of coevolutionary dynamics, the *polymorphic stochastic model.* We refer to the resulting formula as the *generalized replicator equation.*

4.4 An Algorithm for the Polymorphic Stochastic Model

An algorithm for the polymorphic stochastic model derived from equations (4.7,15) is presented in Figure 4.1. In formulating the algorithm we choose first to restrict attention to autonomous coevolutionary communities, i.e. systems without an extra time dependence due to external effects on the environment. In this case the protocol can utilize the *minimal process method* (Gillespie 1976; Feistel 1977) to simulate the functional master equation. As to the validity of the presented algorithm for non-autonomous coevolutionary communities, notice the remark at the end of this section.

Distribution of Waiting Times

According to Step D in Figure 4.1 the waiting times between two events of a stochastic realization follow an *exponential distribution* – the standard result for processes described by master equations that are homogeneous in time.

This inference can easily be apprehended as below. Suppose that the stochastic process at time t is in state p with certainty. Until the next event $p \to p'$ occurs at time $t + \Delta t$ we thus have $P(p', t) = \prod_{i=1}^{N} \Delta(p'_i - p_i)$. In the time interval $(t, t + \Delta t)$ the master equation (4.7) then reduces to

$$\frac{d}{dt} P(p,t) = \; w(p|p,t) \cdot P(p,t) - \int w\big(p'|p,t\big) \; \mathcal{D}p' \cdot P(p,t) \, . \tag{4.16}$$

With $w(p|p,t) = 0$, the abbreviation $T^{-1}(p,t) = \int w(p'|p,t) \; \mathcal{D}p'$ and equation (4.15) we thus obtain for the decay in the probability density $P(p,t)$ of the state p during the considered time interval

$$P(p, t + \Delta t) = \exp \left\{ - \int_{t}^{t+\Delta t} T^{-1}\big(p, t'\big) \; dt' \right\} . \tag{4.17}$$

Since a decrease in the probability density $P(p, t + \Delta t)$ can only be due to an event $p \to p'$ at time $t + \Delta t$, the right hand side of equation (4.17) describes (after normalization) the probability distribution of the waiting time Δt until the next event

An Algorithm for the Polymorphic Stochastic Model

A. Initialize the phenotypic distributions p_i with $i = 1, \ldots, N$ at time $t = 0$ and specify the time t_{end} when to stop the dynamics.

B. Calculate the birth and death probabilities $b_i(s_{ik}, p)$ and $d_i(s_{ik}, p)$ for each individual $i = 1, \ldots, N$, $k = 1, \ldots, n_i$ with phenotype s_{ik} in the environment given by p.

C. Construct the sums $w_{ik} = b_i(s_{ik}, p) + d_i(s_{ik}, p)$, $w_i = \sum_{k=1}^{n_i} w_{ik}$ and $w = \sum_{i=1}^{N} w_i$ with $i = 1, \ldots, N$ and $k = 1, \ldots, n_i$.

D. Choose the waiting time Δt for the next event to occur according to $\Delta t = -\frac{1}{w} \cdot \ln r$ where $0 < r \leq 1$ is a uniformly distributed random number.

E. Choose species i with probability $\frac{1}{w} \cdot w_i$. Choose individual k in species i with probability $\frac{1}{w_i} \cdot w_{ik}$. Choose then a birth or death event with probability $\frac{1}{w_{ik}} \cdot b_i(s_{ik}, p)$ and $\frac{1}{w_{ik}} \cdot d_i(s_{ik}, p)$, respectively.

F. If in Step E a birth event occurs for an individual with phenotype s_{ik}, choose a new phenotype s'_{ik} with probability density $B_i(s_{ik}, s'_{ik} - s_{ik})$.

G. Update time and phenotypic distributions according to $t \to t + \Delta t$ and $p_i \to p_i + \delta_{s'_{ik}}$ or $p_i \to p_i - \delta_{s_{ik}}$ for a birth or death event in species i respectively.

H. Continue from Step B until $t \geq t_{end}$.

Figure 4.1 An algorithm for the polymorphic stochastic model. The protocol employs the minimal process method described in the text.

happens, given that an event just has occurred at time t. For homogeneous master equations T^{-1} is independent of t and equation (4.17) reduces to

$$P(p, t + \Delta t) = \exp\left\{-\Delta t / T(p)\right\} . \tag{4.18}$$

In this case waiting times simply are distributed exponentially with mean $T(p)$.

The Minimal Process Method

The distribution of waiting times, calculated above, is the backbone of the minimal process method (Gillespie 1976; Feistel 1977; see also Fricke and Schnakenberg 1991). The general algorithm can be decomposed into the repetition of four simple steps which are outlined below.

1. Initialization of time and state.
   (→ Step A in Figure 4.1)
2. Calculation of all relevant transition probabilities per unit time.
   (→ Steps B and C in Figure 4.1)
3. Choice of a waiting time according to an exponential distribution.
   (→ Step D in Figure 4.1)
4. Choice of a particular event according to its relative transition probability.
   (→ Steps E and F in Figure 4.1)
5. Update of time and state; unless simulation completed, continuation from Step 2.
   (→ Steps G and H in Figure 4.1)

A set of random numbers r_{ex}, exponentially distributed according to $P_{ex}(r_{ex}) = \exp\{-r_{ex}/\langle r_{ex}\rangle\}/\langle r_{ex}\rangle$ for $r_{ex} \geq 0$ and $P_{ex}(r_{ex}) = 0$ elsewhere, can be obtained from another set of random numbers r_{eq}, equally distributed according to $P_{eq}(r_{eq}) = 1$ for $0 < r_{eq} \leq 1$ and $P_{eq}(r_{eq}) = 0$ elsewhere, by means of the following transformation (see e.g. Schnakenberg 1991)

$$r_{ex} = -\langle r_{ex}\rangle \cdot \ln r_{eq} \; . \tag{4.19}$$

This relation can be used to implement Step 3 above.

The minimal process method turns out advantageous compared to the simulation of a stochastic process employing a constant time step not only because of efficiency but also because of precision. The latter method has to simulate numerous time steps without an event occurring and it can produce arbitrarily large deviations from the exact result for large simulation times (Feistel 1977).

Autonomous and Non-Autonomous Systems

Waiting times of homogeneous master equations (corresponding to autonomous systems) have been shown above to be distributed exponentially.

Since the difference between equations (4.17) and (4.18) becomes negligible for time steps Δt being small compared to the time scale on which $T^{-1}(p, t)$ changes, exponentially distributed waiting times and thus the minimal process method may be applied approximately even to non-homogeneous master equations (corresponding to systems with an external time dependence), provided only that the typical number of events on the timescale of the external perturbations is large. For reasonably large population sizes within the non-autonomous coevolutionary community this simplification will usually hold in good approximation; for more details see Section 8.2.

4.5 Sample Simulations and Further Inquiry

To illustrate the descriptive capacity of the polymorphic stochastic model, we present some stochastic realizations of the generalized replicator equation. Examples are based on the coevolutionary predator-prey community that is described in detail in Chapter 9.

Mutation Catastrophe

A high mutation ratio μ_i for a species i amounts to replicas seldom being true in this population of replicators. Under these circumstances the broadening effect of mutation on the phenotypic distribution p_i is hardly counteracted by the narrowing impact of selection. The variance of the distribution p_i will continually grow, and consequently the information comprised in p_i, when initially narrow, gradually is lost. In resemblance of the *error catastrophe* introduced by Eigen and Schuster (1979) we call this process *mutation catastrophe*.

An example of such an almost unbiased broadening of a phenotypic distribution caused by too large a mutation ratio is shown in Figure 4.2.

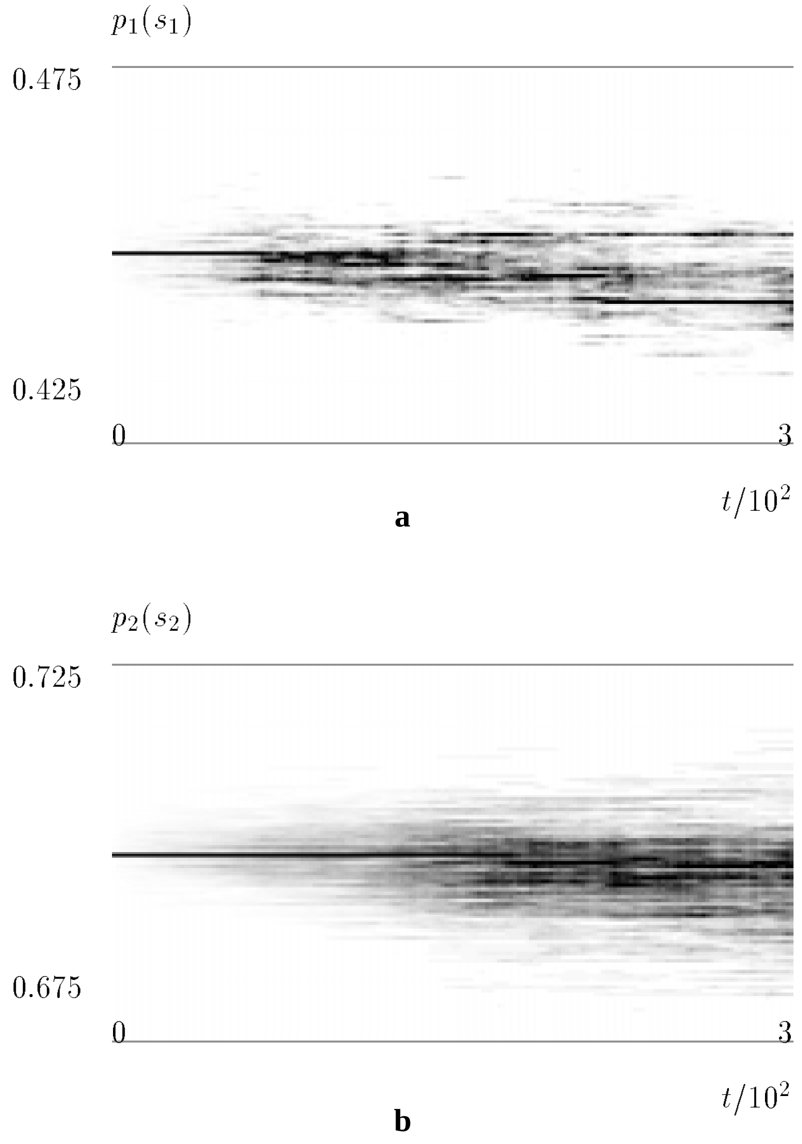

Figure 4.2 Realizations of the polymorphic stochastic model. The phenotypic distributions (a) $p_1(s_1)$ and (b) $p_2(s_2)$ at each point in time are depicted by grayscales (black corresponds to the population number of the prevalent adaptive trait value and white to absent adaptive trait values). The figures show evolutionary dynamics characteristic for high mutation ratios: the broadening effect of mutation on the phenotypic distributions is hardly counteracted by the narrowing impact of selection. The realizations given are made up of roughly 100 000 single birth and death events in each species. Parameters of the coevolutionary predator-prey community are as given in Figure 4.4 except $\mu_1 = 5 \cdot 10^{-2}$, $\mu_2 = 5 \cdot 10^{-1}$ and $\sigma_1 = \sigma_2 = 2 \cdot 10^{-3}$.

Evolutionary Branching

The phenomenon of phenotypic distributions that were unimodal initially to gradually become bimodal in the course of an adaptation process is called *disruptive selection.*

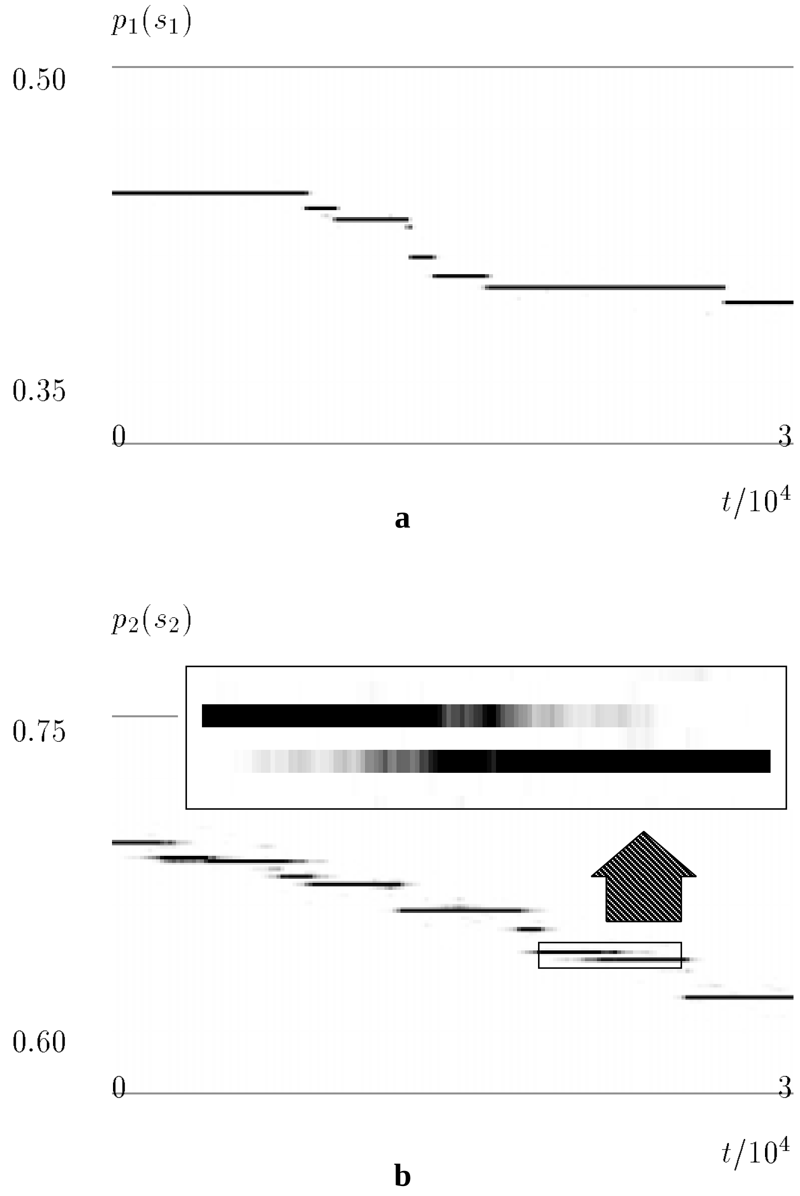

Figure 4.3 Realizations of the polymorphic stochastic model. The phenotypic distributions (a) $p_1(s_1)$ and (b) $p_2(s_2)$ at each point in time are depicted by grayscales (black corresponds to the population number of the prevalent adaptive trait value and white to absent adaptive trait values). The figures show evolutionary dynamics characteristic of the monomorphic regime: evolution occurs via sequences of trait substitutions. The trait substitution sequences given are made up of roughly 10 000 000 single birth and death events in each species. The inset in (b) depicts a single trait substitution, the population of the resident adaptive trait value is decreasing in size while that of the mutant trait value increases until it has completely replaced the former resident. The dynamics displayed in this figure are a subset of that presented in Figure 4.4, for comparison see the dotted box there. Parameters of the coevolutionary predator-prey community are the same as in Figure 4.4.

Evolutionary processes of this kind are important to notice as after the occurrence of disruptive selection has caused the phenotypic distribution in a species to become bimodal, describing the dynamics of this distribution in terms of its average adaptive trait value obviously is misleading.

When phenotypic or mutation variances are large and moreover the environment, in which a particular phenotypic distribution has evolved towards a unimodal shape, is abruptly changed such as to make selection disruptive, bimodality is the expected outcome. On the other hand, if phenotypic and mutation variances are small, disruptive selection is more difficult to generate by external manipulations of the environment. For this reason it is interesting to ask whether the evolutionary or coevolutionary process itself could generate an environment that gives rise to disruptive selection. Such an event has been called *evolutionary branching* by Metz et al. (1994) and has been shown to be feasible when (i) considering only a single species' adaptation to its constant environment or (ii) assuming deterministic population dynamics.

The relevance of evolutionary branching for the present work stems from the fact that its incidence would violate the *principle of mutual exclusion* introduced in Section 5.1. The mathematical system for the description of coevolutionary dynamics as presented in Chapters 5 and 6, resting on this principle, then ought to be extended. Fortunately, the analytic framework developed up to Chapter 7 allows to narrow down substantially the circumstances under which evolutionary branching can occur, see Section 7.3. Even in the remaining cases the potential for evolutionary branching is moot: when allowing both for coevolution and for stochasticity in the species' population dynamics – two requirements met by the generalized replicator equation established above – no instance of evolutionary branching has been observed by the author.

Trait Substitution Sequences

When mutation ratios μ_i are low, $\mu_i \ll 1$, the change of the phenotypic distributions p_i over time takes an altogether different shape compared to the case of the mutation catastrophe.

Now the process of selection is not dominated by that of mutation and consequently the distributions of adaptive trait values remain narrow. In fact, the temporal change of these distributions can accurately be described by a single adaptive trait value in each species being replaced from time to time by another one. This is the characteristic

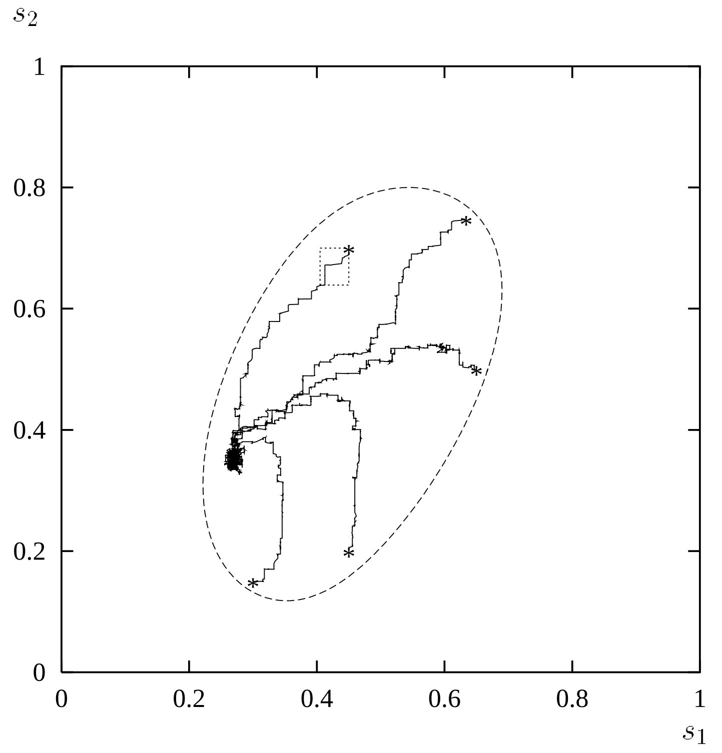

Figure 4.4 Realizations of the polymorphic stochastic model. Trait substitution sequences starting at the five initial conditions (indicated by asterisks) are depicted by continuous lines. Each of these five trait substitution sequences is made up of roughly 500 000 000 single birth and death events. The dotted box indicates the region corresponding to the trait substitution sequences shown in detail in Figure 4.3. The discontinuous oval line is the boundary of the region of coexistence, see Section 5.1. The coevolution of both species drives their adaptive trait values towards a common equilibrium $\hat{s}$. Parameters of the coevolutionary predator-prey community are: $h = 0.2$, $c_1 = 2.0$, $c_2 = 8.0$, $\sigma_1 = \sigma_2 = 5 \cdot 10^{-3}$ and $\mu_1 = 10^{-4}$; the remaining parameters are as given in Figure 9.3.

feature of what we designate the *monomorphic regime*. We call the adaptive trait value that is prevalent at a point in time the *resident* adaptive trait value and the event of its replacement by a mutant adaptive trait value a *trait substitution*. The process of evolution in each species consequently is described in terms of a *trait substitution sequence*. The population processes underlying a single trait substitution are analyzed in Section 5.1. The results obtained there underpin the derivation of the stochastic dynamics for trait substitution sequences in Section 5.2 and 5.3.

Instances of such trait substitution sequences, as described by the generalized replicator equation, are presented in Figure 4.3. The inset shows a single trait substitution: after a mutant trait value has entered the population, it gradually increases in number such that resident and mutant trait values coexist until the mutant one has gone to fixation by replacing the former resident one. In Figure 4.4 we have used the polymorphic stochastic model to picture the combined dynamics of trait substitution sequences in two coevolving species originating from different initial conditions. We will use these five particular coevolutionary processes as running examples to illustrate the parallel predictions made by our three dynamical models of coevolution (Figure 4.4, Figure 5.3, Figure 5.4 and Figure 6.2).

Chapter 5
The Monomorphic Stochastic Model

In this chapter we establish a stochastic description of the monomorphic coevolutionary dynamics. Under certain conditions it is possible to deduce from the generalized replicator equation, which defines the polymorphic stochastic model, a reduced representation of the coevolutionary process; this reduction leads us to the monomorphic stochastic model. The central idea here is to envisage a sequence of trait substitutions as a *directed random walk in trait space* determined by the processes of mutation and selection.

5.1 The Monomorphic Regime and Trait Substitutions

In this section we take the first steps to deduce from the generalized replicator equation the monomorphic stochastic model. In particular we stress the assumptions on which the latter is based.

Conditions for Monomorphism

In Section 4.5 we have seen that the complexity inherent in the polymorphic stochastic model can be substantially alleviated if only two requirements are met. First, when no evolutionary branching occurs in the species $i = 1, \ldots, N$, the phenotypic distributions p_i stay unimodal in the course of the coevolutionary process. There is no disruptive selection acting on the distributions which might turn them bimodal. Second, if μ_i is sufficiently small for all $i = 1, \ldots, N$, the phenotypic distributions p_i in each species will be sharply concentrated on a single phenotype, the resident phenotype. In this case selection is strong enough to counteract the impact of mutation to broaden the phenotypic distributions.

To proceed with the analysis of coevolutionary dynamics we now raise these observations to acquire the status of assumptions.

A1. The mutation ratios μ_i are sufficiently small for all $i = 1, \ldots, N$.

A2. No two adaptive trait values s_i and s_i' can coexist in the populations of species $i = 1, \ldots, N$ for $t \to \infty$ when not renewed by mutations.

These two condition specify what we call the *monomorphic regime*. The second condition is sometimes referred to as the *principle of mutual exclusion*. Prerequisites for this principle are investigated in Section 7.3.

Structure of Trait Substitutions

With these two provisions, we can take the phenotypic distributions as being given by $p_i = n_i \cdot \delta_{s_i}$ at almost any point in time, where n_i is the population size of species $i = 1, \ldots, N$ and s_i its resident phenotype. We call such a distribution of resident phenotypes *monomorphic*.

The simulations presented in Section 4.5 have shown that in this monomorphic regime adaptive change occurs via a sequence of trait substitutions, where a resident phenotype s_j with $j \in 1, \ldots, N$ is replaced by a mutant phenotype s_j'. The time period corresponding to a single such trait substitution $s_j \to s_j'$ can be partitioned into four phases.

1. *Stasis.* Throughout a time interval τ_s the phenotypic distribution p_j in species j is given by $p_j = n_j \cdot \delta_{s_j}$. Mutations occurring during this phase are not successful in invading the resident populations.
2. *Mutation.* At the end of that time interval a mutation occurs introducing a mutant phenotype s_j' into the population of species j such that $p_j = n_j \cdot \delta_{s_j} + \delta_{s_j'}$. This mutant is going to be successful.
3. *Invasion.* The mutant grows in population size to exceed the critical threshold for accidental extinction (Wissel and Stöcker 1991). We then have $p_j = n_j \cdot \delta_{s_j} + n_j' \cdot \delta_{s_j'}$.

4. *Fixation.* The principle of mutual exclusion requires that after invasion the mutant phenotype will replace the once resident phenotype such that $p_j = n'_j \cdot \delta_{s'_j}$, this happens some time τ_f after the mutation had occurred.

Note that in the above equations for p_j the quantities n_j and n'_j denote the population sizes of resident and mutant phenotype at the end of the particular phase considered rather than the same fixed numbers throughout.

The four steps outlined above can be repeated many times. The resulting process is a trait substitution sequence. According to condition A1 above we have $\tau_f \ll \tau_s$ and hence the phases 2, 3 and 4 take place on a timescale much shorter than that of phase 1.

Reduction of the Generalized Replicator Equation

We now utilize the generalized replicator equation (4.7,15) to analyze in detail the successive steps of the trait substitution process.

Let us consider a trait substitution in species j. We formally assign the population of the mutant adaptive trait value the index $i = 0$: $s_0 = s'_j$, $n_0 = n'_j$, $b_0 = b_j$ and $d_0 = d_j$. In the course of this trait substitution the phenotypic distributions in the coevolutionary community are given by

$$\widetilde{p} = \left(n_1 \cdot \delta_{s_1}, \ldots, n_j \cdot \delta_{s_j} + n_0 \cdot \delta_{s_0}, \ldots, n_N \cdot \delta_{s_N}\right) . \tag{5.1}$$

To simplify notation we write $P(n,t) = P(\widetilde{p},t)$, $\widetilde{b}_i^j(s_i,s,n,t) = b_i(s_i,\widetilde{p},t)$ and $\widetilde{d}_i^j(s_i,s,n,t) = d_i(s_i,\widetilde{p},t)$ for $i = 0,\ldots,N$.

When introducing $p = \widetilde{p}$ into equations (4.7) and (4.15) and accounting for the fact that effectively only one mutation ought to be considered during a trait substitution we arrive at

$$\begin{aligned} &\int w(p'|\widetilde{p},t) \cdot P(\widetilde{p},t)\, \mathcal{D}p' \\ &= \sum_{i=0}^{N} \left[\widetilde{d}_i^j(s_i,s,n,t) \cdot n_i + \widetilde{b}_i^j(s_i,s,n,t) \cdot n_i\right] \cdot P(n,t) \end{aligned} \tag{5.2}$$

and

$$\begin{aligned} &\int w(\widetilde{p}\,|p',t) \cdot P(p',t)\, \mathcal{D}p' \\ &= \sum_{i=0}^{N} \Big[\, \widetilde{d}_i^j\big(s_i,s,n+1^i,t\big) \cdot (n_i+1) \cdot P\big(n+1^i,t\big) + \\ &\qquad \widetilde{b}_i^j\big(s_i,s,n-1^i,t\big) \cdot (n_i-1) \cdot P\big(n-1^i,t\big) \,\Big] . \end{aligned} \tag{5.3}$$

The 1^i are vectors with components $1^i_j = \delta_{ij}$ where δ_{ij} denotes the Kronecker symbol. Note that $\widetilde{b}^j_i\big(s_i, s, n - 1^i, t\big) = 0$ for $n_i = 0$. Combining these two results according to equation (4.7) we obtain a stochastic description for the population dynamics in the course of a trait substitution

$$\begin{aligned}\frac{d}{dt}P(n,t) = \sum_{i=0}^{N} \Big[& \widetilde{d}^j_i\big(s_i, s, n + 1^i, t\big) \cdot (n_i + 1) \cdot P\big(n + 1^i, t\big) + \\ & \widetilde{b}^j_i\big(s_i, s, n - 1^i, t\big) \cdot (n_i - 1) \cdot P\big(n - 1^i, t\big) - \\ & \widetilde{d}^j_i(s_i, s, n, t) \cdot n_i \cdot P(n,t) - \\ & \widetilde{b}^j_i(s_i, s, n, t) \cdot n_i \cdot P(n,t) \Big] \, .\end{aligned} \tag{5.4}$$

To account for the single successful mutation in phase 2 of such a trait substitution, see above, we use in equation (5.4) initial conditions $P(n,t) \propto \delta_{0,n_0}$ for phase 1 and $P(n,t) \propto \delta_{1,n_0}$ for phase 3.

Resident Population Dynamics

To further simplify this stochastic description of the population dynamics during a trait substitution we introduce additional assumptions.

A3. The populations of the resident adaptive trait values are sufficiently large during the stasis phase of a trait substitution in order not to be subject to accidental extinction.

A4. The population dynamics of the resident adaptive trait values settle (apart from fluctuations) towards an equilibrium point.

A5. There is no external impact on the environment of the coevolutionary community that renders the system non-autonomous.

Relaxations of conditions A4 and A5 are provided in Section 8.2.

Owing to condition A3 we may safely describe the population dynamics of the resident adaptive trait values during phase 1 of the trait substitution by means of a deterministic approximation

$$\frac{d}{dt}n_i = n_i \cdot \widetilde{f}^j_i(s_i, s, n) \tag{5.5}$$

following from equation (5.4) for resident population sizes $n = (0, n_1, \ldots, n_N)$ treated as continuous variables and with

$$\widetilde{f}^j_i(s_i, s, n) = \widetilde{b}^j_i(s_i, s, n) - \widetilde{d}^j_i(s_i, s, n) \, . \tag{5.6}$$

We then exploit condition A4 in combination with equations (5.5) to define the *equilibrium population sizes* $\hat{n} = (0, \hat{n}_1, \ldots, \hat{n}_N)$ of the resident adaptive trait values s by

$$\widetilde{f}_i^j(s_i, s, \hat{n}(s)) = 0 \tag{5.7}$$

for all $i = 1, \ldots, N$. According to condition A3 these population sizes are also approximately valid in the course of phases 2 and 3 of the trait substitution during which the mutant is rare.

For a given set s of resident adaptive trait values, equations (5.7) determine whether these trait values can coexist. As we are interested in the coevolutionary dynamics of the N-species community, we need to consider the subspace of the *monomorphic trait space* $\widehat{S}$ in which the resident populations of all species have positive population sizes,

$$\widehat{S}_c = \left\{ s \in \widehat{S} \mid \hat{n}_i(s) > 0 \;\text{ for all }\; i = 1, \ldots, N \right\} . \tag{5.8}$$

We call this subspace of $\widehat{S}$ the *region of coexistence*. Since equations (5.5) are only valid for large resident population sizes n_i, extinction of a resident population is not only certain for resident adaptive trait values s outside the region $\widehat{S}_c$ but is also probable for those close to the boundary $\partial\widehat{S}_c$ of $\widehat{S}_c$

Mutant Population Dynamics

By virtue of conditions A3 to A5 together with equation (5.4) we can finally approximate the stochastic population dynamics of the mutant adaptive trait value during phase 3 of the trait substitution by means of the following equation

$$\begin{aligned}\frac{d}{dt}P(n'_j, t) =& \overline{d}_j(s'_j, s) \cdot (n'_j + 1) \cdot P(n'_j + 1, t) + \\ & \overline{b}_j(s'_j, s) \cdot (n'_j - 1) \cdot P(n'_j - 1, t) - \\ & \overline{d}_j(s'_j, s) \cdot n'_j \cdot P(n'_j, t) - \\ & \overline{d}_j(s'_j, s) \cdot n'_j \cdot P(n'_j, t) \; .\end{aligned} \tag{5.9}$$

Here we have introduced the abbreviations

$$\overline{b}_j(s'_j, s) = \widetilde{b}_j^j(s'_j, s, \hat{n}(s)) \tag{5.10}$$

and

$$\overline{d}_j(s'_j, s) = \widetilde{d}_j^j(s'_j, s, \hat{n}(s)) \tag{5.11}$$

for the per capita birth and death rates of a mutant adaptive trait value s'_j in an environment determined by the monomorphic resident populations with adaptive trait values s.

Note that although these probabilities per unit time can formally be combined to yield

$$\overline{f}_j(s'_j, s) = \overline{b}_j(s'_j, s) - \overline{d}_j(s'_j, s) \ , \tag{5.12}$$

the per capita growth rate of a mutant adaptive trait value s'_j in an environment determined by the monomorphic resident populations with adaptive trait values s, it is essential to recognize that a deterministic approximation of mutant population dynamics, $\frac{d}{dt}n'_j = n'_j \cdot \overline{f}_j(s'_j, s)$, is not permitted during the invasion phase 3 as the mutant then is rare. Mutants enter the system at population size 1, hence there is no alternative to a stochastic treatment of their population dynamics.

The equations derived above are the bases of our stochastic description of trait substitution sequences and will be employed in Section 5.3 to derive the monomorphic stochastic model of coevolutionary dynamics.

5.2 Stochastic Description of Trait Substitution Sequences

In this section we present a stochastic description of the monomorphic coevolutionary dynamics by envisaging trait substitution sequences as directed random walks in the monomorphic trait space. The stochastic description is completed by the transition probabilities per unit time derived in the next section.

Markov Property

The adaptive dynamics of the N-species coevolutionary community are taking place in the subspace $\widehat{S}_c$ of the monomorphic trait space of adaptive trait values s. The trait substitution events constitute a stochastic process on $\widehat{S}_c$. Stochasticity is imposed by (i) the process of mutation and (ii) the impact of demographic stochasticity on rare mutants.

The adaptive dynamics possess no memory, for mutation and selection depend only on the present state of the community. The corresponding stochastic process in s thus will be Markovian, provided that the knowledge of s suffices to determine the potential for adaptive change in the immediate future. To meet this requirement for real biological systems, a sufficient number of adaptive traits might need to be considered, see Section 8.1.

Master Equation

The stochastic adaptive dynamics of the N-species community in $\widehat{S}_c$ thus is described by a master equation

$$\frac{d}{dt}P(s,t) = \int \Big[\, w(s|s',t)\cdot P(s',t) - w(s'|s,t)\cdot P(s,t)\,\Big]\, ds'. \tag{5.13}$$

for $P(s,t)$, the probability density of resident adaptive trait values $s = (s_1, \ldots, s_n)$ to be realized at time t. The probabilities per unit time for the transitions $s \to s'$ at time t are denoted by $w(s'|s,t)$.

The equation above in principle is capable of describing the stochastic adaptive process in the coevolutionary community even for environments that are subject to time-dependent external influences. Yet, in the following sections we will restrict attention to autonomous systems, where such a time dependence is absent. The reason for this is that the principle of mutual exclusion, see also Section 7.3, on which in turn the assumption of monomorphism rests, is not generally valid for arbitrarily varying environments. We come back again to the general case in Section 8.2.

5.3 Transition Probabilities per Unit Time

We now turn to the derivation of the transition probabilities per unit time $w(s'|s)$.

From General Events to Trait Substitution Events in a Single Species

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

$$w(s'|s) = \sum_{i=1}^{n} w_i(s_i', s) \cdot \prod_{\substack{j=1 \\ j\neq i}}^{n} \delta(s_j' - s_j) \tag{5.14}$$

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.

From Trait Substitution Events in a Single Species to Mutation and Selection Events

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.

First, as explained in Section 5.1, a trait substitution comprises four phases: stasis, mutation, invasion and fixation. The latter two correspond to the process of selection. As the phases of mutation, invasion and fixation are statistically uncorrelated, the probability per unit time w_i for a complete trait substitution event can be decomposed into the probability per unit time $\mathcal{M}_i$ that the mutant enters the population (phase 2: mutation) times the conditional probability $\mathcal{S}_i$ for invasion given mutation, i.e. the probability of a single mutant individual to successfully escape accidental extinction (phase 3: invasion)

$$w_i(s_i', s) = \mathcal{M}_i(s_i', s) \cdot \mathcal{S}_i(s_i', s) \, . \tag{5.15}$$

An additional factor (phase 4: fixation) would have been required, had we not assumed the principle of mutual exclusion which guarantees that invasion implies fixation. Therefore the corresponding conditional probability of fixation given invasion is of value 1.

Mutation Events

Second, we compute the probability per unit time $\mathcal{M}_i$ that the mutant enters the population.

The processes of mutation in distinct individuals are statistically uncorrelated. Thus the probability per unit time $\mathcal{M}_i$ is given by the product of the following three terms.

1. The per capita mutation rate $\mu_i(s_i) \cdot \bar{b}_i(s_i, s)$ for the trait s_i. The term $\bar{b}_i(s_i, s)$ is the per capita birth rate of resident individuals of the ith species in the environment determined by the monomorphic resident populations with adaptive trait values s, and $\mu_i(s_i)$ denotes the fraction of births that give rise to mutations in the species i.
2. The population size $\hat{n}_i(s)$ of the ith species. The product of this factor with the first term yields the overall mutation rate in the population of species i.
3. The probability distribution $M_i(s_i, s_i' - s_i)$ for the mutation process in the trait s_i.

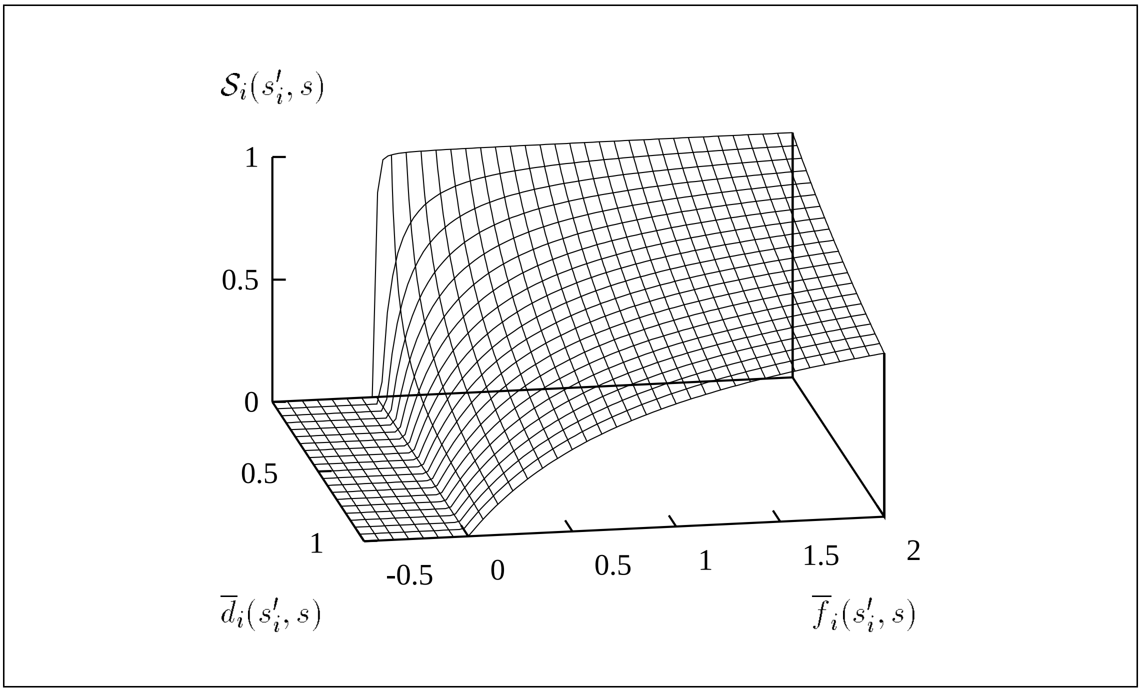

Figure 5.1 Invasion success of a rare mutant. The probability $\mathcal{S}_i(s_i', s)$ of a mutant population initially of size 1 with adaptive trait value s_i' in a community of monomorphic resident populations with adaptive trait values s to grow in size such as to eventually overcome the threshold 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.

Collecting the expressions above we obtain

$$\mathcal{M}_i(s_i', s) = \mu_i(s_i) \cdot \overline{b}_i(s_i, s) \cdot \hat{n}_i(s) \cdot M_i(s_i, s_i' - s_i) \tag{5.16}$$

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

Selection Events

Third, we consider the process of selection determining the probability $\mathcal{S}_i$ of escaping extinction.

Since mutants enter initially in a single individual, the impact of demographic stochasticity on their population dynamics must not be neglected (Fisher 1958). The situation is different, however, for the resident populations; here we have assumed that the equilibrium population sizes $\hat{n}_i(s)$ are large enough for there to be negligible risk of accidental extinction.

Two results stem from this.

1. Frequency-dependent effects on the population dynamics of the mutant can be ignored when the mutant is rare relative to the resident.
2. 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).

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 equation (5.9) and considering the result 1 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) with the per capita birth and death rates of the rare mutant, $b = \overline{b}_i(s_i', s)$ and $d = \overline{d}_i(s_i', s)$. We exploit result 2 by taking the limit $n \to \infty$.

The probability $\mathcal{S}_i$ of escaping extinction is thus given by

$$\begin{aligned} \mathcal{S}_i(s_i', s) &= \begin{cases} 1 - \overline{d}_i(s_i', s)/\overline{b}_i(s_i', s) & \text{for} \quad \overline{d}_i(s_i', s)/\overline{b}_i(s_i', s) < 1 \\ 0 & \text{for} \quad \overline{d}_i(s_i', s)/\overline{b}_i(s_i', s) \geq 1 \end{cases} \\ &= \overline{b}_i^{-1}(s_i', s) \cdot \big(\overline{f}_i(s_i', s)\big)_+ \end{aligned} \tag{5.17}$$

where the function $(\ldots)_+ : \ x \to x \cdot \Theta(x)$ leaves positive arguments unchanged and maps negative ones to zero.

In consequence of equation (5.17), 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 5.1.

Conclusion

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

$$\begin{aligned} w_i(s_i', s) = &\mu_i(s_i) \cdot \overline{b}_i(s_i, s) \cdot \hat{n}_i(s) \cdot M_i(s_i, s_i' - s_i) \cdot \\ &\overline{b}_i^{-1}(s_i', s) \cdot \big(\overline{f}_i(s_i', s)\big)_+ \, . \end{aligned} \tag{5.18}$$

This result completes the stochastic representation of the mutation-selection process in terms of the master equation. By combining equations (5.13), (5.14) and (5.18) we have derived our second model of coevolutionary dynamics, the *monomorphic stochastic model.*

Recovery of Invasion Criterion

From equation (5.18) it is easy to conclude that a sufficient condition for a resident population with adaptive trait value s_i not to be invadable by a mutant adaptive trait value s_i' (in an environment determined by the monomorphic resident populations with adaptive trait values s) is given by $\overline{f}_i(s_i', s) < 0$ or equivalently by

$$\overline{f}_i(s_i, s) > \overline{f}_i(s_i', s) \ . \tag{5.19}$$

This condition closely resembles the inequality (2.1) for evolutionarily stable strategies, which is thus recovered from our stochastic approach.

We only note in passing that when resident populations are not assumed to be sufficiently large for not being subject to accidental extinction, invasion always is possible with some finite probability per unit time.

5.4 An Algorithm for the Monomorphic Stochastic Model

An algorithm for the monomorphic stochastic model derived from equations (5.13,14,18) is presented in Figure 5.2. As in the case of the polymorphic stochastic model we again restrict attention to autonomous coevolutionary communities in order to employ for the algorithm the minimal process method introduced in Section 4.4.

Distribution of Waiting Times

According to Step C in Figure 5.1 the waiting times between two events of a stochastic realization follow an exponential distribution. By the same line of reasoning as given in Section 4.4 we obtain for the distribution of waiting times between two subsequent trait substitution events in the monomorphic stochastic model (apart from normalization)

$$P(s, t + \Delta t) = \exp\left\{ - \int_t^{t+\Delta t} T^{-1}(s, t') \ dt' \right\} \ . \tag{5.20}$$

with $T^{-1}(s,t) = \int w(s'|s,t) \ ds'$. For homogeneous master equations (5.13) equation (5.20) reduces to

$$P(s, t + \Delta t) = \exp\left\{ -\Delta t / T(s) \right\} \ . \tag{5.21}$$

An Algorithm for the
Monomorphic Stochastic Model

A. Initialize the adaptive trait values s_i with $i = 1, \ldots, N$ at time $t = 0$ and specify the time t_{end} when to stop the dynamics.

B. Construct the integrals $w_i = \int w_i(s_i', s)\, ds_i'$ with $i = 1, \ldots, N$ and the sum $w = \sum_{i=1}^{N} w_i$.

C. Choose the waiting time Δt for the next event to occur according to $\Delta t = -\frac{1}{w} \cdot \ln r$ where $0 < r \leq 1$ is a uniformly distributed random number.

D. Choose species i with probability $\frac{1}{w} \cdot w_i$.

E. Choose for species i a new phenotype s_i' with probability density $\frac{1}{w_i} \cdot w_i(s_i', s)$.

F. Update time and adaptive trait values according to $t \rightarrow t + \Delta t$ and $s_i \rightarrow s_i'$.

G. Continue from Step B until $t \geq t_{end}$.

Figure 5.2 An algorithm for the monomorphic stochastic model. The protocol employs the minimal process method described in Section 4.4.

Autonomous and Non-Autonomous Systems

The remarks in Section 4.4 on the validity of the presented algorithm for non-autonomous coevolutionary communities apply equally to the monomorphic stochastic model. For time steps Δt being small compared to the time scale on which $T^{-1}(s, t)$ changes, exponentially distributed waiting times and thus the minimal process method may be applied approximately even to non-homogeneous master equations (corresponding to systems with an external time dependence), provided only that the typical number of events on the timescale of the external perturbations is large.

This prerequisite coincides with the condition that is required for the principle of mutual exclusion to hold even in the case of varying environments. For more details see Sections 7.3 and 8.2.

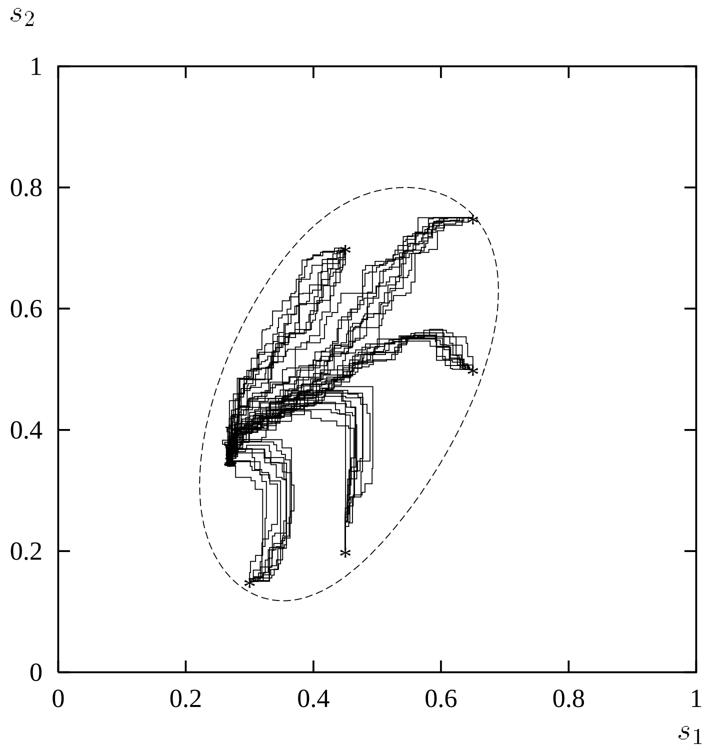

Figure 5.3 Realizations of the monomorphic stochastic model. Five directed random walks in trait space for each of the five initial conditions (indicated by asterisks) are depicted by continuous lines. The discontinuous oval line is the boundary of the region of coexistence. The coevolution of both species drives their adaptive trait values towards a common equilibrium $\hat{s}$. Parameters of the coevolutionary predator-prey community are the same as in Figure 4.4.

5.5 Sample Simulations and Further Inquiry

The information contained in the stochastic representation of the adaptive process can be used in several respects.

Bundles of Trait Substitution Sequences

First, we can employ the algorithm presented in the last section to obtain actual realizations of the stochastic mutation-selection process.

We again illustrate this method by means of an example of predator-prey coevolution. A portion of the two-dimensional monomorphic trait space $\widehat{S}$ of this system is depicted in Figure 5.3. The dashed line surrounds the region of coexistence $\widehat{S}_c$. Within this region several trait substitution sequences $(s_1(t), s_2(t))$ are displayed by continuous lines.

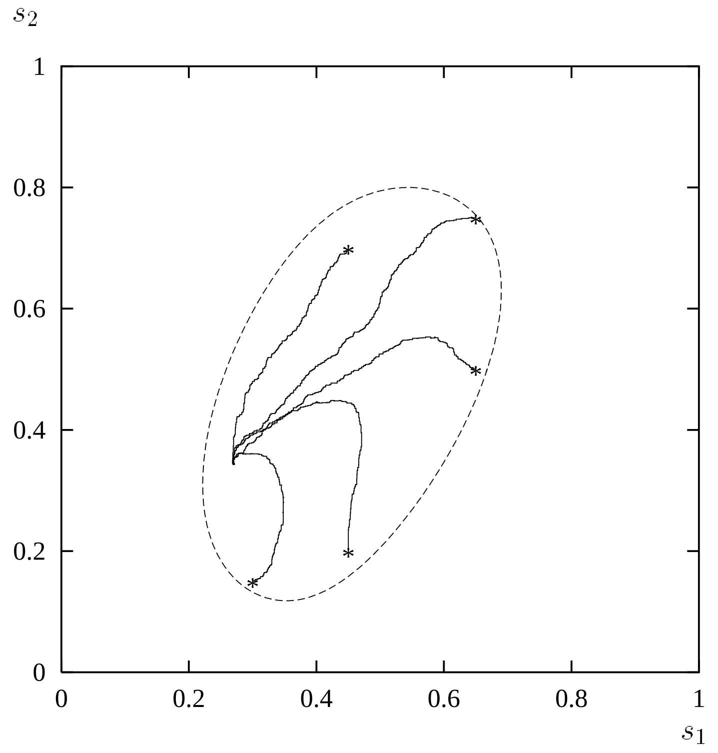

Figure 5.4 Mean paths of the monomorphic stochastic model. Ten trait substitution sequences for each of the five initial conditions (indicated by asterisks) are combined to obtain the mean paths, depicted by continuous lines. The jaggedness of these lines is caused by the finite number of ten trait substitution sequences used for constructing the mean paths. The discontinuous oval line is the boundary of the region of coexistence. The coevolution of both species drives their adaptive trait values towards a common equilibrium $\hat{s}$. Parameters of the coevolutionary predator-prey community are the same as in Figure 4.4.

Note that trait substitution sequences starting from the same initial state are not identical. This underlines the unique, historical nature of any evolutionary process. But, though these paths are driven apart by the process of mutation, they are kept together by the directional impact of selection.

Definition of Mean Paths

Second, the latter observation underpins the introduction of a further concept from stochastic process theory.

By imagining a large number r of independent trait substitution sequences $s^j(t) = \big(s_1^j(t), \ldots, s_N^j(t)\big)$, with $j = 1, \ldots, r$, 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

$$\langle s\rangle(t) = \lim_{r\to\infty} \frac{1}{r} \cdot \sum_{j=1}^{r} s^j(t)\ . \tag{5.22}$$

The construction of these mean paths is illustrated in Figure 5.4 for the case of predator-prey coevolution. By comparison of Figure 5.4 to Figures 5.3 and 4.4 it can be seen that the mean paths appear to capture the essential features of the adaptive process. This observation is further exploited in the next chapter.

Chapter 6
The Monomorphic Deterministic Model

The mean paths of the monomorphic stochastic model, introduced in Section 5.5, obviously summarize the essential features of the adaptive process. Hence it is desirable to obtain an explicit expression for computing the *mean path dynamics*.

Rather than averaging over lots of stochastic realizations as shown in Section 5.5, in this chapter we derive a system of ordinary differential equations that directly serves as a deterministic approximation of the mean path dynamics.

6.1 Dynamics of Mean Path and Deterministic Path

The mean path has been defined in equation (5.22) as the average over an infinite number of independent realizations of the stochastic process.

Mean Path Dynamics

Equivalently, we can employ the probability distribution $P(s,t)$ considered in the last chapter to define the mean of an arbitrary function $F(s)$ by $\langle F(s)\rangle(t) = \int F(s) \cdot P(s,t)\, ds$ (Gardiner 1985).

In particular we thereby obtain for the mean path

$$\langle s\rangle(t) = \int s \cdot P(s,t)\, ds \; . \tag{6.1}$$

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

$$\frac{d}{dt}\langle s\rangle(t) = \int s \cdot \frac{d}{dt}P(s,t)\, ds \,. \tag{6.2}$$

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

$$\frac{d}{dt}\langle s\rangle(t) = \int\int \big(s' - s\big) \cdot w\big(s'|s\big) \cdot P(s,t)\, ds'\, ds \,. \tag{6.3}$$

By exploiting the δ-function property of $w(s'|s)$, see equation (5.14), and introducing the *jth jump moment of the ith species*,

$$a_{ji}(s) = \int \big(s_i' - s_i\big)^j \cdot w_i\big(s_i', s\big)\, ds_i' \tag{6.4}$$

with $a_j = \big(a_{j1}, \ldots, a_{jN}\big)$, we obtain

$$\frac{d}{dt}\langle s\rangle(t) = \langle a_1(s)\rangle(t) \,. \tag{6.5}$$

Deterministic Path Dynamics

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

$$\frac{d}{dt}\langle s\rangle(t) = a_1(\langle s\rangle(t)) \,. \tag{6.6}$$

However, the adaptive 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.

As an alternative to the classical Kramers-Moyal expansion, the result (6.6) can be derived via a controlled series expansion, called the *omega-expansion* (van Kampen 1962, 1981). Without going into details we only mention that for this purpose one can utilize σ_i^{-1}, the inverses of the standard deviations of the mutation distributions M_i, as *system size parameters*. Similar to constructing the thermodynamic limit in statistical mechanics (see e.g. Huang 1987), one can then show that the dynamics (6.5) of the mean path of the adaptive process converge to equation (6.6) for large system size parameters. For details on this method see van Kampen (1962, 1981) and Kubo et al. (1973). In order to distinguish between the mean path itself and that actually described by equation (6.6), the latter is called the *deterministic path* (Serra et al. 1986).

6.2 Deterministic Approximation in First Order

In this section we derive an equation for the deterministic approximation of the adaptive process. We show that when taking the approximation only to first order and invoking further simplifying assumptions as to the mutation process, we recover the canonical equation of adaptive dynamics as described in Section 2.3.

However, the mathematical framework developed here is capable (i) of providing higher order correction terms to the canonical equation and (ii) of allowing for more general ecological and evolutionary scenarios than the canonical result. In the next section we start to develop these generalizations, further extensions are provided in Chapter 8.

The Deterministic Path of the Adaptive Process

We can calculate the deterministic path of the coevolutionary dynamics by substituting equation (5.18) into (6.4) and the result into (6.6). Since in the remainder of this chapter we concentrate on the deterministic approximation, we will cease denoting it by angle brackets $\langle \ldots \rangle$. For the purpose of comparison to the canonical equation of adaptive dynamics as presented in Section 2.3, in this section we are interested in a description of the adaptive dynamics that is as simple as possible. For this reason we temporarily assume mutation processes to be symmetric. We again return to general mutation processes in the next section.

By proceeding as described above we obtain

$$\begin{aligned}\frac{d}{dt}s_i =& \mu_i(s_i) \cdot \bar{b}_i(s_i, s) \cdot \hat{n}_i(s) \cdot \\ & \int_{R_i(s)} (s_i' - s_i) \cdot M_i(s_i, s_i' - s_i) \cdot \bar{b}_i^{-1}(s_i', s) \cdot \bar{f}_i(s_i', s)\, ds_i'\end{aligned} \tag{6.7}$$

where, as an alternative to employing the function $(\ldots)_+$ in the integrand, see equation (5.18), in equation (6.7) we have restricted the *range of integration* to $s_i' \in R_i(s)$ with

$$R_i(s) = \left\{ s_i' \in \widehat{S}_i \mid \bar{f}_i(s_i', s) > 0 \right\}. \tag{6.8}$$

Note that the process of mutation causes the evolutionary rate $\frac{d}{dt}s_i$ to be dependent on the per capita growth and birth rates of all possible mutant traits s_i'. This dependence is manifested both by the integrand of (6.7) and in the range of integration (6.8).

First Order Result

In order to transform the described global coupling into a local one we apply a Taylor expansion to $\overline{f}_i(s_i', s)$ in equation (6.8) and $\overline{b}_i^{-1}(s_i', s) \cdot \overline{f}_i(s_i', s)$ in equation (6.7) about $s_i' = s_i$. Higher orders in these expansions are discussed in Section 6.3; in this section we will use the results only up to first order,

$$\overline{f}_i(s_i', s) = \partial_i' \overline{f}_i(s_i, s) \cdot (s_i' - s_i) \tag{6.9}$$

and

$$\overline{b}_i^{-1}(s_i', s) \cdot \overline{f}_i(s_i', s) = \overline{b}_i^{-1}(s_i, s) \cdot \partial_i' \overline{f}_i(s_i, s) \cdot (s_i' - s_i) \, . \tag{6.10}$$

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 frequently, we apply the abbreviated notations

$$\partial_i' \overline{f}_i = \frac{\partial}{\partial s_i'} \overline{f}_i \, , \qquad \partial_i \overline{f}_i = \frac{\partial}{\partial s_i} \overline{f}_i \tag{6.11}$$

and analogously for all functions taking the arguments (s_i', s).

From equations (6.8) and (6.9) 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 $\partial_i' \overline{f}_i(s_i, s)$. As we assumed the mutation distribution M_i to be symmetric in its argument $s_i' - s_i$, we obtain the same result in both cases by substituting equation (6.10) into (6.7)

$$\frac{d}{dt} s_i = \frac{1}{2} \cdot \mu_i(s_i) \cdot \sigma_i^2(s_i) \cdot \hat{n}_i(s) \cdot \partial_i' \overline{f}_i(s_i, s) \tag{6.12}$$

where

$$\sigma_i^2(s_i) = \int \Delta s_i^2 \cdot M_i(s_i, \Delta s_i) \, d\Delta s_i \tag{6.13}$$

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 (6.12) provides a first order, deterministic approximation of the coevolutionary dynamics. These equations define a simple version of the *monomorphic deterministic model*; a more refined one is provided in form of equations (6.19).

Interpretation of the First Order Result

From equation (6.12) we see that the rate of evolution in the trait s_i is determined by two factors.

1. The first terms in equation (6.12) 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

$$\begin{aligned}\partial_i' \overline{f}_i(s_i, s) &= \frac{\partial}{\partial s_i'} f_i(s_i', s) \Big|_{s_i'=s_i} \\ &= \lim_{\Delta s_i \to 0} \frac{1}{\Delta s_i} \cdot \left[\overline{f}_i(s_i + \Delta s_i, s) - \overline{f}_i(s_i, s) \right] \\ &= \lim_{\Delta s_i \to 0} \frac{1}{\Delta s_i} \cdot \overline{f}_i(s_i + \Delta s_i, s)\end{aligned} \tag{6.14}$$

   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 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 Section 7.2 we demonstrate that this information in general is not sufficient to predict evolutionary attractors.

Recovery of the Canonical Equation of Adaptive Dynamics

By means of equation (6.12) we have recovered the canonical equation (2.3) of adaptive dynamics from the stochastic ecological processes underlying the coevolutionary process.

For the evolutionary rate coefficients we obtain

$$k_i(s) = \frac{1}{2} \cdot \mu_i(s_i) \cdot \sigma_i^2(s_i) \cdot \hat{n}_i(s) \, . \tag{6.15}$$

In addition, we have shown the appropriate measure of “fitness” to be given by the per capita growth rate of a rare mutant

$$W_i(s_i', s) = \overline{f}_i(s_i', s)\,. \tag{6.16}$$

In the next section and in Chapter 8 we indicate how the canonical result can be generalized.

6.3 Deterministic Approximation in Higher Orders

The result (6.12) for the deterministic approximation of the adaptive process needs to be generalized for two reasons.

1. The process of mutation has induced a global coupling in the adaptive dynamics (6.7). 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.
2. Rather than restricting mutation distributions M_i to be symmetric, general distribution functions ought to be allowed (Mackay 1990).

Higher Order Result

The rth order results for 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 $s_i' = s_i$ are given by

$$\overline{f}_i(s_i', s) = \sum_{j=1}^{r} (s_i' - s_i)^j \cdot \frac{1}{j!} \cdot \partial_i'^{j}\, \overline{f}_i(s_i, s) \tag{6.17}$$

and

$$\begin{aligned} &\overline{b}_i^{-1}(s_i', s) \cdot \overline{f}_i(s_i', s) \\ &= \sum_{j=1}^{r} (s_i' - s_i)^j \cdot \frac{1}{j!} \cdot \sum_{j'=1}^{j} \binom{j}{j'} \cdot \partial_i'^{j'}\, \overline{f}_i(s_i, s) \cdot \partial_i'^{j-j'}\, \overline{b}_i^{-1}(s_i, s)\,. \end{aligned} \tag{6.18}$$

Again we have already accounted for $\overline{f}_i(s_i, s) = 0$.

Substituting equations (6.18) into (6.7) yields the result for the deterministic approximation of the coevolutionary dynamics in rth order

$$\begin{aligned} \frac{d}{dt} s_i &= \mu_i(s_i) \cdot \hat{n}_i(s) \cdot \\ &\sum_{j=1}^{r} m_{j+1,i}(s) \cdot \frac{1}{j!} \cdot \sum_{j'=1}^{j} \binom{j}{j'} \cdot \partial_i'^{j'}\, \overline{f}_i(s_i, s) \cdot \partial_i'^{j-j'}\, \overline{b}_i^{-1}(s_i, s) \end{aligned} \tag{6.19}$$

with

$$m_{ji}(s) = \int_{R_i(s)} \left(s'_i - s_i\right)^j \cdot M_i\left(s'_i - s_i\right) \, ds'_i \, . \tag{6.20}$$

The range of integration in (6.20) is given by substituting (6.17) into (6.8)

$$R_i(s) = \{ s'_i \in \widehat{S}_i \mid \sum_{j=1}^{r} \left(s'_i - s_i\right)^j \cdot \frac{1}{j!} \cdot \partial_i'^j \overline{f}_i(s_i, s) > 0 \} \, . \tag{6.21}$$

The interpretation of the adaptive dynamics (6.19) is analogous to that given for (6.12) in the last section. The $m_{ji}(s)$ are called the *jth mutation moments of the ith species*. They actually coincide with the jth moments of the mutation distribution M_i only if the range of integration $R_i(s)$ is $(-\infty, +\infty)$. However, as (6.21) indicates, this is generally 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 distributions such that the result (6.19) is independent of this assumption.

Comparison to First Order Result

The corrections arising from the higher order result (6.19) in comparison to the first order result (6.12) 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 jth order derivatives $\partial_i'^j \left[\, \overline{b}_i^{-1}(s_i, s) \cdot \overline{f}_i(s_i, s) \, \right]$ with $j > 1$ 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 $m_{j+1,i}(s)$ with $j > 1$ are negligible compared to the second order mutation moment.

We conclude that in either limit – that of vanishing nonlinearity or that of vanishing variance – the first order result (6.12) of the adaptive dynamics becomes an exact representation of the deterministic path. The virtue of the dynamics (6.12) is its simplicity combined with good accuracy as long as one of the two conditions above is met. The virtue of the dynamics (6.19) 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.

Note that even for $r = 1$ equations (6.12) and (6.19) are in general not equivalent. When the mutation process is asymmetric, $\frac{1}{2} \cdot \sigma_i^2(s_i)$ will not coincide with $m_{2i}(s)$. In particular, the value of $m_{2i}(s)$ then depends on the distribution of advantageous mutant trait values s_i' around the resident trait value s_i.

The importance of the higher order correction terms is discussed in Section 7.4. We there describe two special consequences. One effect, the *shifting of evolutionary isoclines*, only occurs in the second order result for asymmetric mutation processes, for symmetric mutation processes the third order corrections are to be considered. The other effect, the phenomenon of *evolutionary slowing down*, can be understood by means of the second order result.

6.4 An Algorithm for the Monomorphic Deterministic Model

An algorithm for the monomorphic deterministic model derived from equations (6.12) or (6.19) is presented in Figure 6.1. It employs the *fourth order Runge-Kutta method* described below.

The Euler Method

The simplest choice for an update method in Step C of the algorithm for the monomorphic deterministic model could be based on the Euler method

$$t \to t + dt, \qquad s_i \to s_i + w_i \tag{6.22}$$

with $w_i = dt \cdot \dot{s}_i(s)$. Here, $\dot{s}_i(s)$ denotes the right hand side of either equation (6.12) or (6.19).

However, the error for this method of numerical integration is of order $\mathcal{O}(dt^2)$. For results of sufficient accuracy thus small time steps dt are required.

An Algorithm for the Monomorphic Deterministic Model

A. Initialize the adaptive trait values s_i with $i = 1, \ldots, N$ at time $t = 0$ and specify the time step dt as well as the time t_{end} when to stop the dynamics.

B. Construct the vectors $w_{1i} = dt \cdot \dot{s}_i(s)$, $w_{2i} = dt \cdot \dot{s}_i\big(s + \frac{1}{2} \cdot w_1\big)$, $w_{3i} = dt \cdot \dot{s}_i\big(s + \frac{1}{2} \cdot w_2\big)$ and $w_{4i} = dt \cdot \dot{s}_i(s + w_3)$ with $i = 1, \ldots, N$.

C. Update time and adaptive trait values according to $t \rightarrow t + dt$ and $s_i \rightarrow s_i + \frac{1}{6} \cdot (w_{1i} + 2 \cdot w_{2i} + 2 \cdot w_{3i} + w_{4i})$.

D. Continue from Step B until $t \geq t_{end}$.

Figure 6.1 An algorithm for the monomorphic deterministic model. The protocol employs the fourth order Runge-Kutta method described in the text.

The Fourth Order Runge-Kutta Method

A better choice is provided by the fourth order Runge-Kutta method

$$t \rightarrow t + dt, \qquad s_i \rightarrow s_i + \frac{1}{6} \cdot (w_{1i} + 2 \cdot w_{2i} + 2 \cdot w_{3i} + w_{4i}) \tag{6.23}$$

with w_{1i} to w_{4i} as defined in Step B of Figure 6.1.

Here, the error inevitably associated with any method of numerical integration is only of order $\mathcal{O}\big(dt^5\big)$. As time steps dt thus may be larger while producing the same error, this method is advantageous to the simpler Euler method.

6.5 Sample Simulations and Further Inquiry

The deterministic approximation of the monomorphic stochastic model opens up ample opportunity for further investigation of the adaptive dynamics in coevolutionary communities. We will utilize this representation in Chapters 7 and 9; here we only outline some general perspectives.

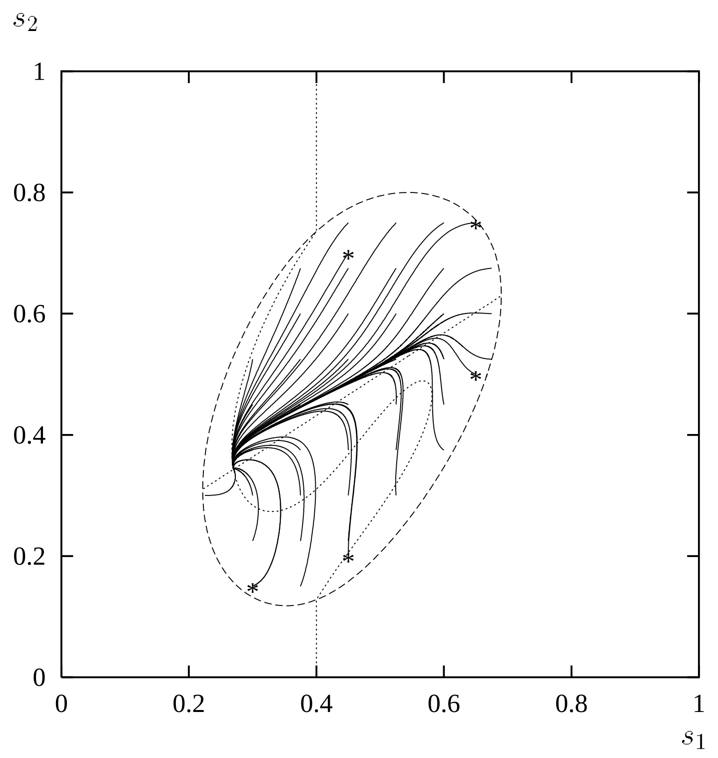

Figure 6.2 Orbits of the monomorphic deterministic model. The deterministic trajectories which correspond to the trait substitution sequences in Figure 5.3, to the mean paths in Figure 5.4 and to the realizations of the polymorphic stochastic model in Figure 4.4 are depicted by continuous lines with initial conditions indicated by asterisks. More 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), see Section 7.1. Parameters of the coevolutionary predator-prey community are the same as in Figure 5.4.

Phase Portraits

The deterministic approximations (6.12) and (6.19) readily allow us to calculate *phase portraits* of the adaptive dynamics.

An application to predator-prey coevolution is depicted in Figure 6.2. The evolutionary trajectories, following the deterministic path, coincide with the mean paths calculated from the stochastic process itself, see Figure 5.4. We could easily supplement the picture by considering a large number of trajectories.

A variety of such phase portraits is obtained in the investigation of the coevolutionary predator-prey community in Chapter 9, see Figures 9.4, 9.5 and 9.6.

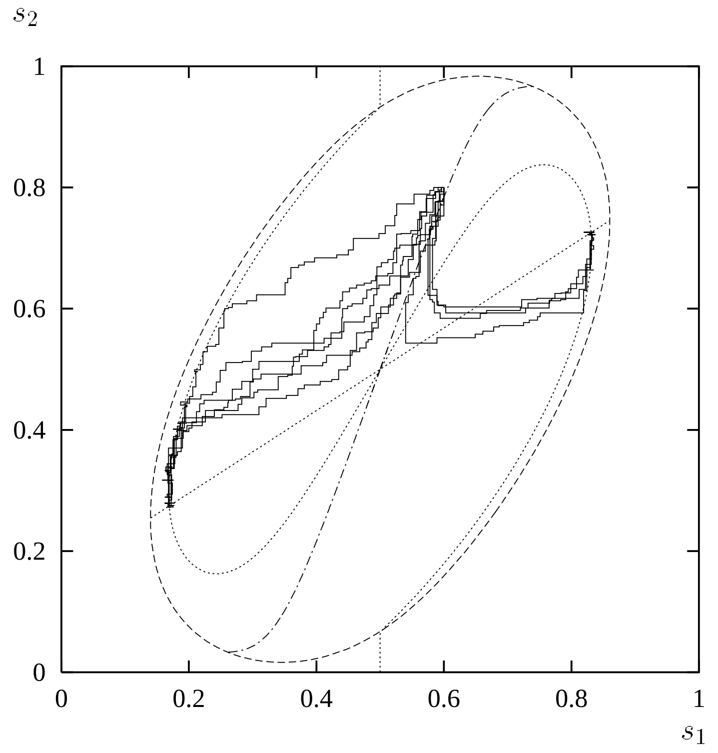

Figure 6.3 The monomorphic models and multiple attractors in trait space. Ten trait substitution sequences with a common initial condition are obtained as stochastic realizations of the monomorphic stochastic model and depicted by continuous lines. The set of these trait substitution sequences splits permanently into two separate bundles since the initial condition is close to a basin boundary, a feature that cannot be captured by a deterministic description. The basin boundary or separatrix is obtained from the monomorphic deterministic model and is depicted by the dashed and dotted line. The basin boundary is the unstable manifold of a saddle, which is located at the middle intersection of the inner evolutionary isoclines depicted as dotted curves. The outer two fixed points are stable nodes. To construct the basin boundary the direction of time is to be reversed in the monomorphic deterministic model in order to stabilize the unstable manifold. The discontinuous oval curve is the boundary of the region of coexistence. Parameters of the coevolutionary predator-prey community are as given in Figure 9.3 except for $\sigma_1 = \sigma_2 = 5 \cdot 10^{-3}$.

Bifurcation Analysis

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 approximations (6.12) or (6.19).

The effects of varying different ecological parameters, which have an impact on the adaptive dynamics, can then be explored systematically, see Sections 7.2 and 9.4 and in particular Figure 9.7.

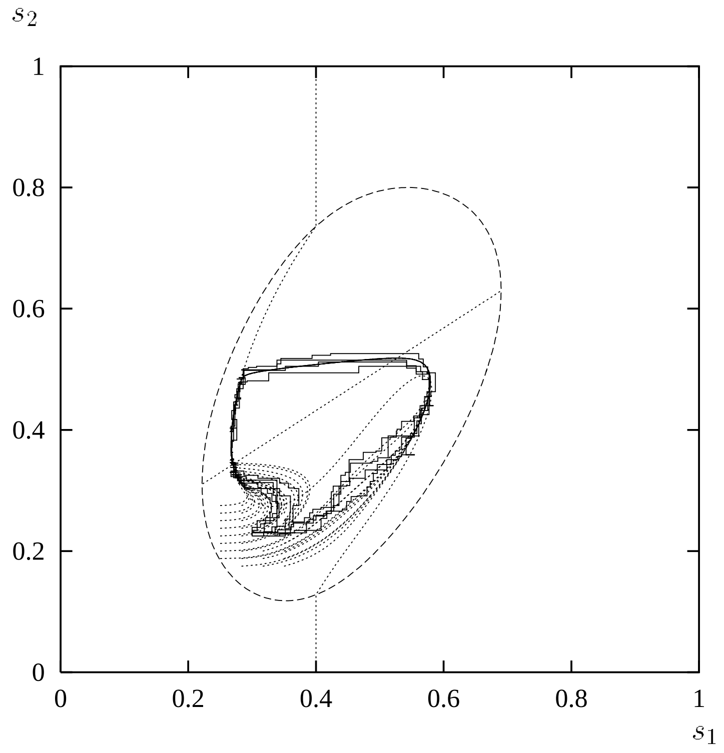

Figure 6.4 The monomorphic models and expanding flow in trait space. Ten trait substitution sequences with a common initial condition are obtained as stochastic realizations of the monomorphic stochastic model and depicted by continuous lines. The set of these trait substitution sequences splits temporarily into two separate bundles since the initial condition is situated in a region of expanding flow, a feature that cannot be captured by a deterministic description. The flow is defined in terms of the monomorphic deterministic model and its orbits are depicted by the dotted lines. The discontinuous oval curve is the boundary of the region of coexistence. Parameters of the coevolutionary predator-prey community are the same as in Figure 6.2 except for $\mu_1 = 10^{-3}$.

Caveats

Some caveats are however necessary for understanding the validity of any deterministic approximation of a stochastic process.

First, if the adaptive dynamics turn out to be multistable, it will be possible for trait substitution sequences to exhibit jumps between the existing basins of attraction. No deterministic approximation is capable of capturing this feature. This must be kept in mind while applying the deterministic approximation to initial states very close to the basin boundary. Figure 6.3 illustrates this point. Moreover, large fluctuations between the multiple stable states themselves in principle can happen. However, due to the shape of the mutation distributions the latter will typically be associated with such extremely small probabilities per unit time that are negligible on ecological and even on evolutionary timescales.

Second, if the flow of the dynamical system describing the deterministic path is expanding, i.e. trajectories are diverging, 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. An example is given in Figure 6.4. Note, however, 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 Figures 5.3 and 6.2.

Third, if the adaptive dynamics possess nonequilibrium attractors, 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 a stochastic limit cycle dynamics is not defined, though the asymptotic mean period is accurately described. This point is demonstrated in Figure 9.8.

Chapter 7
Analysis of the Monomorphic Models

In this chapter we utilize the descriptions of the monomorphic stochastic model and the monomorphic deterministic model, derived in the previous two chapters, to examine in detail some of the rich variety of features that coevolutionary dynamics of this sort can exhibit.

7.1 Characteristics of Isoclines

Given equation (6.12) which describes the coevolutionary dynamics of the monomorphic deterministic model to first order, we can now investigate the conditions under which evolution in single traits or in the whole community comes to a halt.

Definition of Isoclines

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 (6.12) 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.

In a second step, the impact of mutational steps being finite rather than infinitesimal can by investigated by means of the higher order correction terms provided by equation (6.19). This case will be considered in Section 7.4.

Classification of Isoclines

Inner evolutionary s_i-isoclines can be classified as below.

1. Inner isoclines on which

$$\partial_i^{\prime 2}\overline{f}_i(s_i, s) < 0 \tag{7.1}$$

   holds are called δ-stable or *non-invadable*.
2. Inner isoclines whose points satisfy

$$\partial_i^{\prime 2}\overline{f}_i(s_i, s) - \partial_i^{2}\overline{f}_i(s_i, s) < 0 \tag{7.2}$$

   are called m-stable or *convergent*.
3. Inner isoclines characterized by

$$\partial_i^{\prime 2}\overline{f}_i(s_i, s) + \partial_i^{2}\overline{f}_i(s_i, s) < 0 \tag{7.3}$$

   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).

The notion of non-invadability is that on the s_i-isoclines mutants s_i' in species i with phenotypes close to s_i should not be able to invade; this idea is familiar from ESS theory (Maynard Smith and Price 1973; Maynard Smith 1982; Parker and Maynard Smith 1990) and the arguments of Roughgarden (1983) and Brown and Vincent (1987a, 1987b).

The term convergence was introduced to refer to the property of successive mutations s_i' to cause evolution towards the s_i-isocline. Attention was first drawn to the distinction between this and non-invadability by Eshel and Motro (1981) and Eshel (1983), and

Class	Inequality			Set of invasion angles		
	(7.1)	(7.2)	(7.3)	$\alpha_{min} <$	α_i	$< \alpha_{max}$
	non-invadability........................	...............convergence	................no mutual invadability			
1	yes	yes	yes	$3 \cdot \frac{\pi}{4}$		$5 \cdot \frac{\pi}{4}$
2	yes	yes	no	$2 \cdot \frac{\pi}{4}$		$3 \cdot \frac{\pi}{4}$
3	no	yes	no	$1 \cdot \frac{\pi}{4}$		$2 \cdot \frac{\pi}{4}$
4	no	no	no	$7 \cdot \frac{\pi}{4} - 2 \cdot \pi$		$1 \cdot \frac{\pi}{4}$
5	no	no	yes	$6 \cdot \frac{\pi}{4}$		$7 \cdot \frac{\pi}{4}$
6	yes	no	yes	$5 \cdot \frac{\pi}{4}$		$6 \cdot \frac{\pi}{4}$

Figure 7.1 Definition of the six different classes of evolutionary isoclines.

was discussed in more detail by Taylor (1989) as well as by Takada and Kigami (1991). Note that the dynamical interpretation suggested by the term convergent is different for coevolutionary communities with $N = 1$ and for those with $N > 1$; this distinction will be clarified in the next section.

Mutual invadability refers to the property of a pair of phenotypes s_i' and s_i'' at opposite sides of the s_i-isocline both to invade and to be invaded by the other phenotype; Christiansen (1991) noted that neither phenotype can go to fixation in this case. If an isocline has this property at a fixed point, the system could evolve from the fixed point to a state in which two phenotypes are present in species i; the principle of mutual exclusion guaranteeing that each mutant either replaces the previous resident or goes to extinction would no longer hold. Identifying such fixed points thus is important, because they indicate when the assumption of monomorphism (see Section 5.1) might become inappropriate. For more details on this issue see the discussion in Sections 7.2 and 7.3.

The inequalities (7.1), (7.2) and (7.3) permit six classes of isoclines (Metz et al. 1994), as summarized in Figure 7.1. There are only 6 rather than $2^3 = 8$ classes, as convergence and absence of mutual invadability imply non-invadability; similarly, divergence and mutual invadability imply invadability. The class of an isocline can readily be determined: to do this we suggest a new mathematical tool, the *invasion angle*

$$\alpha_i(s) = \arctan\left(\partial_i'^2 \overline{f}_i(s_i, s), \partial_i^2 \overline{f}_i(s_i, s)\right) \tag{7.4}$$

where the function $\arctan(x, y)$ returns the angular polar coordinate corresponding to the two Cartesian coordinates x and y. The invasion angle α_i, evaluated at a point on a s_i-isocline, unambiguously identifies the class of the isocline at that point (see Figure 7.1) and, in consequence, there is only a single degree of freedom in the classification scheme of isoclines.

Illustration of the Classification

To understand the significance of the invasion angle and of the three inequalities above we expand $\overline{f}_i(s_i', s)$, the per capita growth rate of a mutant s_i' in a community of resident species with adaptive trait values s, to second order into a Taylor series in s_i' and s_i around a point $\hat{s}$ situated on a s_i-isocline

$$\begin{aligned}\overline{f}_i(s_i', s) =& \overline{f}_i(\hat{s}_i, \hat{s}) + \\ & (s_i' - \hat{s}_i) \cdot \partial_i' \overline{f}_i(\hat{s}_i, \hat{s}) + \\ & (s_i - \hat{s}_i) \cdot \partial_i \overline{f}_i(\hat{s}_i, \hat{s}) + \\ & (s_i' - \hat{s}_i)^2 \cdot \partial_i'^2 \overline{f}_i(\hat{s}_i, \hat{s}) + \\ & (s_i' - \hat{s}_i) \cdot (s_i - \hat{s}_i) \cdot 2 \cdot \partial_i' \partial_i \overline{f}_i(\hat{s}_i, \hat{s}) + \\ & (s_i - \hat{s}_i)^2 \cdot \partial_i^2 \overline{f}_i(\hat{s}_i, \hat{s})\end{aligned} \tag{7.5}$$

By accounting for the constraint $\overline{f}_i(s_i', s) = 0$ which holds for all $s_i' = s_i$, we obtain the identities

$$\overline{f}_i(\hat{s}_i, \hat{s}) = 0\ , \tag{7.6}$$

$$\partial_i' \overline{f}_i(\hat{s}_i, \hat{s}) + \partial_i \overline{f}_i(\hat{s}_i, \hat{s}) = 0 \tag{7.7}$$

and

$$\partial_i'^2 \overline{f}_i(\hat{s}_i, \hat{s}) + 2 \cdot \partial_i' \partial_i \overline{f}_i(\hat{s}_i, \hat{s}) + \partial_i^2 \overline{f}_i(\hat{s}_i, \hat{s}) = 0\ . \tag{7.8}$$

From the first order result of the monomorphic deterministic model, equation (6.12), we know that points $\hat{s}$ on inner evolutionary s_i-isoclines are characterized by $\partial_i' \overline{f}_i(\hat{s}_i, \hat{s}) = 0$. With the three identities (7.6), (7.7) and (7.8) there thus remain only two degrees of freedom in equation (7.5). One can be eliminated by normalization, the other is given by the invasion angle α_i. When choosing normalization to be given by

$$\max_{\left(s'_i-\hat{s}'_i,s_i-\hat{s}'_i\right)\in(-1,+1)^2} \left|\overline{f}_i(s'_i,s)\right| = 1 \tag{7.9}$$

we obtain in lieu of equation (7.5)

$$\begin{aligned}\overline{f}_i(s'_i,s) =& c'\cdot\left(s'_i-\hat{s}_i\right)^2 - \\ & \frac{1}{2}\cdot\left(c'+c\right)\cdot\left(s'_i-\hat{s}_i\right)\cdot\left(s_i-\hat{s}_i\right)+ \\ & c\cdot\left(s_i-\hat{s}_i\right)^2\end{aligned} \tag{7.10}$$

with $c' = r\cdot\cos\alpha_i$, $c = r\cdot\sin\alpha_i$ and $r = \frac{1}{2}\cdot\left|\cos\alpha_i+\sin\alpha_i\right|^{-1}$.

The *saddle-surfaces* described by equation (7.10), that correspond to the six classes of isoclines are illustrated in Figure 7.2. These surfaces intersect the plane $\overline{f}_i(s'_i,s) = 0$ at two straight lines. Whereas one of these lines corresponds to $(s'_i-\hat{s}_i)/(s_i-\hat{s}_i) = 1$, one easily sees that the invasion angle α_i determines the location of the second line which is described by $(s'_i-\hat{s}_i)/(s_i-\hat{s}_i) = \tan\alpha_i$.

7.2 Characteristics of Fixed-Points

Much of the interest in models of coevolution has been to characterize properties of fixed points in trait space at which the selection pressures generated by interacting species are balanced, so that there is no further phenotypic evolution of the system. The motivation for this work has come primarily from evolutionary game theory, and a dynamic is often not made explicit in this context.

In this section we show that dynamical considerations are indispensable in a coevolutionary context.

Communities with N=1

The three inequalities (7.1), (7.2) and (7.3) have been employed in the literature to analyze fixed points of the evolutionary dynamics in communities comprising only a single species, $N = 1$ (Eshel and Motro 1981; Eshel 1983; Taylor 1989; Takada and Kigami 1991; Metz et al. 1994). In this case the s_1-isocline coincides with the fixed points of the evolutionary dynamics. Please note that the properties of such fixed points – given below as encountered in the literature – only hold in the simple special case $N = 1$.

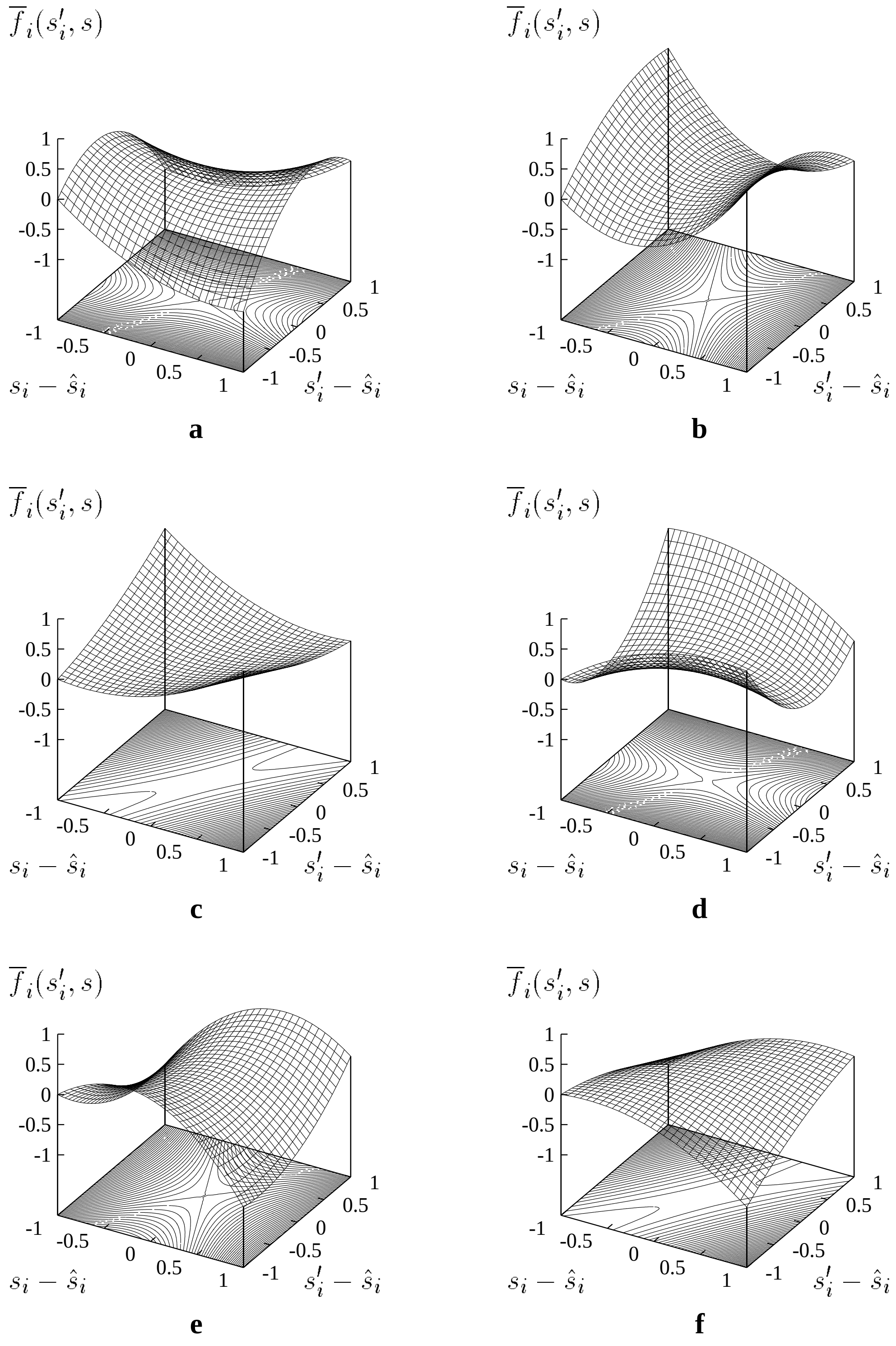

Figure 7.2 Illustration of the different classes of isoclines. In the vicinity of an isocline the surface $\overline{f}_i(s_i', s)$ to second order is saddle-like in the arguments $s_i' - \hat{s}_i$ and $s_i - \hat{s}_i$. Figures (a) to (f) correspond to classes 1 to 6 of isoclines as given in Figure 7.1.

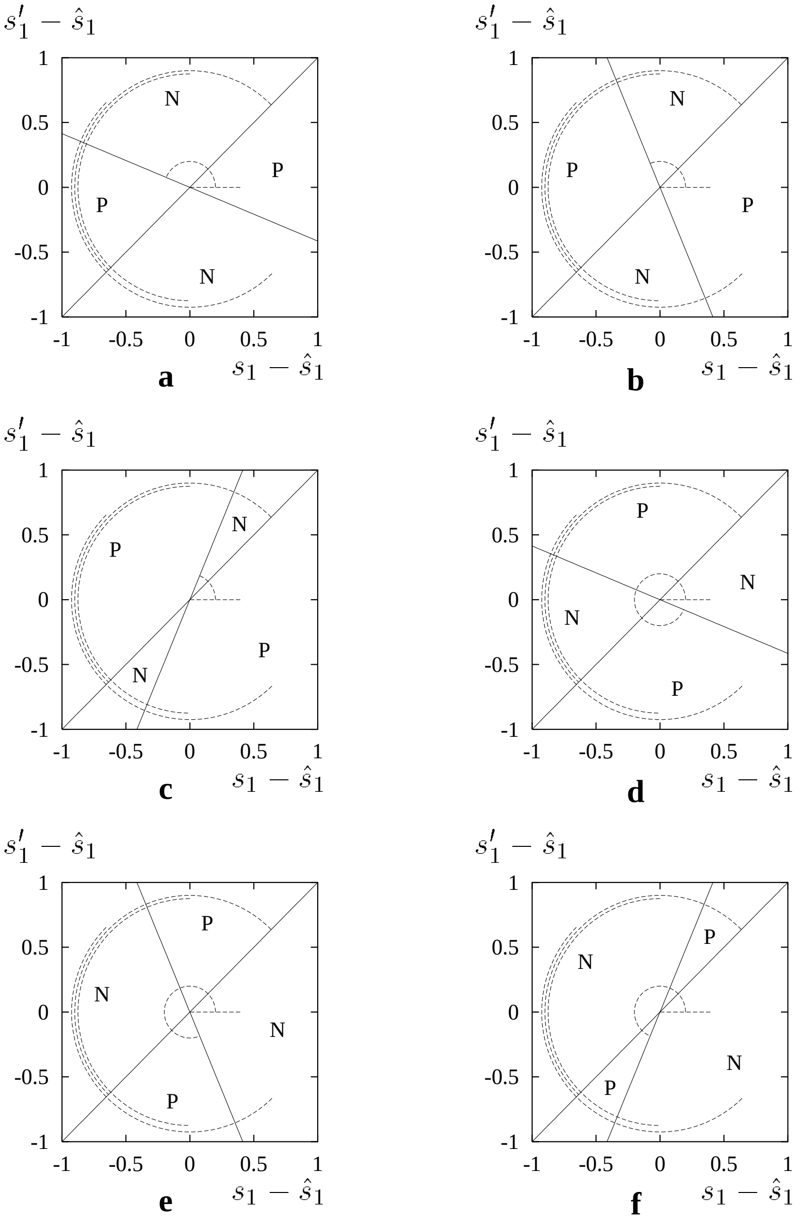

Figure 7.3 The vicinity of the different classes of fixed-points for $N = 1$. The sign of $\overline{f}_1(s'_1, s_1)$ is shown by letters (P: positive; N: negative). The two straight lines correspond to $\overline{f}_1(s'_1, s_1) = 0$. The small arc at the center measures the invasion angle α_1. The three large arcs indicate the range of invasion angles that fulfill the inequalities (7.1), (7.2) and (7.3) (inner: non-invadability; middle: convergence; outer: no mutual invadability). It is helpful to compare this figure to Figure 7.2. After choosing a specific resident adaptive trait value s_1, the above figures can be utilized to determine those mutant adaptive trait values s'_1 that could invade the resident population. In this vein the meaning of the three inequalities (7.1), (7.2) and (7.3) can be understood (non-invadability/invadability: consider the range of mutants being able to invade the resident at the fixed point; convergence/divergence: consider a sequence of trait substitutions in the vicinity of the fixed point; no mutual invadability/mutual invadability: consider the range of mutants being able to invade the resident in the vicinity of the fixed point and vice versa).

Fixed points of classes 1 and 2 cause convergence, see Figure 7.3. In contrast to class 1, a system tending to a class 2 fixed point can go through a transient period of polymorphism before reaching the fixed point; Metz et al. (1994) refer to this as a *contracting polymorphism*. Class 3 also gives convergence to the fixed point but, at the fixed point itself, mutants at opposite sides can invade and coexist. This then corresponds to Prout's (1968) notion of a *protected polymorphism*, referred to as a *polymorphic evolutionarily attainable trait* by Christiansen (1991), and as an *expanding polymorphism* by Metz et al. (1994). Fixed points of classes 4 and 5 are invadable and divergent; that class 4 in contrast to class 5 allows for mutual invadability might only be important when starting the evolutionary process in the vicinity of the fixed point which in the former case can give rise to a short initial period during which a transient polymorphism can occur. A class 6 fixed point is non-invadable but divergent, i.e. it would be uninvadable if the system started on at the fixed point, but starting from other points in the neighborhood the system evolves away from it; such a configuration has aptly been called a *Garden of Eden configuration* by Hofbauer and Sigmund (1990).

The six different classes of fixed points for $N = 1$ are illustrated in Figure 7.3. Notice that the information presented in this figure can by inferred from Figure 7.2. Thus both figures apply to communities with $N > 1$; however, interpreting the diagrams of Figure 7.3 in the sense described in the figure legend is only possible in the case $N = 1$.

The relationship between the properties of fixed points given above and dynamical stability is trivial for systems in which only one species evolves. It is readily shown that the condition for dynamical stability of a fixed point under dynamics given by the first order of the monomorphic deterministic model coincides with the condition for convergence, inequality (7.2). To see this, consider the Jacobian of dynamics (6.12)

$$J = k_1(s_1) \cdot \left[\partial_1'^2 \overline{f}_1(s_1, s_1) + \partial_1' \partial_1 \overline{f}_i(s_1, s_1)\right] \tag{7.11}$$

evaluated at the fixed point $\hat{s}_1$; for the definition of the evolutionary rate coefficients $k_i(s)$ see equation (6.15). By employing equation (7.8) we obtain for the Jacobian at the fixed point

$$J = k_1(\hat{s}_1) \cdot \frac{1}{2} \cdot \left[\partial_1'^2 \overline{f}_1(\hat{s}_1, \hat{s}_1) - \partial_1^2 \overline{f}_1(\hat{s}_1, \hat{s}_1)\right] . \tag{7.12}$$

Since the local stability of fixed points in one-dimensional systems depends only on the sign of the Jacobian evaluated at these points, with inequality (7.2) we can conclude that dynamically stable fixed points ($J < 0$) are convergent and that unstable ones ($J > 0$) are divergent. Moreover, since the condition for non-invadability is independent of the condition for convergence, dynamical stability of the fixed point does not require non-invadability.

Communities with N>1

We now turn to the coupled evolution of two species to see how the properties of isoclines relate to dynamical stability of two-dimensional systems. Here the inner fixed points are given by the intersection of the inner isoclines $\partial_1' \overline{f}_1(s_1', s) = 0$ and $\partial_2' \overline{f}_2(s_2', s) = 0$. The six classes of isoclines above allow 36 types of fixed points, of which 21 are distinct under permutation of the two species. With dynamics (6.12) the Jacobian at the fixed point $\hat{s} = (\hat{s}_1, \hat{s}_2)$ is

$$J = \begin{pmatrix} J_{11} & J_{12} \\ J_{21} & J_{22} \end{pmatrix} \tag{7.13}$$

with

$$\begin{aligned} J_{11} &= k_1(s) \cdot \left[\partial_1'^2 \overline{f}_1(\hat{s}_1, \hat{s}) + \partial_1' \partial_1 \overline{f}_1(\hat{s}_1, \hat{s})\right] , \\ J_{12} &= k_1(s) \cdot \partial_1' \partial_2 \overline{f}_1(\hat{s}_1, \hat{s}) , \\ J_{21} &= k_2(s) \cdot \partial_2' \partial_1 \overline{f}_2(\hat{s}_2, \hat{s}) , \\ J_{22} &= k_2(s) \cdot \left[\partial_2'^2 \overline{f}_2(\hat{s}_2, \hat{s}) + \partial_2' \partial_2 \overline{f}_2(\hat{s}_2, \hat{s})\right] . \end{aligned} \tag{7.14}$$

As in the one-dimensional case, the bracketed terms $[\ldots]$ on the diagonal are the same (apart from a positive factor of 2) as the expressions given in inequality (7.2), and are therefore related to the isoclinic conditions for convergence of each species. But there is a much more indirect relationship between these convergence conditions and dynamical stability; we collect together the relevant results in the next paragraph.

A necessary and sufficient condition for local stability of fixed points in two-dimensional systems is that $\operatorname{tr} J < 0$ and $\det J > 0$. From this the following results can be obtained; see also Abrams et al. (1993). (i) Convergence of each species (i.e. bracketed terms $[\ldots]$ in J negative) is neither necessary nor sufficient for local asymptotic stability of the fixed point. Convergence is not sufficient because, although convergence implies $\operatorname{tr} J < 0$, the sign of $\det J$ depends on the off-diagonal mixed partial derivatives. Convergence is not necessary because it is possible to have $\operatorname{tr} J < 0$ and $\det J > 0$ when only one species is convergent and the other divergent. (ii) If each species is divergent, i.e. both bracketed terms in J are positive, we have $\operatorname{tr} J > 0$ and hence the fixed point is unstable. Thus six of the 21 types of fixed points are definitely evolutionary repellors, but the remaining 15 could be either repellors or attractors. However, by allowing for 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 ratio of the evolutionary rate coefficients $k_1(\hat{s})/k_2(\hat{s})$.

We conclude from these results that the simple identity of the condition for convergence with that for local dynamical stability, which holds for single-species evolution, has no counterpart in multispecies coevolution. The attractors of the coevolutionary process can depend critically on detailed dynamical features of the coevolving system. In particular, as the mutation process influences the evolutionary rate constants $k_i(s)$, in general no inferences as to the dynamical stability of evolutionary fixed points for $N > 1$ can be made when considering the process of selection alone. For a contrasting view on this issue see Rand et al. (1993).

Figure 7.4 illustrates the considerations above. Depicted are adaptive dynamics in a coevolutionary community comprising two species. Species 1 has a s_1-isocline that changes along its length between classes 2, 3, and 4, see Figure 7.4a. At the point of intersection with the s_2-isocline, the isocline of species 1 has the properties of invadability, divergence and mutual invadability, whereas the isocline of species 2 is of class 1 having the properties of non-invadability, convergence and no mutual invadability. This example is interesting for several reasons.

First, the fixed point is an instance of case (v) above, i.e. its dynamical stability depends on the evolutionary rate constants. If the mutation ratios of species 1 and 2 are chosen in the ratio 1:10, allowing faster evolution in species 2, the fixed point is stable and serves as an attractor for the adaptive dynamics, see Figure 7.4b. On the other hand, if the mutation ratios are chosen in the ratio 1:1, the fixed point is unstable and the attractor is given by a limit cycle, see Figure 7.4c.

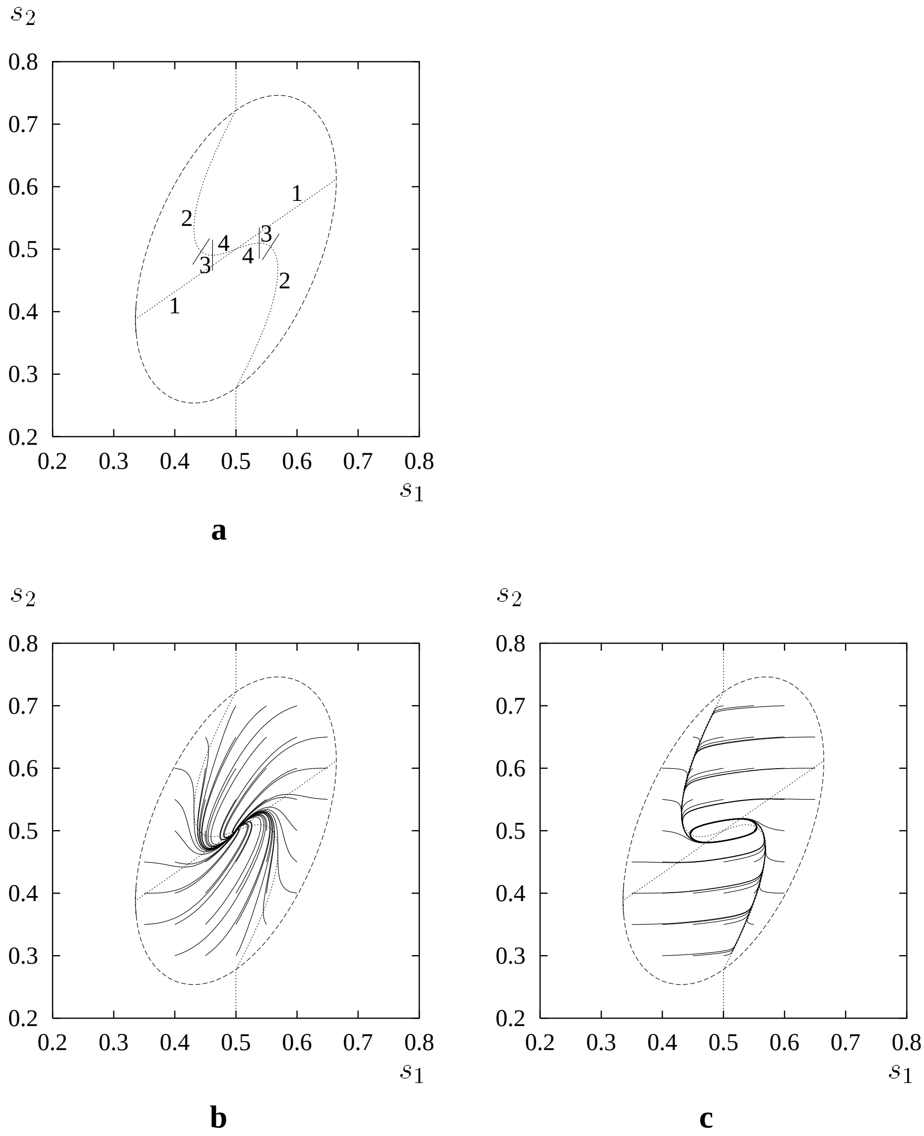

Figure 7.4 Tuning of evolutionary stability by means of the mutation process. The discontinuous oval curve is the boundary of the region of coexistence. The dotted curves are the inner evolutionary isoclines of the two species (straight line: predator, curved line prey). (a) The sections of the isoclines are labeled according to their class, see Figure 7.1. The fixed point at the intersection of the two isoclines is an instance of case (v) described in the text. Here, evolutionary stability can be tuned just by varying the ratio of the evolutionary rate coefficients. (b) The fixed point is stable for mutation ratios of the two species obeying $\mu_1/\mu_2 = 0.1$. Orbits of the monomorphic deterministic model are depicted by continuous lines. (c) The fixed point is unstable and is surrounded by a stable limit cycle for mutation ratios of the two species obeying $\mu_1/\mu_2 = 1$. These distinct mutation ratios are the only difference between the systems displayed in figures (b) and (c). Parameters of the coevolutionary predator-prey community are as given in Figure 9.3 with $h = 0.11$ except in figure (b) where $\mu_1 = 10^{-4}$.

Second, the example illustrates how dynamical stability is independent of non-invadability of the fixed point. It can be seen that $\hat{s}$ can be an attractor, see again Figure 7.4b, notwithstanding the fact that coevolution, according to the class 4 of the s_1-isocline, leads to a local minimum for the per capita growth rate of species 1. Also Takada and Kigami (1991) and Abrams et al. (1993) have noted that a system of coevolving species may be driven to a fixed point where one species is at a local “fitness” minimum.

Third, in the system illustrated in Figure 7.4, the three basic kinds of selection are all present: selection is directional for both species away from the isoclines, stabilizing for species 2 around its isocline and disruptive for species 1 at its isocline in the neighborhood of the fixed point.

From the discussion above we draw two conclusions.

1. For coevolutionary communities with $N > 1$, comprising several species, the notion of convergence, which proved useful in the classification of fixed-points for the special case $N = 1$, has to be replaced by the more general definition of dynamical stability as demonstrated above.
2. In contrast, the concepts of invadability and mutual invadability generalize without problems to communities with $N > 1$. As in the case $N = 1$, the presence of mutual invadability at a fixed-point indicates the possibility of polymorphism. If mutual invadability is accompanied by invadability, there can even be potential for the emergence of a protected polymorphism, i.e. for the occurrence of evolutionary branching.

Whereas the first conclusion is essential for appreciating the impossibility of stripping away the mutation process from the consideration of evolutionary outcomes; the second conclusion is a first step in analyzing the prerequisites for the assumption of monomorphism, introduced in Section 5.1. In the next section we take this investigation further by proving the principle of mutual exclusion for a certain type of coevolutionary communities.

7.3 The Principle of Mutual Exclusion

We have assumed in Section 5.1 that without mutations two or more values of the adaptive trait s_i within a species cannot coexist in the limit $t \to \infty$, only the single most advantageous trait value surviving. This principle of mutual exclusion can be proved for the case of Lotka-Volterra population dynamics.

The Principle of Mutual Exclusion for Lotka-Volterra Communities

The theorem is as follows. Consider in species $j \in 1, \dots, N$ two populations with sizes n_j and n'_j of a resident adaptive trait value s_j and a sufficiently close mutant trait value s'_j, respectively, in an environment determined by traits s_i with population sizes n_i, $i = 1, \dots, N$. The dynamics of the population sizes in the community are assumed to be of Lotka-Volterra type.

When the mutant is absent, we call the remaining population dynamics *resident system*, when the resident is absent *mutant system*, and when both are present *combined system*. Provided that

1. the selection derivative $\partial'_j \overline{f}_j(s_j, s)$ does not vanish,
2. the Lotka-Volterra interaction matrix of the combined system (i) is not singular, and (ii) its elements for species j vary smoothly with s_j,

we show that there cannot exist a fixed point of the combined system in R_+^{N+1}. From this it can then be inferred that the mutant will either go to fixation or to extinction.

Notation of Proof

As in Section 5.1 we formally assign the population of the mutant adaptive trait value the index $i = 0$: $s_0 = s'_j$, $n_0 = n'_j$, $b_0 = b_j$ and $d_0 = d_j$. In the course of a trait substitution $s_j \to s'_j$ the phenotypic distributions in the coevolutionary community are given by

$$\widetilde{p} = \big(n_1 \cdot \delta_{s_1}, \dots, n_j \cdot \delta_{s_j} + n_0 \cdot \delta_{s_0}, \dots, n_N \cdot \delta_{s_N}\big) \; . \tag{7.15}$$

From the stochastic description of the invasion process

$$\begin{aligned} \frac{d}{dt} P(n,t) = \sum_{i=0}^{N} \Big[& \widetilde{d}_i^j\big(s_i, s, n + 1^i\big) \cdot (n_i + 1) \cdot P\big(n + 1^i, t\big) + \\ & \widetilde{b}_i^j\big(s_i, s, n - 1^i\big) \cdot (n_i - 1) \cdot P\big(n - 1^i, t\big) - \\ & \widetilde{d}_i^j(s_i, s, n) \cdot n_i \cdot P(n,t) - \\ & \widetilde{b}_i^j(s_i, s, n) \cdot n_i \cdot P(n,t) \Big] \; , \end{aligned} \tag{7.16}$$

see equation 5.4, we can formally construct a deterministic system describing resident and mutant population dynamics when treating population sizes as continuous variables and neglecting fluctuations

$$\frac{d}{dt} n_i = n_i \cdot \widetilde{f}_i^j(s_i, s, n) \tag{7.17}$$

with $\widetilde{f}_i^j(s_i, s, n) = \widetilde{b}_i^j(s_i, s, n) - \widetilde{d}_i^j(s_i, s, n)$ and $n = (n_0, n_1, \dots, n_N)$. The assumption of continuous population sizes and negligible fluctuations is only justified for large populations, $n_0, n_1, \dots, n_N \gg 1$. As we have frequently pointed out, this is not the case when considering a mutant population which initially is of size 1. Thus the equations (7.17) are not capable of describing the dynamics of the invasion process, for this purpose we have to rely on the stochastic representation (7.16). We only may use the dynamical system (7.17) in circumstances when all considered populations (i.e. those with positive sizes) are large. This constraint will be respected below.

The assumption that population dynamics are of Lotka-Volterra type is expressed by

$$\widetilde{f}_i^j(s_i, s, n) = r_i(s_i) + \sum_{j=0}^{N} \alpha_{ij}(s_i, s_j) \cdot n_j \qquad \text{for all} \qquad i = 0, \dots, N\,. \tag{7.18}$$

The fixed-points of the population dynamics of the combined system, denoted by $\hat{n} = (\hat{n}_0, \hat{n}_1, \dots, \hat{n}_N)$, are defined by $\widetilde{f}_i^j(s_i, s, \hat{n}(s)) = 0$ for all $i = 0, \dots, N$. Similarly, we define the fixed-points $\hat{n}^{(0)} = (0, \hat{n}_1^{(0)}, \hat{n}_2^{(0)}, \dots, \hat{n}_N^{(0)})$ and $\hat{n}^{(1)} = (\hat{n}_0^{(1)}, 0, \hat{n}_2^{(0)}, \dots, \hat{n}_N^{(1)})$ of the resident and of the mutant system, respectively, by $\widetilde{f}_i^j(s_i, s, \hat{n}^{(1)}(s)) = 0$ for all $i = 1, 2, \dots, N$ and by $\widetilde{f}_i^j(s_i, s, \hat{n}^{(0)}(s)) = 0$ for all $i = 0, 2, \dots, N$. The superscript thus refers to the index of the absent population.

To shorten notation, below we do not continue to repeat the dependence of the quantities $\widetilde{f}_i$, r, α, $\hat{n}$, $\hat{n}^{(0)}$ and $\hat{n}^{(1)}$ on the vector $s = (s_0, s_1, \dots, s_N)$ and the index j which are constant throughout a particular trait substitution.

We denote minors of a matrix A by $m^{ij}(A)$; here the ith row and the jth column have been eliminated. We further define the matrices $z^{ij}(A)$ derived from a matrix A by replacing the elements of the ith row and the jth column by 0, except for the element A_{ij} itself which is replaced by 1; successive mappings of this sort are denoted by $z^{ij,kl}(A) = z^{ij}\big(z^{kl}(A)\big)$. Similarly, the vector $z^i(a)$ is obtained from a vector a by setting a_i to 0.

Outline of Proof

The proof of the above theorem is divided into four steps.

1. First, we prove the equation
$$\begin{aligned}\hat{n}_0 \cdot \hat{n}_1 = &\big[\det{}^{-2}\,\alpha\big] \cdot \\ &\big[\det m^{00}(\alpha) \cdot \det m^{11}(\alpha)\big] \cdot \\ &\Big[\widetilde{f}_0(\hat{n}^{(0)}) \cdot \widetilde{f}_1(\hat{n}^{(1)})\Big]\,.\end{aligned} \tag{7.19}$$
2. Then, we show
$$\det m^{00}(\alpha) \;\gtreqless\; 0 \qquad \Leftrightarrow \qquad \det m^{11}(\alpha) \;\gtreqless\; 0\,. \tag{7.20}$$
3. Next, we demonstrate
$$\widetilde{f}_0(\hat{n}^{(0)}) \;\gtreqless\; 0 \qquad \Leftrightarrow \qquad \widetilde{f}_1(\hat{n}^{(1)}) \;\lesseqgtr\; 0\,. \tag{7.21}$$

In consequence of these results of parts 1 to 3, $\hat{n}_0$ and $\hat{n}_1$ have to be of opposite sign, thus there is no fixed-point of the combined system in R_+^{N+1}.

4. Finally, we exploit the fact that if there is no fixed-point of the combined system in R_+^{N+1} there can be no attractor at all in R_+^{N+1} .

Hence, under the two conditions mentioned above, the two adaptive trait values s_j and s'_j cannot coexist. As then the mutant will either go to fixation or to extinction, the principle of mutual exclusion is proved.

Proof, Part 1

In this part of the proof we will use Kramer's rule

$$x_j = \det{}^{-1} A \cdot \sum_i a_i \cdot (-1)^{i+j} \cdot \det m^{ij}(A) \tag{7.22}$$

to solve systems $A \cdot x = a$ of linear equations, and Steiner's rule

$$\det A = \sum_j A_{ij} \cdot (-1)^{i+j} \cdot \det m^{ij}(A) \tag{7.23}$$

to evaluate the determinant of a matrix A by expanding it with respect to its ith row. Note also that for any matrix A the identity

$$\det m^{ij}(A) = \det z^{ij}(A) \tag{7.24}$$

holds.

In a *first step* we evaluate the fixed-points of the combined, the resident and the mutant system. The former are defined by the equations

$$r_j + \sum_{i=1}^{N} \alpha_{ij} \cdot \hat{n}_i = 0 \tag{7.25}$$

holding for all $j = 0, \ldots, N$. By solving this system of linear equations we obtain for $\hat{n}$

$$\hat{n}_j = \det^{-1} \alpha \cdot \sum_{i=0}^{N} (-r_i) \cdot (-1)^{i+j} \cdot \det m^{ij}(\alpha) \, . \tag{7.26}$$

Similarly we get for $\hat{n}^{(0)}$ and $\hat{n}^{(1)}$

$$\hat{n}_j^{(0)} = \det^{-1} z^{00}(\alpha) \cdot \sum_{i=0}^{N} \big(-z^0(r_i)\big) \cdot (-1)^{i+j} \cdot \det m^{ij}\big(z^{00}(\alpha)\big) \tag{7.27}$$

and

$$\hat{n}_j^{(1)} = \det^{-1} z^{11}(\alpha) \cdot \sum_{i=0}^{N} \big(-z^1(r_i)\big) \cdot (-1)^{i+j} \cdot \det m^{ij}\big(z^{11}(\alpha)\big) \, . \tag{7.28}$$

In a *second step* we compute the product $\widetilde{f}_0(\hat{n}^{(0)}) \cdot \widetilde{f}_1(\hat{n}^{(1)})$ according to equation (7.18)

$$\begin{aligned} &\widetilde{f}_0(\hat{n}^{(0)}) \cdot \widetilde{f}_1(\hat{n}^{(1)}) \\ &= \left[r_0 + \sum_{j=0}^{N} \alpha_{0j} \cdot \hat{n}_j^{(0)} \right] \cdot \\ &\quad \left[r_1 + \sum_{j=0}^{N} \alpha_{1j} \cdot \hat{n}_j^{(1)} \right] . \end{aligned} \tag{7.29}$$

By utilizing equations (7.27) and (7.28) we get

$$\begin{aligned} &\widetilde{f}_0(\hat{n}^{(0)}) \cdot \widetilde{f}_1(\hat{n}^{(1)}) \\ &= \left[r_0 + \det^{-1} z^{00}(\alpha) \cdot \sum_{i,j=0}^{N} \alpha_{0j} \cdot \big(-z^0(r_i)\big) \cdot (-1)^{i+j} \cdot \det z^{ij}\big(z^{00}(\alpha)\big) \right] \cdot \\ &\quad \left[r_1 + \det^{-1} z^{11}(\alpha) \cdot \sum_{i,j=0}^{N} \alpha_{1j} \cdot \big(-z^1(r_i)\big) \cdot (-1)^{i+j} \cdot \det z^{ij}\big(z^{11}(\alpha)\big) \right] . \end{aligned} \tag{7.30}$$

Then we decompose the two sums into several separate terms

$$\begin{aligned}
&\widetilde{f}_0(\hat{n}^{(0)}) \cdot \widetilde{f}_1(\hat{n}^{(1)}) \\
=\ &\det{}^{-1} z^{00}(\alpha) \cdot \det{}^{-1} z^{11}(\alpha) \cdot \\
&\Bigg[r_0 \cdot \det z^{00}(\alpha) - r_1 \cdot \alpha_{01} \cdot \det z^{11,00}(\alpha) + \\
&r_1 \cdot \sum_{j=2}^{N} \alpha_{0j} \cdot (-1)^j \cdot \det z^{1j,00}(\alpha) + \\
&\alpha_{01} \cdot \sum_{i=2}^{N} r_i \cdot (-1)^i \cdot \det z^{i1,00}(\alpha) - \\
&\sum_{i,j=2}^{N} \alpha_{0j} \cdot r_i \cdot (-1)^{i+j} \cdot \det z^{ij,00}(\alpha) \Bigg] \cdot \\
&\Bigg[r_1 \cdot \det z^{11}(\alpha) - r_0 \cdot \alpha_{10} \cdot \det z^{00,11}(\alpha) + \\
&r_0 \cdot \sum_{j=2}^{N} \alpha_{1j} \cdot (-1)^j \cdot \det z^{0j,11}(\alpha) + \\
&\alpha_{10} \cdot \sum_{i=2}^{N} r_i \cdot (-1)^i \cdot \det z^{i0,11}(\alpha) - \\
&\sum_{i,j=2}^{N} \alpha_{1j} \cdot r_i \cdot (-1)^{i+j} \cdot \det z^{ij,11}(\alpha) \Bigg] .
\end{aligned} \tag{7.31}$$

In the last transformation we have used (i) $z^0(r_i) = 0$ for $i = 0$, $z^0(r_i) = r_i$ for $i \neq 0$, (ii) $z^1(r_i) = 0$ for $i = 1$, $z^1(r_i) = r_i$ for $i \neq 1$ and (iii) $\det z^{ij,kl}(\alpha) = 0$ for $i = k$ and $j \neq l$ or $i \neq k$ and $j = l$.

In a *third step* we compute the product $\hat{n}_0 \cdot \hat{n}_1$ utilizing equation (7.26)

$$\begin{aligned}
&\hat{n}_0 \cdot \hat{n}_1 \\
=\ &\left[\det{}^{-1} \alpha \cdot \sum_{i=0}^{N} (-r_i) \cdot (-1)^{i+0} \cdot \det z^{i0}(\alpha) \right] \cdot \\
&\left[\det{}^{-1} \alpha \cdot \sum_{i=0}^{N} (-r_i) \cdot (-1)^{i+1} \cdot \det z^{i1}(\alpha) \right] .
\end{aligned} \tag{7.32}$$

By expanding $\det z^{i0}(\alpha)$ with respect to its 0th row and $\det z^{i1}(\alpha)$ with respect to its 1st row we obtain

$$\begin{aligned}
&\hat{n}_0 \cdot \hat{n}_1 \\
&= \det{}^{-2} \alpha \cdot \\
&\Big[\sum_{i=0}^{N} r_i \cdot (-1)^{i+0} \cdot \sum_{j=0}^{N} z^{i0}_{0j}(\alpha) \cdot (-1)^{0+j} \cdot \det z^{0j}\big(z^{i0}(\alpha)\big) \Big] \cdot \\
&\Big[\sum_{i=0}^{N} r_i \cdot (-1)^{i+1} \cdot \sum_{j=0}^{N} z^{i1}_{1j}(\alpha) \cdot (-1)^{1+j} \cdot \det z^{1j}\big(z^{i1}(\alpha)\big) \Big] .
\end{aligned} \tag{7.33}$$

Again, we write some terms of the sums explicitly

$$\begin{aligned}
&\hat{n}_0 \cdot \hat{n}_1 \\
&= \det{}^{-2} \alpha \cdot \\
&\Big[r_0 \cdot \det z^{00}(\alpha) - r_1 \cdot \alpha_{01} \cdot \det z^{11,00}(\alpha) + \\
&\quad r_1 \cdot \sum_{j=2}^{N} \alpha_{0j} \cdot (-1)^j \cdot \det z^{1j,00}(\alpha) + \\
&\quad \alpha_{01} \cdot \sum_{i=2}^{N} r_i \cdot (-1)^i \cdot \det z^{i1,00}(\alpha) - \\
&\quad \sum_{i,j=2}^{N} \alpha_{0j} \cdot r_i \cdot (-1)^{i+j} \cdot \det z^{ij,00}(\alpha) \Big] \cdot \\
&\Big[r_1 \cdot \det z^{11}(\alpha) - r_0 \cdot \alpha_{10} \cdot \det z^{00,11}(\alpha) + \\
&\quad r_0 \cdot \sum_{j=2}^{N} \alpha_{1j} \cdot (-1)^j \cdot \det z^{0j,11}(\alpha) + \\
&\quad \alpha_{10} \cdot \sum_{i=2}^{N} r_i \cdot (-1)^i \cdot \det z^{i0,11}(\alpha) - \\
&\quad \sum_{i,j=2}^{N} \alpha_{1j} \cdot r_i \cdot (-1)^{i+j} \cdot \det z^{ij,11}(\alpha) \Big] .
\end{aligned} \tag{7.34}$$

To obtain the last equation we have used (i) $z^{ij,ij}(\alpha) = z^{ij}(\alpha)$, (ii) $z^{ij,kl}(\alpha) = -z^{kj,il}(\alpha)$ and (iii) $z^{ij}_{kl}(\alpha) = 0$ for $i = k$ and $j \neq l$ or $i \neq k$ and $j = l$, $z^{ij}_{kl}(\alpha) = 1$ for $i = k$ and $j = l$, $z^{ij}_{kl}(\alpha) = \alpha_{kl}$ for $i \neq k$ and $j \neq l$.

In a *fourth step* we compare the results (7.31) and (7.34). This completes the proof of equation (7.19).

Proof, Part 2

In this part of the proof we investigate the relative signs of $\det m^{00}(\alpha)$ and $\det m^{11}(\alpha)$.

For this purpose we expand $\det m^{11}(\alpha)$ to first order in the mutant adaptive trait value s'_j around the resident trait value s_j

$$\det m^{11}(\alpha) = \det m^{00}(\alpha) + \left(s'_j - s_j\right) \cdot \frac{\partial}{\partial s'_j} \det m^{11}(\alpha) \Big|_{s'_j = s_j} . \tag{7.35}$$

Provided that (i) all interaction coefficients α_{ij} and α_{ji} vary smoothly with the trait value s'_j, (ii) the resident system is not singular, $\det m^{00}(\alpha) \neq 0$, and (iii) the mutant trait value is sufficiently close to the resident trait value,

$$\left|s'_j - s_j\right| < \det m^{00}(\alpha) / \frac{\partial}{\partial s'_j} \det m^{11}(\alpha) \Big|_{s'_j = s_j} , \tag{7.36}$$

we thus can conclude that $\det m^{00}(\alpha)$ and $\det m^{11}(\alpha)$ are of the same sign. Consequently, their product is positive.

Proof, Part 3

This part of the proof is concerned with the relative signs of $\widetilde{f}_0(\hat{n}^{(0)})$ and $\widetilde{f}_1(\hat{n}^{(1)})$.

With equations (5.10,11,12) we have $\widetilde{f}_0(\hat{n}^{(0)}) = \overline{f}_j(s'_j, s)$ and $\widetilde{f}_1(\hat{n}^{(1)}) = \overline{f}_j(s_j, s')$ where s' has components $s'_i = s_i$ for all $i = 1, \ldots, N \neq j$ and $s'_i = s'_j$ for $i = j$.

Expansion of these functions to first order in the mutant adaptive trait value s'_j around the resident trait value s_j yields

$$\begin{aligned} \widetilde{f}_0(\hat{n}^{(0)}) &= \overline{f}_j(s_j, s) + \left(s'_j - s_j\right) \cdot \partial'_j \overline{f}_j(s_j, s), \\ \widetilde{f}_1(\hat{n}^{(1)}) &= \overline{f}_j(s_j, s) + \left(s'_j - s_j\right) \cdot \partial_j \overline{f}_j(s_j, s) . \end{aligned} \tag{7.37}$$

We exploit equations (7.6) and (7.7) and obtain

$$\begin{aligned} \widetilde{f}_0(\hat{n}^{(0)}) &= +\left(s'_j - s_j\right) \cdot \partial'_j \overline{f}_j(s_j, s), \\ \widetilde{f}_1(\hat{n}^{(1)}) &= -\left(s'_j - s_j\right) \cdot \partial'_j \overline{f}_j(s_j, s) . \end{aligned} \tag{7.38}$$

From this we conclude that $\widetilde{f}_0(\hat{n}^{(0)})$ and $\widetilde{f}_1(\hat{n}^{(1)})$ will be of opposite sign unless the selection derivative $\partial'_j \overline{f}_j(s_j, s)$ vanishes. Hence their product is negative.

Proof, Part 4

This part of the proof is standard, it can be found e.g. in Hofbauer and Sigmund (1988, see Theorem 1 in their Section 9).

The Monomorphic Regime apart from Isoclines

In Section 5.1 we have based the assumption of monomorphism on two separate conditions, the smallness of mutation ratios and the principle of mutual exclusion. The latter has now been clarified for coevolutionary Lotka-Volterra communities. For generic communities of this type (having an interaction matrix that depends smoothly on trait values and that is not singular) and for sufficiently small mutational steps, the principle of mutual exclusion in species j is valid apart from the s_j-isoclines of the adaptive dynamics (where the selection derivative $\partial_j' \overline{f}_j(s_j, s)$ does vanish).

In a last step we hence investigate under what conditions the assumption of monomorphism holds in the vicinity of these isoclines.

The Monomorphic Regime in the Vicinity of Isoclines

The investigation of the two conditions for the assumption of monomorphism, the smallness of mutation ratios and the principle of mutual exclusion, requires particular care in the vicinity of evolutionary isoclines. A violation of the first condition 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 and a close mutant trait will differ only slightly. For this reason it may take a long time until the mutant replaces the former resident. We have seen above that for Lotka-Volterra communities the second condition may not hold, either, in the vicinity of an inner evolutionary s_i-isocline. From Sections 7.1 and 7.2 we know that this might be the case for isoclines which are mutually invadable.

Nevertheless, the breach of the assumption of monomorphism, in the cases mentioned here, can be of minor relevance. There are several reasons for this supposition and we discuss the possible cases in turn.

1. Close to an evolutionary isocline that is not mutually invadable, the only problem is the lack of the timescale separation between the population dynamics, forcing deleterious mutants to go extinct, and the process of mutation, enabling new mutants to enter the population. Here, a polymorphic distribution around the isocline can build up, for relatively long time is required to drive out the deleterious mutants. However, after a sufficient time the most advantageous mutant will eventually have succeeded in banishing the other trait values such that the polymorphic distribution is only present for an intermediate time interval. In addition, when the mutation

ratio μ_i is not too high or the mutation variance σ_i^2 too large, this distribution is sharply peaked on the isocline.

2. In the vicinity of an evolutionary isocline that is mutually invadable the principle of mutual exclusion may fail to hold. If the isocline is non-invadable, mutants on opposite sides of the isocline may temporarily coexist. But, due to non-invadability, only one trait value remains when the isocline is reached. Again, when the mutation variance σ_i^2 is small, this temporal deviation from monomorphism may be neglected. We thus conclude that in both cases 1 and 2 the monomorphic framework can be retained as an approximation.
3. If an evolutionary isocline is both mutually invadable and also invadable, mutants on opposite sides of the isocline can coexist permanently. This process may give rise to *evolutionary branching* (Metz et al. 1994). However, as remarked in Section 4.5, evolutionary branching has not been observed by the author in the monomorphic regime of the generalized replicator equation. It appears that the incidence of evolutionary branching is not robust under coevolutionary dynamics when treated stochastically. We thus conjecture that even in this case 3 the monomorphic description can be retained. Nevertheless, further investigation of this issue is suggested.

There is yet another incentive for relying on the monomorphic framework in the vicinity of isoclines. Though we have $\frac{d}{dt}s_i = 0$ for a point $\hat{s}$ situated on an evolutionary isocline of species i, in a coevolutionary context the adaptive trait values of the other species usually are still bound to change, $\frac{d}{dt}s_j \neq 0$ for $j = 1, \ldots, N \neq i$. This will hold unless $\hat{s}$ is a fixed-point of the coevolutionary dynamics or the adaptive change in s_i happens on a faster timescale than that of all s_j. In consequence, the dynamics in the other species will drive the adaptive trait values s away from the s_i-isocline and the phenomena described under 1 to 3 above cannot occur.

Conclusions

We summarize the analysis of this section in terms of the following statements.

1. For generic Lotka-Volterra communities with small mutation ratios in all species and small mutational steps, a monomorphic description will hold apart from the isoclines of the adaptive dynamics.

2. In cases not covered by 1, a monomorphic description will hold if the isocline of a species is only traversed owing to adaptive change in the other species.
3. In cases not covered by 1 or 2, a monomorphic description will hold approximately if the considered isocline is not mutually invadable or mutually invadable but non-invadable.
4. In cases not covered by 1, 2 or 3, a monomorphic description will hold when considering stochastic coevolutionary dynamics.

Please note that, although the principle of mutual exclusion has been taken for granted in the exploration of coevolutionary communities which are not of Lotka-Volterra type (e.g. Rand et al. 1993; Rand and Wilson 1994), our proof is restricted to the class of Lotka-Volterra communities. To our knowledge, there exists no proof of this principle for population dynamics of arbitrary type.

7.4 Consequences of Higher Order Corrections

The higher order correction terms to the monomorphic deterministic model can have important consequences in specific circumstances. Here, we describe two special effects.

1. Finite mutation variances give rise to inner evolutionary isoclines that are displaced relative to those obtained for infinitesimal mutation variances. This shifting of isoclines already occurs in the second order result for asymmetric mutation processes whereas for symmetric mutation processes the third order corrections are to be considered.
2. The other effect, the phenomenon of evolutionary slowing down, can be demonstrated by means of the second order result. Its investigation leads to the conclusion that fixed points lying on non-invadable inner evolutionary isoclines for some traits are attained at a rate which is algebraically slow rather than exponentially fast in those traits.

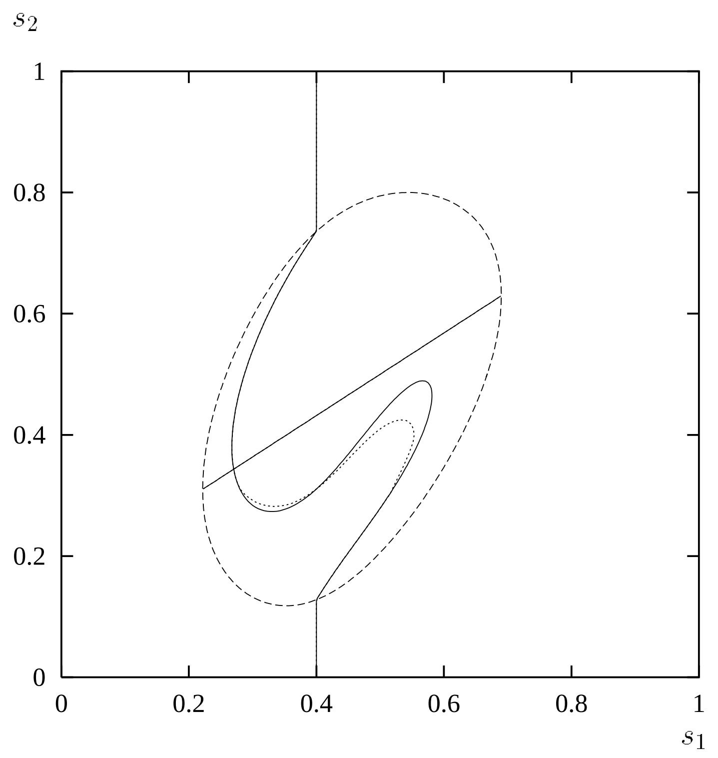

Figure 7.5 Shifting of evolutionary isoclines. The continuous curves are the inner evolutionary isoclines of the two species (straight line: predator, curved line: prey) for infinitesimal mutation variances, $\sigma_1 \longrightarrow 0$ and $\sigma_2 \longrightarrow 0$. The dotted curves are the inner evolutionary isoclines of the two species for finite mutation variances, $\sigma_1 = \sigma_2 = 5 \cdot 10^{-2}$. The discontinuous oval curve is the boundary of the region of coexistence. Except for the mutation variances parameters of the coevolutionary predator-prey community are the same as in Figure 6.2.

Shifting of Evolutionary Isoclines

We now analyze inner evolutionary s_i-isoclines in the context of the higher order result (6.19). In other words, we investigate the impact of allowing mutational steps to be finite in size rather than infinitesimal. The class of an isocline in this case is determined by that of the corresponding isocline in the first order result. As to the location of the isoclines the results are as follows.

First, we consider the second order result. According to equation (6.21) the range of integration here is given by $R_i(s) = \left\{s'_i \in \widehat{S}_i \mid (s'_i - s_i) \cdot \partial'_i \overline{f}_i(s_i, s) + (s'_i - s_i)^2 \cdot \frac{1}{2} \cdot \partial'^2_i \overline{f}_i(s_i, s) > 0\right\}$. For $\partial'_i \overline{f}_i(s_i, s) = 0$ this range either vanishes or extends to $(-\infty, +\infty)$, depending on the sign of $\partial'^2_i \overline{f}_i(s_i, s)$. If thus an inner s_i-isocline is non-invadable, the mutation moment $m_{3i}(s)$, see equation (6.20), and in consequence the second order correction in equation (6.19) 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 $\partial_i'^j \overline{f}_i(s_i, s)$ and the first and higher order derivatives $\partial_i'^{j-j'} \overline{b}_i^{-1}(s_i, s)$ in equation (6.19) 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 (6.12) this manifold would be called an evolutionary s_i-isocline. In terms of the more general higher order result (6.19) 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 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.

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, see Chapter 9, by the dotted curves in Figure 7.5. 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.

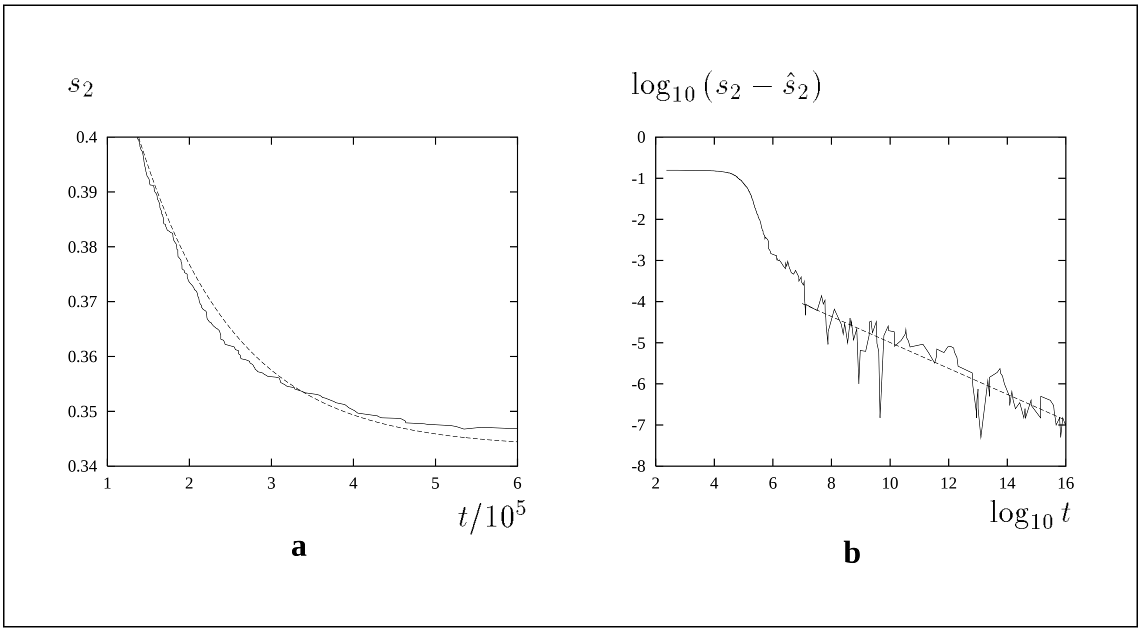

Figure 7.6 Evolutionary slowing down. (a) The continuous curve shows the mean path dynamics of the predator's trait close to the evolutionary equilibrium $\hat{s}$ in Figure 5.4 (constructed from 20 trait substitution sequences). The fixed point $\hat{s}$ lies on a non-invadable predator isocline. In 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. (b) A double logarithmic plot of the considered time series confirms the derived power law $s_2(t) - \hat{s}_2 \propto t^{-1/3}$, the jaggedness of the continuous curve stems from the extreme amplification of the impact of single trait substitutions due to the logarithmic scale. The 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 $-1/3$, thus confirming the prediction of fourth order slowing down. Parameters of the coevolutionary predator-prey community are the same as in Figures 5.3, 5.4 and 6.2.

Conditions for Evolutionary Slowing Down

For the purpose of illustration let us start by considering 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, $\frac{d}{dx}\frac{d}{dt}x = 0$.

In general, a dynamical system $\frac{d}{dt}x = F(x)$ is said to exhibit rth order slowing down at a fixed point $\hat{x}$ if $F(x) = \sum_{j=r}^{\infty} a_{j\pm} \cdot (x - \hat{x})^j$ around $x = \hat{x}$ with (i) $r > 1$ and with (ii) $\pm a_{r\pm} < 0$ for r even and $a_{r\pm} < 0$ for r odd. The distinction $\pm$ 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 $x(t) - \hat{x} \propto \pm(a_{r\pm} \cdot t)^{1/(1-r)}$.

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 equation (6.21) 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 slowing down, we examine the coefficients $a_{j\pm}$ defined above in the case of the adaptive dynamics described by equation (6.7). 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 fourth order slowing down. 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. In the theory of phase transitions a related phenomenon is known as *critical slowing down* (Huang 1987). Here, the algebraically slow relaxation towards an equilibrium point occurs at a critical value of a control parameter, e.g. temperature, that is external to the considered system. In such systems, fluctuations around the equilibrium point are much larger at the critical value than apart from it. In contrast, the phenomenon of evolutionary slowing down causes fluctuations to vanish at the equilibrium point and, moreover, it is an effect which is internally driven (one could interpret the range of integration $R_i(s)$ as a control parameter that is tuned towards its critical value while the adaptive dynamic approaches the non-invadable isocline).

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 7.6a 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 Figure 7.6b 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.

7.5 Construction of Adaptive Landscapes

The dynamic of evolutionary processes is frequently associated with the concept of optimization, optimization in turn being interpreted in the sense of maximization (Lewontin 1987; Emlen 1987). The influential metaphor of the adaptive landscape, introduced by Wright (1931), see Section 2.3, has helped to support this tendency. In this section we advance arguments why we think that the notion of hill-climbing on an adaptive landscape is tempting but obsolete in a coevolutionary context.

Problems with the Hill-climbing Metaphor in a Coevolutionary Context

First, we have seen in Section 7.2 that the determination of coevolutionary endpoints may not be decomposed into analyzing the impacts of mutation and selection separately. The quantitative details of the mutation process can be essential for predicting the direction of coevolutionary change. In contrast, the metaphor of the adaptive landscape suggests that directionality is imposed on the evolutionary dynamics by a “fitness" function which is only dependent on the process of selection.

Second, the adaptive landscape for coevolutionary processes ought to be a variable one. For a particular species, its shape has to undergo transformations according to the altering biotic environment generated by the other species which in turn are subject to adaptive change. We show that once the variability of the landscape is tolerated, it is possible to cast an arbitrary dynamical system in a mathematical form that corresponds to a hill-climbing process on a variable adaptive landscape. To see this we consider the set of equations

$$\frac{d}{dt}x = F(x) \tag{7.39}$$

with $x = (x_1, \ldots, x_N)$ and $F = (F_1, \ldots, F_N)$. It can easily be checked (using Leibnitz' rule for differentiation with respect to integration limits) that equation (7.39) is mathematically equivalent to

$$\frac{d}{dt}x_i = \frac{\partial}{\partial x_i'} W_i(x_i', x) \Big|_{x_i' = x_i} \qquad \text{for} \quad i = 1, \ldots, N \tag{7.40}$$

with

$$W_i(x_i', x) = \int_{x_i}^{x_i'} F(x) \Big|_{x_i = x_i''} \, dx_i'' \, . \tag{7.41}$$

Alternatively, we can write

$$\frac{d}{dt}x = \nabla_{x'} W(x', x) \Big|_{x' = x} \tag{7.42}$$

and

$$W(x', x) = \sum_{i=1}^{N} W_i(x_i', x) \tag{7.43}$$

with $\nabla_{x'} = \left(\partial/\partial x_1', \ldots, \partial/\partial x_N'\right)$. Equation (7.40) describes the dynamics of the arbitrary system (7.39) as an interplay of several hill-climbing processes on N separate adaptive landscapes $W_i(x_i', x)$ for species $i = 1, \ldots, N$. In contrast, equation (7.42) corresponds to a hill-climbing process on a single landscape $W(x', x)$. Note that these landscapes are extended in the space of all x' whereas their shape is parametrized by the value of x, the current state of the dynamical system.

Envisaging Coevolutionary Dynamics on Variable Adaptive Landscapes

The canonical equation (2.3) of adaptive dynamics, which we have underpinned by a formal derivation in Section 6.2, is also inspired by the idea of envisaging adaptation as a hill-climbing process. However, when the evolutionary rate coefficients $k_i(s)$ are allowed to depend on the adaptive state s (Abrams et al. 1993), the adaptive dynamics can deviate from the path given by the direction of steepest ascent on the landscape described by $\overline{f}_i(s_i', s)$.

To cast our coevolutionary dynamics in terms of a process of hill-climbing on a variable adaptive landscape we set in equation (7.39) $x = s$ and, in accordance with equation (6.12), $F(s) = \frac{1}{2} \cdot \mu_i(s_i) \cdot \sigma_i^2(s_i) \cdot \hat{n}_i(s) \cdot \partial_i' \overline{f}_i(s_i, s)$. From equations (7.41) and (7.43) we obtain the adaptive landscape for the coevolutionary dynamics of the monomorphic deterministic model

$$W(s', s) = \frac{1}{2} \cdot \sum_{i=1}^{N} \int_{s_i}^{s_i'} \left[\mu_i(s_i) \cdot \sigma_i^2(s_i) \cdot \hat{n}_i(s) \cdot \partial_i' \overline{f}_i(s_i, s)\right] \Big|_{s_i = s_i''} \, ds_i'' \; . \tag{7.44}$$

Here, setting the arbitrary lower integration limit to s_i amounts to normalizing the absolute height of the adaptive landscape to zero for the current combination of trait values, $W(s, s) = 0$. To recover the dynamics we use the transcription of equation (7.42)

$$\frac{d}{dt} s = \nabla_{s'} W(s', s) \Big|_{s' = s} \; . \tag{7.45}$$

We see that if we wish to describe the adaptive dynamics by a process of gradient ascent (following the direction of steepest slope on an adaptive landscape) we ought to incorporate features of the mutation process into the definition of the landscape. This is why (i) the canonical equation (2.3) of adaptive dynamics can give rise to dynamics leading to minima of the adaptive landscape functions $\overline{f}_i(s_i', s)$ and why (ii) evolutionary stability can be tuned without altering these landscape functions, see Section 7.2.

In Figures 7.7 and 7.8 we give two examples of employing equation (7.44) together with (7.45) to generate variable adaptive landscapes for coevolutionary dynamics. Both examples are based on the coevolutionary predator-prey community which is analyzed in Chapter 9.

Visualizing the adaptive dynamics by means of a variable adaptive landscape might help our imagination. First, we might take the transformation of the landscape's shape in the course of the coevolutionary process as picturing the alteration of the

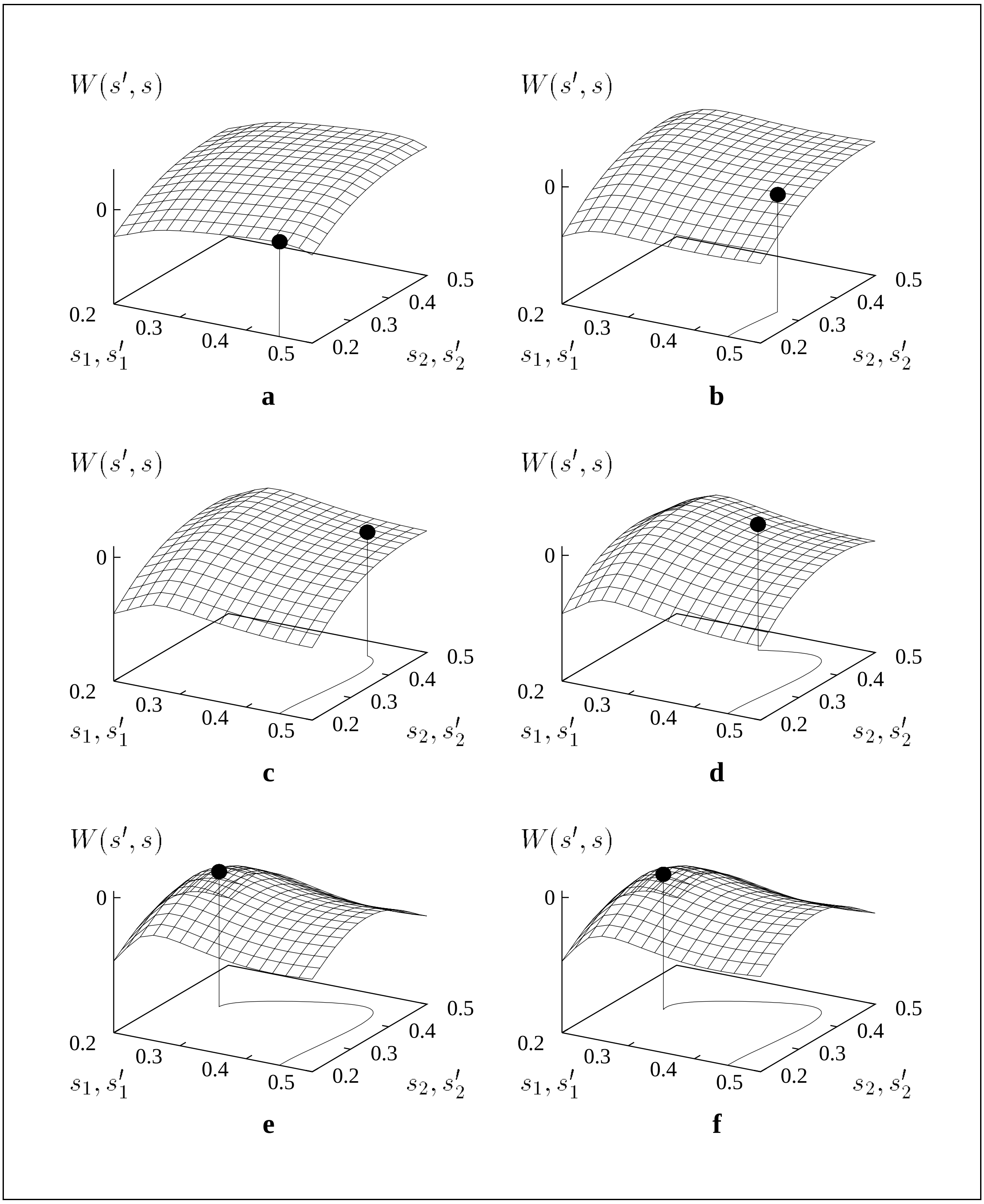

Figure 7.7 Coevolution towards an evolutionarily stable fixed point envisaged on a variable adaptive landscape. The trajectory of the adaptive dynamics is given on the bottom plane; according to equation (7.44) it can be understood as being determined by a hill-climbing process on the variable adaptive landscape. The sphere upon the landscape shows the current state of the adaptive trait values. The coordinates for the trajectory and the current state of the adaptive dynamics are (s_1, s_2), those for the variable adaptive landscape (s'_1, s'_2). Times shown are (a) $t = 0$, (b) $t = 5 \cdot 10^4$, (c) $t = 3 \cdot 10^5$, (d) $t = 5 \cdot 10^5$, (e) $t = 8 \cdot 10^5$, and (f) $t = 8 \cdot 10^6$. Parameters of the coevolutionary predator-prey community are the same as in Figure 4.4.

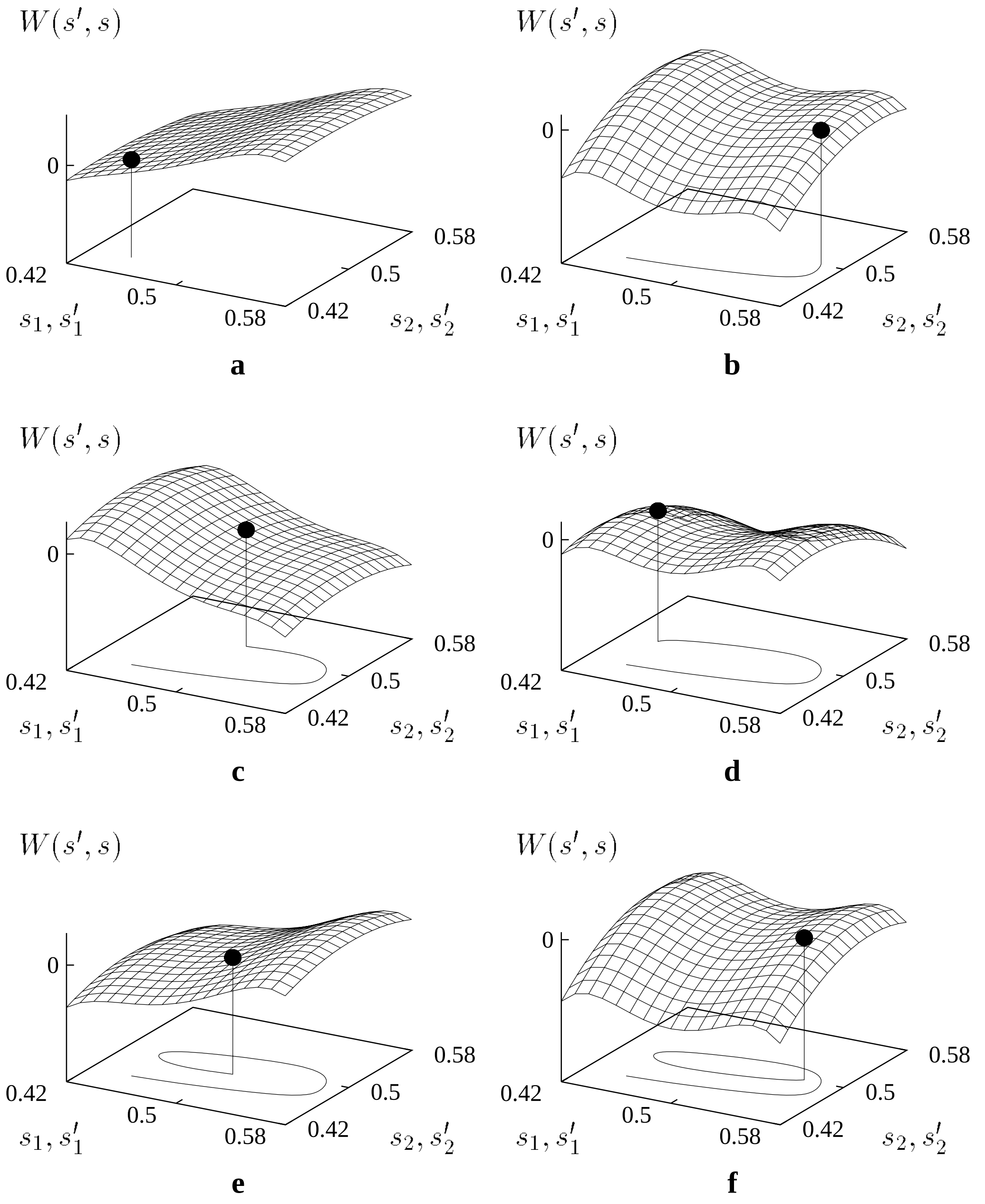

Figure 7.8 Coevolution towards an evolutionarily stable limit cycle envisaged on a variable adaptive landscape. The trajectory of the adaptive dynamics is given on the bottom plane; according to equation (7.44) it can be understood as being determined by a hill-climbing process on the variable adaptive landscape. The sphere upon the landscape shows the current state of the adaptive trait values. The coordinates for the trajectory and the current state of the adaptive dynamics are (s_1, s_2), those for the variable adaptive landscape (s'_1, s'_2). Times shown are (a) $t = 0$, (b) $t = 1.2 \cdot 10^6$, (c) $t = 2.7 \cdot 10^6$, (d) $t = 3.4 \cdot 10^6$, (e) $t = 4.9 \cdot 10^6$, and (f) $t = 5.5 \cdot 10^6$. The phenomenon of evolutionary cycling is discussed in detail in Chapter 9. Parameters of the coevolutionary predator-prey community are as given in Figure 9.3 with $h = 0.11$.

species' environment caused by and also causing their adaptive change. Second, one could be tempted to interpret the constant height of the current adaptive state of the coevolutionary community on the landscape as illustrating a point made by Fisher (1958) that the changes brought about by natural selection must be offset against the resulting deterioration of the environment (Frank and Slatkin 1992). But still, as demonstrated above there is no explanatory potential in describing evolution as hill-climbing in a coevolutionary context. The adaptive dynamics, equation (6.12), precedes the adaptive landscape, equation (7.44), and not vice versa.

Chapter 8
Extension of the Polymorphic and Monomorphic Models

In this chapter we discuss generalizations of the dynamical theory of coevolution as developed in Chapters 4 to 6. We point out how to extend the theoretical framework presented there, in order to cover more complicated ecological and evolutionary scenarios.

8.1 Multi-trait Coevolution and Functional Constraints

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.

Multiple Traits

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

$$s_i = (s_{il}) \tag{8.1}$$

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.

Constraints

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 traits is further restricted by constraints on the combinations of different traits. 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 subspace 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 subspace $\widehat{S}_C$ of $\widehat{S}$ with

$$\widehat{S}_C = \widehat{S}_c \cap \widehat{S}_{c'} \tag{8.2}$$

   where $\widehat{S}_c$ denotes the region of coexistence as defined in equation (5.8).

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 $M_{il}(s_i, \Delta s_{il})$.

Below we generalize the results obtained in the previous sections to match the extended framework of multiple-trait coevolution.

Extension of the Polymorphic Stochastic Model

No notational changes are required to extend the results of Chapter 4 to multiple-trait coevolution. Note only that the phenotypic distributions p_i as well as the mutation and offspring distributions M_i and B_i now are multivariate, that the delta functions in equation (4.1) and (4.9) take vectors as parameters such that the usual definitions $\delta_{s_i} = \prod_{l=1}^{\nu_i} \delta_{s_{il}}$ and $\delta(s_i' - s_i) = \prod_{l=1}^{\nu_i} \delta\big(s_{il}' - s_{il}\big)$ apply, and that the integrations ds_i' and ds_i in equation (4.15) now stand for $ds_i' = \prod_{l=1}^{\nu_i} ds_{il}'$ and $ds_i = \prod_{l=1}^{\nu_i} ds_{il}$.

Extension of the Monomorphic Stochastic Model

Similarly, the results for the stochastic representation in Chapter 5, in particular equations (5.13), (5.14) and (5.18), carry over without alteration. The delta functions in equation (5.14) now take vectors as arguments, such that again $\delta(s_i' - s_i) = \prod_{l=1}^{\nu_i} \delta\big(s_{il}' - s_{il}\big)$ applies, the mutation distribution in equation (5.18) is multivariate and the integration ds' in equation (5.13) now is given by $ds' = \prod_{i=1}^{N} ds_i' = \prod_{i=1}^{N} \prod_{l=1}^{\nu_i} ds_{il}'$.

Extension of the Monomorphic Deterministic Model

The results of Chapter 6 for the deterministic approximation to the monomorphic coevolutionary dynamics generalize as below. No modifications are required in equations (6.7) and (6.8). However, the integral in equation (6.7) now is multi-dimensional with $ds_i = \prod_{l=1}^{\nu_i} ds_{il}$, and consequently the range $R_i(s)$ of integration in (6.8) now becomes a subspace of dimension ν_i instead of a mere interval.

In generalizing equation (6.12) we obtain

$$\frac{d}{dt} s_i = \frac{1}{2} \cdot \mu_i(s_i) \cdot \sigma_i^2(s_i) \cdot \hat{n}_i(s) \cdot \nabla_i' \overline{f}_i(s_i, s) \tag{8.3}$$

as the first order result for the deterministic approximation of the multiple-trait coevolutionary dynamics in $\widehat{S}_C$. Here $\nabla_i' \overline{f}_i(s_i, s)$ with $\nabla_i' = \big(\partial_{i1}', \ldots, \partial_{i\nu_i}'\big)$ 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 multiple-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

$$\sigma_{i,ll'}^2(s_i) = \int \Delta s_{il} \cdot \Delta s_{il'} \cdot M_i(s_i, \Delta s_i)\, d\Delta s_i \tag{8.4}$$

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 an altered 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 (8.3) for species i are now given by those manifolds in $\widehat{S}_C$ 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 $\sigma_i^2(s_i)$. The location and type of boundary isoclines on $\partial\widehat{S}_C$ is less easy to settle and phase portraits of the system (8.3) will prove useful in this circumstance.

8.2 Nonequilibrium Population Dynamics and Varying Environments

In this section we analyze the issues of coevolution under nonequilibrium population dynamics and under varying external influences on the environment.

In relaxing the assumption of a fixed point attractor $\hat{n}(s)$ in population size space made in Section 5.1, we now allow for arbitrary attractors $A(s)$ that give rise to *periodic, quasi-periodic or chaotic population dynamics*. Similarly, external influences can impose an extra time dependence on the coevolutionary community thus rendering the system nonautonomous. Although both effects give rise to changes in the environment experienced by an individual within the coevolutionary community, the term *varying environment* usually is used as an abbreviation for the latter, since only in this case the coevolutionary community, considered as a single system, is exposed to variation from beyond its boundary.

After discussing relations between different timescales in the coevolutionary community, we provide generalizations of the two monomorphic models of coevolutionary processes to nonequilibrium population dynamics and varying environments. In the literature different invasion criteria have been suggested in this context. We outline the mathematical concepts and finally investigate in how far these criteria can be approved in the light of the formalism developed in this work.

Timescales in the Coevolutionary Community

Already in the case of a fixed point attractor in population size space we had to distinguish between the timescale τ_a of adaptive change and the timescale τ_f on which a mutant either goes extinct or reaches fixation while the population dynamics of the combined system attain its attractor. Both τ_a and τ_f are larger than the typical time τ_i between birth or death events of individuals in the coevolutionary community.

When population dynamics settles to a nonequilibrium attractor $A(s)$ in population size space, an additional timescale τ_p for the motion on this attractor is introduced. Moreover, variation of the environment due to external influences on a timescale τ_e imposes an extra time dependence on the coevolutionary community.

No premises as to the relations between the five timescales above enter the derivation of the polymorphic stochastic model. For the monomorphic models, resident populations are considered sufficiently large in order not to be subject to accidental extinction, consequently $\tau_a, \tau_f, \tau_p \gg \tau_i$ obtains. Moreover, the assumption of small mutation ratios implies $\tau_a \gg \tau_f$. The assumptions of equilibrium population dynamics and the absence of an external time dependence in the coevolutionary community are formally expressed by $\tau_p, \tau_e \to \infty$. In summary, the considerations in Chapters 5, 6 and 7 have been underlined by the relations

$$\tau_a \gg \tau_f \gg \tau_i \ \wedge \ \tau_p, \tau_e \to \infty. \tag{8.5}$$

In this section we investigate the consequences of relaxing the last two assumptions $\tau_p \to \infty$ and $\tau_e \to \infty$.

Consideration of the Polymorphic Stochastic Model

External variation of the environment of the coevolutionary community is explicitly allowed in the polymorphic stochastic model, see equations (4.7) and (4.15). However, the particular algorithm presented for the polymorphic stochastic model in Chapter 4 is based on the minimal process method, and thus is exact for $\tau_e \to \infty$. As explained in Section 4.4 this algorithm can be used as an approximation even for environments which are subject to external variation provided that $\tau_e \gg \tau_i$. For $\tau_e \not\gg \tau_i$ other algorithms should be devised, whereas the polymorphic stochastic model itself stays valid.

No assumptions as to the attractors of the population dynamics of the different species in the coevolutionary community have been made when deriving the polymorphic stochastic model. In fact, population dynamics and adaptive dynamics are not formally treated separately in this model. In consequence, the polymorphic stochastic model is fully capable of describing coevolutionary communities with nonequilibrium population dynamics.

Extension of the Monomorphic Stochastic Model

In the case $\tau_f \gg \tau_p \wedge \tau_e \to \infty$ invasion and fixation of a successful mutant happen slowly compared to the dynamics on the attractor $A(s)$. This will typically be the case for mutants whose adaptive trait values s_i' are sufficiently close to the resident trait value s_i. To determine the fate of a rare mutant we then can take its per capita rates on $A(s)$ to be effectively given by $\overline{b}_i(s_i', s)$, $\overline{d}_i(s_i', s)$, defined in analogy to

$$\overline{f}_i(s_i', s) = \lim_{T \to \infty} \frac{1}{T} \cdot \int_0^T \widetilde{f}_i^i\big(s_i', s, n(t)\big)\, dt \tag{8.6}$$

where the bar here denotes the time average along a trajectory $n(t)$ on $A(s)$. The dynamics of $n(t)$ is described by equation (5.5). Due to ergodicity the choice of $n(0)$ is not affecting these averages and the time average can effectively be replaced by a phase average on the attractor $A(s)$

$$\overline{f}_i(s_i', s) = \int_{A(s)} \widetilde{f}_i^i(s_i', s, n)\, d\nu(n)\ , \tag{8.7}$$

see the remark on the natural measure $d\nu(n)$ of $A(s)$ further below. In generalizing equations (5.18) we obtain for the probabilities per unit time in the stochastic representation

$$\begin{aligned} w_i(s_i', s) = &\mu_i \cdot \overline{b}_i(s_i, s) \cdot \overline{n}_i(s) \cdot M_i(s_i, s_i' - s_i) \cdot \\ &\overline{b}_i^{-1}(s_i', s) \cdot (\overline{f}_i(s_i', s))_+\ . \end{aligned} \tag{8.8}$$

Similar conclusions can be drawn for the case $\tau_f \gg \tau_e \wedge \tau_p \to \infty$ where the invasion of a successful mutant happens slowly compared to the dynamics of the external influences on the environment. Equation (8.8) carries over and $\overline{f}_i(s_i', s)$ now indicates a time average over the change of the external influences on the environment. When the varying external influences possess a stationary frequency distribution, the time average again can be obtained instead as an average over these external influences weighted by their probability to occur.

Evidently, for coevolutionary communities with both nonequilibrium population dynamics and varying environment the above arguments can be combined provided that $\tau_f \gg \tau_p, \tau_e$. In this case $\overline{f}_i(s'_i, s)$ is given by a twofold average.

Another extreme is described by the condition $\tau_e \gg \tau_f \wedge \tau_p \to \infty$. Here, the environment of a mutant is practically constant during its successful or unsuccessful invasion. Instead of equation (8.9) we therefore have

$$\begin{aligned} w_i(s'_i, s, t) = &\mu_i \cdot b_i(s_i, s, t) \cdot \hat{n}_i(s, t) \cdot M_i(s_i, s'_i - s_i) \cdot \\ &\overline{b}_i^{-1}(s'_i, s, t) \cdot (\overline{f}_i(s'_i, s, t))_+ \, . \end{aligned} \tag{8.9}$$

Notice that in this case the capability of mutants to invade a community of resident species not only depends on the resident trait values s but also on the states of the external influences on the environment at the particular time of invasion.

The cases with $\tau_p \gg \tau_f$ are more involved and will not be covered here.

When the environment of a mutant changes due to nonequilibrium population dynamics or due to external influences on a timescale that is comparable to τ_f, the fate of the mutant cannot be decided upon its initial per capita growth rate. The assumption of invasion implying fixation, see Section 5.1, which in turn rests on the principle of mutual exclusion, is likely not to hold in this case. In such cases retreat to the polymorphic stochastic model is recommended.

However, for small mutational steps, the timescale τ_f for fixation of successful mutants will not be too small, such that the feasible cases, see equation (8.8), can be taken as the relevant ones.

Extension of the Monomorphic Deterministic Model

The discussion provided above for the monomorphic stochastic model directly applies to the monomorphic deterministic model. In generalizing equation (6.12) and by using equation (8.8) in the case $\tau_f \gg \tau_p, \tau_e$ we obtain for the deterministic approximation of the adaptive dynamics in first order

$$\frac{d}{dt} s_i = \mu_i \cdot m_{2i}(s) \cdot \overline{n}_i(s) \cdot \partial'_i \overline{f}_i(s_i, s) \, . \tag{8.10}$$

For the case $\tau_e \gg \tau_f \wedge \tau_p \to \infty$ we employ equation (8.9) to get

$$\frac{d}{dt} s_i = \mu_i \cdot m_{2i}(s) \cdot \hat{n}_i(s, t) \cdot \partial'_i \overline{f}_i(s_i, s, t) \, . \tag{8.11}$$

In equations (8.10) and (8.11) we have used the second mutation moment m_{2i} rather than $\frac{1}{2} \cdot \sigma_i^2$ in order to allow for asymmetric mutation distributions.

The construction of the higher order deterministic approximations for the adaptive dynamics follows the same scheme as in Section 6.3 and is not repeated here.

Invasion Criteria from the Literature

As a special application of the monomorphic stochastic model, we can use our mathematical framework to deduce a criterion for resolving whether or not a given mutant can successfully invade a coevolutionary community comprising given resident populations. We already have obtained such a criterion in Section 5.3, equation (5.19), assuming equilibrium population dynamics. It is of particular interest to investigate how this result generalizes to encompass nonequilibrium population dynamics. Before we establish our own criterion, we briefly review some mathematical concepts suggested for this purpose in the literature.

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

$$E_1(s_i', s) = \lim_{T \to \infty} \frac{1}{T} \cdot \int_0^T \widetilde{f}_i^i(s_i', s, n(t))\, dt\,, \tag{8.12}$$

$$E_2(s_i', s) = \lim_{T \to \infty} \frac{1}{T} \cdot \ln \frac{|\Delta n(T)|}{|\Delta n(0)|}\,, \tag{8.13}$$

$$E_3(s_i', s) = \int_{A(s)} \widetilde{f}_i^i(s_i', s, n)\, d\nu(n)\,. \tag{8.14}$$

In the literature, the invasion criterion for the initial increase of the rare mutant is taken to be $E_k > 0$ with $k = 2$ or 3 (Metz et al. 1992, Rand et al. 1993). For the notions of resident and combined systems, used below, see Section 7.3.

The first quantity E_1 equals $\overline{f}_i(s_i', s)$, 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, see equation (8.6). We have introduced E_1 as it serves as a convenient common denominator for the other two quantities E_2 and E_3, see below.

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 of the resident system. Lyapunov exponents in general are given by the average logarithmic growth rate of the distance between two specific trajectories. Here, the first trajectory $n(t)$ starts from $n(0)$ on the attractor A itself, the second trajectory $n'(t)$ has initial conditions $n'(0) = n(0) + \Delta n(0)$ 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 $\Delta n(t) = n'(t) - n(t)$, where the particular choice of the distance function $|\ldots|$ does not affect the result (Oseledec 1968). Note that the mathematical definition of a Lyapunov exponent requires the time development of $n'(t)$ to be evaluated according to the linearization of the dynamics of the combined system along the attractor A (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 $(0, T)$; in order to nonetheless cover the attractor A sufficiently, several repetitions of this procedure usually are necessary where each single repetition is followed by a re-scaling $\alpha \cdot \Delta n(T) \to \Delta n(0)$ 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 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 is chaotic (Ott 1993). For practical applications this caveat however is spurious due to the noise inevitably associated with any numerical estimation (Schuster 1989).

Equivalence of Invasion Criteria

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 $n'(0)$ 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 $\frac{d}{dt}\Delta n'_i(t) = \widetilde{f}_i^{\,i}(s'_i, s, n)|_{n=n(t)} \cdot \Delta n'_i(t)$. From these equations we conclude $|\Delta n(T)|/|\Delta n(0)| = \exp \int_0^T \widetilde{f}_i^{\,i}(s'_i, s, n(t))\, dt$. Comparing this result to equations (8.12) and (8.13) completes the proof of $E_1 = E_2$.

Recovery of Invasion Criteria

We now 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.

A rare mutant s'_i can successfully invade a community given by the resident traits 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, if we consider only the case $\tau_f \gg \tau_p \wedge \tau_e \to \infty$, our stochastic approach yields the criterion $E_1 > 0$ which is equivalent to those proposed previously. To see this, consider equation (8.8) together with the definitions of $(\ldots)_+$ and that of $\overline{f}_i(s'_i, s)$ in equation (8.6).

In addition to recovering this result suggested in the literature, we analogously can establish corresponding criteria for the other cases analyzed in this section. Furthermore, our analysis has not only furnished us with these criteria for the initial increase of a rare mutant but provides a full dynamical description of the stochastic adaptive process.

Part C

Application of the Dynamical Theory of Coevolution

The population dynamics of predator-prey systems are a classical model of theoretical ecology. The question as to the consequences of superimposing an adaptive process onto the population dynamics of predator and prey has fostered a variety of theoretical models of phenotypic coevolution in such communities.

In this part we utilize the three models of coevolution derived in the last chapters to investigate the variety of possible evolutionary dynamics in a prototypical predator-prey community. In particular we focus on the potential for evolutionary cycling – a type of evolutionary change belonging to the class of Red Queen dynamics – and demonstrate that this mode of coevolution is a feasible outcome in predator-prey communities. This finding corroborates speculations put forward in the literature and once again underlines the necessity for a dynamical theory of coevolution.

Chapter 9
Predator-Prey Coevolution

9.1 Background

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).

Arms Races

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 favors predator phenotypes best able to consume the prey, whereas selection by the predator on the prey favors 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.

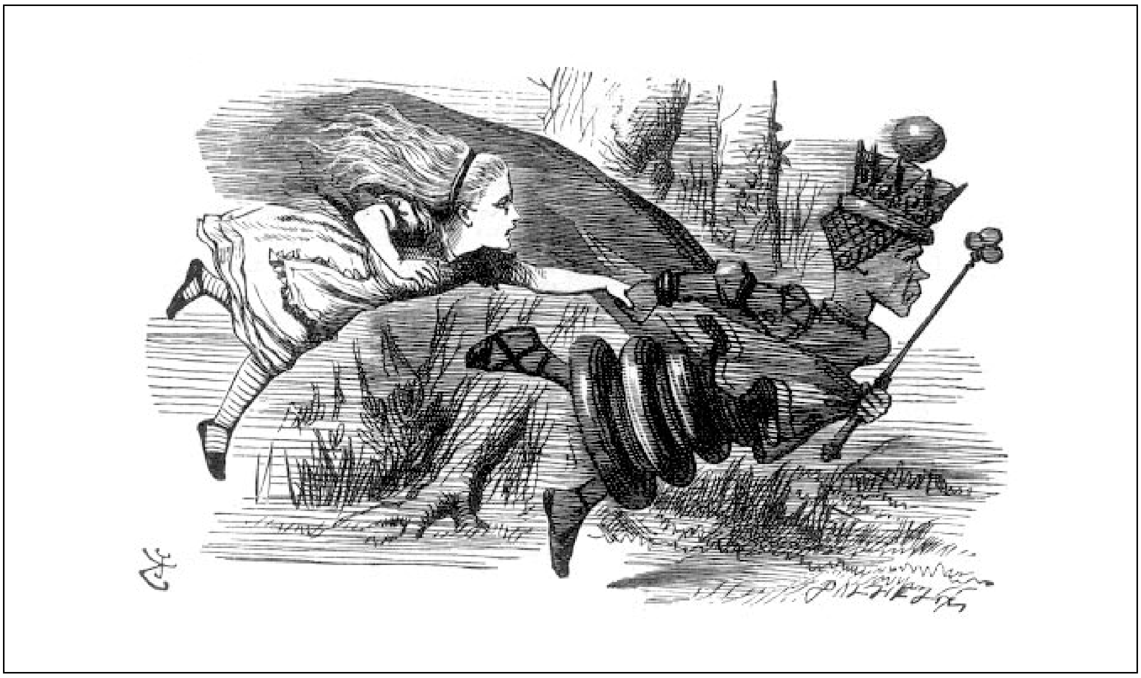

Figure 9.1 "Well, in *our* country," said Alice, still panting a little, "you'd generally get to somewhere else – if you ran very fast for a long time as we've been doing." "A slow sort of country!" said the Queen. "Now, *here*, you see, it takes all the running *you* can do, to keep in the same place." (after Carroll 1871) Since Van Valen (1973) the Red Queen serves as a metaphor for the deterioration of a species' environment owing to continual coevolution with other species. This process can give rise to Red Queen dynamics, i.e. continuous evolutionary change in a community in the absence of external forcing.

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, for more details see Section 1.2. 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".

The Red Queen

Of some interest has thus been the general 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; Maynard Smith 1982).

Following Van Valen's (1973) Red Queen's hypothesis, the alternative – the interaction between species prevents attainment of an equilibrium point such that there is continuous evolutionary change in their phenotypes – has become known as *Red Queen dynamics* (Stenseth and Maynard Smith 1984; Rosenzweig et al. 1987; Marrow et al. 1992). Such dynamics are interpreted to indicate the continuous deterioration of a species' environment owing to the continual evolution of other species (Futuyma 1986; Ebeling and Feistel 1982). The name was inspired by the book “Through the Looking-Glass, and What Alice Found There” by Lewis Carroll (1871) where the Red Queen explains: ”Now, here, you see, it takes all the running you can do, to keep in the same place.” We refer 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.

Outline of Analysis

To investigate whether Red Queen dynamics are possible, prototypical coevolutionary predator-prey communities have been devised (Marrow et al. 1992; Marrow and Cannings 1993). Analysis of these communities has been interpreted to suggested that, over the course of evolution, the phenotypes could either tend to equilibrium or to nonequilibrium asymptotic states. However, the models considered in these analyses were not dynamical and the time-dependence owing to the processes of mutation and selection was not incorporated. We have seen in Section 7.2 that under these circumstances prediction of evolutionary outcomes generally is impossible; to determine the asymptotic states of coevolving systems it is necessary to employ a dynamical framework. Consequently, we here analyze the coevolutionary predator-prey community in terms of our three dynamical models of coevolution.

Section 9.2 introduces the ecological interactions which define the predator-prey community. In Section 9.3 we illustrate different coevolutionary outcomes in this community and demonstrate that these can be grouped into three classes: (i) the predator goes extinct, (ii) coevolution leads to constant phenotypes in predator and prey, and (iii) the phenotypes in both species undergo coupled and sustained oscillations on a limit cycle corresponding to Red Queen dynamics. Section 9.4 analyzes in detail 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.

9.2 Specification of the Coevolutionary Community

According to the framework established in Section 4.1 we base our dynamical models of predator-prey coevolution on the ecological processes in the predator-prey community. In doing so we ensure 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.

Birth and Death Events

For simplicity, we focus on a single adaptive 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.

Figure 9.2 provides a characterization of the coevolutionary predator-prey community by specifying the fundamental birth and death processes. In particular, Figure 9.2a 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 Figure 9.2b.

<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 $s_1 \rightarrow s_1'$</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 $s_2 \rightarrow s_2'$</td><td>$(1-\mu_2) \cdot \delta(s_2' - s_2) + \mu_2 \cdot M_2(s_2' - s_2)$</td></tr>
</table>

Figure 9.2 Specification of birth, death and mutation processes for a prey individual with phenotype s_1 and predator with phenotype s_2 in the coevolutionary predator-prey community.

Mutation

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.

Figure 9.2c 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. These distributions are assumed to be Gaussian with mean 0 and variances σ_1^2 and σ_2^2 respectively.

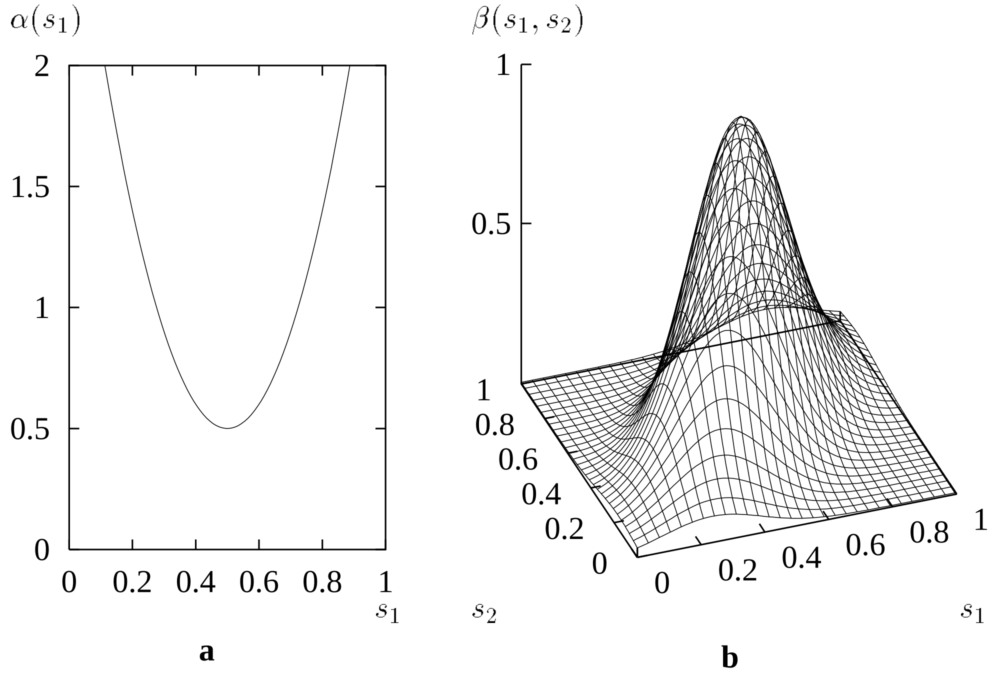

Figure 9.3 Specification of the interactions in the coevolutionary predator-prey community as introduced in Figure 9.2. The functions used to describe the effect of phenotypes on the birth and death probabilities arising from encounters between individuals are: (a) prey self-limitation $\alpha(s_1) = u \cdot \{c_1 - c_2 \cdot s_1 + c_3 \cdot s_1^2\}$, (b) effect of predator on prey $\beta(s_1, s_2) = u \cdot \exp\{-\delta_1^2 + 2 \cdot c_4 \cdot \delta_1 \cdot \delta_2 - \delta_2^2\}$, where $\delta_1 = (s_1 - c_3)/c_5$ and $\delta_2 = (s_2 - c_7)/c_8$. $u = 10^{-3}$ 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 are: $\mu_1 = 10^{-3}$, $\mu_2 = 10^{-3}$; $\sigma_1 = 2 \cdot 10^{-3}$, $\sigma_2 = 2 \cdot 10^{-3}$. The given parameter values are used throughout except where otherwise stated.

Selection

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 9.3.

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 9.3a). The function β describing the effect of a predator on the probability of death of the prey is taken to be bivariate Gaussian (Figure 9.3b), 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*.

Simple though this example is, it illustrates some features of a coevolving predator-prey system. In particular, it shows the tension typical of predator-prey coevolution: the predator gains its greatest benefit from the prey at the combination of adaptive trait values $s_1 = 0.5$, $s_2 = 0.5$ where in contrast the prey suffers its greatest loss.

Resume

The ecological community presented here extends the model of Marrow et al. (1992) by (i) providing a full dynamical description of the birth, death and mutation processes. It further generalizes the former account in the sense that (ii) it allows stochastic population dynamics arising from individual-based encounters, and (iii) it permits the populations to have polymorphic phenotypic distributions since multiple adaptive trait values may be present simultaneously in each species.

As a special case of our description, we recover the well-known Lotka-Volterra equations

$$\begin{aligned} \frac{d}{dt} n_1 &= n_1 \cdot (+r_1 - \alpha(s_1) \cdot n_1 - \beta(s_1, s_2) \cdot n_2)\,, \\ \frac{d}{dt} n_2 &= n_2 \cdot (-r_2 + \gamma(s_1, s_2) \cdot n_1) \end{aligned} \tag{9.1}$$

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 is present within each species).

9.3 Investigation of Evolutionary Outcomes

Here we describe the variety of possible evolutionary outcomes in a predator-prey community, using the monomorphic deterministic model as a starting point of our investigation. 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.

The Region of Coexistence

In the case of the monomorphic dynamics we can immediately infer from equations (9.1) that there is a region $\widehat{S}_c$ in the monomorphic trait space $\widehat{S}$ where both species can coexist with positive population densities.

The boundary of this region is depicted by the oval discontinuous curves in Figures 9.4, 9.5 and 9.6. 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 (9.1). Accordingly, coevolution of the predator and prey can only be observed within this region of coexistence. It is possible for a sequence of trait substitutions in the prey to lead to extinction of the predator, as illustrated e.g. in Figure 9.5.

On the other hand, 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, as there is no region of trait space in which neither species has a positive equilibrium population density.

Classification of Evolutionary Outcomes in Predator-Prey Coevolution

By tuning the shape of the interaction functions depicted in Figure 9.3, the variety of possible coevolutionary outcomes in this predator-prey community can be explored. A survey is given in Marrow et al. (1992).

This diversity of different coevolutionary outcomes can be grouped into a small number of classes. For a coevolving predator-prey community starting with phenotypes in the region of coexistence, there are eventually only three classes of possible outcomes. We illustrate these classes in Figures 9.4 to 9.6 by means of typical instances.

1. *Evolution to a fixed point.* In Figure 9.4a, the adaptive trait 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 in this example, as can be seen from the accompanying phase portrait (Figure 9.4b); two of these are attractors and they are separated by the unstable 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

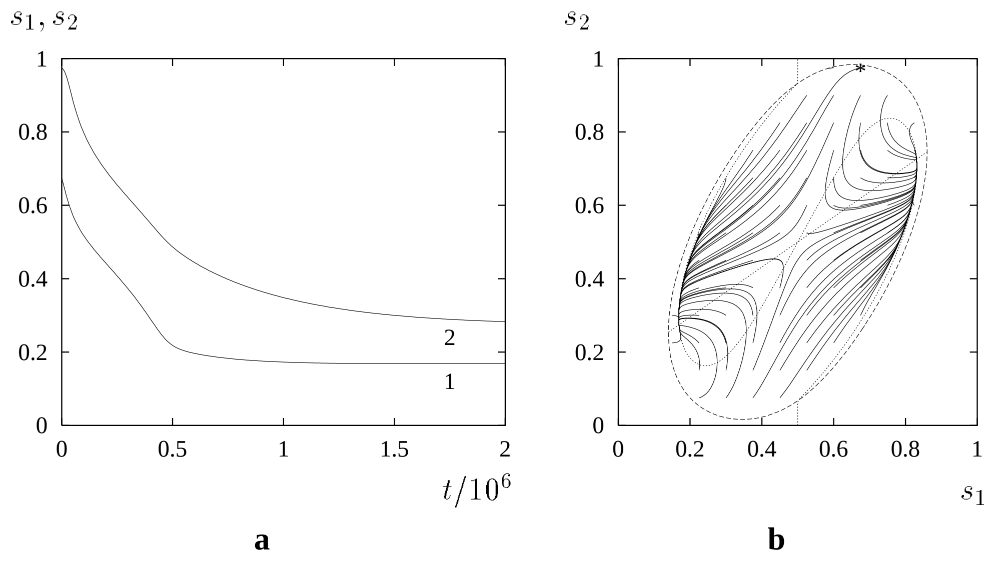

Figure 9.4 Patterns of evolution of prey (s_1) and predator (s_1) phenotypes obtained from the monomorphic deterministic model. (a) Solution that tends to an equilibrium point over the course of time obtained using the parameter values from Figure 9.3 with $h = 1.0$. (b) Phase portrait of the trait space from which (a) is drawn with orbits shown as continuous lines. The starting point of the orbit shown in (a) is indicated by an asterisk. The boundary of the region $\widehat{S}_c$ 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); fixed points occur at the intersection of the isoclines.

observed asymptotic state than the more or less arbitrary initial conditions of the adaptive process.

2. *Evolution to extinction.* In Figure 9.5a the coevolutionary process drives the phenotypic values towards the boundary of the region of coexistence (see Figure 9.5b). There the predator population goes extinct and the predator phenotype is no longer defined. The trait 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 adaptive dynamics in (s_1, s_2) and not merely by the population dynamics in (n_1, n_2).
3. *Evolutionary cycling.* In Figure 9.6a, 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 9.6b, the attractor is a limit

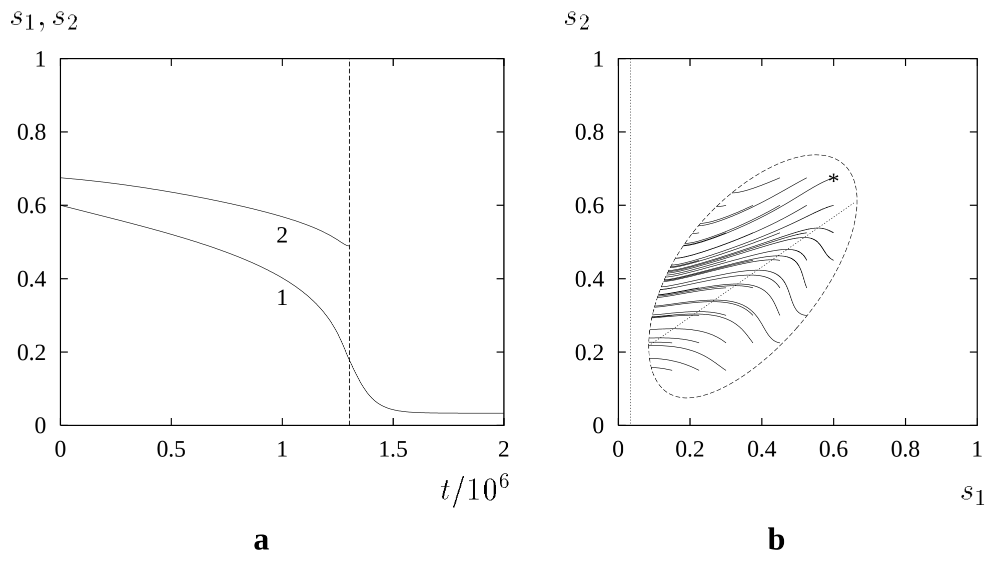

Figure 9.5 Patterns of evolution of prey (s_1) and predator (s_1) phenotypes obtained from the monomorphic deterministic model. (a) Solution for a community that evolves to predator extinction at time $t = 1.3 \cdot 10^6$. After this time, the prey continues to evolve in the absence of the predator. Parameter values as in Figure 9.3, except $c_1 = 1.0$, $c_2 = 1.0$, $c_3 = 15.0$, and with $h = 1.0$. (b) Phase portrait of the trait space from which solution (a) is drawn. The starting point of the orbit shown in (a) is indicated by an asterisk. Isoclines are shown as dotted lines (straight line: predator; vertical line: prey). The prey isocline lies outside the region $\widehat{S}_c$ of coexistence and orbits touch the boundary of this region, given as the discontinuous oval line, at which point the predator goes extinct.

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.

9.4 Analysis of Evolutionary Cycling

This section investigates 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 the incidence of evolutionary cycling. Second, we examine the monomorphic stochastic model and finally the polymorphic stochastic model to see how robust

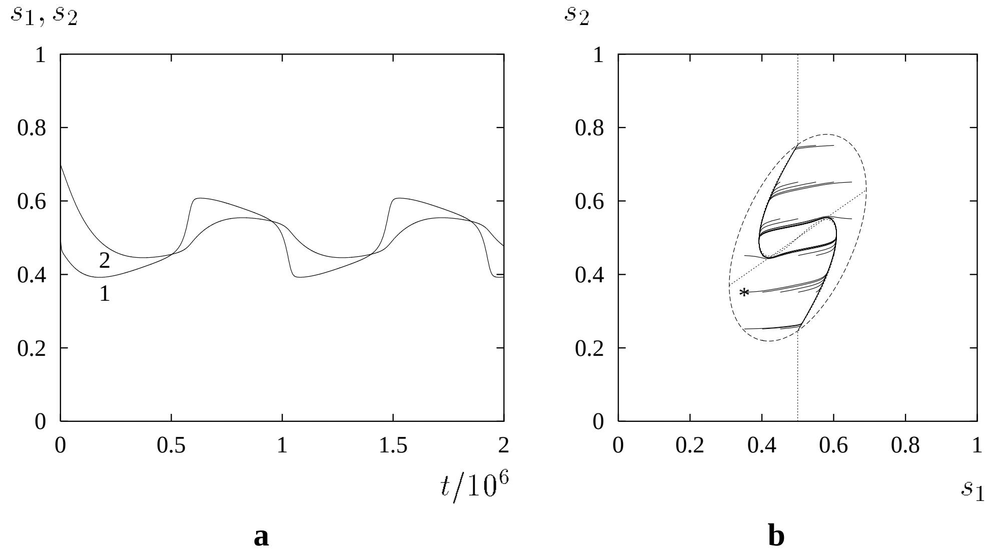

Figure 9.6 Patterns of evolution of prey (s_1) and predator (s_1) phenotypes obtained from the monomorphic deterministic model. (a) Solution exhibiting evolutionary cycling of predator and prey phenotypes. Parameter values for this case are as in Figure 9.3 with $h = 0.14$. The starting point of the orbit shown in (a) is indicated by an asterisk. (b) Phase portrait corresponding to (a) illustrating the basin of attraction for cyclic solutions shown as continuous lines. The boundary of the region $\widehat{S}_c$ 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); an unstable fixed point is located at the intersection of the isoclines.

the phenomenon of evolutionary cycling is when the simplifying assumptions of the monomorphic deterministic model are removed.

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

$$h = \frac{\gamma}{\beta} \, , \tag{9.2}$$

and secondly the ratio of the evolutionary rate constants

$$r = \frac{\mu_1 \cdot \sigma_1^2}{\mu_2 \cdot \sigma_2^2} \, . \tag{9.3}$$

The existence, number and location of fixed points of the monomorphic deterministic model that lie within the region of coexistence $\widehat{S}_c$ can be obtained in first order from the simultaneous solutions $\hat{s}$ of

$$\partial_i' \overline{f}_i(\hat{s}_i, \hat{s}) = 0 \tag{9.4}$$

for $i = 1, 2$. According to section 9.2 the per capita growth rates $\overline{f}_i(s_i', s)$ of rare mutants s_i' in a community of resident trait s are given by

$$\begin{aligned} \overline{f}_1\big(s_1', s\big) &= +r_1 - \alpha\big(s_1'\big) \cdot \hat{n}_1(s) - \beta\big(s_1', s_2\big) \cdot \hat{n}_2(s) \;, \\ \overline{f}_2\big(s_2', s\big) &= -r_2 + \gamma\big(s_1, s_2'\big) \cdot \hat{n}_1(s) \;, \end{aligned} \tag{9.5}$$

where the equilibrium population sizes $\hat{n}(s)$ in $\widehat{S}_c$ from equations (9.1) are obtained as

$$\begin{aligned} \hat{n}_1(s) &= \frac{r_2}{\gamma(s_1, s_2)} \;, \\ \hat{n}_2(s) &= \frac{r_1 \cdot \gamma(s_1, s_2) - r_2 \cdot \alpha(s_1)}{\beta(s_1, s_2) \cdot \gamma(s_1, s_2)} \;. \end{aligned} \tag{9.6}$$

The stability of the fixed points $\hat{s}$ can be checked by evaluating at these points the Jacobian of the first order approximation of the monomorphic deterministic model. This Jacobian J has been computed in Section 7.2, see equations (7.13,14). From the conditions $\det J > 0$ and $\operatorname{tr} J < 0$ we infer that the fixed point $\hat{s}$ is stable if, and only if,

$$\begin{aligned} &\big[\partial_1'^2 \overline{f}_1(\hat{s}_1, \hat{s}) + \partial_1' \partial_1 \overline{f}_1(\hat{s}_1, \hat{s})\big] \cdot \\ &\big[\partial_2'^2 \overline{f}_2(\hat{s}_2, \hat{s}) + \partial_2' \partial_2 \overline{f}_2(\hat{s}_2, \hat{s})\big] - \\ &\partial_1' \partial_2 \overline{f}_1(\hat{s}_1, \hat{s}) \cdot \partial_2' \partial_1 \overline{f}_2(\hat{s}_2, \hat{s}) > 0 \end{aligned} \tag{9.7}$$

and

$$\begin{aligned} &r \cdot \frac{\hat{n}_1(s)}{\hat{n}_2(s)} \cdot \\ &\big[\partial_1'^2 \overline{f}_1(\hat{s}_1, \hat{s}) + \partial_1' \partial_1 \overline{f}_1(\hat{s}_1, \hat{s})\big] - \\ &\big[\partial_2'^2 \overline{f}_2(\hat{s}_2, \hat{s}) + \partial_2' \partial_2 \overline{f}_2(\hat{s}_2, \hat{s})\big] < 0 \;. \end{aligned} \tag{9.8}$$

From the first condition, inequality (9.7), we obtain those intervals of values h where the fixed point $\hat{s}$ could be stable; within these intervals we then employ the second condition, inequality (9.8), to determine those combinations (h, r) for which the fixed point actually is stable.

Since the adaptive dynamics in the predator-prey community are two-dimensional, the only possible attractors are fixed points and limit cycles. From the Poincaré-Bendixon

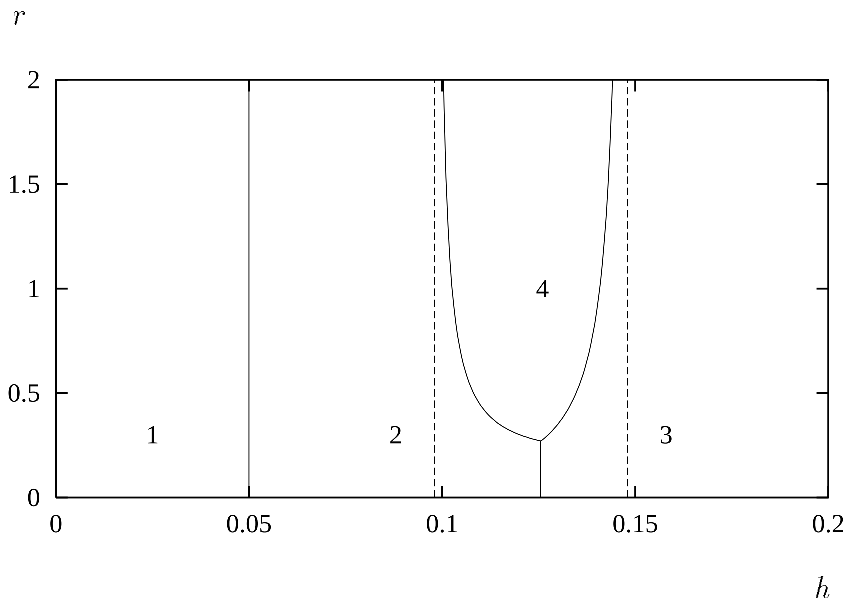

Figure 9.7 Results of the bifurcation analysis, showing the effect of the harvesting efficiency h, and the ratio of the evolutionary rate constants r on the dynamics of the monomorphic deterministic model. Regions are: (1) predator absent, (2) one fixed point, which is an attractor, (3) three fixed points, two of which are attractors, (4) limit-cycle attractor.

theorem, a sufficient condition for the existence of a stable limit cycle is the existence of a region in trait space that (i) a trajectory of the adaptive dynamics cannot leave and that (ii) contains no stable fixed point. Using the signs of the two selection derivatives $\partial_1' \overline{f}_1(s_1, s)$ and $\partial_2' \overline{f}_2(s_2, s)$ between the isoclines, a region that cannot be left is easily established; the stability of the fixed point(s) in this region is then checked as described above.

Requirements for Evolutionary Cycling

The results of the bifurcation analysis are presented in Figure 9.7. 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.

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 (as indicated in Figure 9.7), 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 $h = 12.6\%$.

In summary, we have revealed two types of local bifurcations in this system, both being of codimension 1. The transition at $h = 12.6\%$, where the number of fixed points changes from one to three is called a *pitchfork bifurcation*. The transition across the boundary of region 4, where a fixed point looses stability and gives rise to a stable limit cycle, amounts to a *Hopf bifurcation*.

In completion of the local bifurcation analysis outlined so far, the potential for the incidence of *global bifurcations* ought to be checked. From this it follows that 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 two 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.

Evolutionary Cycling in the Monomorphic Stochastic Model

A realization of the monomorphic stochastic dynamics is given in Figures 9.8c and 9.8d. The parameter values used are the same as those in Figures 9.8a and 9.8b where the dynamics of the monomorphic deterministic model are depicted, and we see that the cyclic behavior 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 as *phase diffusion* (Tomita et al. 1974) or *dephasing* (Schnakenberg 1993), comes about because stochastic perturbations along the limit cycle are not balanced by a counteracting force, whereas those orthogonal to the limit cycle are.

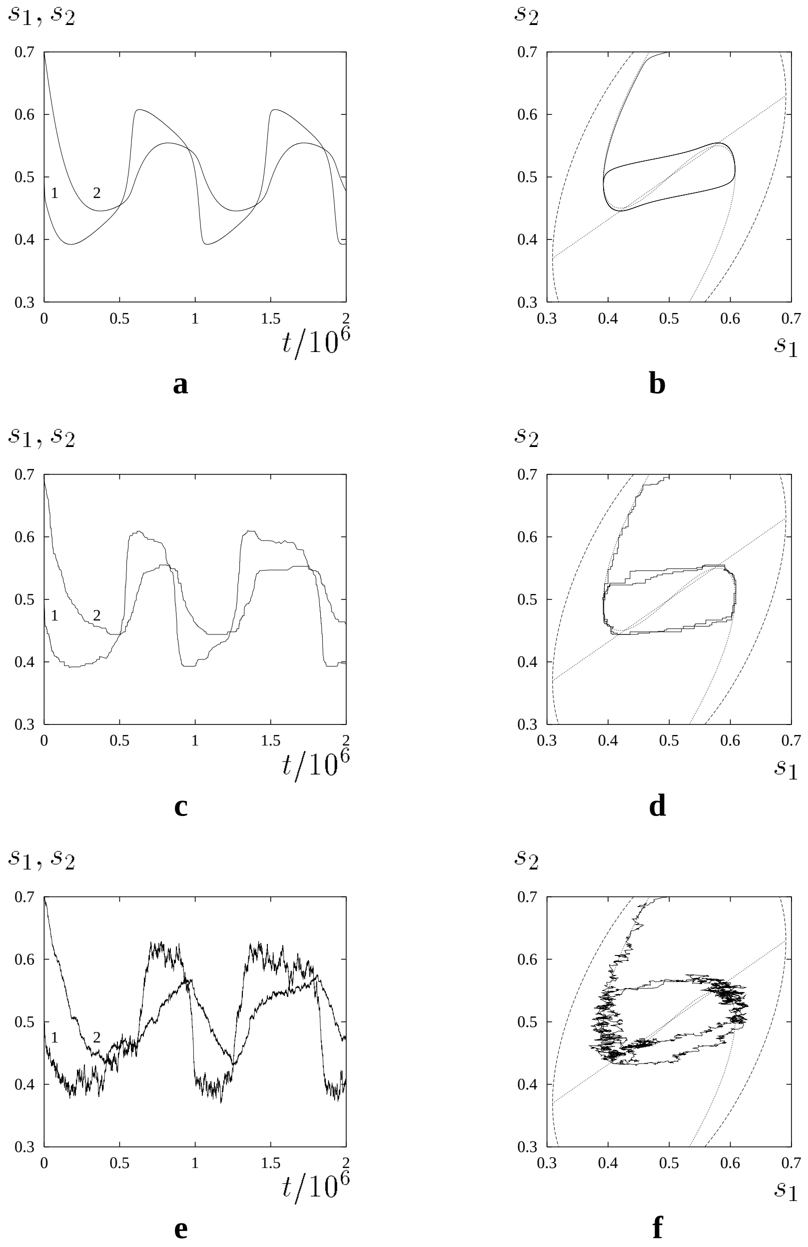

Figure 9.8 Evolutionary cycling as exhibited by the three models of coevolutionary dynamics. The monomorphic deterministic model is used in (a) and (b), the monomorphic stochastic model in (c) and (d), and the polymorphic stochastic model in (e) and (f). Graphs (a), (c) and (e) show the resident values of the prey (s_1) and predator (s_2) phenotypes as functions of time t. The corresponding orbits are shown as continuous lines in the phase portraits given in graphs (b), (d) and (f). In the case of the polymorphic stochastic model the displayed time series is made up of roughly 10 000 000 000 single birth and death events. The boundary of the region $\widehat{S}_c$ of coexistence of predator and prey is given as the discontinuous oval line. Isoclines are shown as dotted lines (straight line: predator; curved line: prey). Parameter values for these simulations are identical and are set as given in Figure 9.3 with $h = 0.14$, except $\mu_1 = \mu_2 = 10^{-2}$.

Second, limit cycles whose extension in trait space is small relative to the typical mutational step sizes (given by σ_1 and σ_2) will be obscured by the stochastic noise. The boundaries of region 4, see Figure 9.7, will then be less sharp than those in the monomorphic deterministic model. Thus, if the evolutionary cycling is to be visible, the mutational steps must not be too large.

Evolutionary Cycling in the Polymorphic Stochastic Model

A realization of the polymorphic stochastic model is shown in Figures 9.8e and 9.8f, using as before the parameter values of Figures 9.8a and 9.8b. The phenomenon of evolutionary cycling still persists despite the phenotypic distributions now being polymorphic.

In addition, this model allows investigating the effects of demographic stochasticity not only of the mutant but also of the resident phenotypes. 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 models.

9.5 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 behavior 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.

Interpretation of the Requirements for Evolutionary Cycling

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 attain in the absence of the predator (h not too low), (ii) sufficient pressure 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.

Related Work

That cyclic phenotype dynamics can occur in coevolution 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 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.

Revival of the Red Queen

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 Section 9.1, 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 nonequilibrium attractors; for instance in systems with more than two coevolving species, chaotic attractors could be found.

Conclusion

It seems therefore that there is a large variety of coevolutionary communities with the potential for nonequilibrium evolutionary attractors. 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 nonequilibrium asymptotic states.

The prevailing view among evolutionary biologists, centered on equilibrium points, needs to be extended to a dynamical framework to assimilate the Red Queen.

Summary and Conclusions

In this thesis we have presented first steps towards a dynamical theory of coevolution. In contrast to evolutionary game theory, our approach is based on a dynamical framework, thus incorporating the description of evolutionary transients and nonequilibrium evolutionary attractors. Unlike standard replicator dynamics, it accounts for the continuous introduction of new adaptive trait values to the evolutionary community and allows for arbitrary ecological interactions within the community, these interactions can be specified at the level of individuals. Different to the canonical equation of adaptive dynamics, our results provide a stochastic treatment of the adaptive process and higher order correction terms to the canonical equation are derived.

Figure 1 summarizes the hierarchy of deductions given in this thesis. Taking the general replicator concept as a starting point, these deductions connect the three dynamical models of coevolution presented in Chapters 4, 5 and 6. The necessary assumptions are displayed to indicate the domain of validity of these models. We have recovered the canonical equation of adaptive dynamics as a special case from our framework – in fact, from the results of Sections 5.3, 4.3 and 6.2 it is clear that the standard models of evolutionary game theory, replicator dynamics and adaptive dynamics form a subset of our hierarchy. In particular, when we read the diagram in Figure 1 from below, we see that the limitations of the canonical equation of adaptive dynamics have been relaxed to a substantial degree.

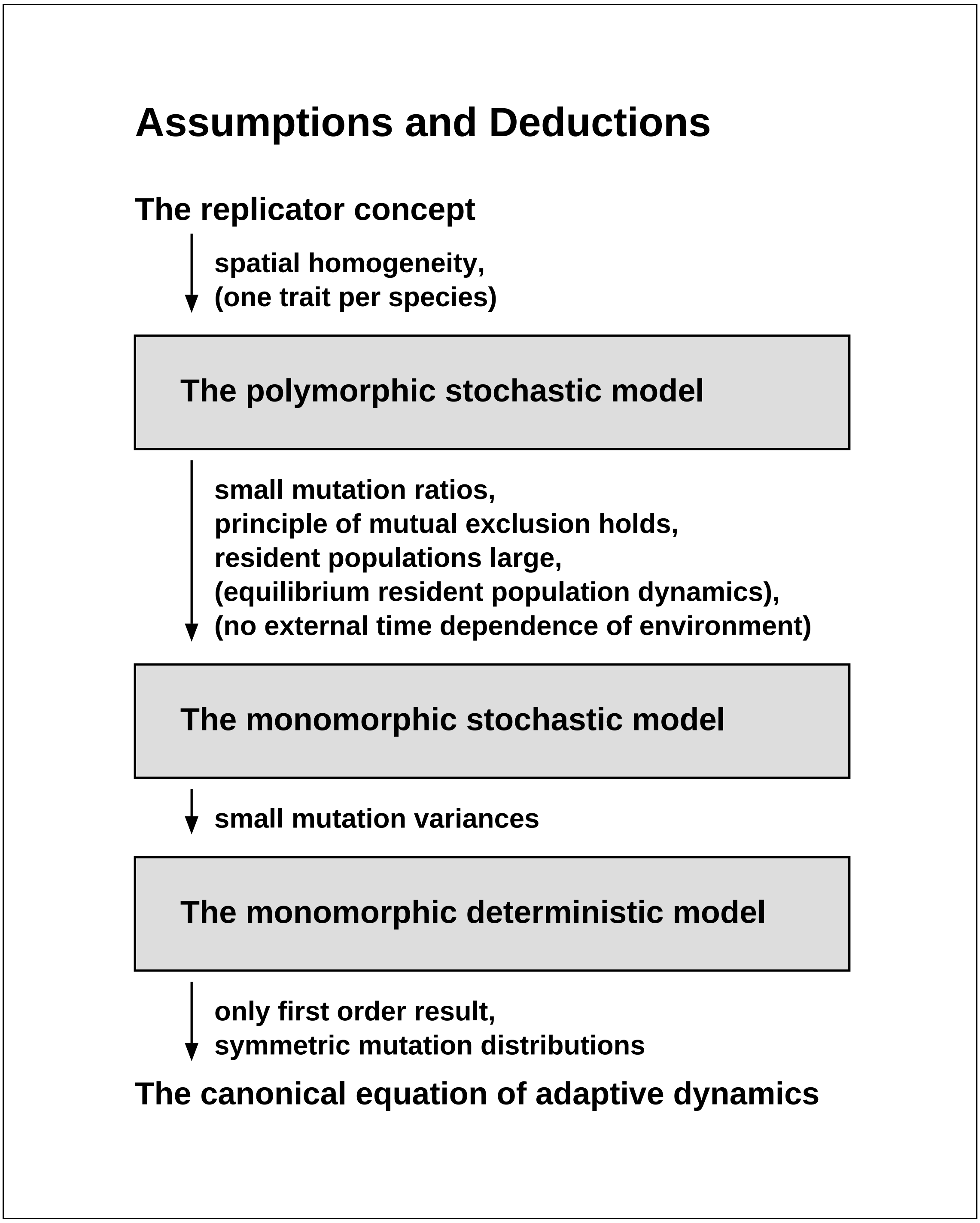

Figure 1 Assumptions and deductions in this thesis. The derivations connecting the three dynamical models of coevolution given in Chapters 4, 5 and 6 are depicted by arrows. The assumptions that enter these derivations are mentioned, those in parentheses are relaxed in Chapter 8. With every additional assumption analytic tractability of the models is increased while at the same time interesting evolutionary phenomena might be sacrificed.

To conclude, we briefly summarize these extensions.

1. To obtain the canonical equation of adaptive dynamics from a mutation-selection process, symmetry properties of the mutation distributions are needed, see Section 6.2. Both our monomorphic deterministic model in Section 6.3 and the two stochastic models remove this assumption.
2. 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. In these circumstances consideration of higher order corrections, as provided in Section 6.3, is recommended.
3. Due to such higher order corrections, there can arise new evolutionary phenomena not described by the canonical equation, like shifting of evolutionary isoclines and evolutionary slowing down. Conditions for such effects can be established analytically, see Section 7.4.
4. Being a deterministic description of the adaptive dynamics, the canonical equation can only describe the mean evolutionary path, as derived in Sections 5.5 and 6.1, and thus does not cover the full richness of dynamical effects that can occur in stochastic mutation-selection systems. In contrast, the monomorphic and polymorphic stochastic models account for such features as splitting probabilities at evolutionary basin boundaries, multiple evolutionary pathways (see Section 6.5) and phase diffusion (see Section 9.4).
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 8.2 that this limitation can be partially overcome such that more general ecological scenarios may be tackled.
6. The canonical equation is restricted to describing the adaptive dynamics of the community. Only when both adaptive dynamics and population dynamics are derived from the joint coevolutionary dynamics of the community, phenomena like evolutionary extinction, see Section 9.3, can be analyzed.
7. Coevolutionary stability cannot be determined by considering non-invadability. In Section 7.2 we have established and illustrated this result; in order to gain a full

picture of coevolutionary stability, it is necessary to supplement the notion of non-invadability (from evolutionary game theory) by that of dynamical stability (from adaptive dynamics) and vice versa.

8. The canonical equation of adaptive dynamics does not permit interdependencies between several traits within one species. In Section 8.1 we have shown how the stochastic approach naturally leads to the introduction of the variance-covariance matrix for the mutation distributions. Off-diagonal terms of the latter can give rise to altered pathways towards evolutionary attractors.
9. Even if one of the key assumptions for monomorphism, see Section 5.1, cannot be taken for granted, still the polymorphic stochastic model can be utilized to obtain a full description of the coevolutionary dynamics. Examples are the mutation catastrophe discussed in Section 4.5 and the increased variation of the adaptive process, see Section 9.4, when resident population sizes are not large.

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 might indeed be sufficient for specific goals, but this depends on what assumptions can reasonably be made. We have shown in this thesis 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.

Acknowledgments

I would like to thank my advisor, Dr. Richard Law, for lots of interesting and fruitful discussions and for constant support during all stages of my work, Prof. Dr. Jürgen Schnakenberg, my supervisor at the "Institut für Theoretische Physik" of the RWTH Aachen, for valuable comments and for his interest in the application of stochastic processes to the theory of coevolution, and all members of the "Arbeitsgruppe Modellierung in Umweltforschung und Lebenswissenschaften" at the Forschungszentrum Jülich where I have benefitted from the stimulating atmosphere and numerous talks given and attended. In particular, many thanks to Ralf Engbert, Prof. Dr. Frank Pasemann, Dr. Friedhelm Drepper, Michael Schiek, Dr. Heinz Vos, Prof. Dr. Jakob Weiner, Margret Spatzek and Dr. Wolfgang Speier for their encouragement and help and to Prof. Dr. Jacqueline McGlade for vividly supporting my interest in theoretical ecology.

For valuable discussions on various topics of this work I thank Prof. Dr. Hans Metz, Prof. Dr. Odo Dickmann, Prof. Dr. Lutz Schimansky-Geier, Prof. Dr. Paulien Hogeweg, Prof. Dr. Gert Eilenberger, Prof. Dr. Vivian Hutson, Prof. Dr. David Gray, Prof. Dr. David Rand, Dr. Paul Marrow, Dr. Stefan Geritz, Dr. Jan van der Laan, Dr. Vincent Jansen, Daniel Morton and Andrew Mclellan.

Finally, I would like to thank my "physics friends" in Aachen, Georg Friberg, Eckhard Karden, Burkhard Neinhüs, Juan Rechid, Martin Rüttgers, Jan Schlipf and Barbara Willkommen for continuous interest in my work and for providing a personal atmosphere that made the last years special.

Developed Software

The software for the present work has been developed in ANSI C[*]. There are four packages,

1. **`coevolve_def.c`**,
2. **`coevolve_aux.c`**,
3. **`coevolve_det.c`**, and
4. **`coevolve_sto.c`**.

All four packages are integrated in the program **`coevolve.c`**.

The first package, `coevolve_def.c`, contains the constants and functions that serve to specify a particular coevolutionary community. The second package, `coevolve_aux.c`, defines several functions commonly used in the other three packages. The third package, `coevolve_det.c`, contains functions for the investigation of the monomorphic coevolutionary dynamics and in particular the implementation of the monomorphic deterministic model. The fourth package, `coevolve_sto.c`, comprises the implementation of the monomorphic and the polymorphic stochastic models.

The listings of the four packages and the integrating program are provided at the end of this chapter, see Listings 1 to 4 and 5. No part of these packages may be used without permission of the author. Below a command reference of the developed functions is given.

---

[*] For compilation the AT&T C++ Translator, version 2.1.03, datemark 08/31/90 has been used.

Function `birth_mono()` Package `coevolve_def.c`

■ Description

User-defined function. Implementation of the per capita birth rate $\overline{b}_i(s_i', s)$.

■ Input

`community_size`	Number N of species making up the coevolutionary community.
`species`	Species index i.
`s`	Adaptive trait value s_i'.
`s_res`	Vector $s = (s_1, \ldots, s_N)$ of the resident trait values.

Additional functions and parameters may be supplied by the user within the package `coevolve_def.c` to facilitate the set-up of the function `birth_mono()`.

■ Output

Internal. Returns $\overline{b}_i(s_i', s)$.

Function `death_mono()` Package `coevolve_def.c`

■ Description

User-defined function. Implementation of the per capita death rate $\overline{d}_i(s_i', s)$.

■ Input

See function `birth_mono()`.

■ Output

Internal. Returns $\overline{d}_i(s_i', s)$.

Function `birth_polysto()` Package `coevolve_def.c`

■ Description

User-defined function. Implementation of the per capita birth rate $b_i(s_i', p)$.

■ Input

`community_size`	Number N of species making up the coevolutionary community.
`species`	Species index i.
`s`	Adaptive trait value s_i'.
`firstgroupP`	Vector of N pointers. Each is directed to a group of individuals in p_i which all have the same trait value s_i'. These pointers determine one end of bidirectionally connected lists giving access to all such groups in p_i; elements of these lists are of type `grouptype` as defined in the package `coevolve_aux.c`.

Additional functions and parameters may be supplied by the user within the package `coevolve_def.c` to facilitate the set-up of the function `birth_polysto()`.

■ Output

Internal. Returns $b_i(s_i', p)$.

Function `death_polysto()` Package `coevolve_def.c`

■ Description

User-defined function. Implementation of the per capita death rate $d_i(s'_i, p)$.

■ Input

See function `birth_polysto()`.

■ Output

Internal. Returns $d_i(s'_i, p)$.

Function `n_hat()` Package `coevolve_def.c`

■ Description

User-defined function. Implementation of the equilibrium population size $\hat{n}_i(s)$.

■ Input

`community_size`	Number N of species making up the coevolutionary community.
`species`	Species index i.
`s`	Vector $s = (s_1, \dots, s_N)$ of the resident trait values.

Additional functions and parameters may be supplied by the user within the package `coevolve_def.c` to facilitate the set-up of the function `n_hat()`.

■ Output

Internal. Returns $\hat{n}_i(s)$.

Function `m()` Package `coevolve_def.c`

■ Description

User-defined function. Implementation of the mutation distribution $M_i(s'_i - s_i)$.

■ Input

`species`	Species index i.
`delta_s`	Difference $s'_i - s_i$ between the resident trait value and the mutant trait value.

Additional functions and parameters may be supplied by the user within the package `coevolve_def.c` to facilitate the set-up of the function `m()`. In particular, providing the vector $\sigma = (\sigma_1, \dots, \sigma_N)$ of mutation standard deviations can be useful.

■ Output

Internal. Returns $M_i(s'_i - s_i)$.

Function `monodet()` Package `coevolve_det.c`

■ Description

Implementation of the monomorphic deterministic model.

■ Input

`community_size`	Number N of species making up the coevolutionary community.
`birth_mono()`	Function providing the per capita birth rates in the community, see above.
`death_mono()`	Function providing the per capita death rates in the community, see above.
`sigma`	Vector $\sigma = (\sigma_1, \dots, \sigma_N)$ of mutation standard deviations.
`mu`	Vector $\mu = (\mu_1, \dots, \mu_N)$ of mutation ratios.

s_init	Vector $s = (s_1, \ldots, s_N)$ of adaptive trait values that are resident initially.
t_end	Time t at which simulation is to be aborted.
t_monodet_step	Time step for numerical integration.
t_monodet_out	Time step for output to be written to the file `monodet.dat`.
monodet_method	Flag. When set to 0, the Euler method is used for numerical integration; when set to 1, the fourth order Runge-Kutta method is employed.
monodet_order	Order in series expansion of the monomorphic deterministic model (can be 1, 2 or 3; when set to 0, no series expansion is made).
monodet_logplot	Flag. When set to 1, values $\log_{10} \lvert s_i(t) - \hat{s}_i \rvert$ instead of $s_i(t)$ are written to the file `monodet.dat`.
s_fixedpoint	Vector of trait values at a fixed point $\hat{s}$, only used when `monodet_logplot` is set to 1.
monodet_direction	Flag. When set to $+1$, direction of time is forward, when set to -1, backward.
extinction_continuation	Flag. When set to 1, simulation of the monomorphic deterministic model continues after a species has gone extinct, otherwise simulation is aborted.
extinction_init	Vector of flags. When the element corresponding to species i is set to 0, this species is present initially, otherwise it is extinct.
monitor_level	Flag controlling the extent of information written to `stdout` (can be 1, 2, 3 or 0; corresponding to basic, normal, detailed or no output).
run_monodet	Flag. When set to 1, the function `monodet()` is executed.

■ Output

To file `monodet.dat`. First column: time t; following columns: resident adaptive trait values $s_1(t)$ to $s_N(t)$. In addition, some information can be written to `stdout`.

Function `portrait()` Package `coevolve_det.c`

■ Description

Construction of a phase portrait for the monomorphic deterministic model. Application is restricted to coevolutionary communities with $N = 2$ or $N = 3$.

■ Input

community_size	Number N of species making up the coevolutionary community.
birth_mono()	Function providing the per capita birth rates in the community, see above.
death_mono()	Function providing the per capita death rates in the community, see above.
sigma	Vector $\sigma = (\sigma_1, \ldots, \sigma_N)$ of mutation standard deviations.
mu	Vector $\mu = (\mu_1, \ldots, \mu_N)$ of mutation ratios.
t_end	Time t at which simulation is to be aborted.
t_monodet_step	Time step for numerical integration.
t_monodet_out	Time step for output to be written to the file `monodet.dat`.
monodet_method	Flag. When set to 0, the Euler method is used for numerical integration; when set to 1, the fourth order Runge-Kutta method is employed.
monodet_order	Order in series expansion of the monomorphic deterministic model (can be 1, 2 or 3; when set to 0, no series expansion is made).
monodet_direction	Flag. When set to $+1$, direction of time is forward, when set to -1, backward.
extinction_continuation	Flag. When set to 1, simulation of the monomorphic deterministic model continues after a species has gone extinct, otherwise simulation is aborted.
extinction_init	Vector of flags. When the element corresponding to species i is set to 0, this species is present initially, otherwise it is extinct.
portrait_type	Flag. When set to 1 starting points are distributed randomly, otherwise they are choosen to lay on a two-dimensional rectangular grid.
portrait_grid	Vector of incremental steps determining the density of starting points in the two directions.

s_mindisplay	Vector of lower bounds for s to be displayed.
s_maxdisplay	Vector of upper bounds for s to be displayed.
random_seed	Seed for the random number generator.
monitor_level	Flag controlling the extent of information written to `stdout` (can be 1, 2, 3 or 0; corresponding to basic, normal, detailed or no output).
run_portrait	Flag. When set to 1, the function `portrait()` is executed.

■ Output

To file `monodet.dat`. First column: time t; following columns: resident adaptive trait values $s_1(t)$ to $s_N(t)$. Trajectories from different starting points are separated by blank lines. In addition, some information can be written to `stdout`.

Function `sketch()` Package `coevolve_det.c`

■ Description

Coarse survey of the sign structure of $\partial_i'\overline{f}_i(s_i, s)$ and $\hat{n}_i(s)$. Application is restricted to coevolutionary communities with $N = 2$.

■ Input

community_size	Number N of species making up the coevolutionary community.
birth_mono()	Function providing the per capita birth rates in the community, see above.
death_mono()	Function providing the per capita death rates in the community, see above.
sketch_grid	Vector of incremental steps determining the density of cells in the two directions.
s_mindisplay	Vector of lower bounds for s to be displayed.
s_maxdisplay	Vector of upper bounds for s to be displayed.
monitor_level	Flag controlling the extent of information written to `stdout` (can be 1, 2, 3 or 0; corresponding to basic, normal, detailed or no output).
run_sketch	Flag. When set to 1, the function `sketch()` is executed.

■ Output

To file `sketch.dat`. Each cell comprises two digits (in order to roughly conserve aspect ratio). Key:

11	$\partial_1'\overline{f}_1(s_1, s) > 0$	$\partial_2'\overline{f}_2(s_2, s) > 0$	$\hat{n}_1(s) > 0$	$\hat{n}_2(s) > 0$
22	$\partial_1'\overline{f}_1(s_1, s) > 0$	$\partial_2'\overline{f}_2(s_2, s) < 0$	$\hat{n}_1(s) > 0$	$\hat{n}_2(s) > 0$
33	$\partial_1'\overline{f}_1(s_1, s) < 0$	$\partial_2'\overline{f}_2(s_2, s) < 0$	$\hat{n}_1(s) > 0$	$\hat{n}_2(s) > 0$
44	$\partial_1'\overline{f}_1(s_1, s) < 0$	$\partial_2'\overline{f}_2(s_2, s) > 0$	$\hat{n}_1(s) > 0$	$\hat{n}_2(s) > 0$
55	$\partial_1'\overline{f}_1(s_1, s) > 0$		$\hat{n}_1(s) > 0$	$\hat{n}_2(s) = 0$
66	$\partial_1'\overline{f}_1(s_1, s) < 0$		$\hat{n}_1(s) > 0$	$\hat{n}_2(s) = 0$
77		$\partial_2'\overline{f}_2(s_2, s) > 0$	$\hat{n}_1(s) = 0$	$\hat{n}_2(s) > 0$
88		$\partial_2'\overline{f}_2(s_2, s) < 0$	$\hat{n}_1(s) = 0$	$\hat{n}_2(s) > 0$
99			$\hat{n}_1(s) = 0$	$\hat{n}_2(s) = 0$

In addition, some information can be written to `stdout`.

Function `contour()` Package `coevolve_det.c`

■ Description

Fine survey of the sign structure of $\frac{d}{dt}s_i(s)$ and $\hat{n}_i(s)$. Application is restricted to coevolutionary communities with $N = 2$.

■ Input

community_size	Number N of species making up the coevolutionary community.
birth_mono()	Function providing the per capita birth rates in the community, see above.
death_mono()	Function providing the per capita death rates in the community, see above.

contour_plot:: func	Flag contolling the function whose sign structure is to be depicted. Can be 1, 2, 3 or 4 corresponding to $\frac{d}{dt}s_1(s)$, $\frac{d}{dt}s_2(s)$, $\hat{n}_1(s)$ or $\hat{n}_2(s)$.
contour_plot:: contour_height	The contour lines, where the surfaces $\frac{d}{dt}s_i(s)$ and $\hat{n}_i(s)$ have the height `contour_height`, are written to the output files. Depiction of sign structure corresponds to setting this value to 0.
contour_plot:: dev_tol	Upper bound for the deviation of the height of the contour lines written to the output files from `contour_height`.
contour_plot:: s1_init	Starting value s_1 for search of contour lines.
contour_plot:: s2_init	Starting value s_2 for search of contour lines.
contour_plot:: dir_init	Direction in which to start search of contour lines.
contour_plot:: s_step	Incemental step between two successive points written to the output files.
contour_plot:: dir_step	Incremental step for two succesive directions in which to search of countour lines.
contour_plot:: max_points	Upper bound for the number of points written to the output files.
s_mindisplay	Vector of lower bounds for s to be displayed.
s_maxdisplay	Vector of upper bounds for s to be displayed.
monitor_level	Flag controlling the extent of information written to `stdout` (can be 1, 2, 3 or 0; corresponding to basic, normal, detailed or no output).
run_contour	Flag. When set to 1, the function `contour()` is executed.

Please note that due to the multitude of parameter choices which can be made for each individual contour line to be plotted, the parameters above that start with `contour_plot::` have to be specified in the source code of the package `coevolve_det.c`. In order to depict two or more contour lines for a particular function, `contour_plot()` has to be called twice or more times.

■ Output

To files `contour_iso1.dat`, `contour_iso2.dat` and `contour_coex.dat`. First columns: trait value s_1, second columns: trait value s_2. In addition, some information can be written to `stdout`.

Function isotest() Package coevolve_det.c

■ Description

Classification of isoclines $\frac{d}{dt}s_i(s) = 0$ and $\hat{n}_i(s)$ according to the categories non-invadable or invadable, convergent or divergent, not mutually invadable or mutually invadable. Application is restricted to coevolutionary communities with $N = 2$.

■ Input

contour_plot:: isotest_displace	Amount of displacement of lines written to the output files relative to contour lines in the normal direction of the contour line.
run_isotest	Flag. When set to 1, the function `isotest()` is executed.

For further inputs see function `contour()`.

■ Output

To files:

isotest1.dat	Non-invadable isoclines.
isotest2.dat	Invadable isoclines.
isotest3.dat	Convergent isoclines.
isotest4.dat	Divergent isoclines.
isotest5.dat	Not mutually invadable isoclines.
isotest6.dat	Mutually invadable isoclines.

First columns: trait value s_1, second columns: trait value s_2. In addition, some information can be written to `stdout`.

Function `landscape()` Package `coevolve_det.c`

Description

Depiction of the variable adaptive landscapes corresponding to the monomorphic deterministic model. Application is restricted to coevolutionary communities with $N = 2$.

Input

`community_size`	Number N of species making up the coevolutionary community.
`birth_mono()`	Function providing the per capita birth rates in the community, see above.
`death_mono()`	Function providing the per capita death rates in the community, see above.
`sigma`	Vector $\sigma = (\sigma_1, \ldots, \sigma_N)$ of mutation standard deviations.
`mu`	Vector $\mu = (\mu_1, \ldots, \mu_N)$ of mutation ratios.
`s_init`	Vector $s = (s_1, \ldots, s_N)$ of adaptive trait values that are resident initially.
`t_end`	Time t at which simulation is to be aborted and the adaptive landscape is to be constructed.
`t_monodet_step`	Time step for numerical integration.
`t_monodet_out`	Time step for output to be written to the file `monodet.dat`.
`monodet_method`	Flag. When set to 0, the Euler method is used for numerical integration; when set to 1, the fourth order Runge-Kutta method is employed.
`monodet_order`	Order in series expansion of the monomorphic deterministic model (can be 1, 2 or 3; when set to 0, no series expansion is made).
`monodet_direction`	Flag. When set to $+1$, direction of time is forward, when set to -1, backward.
`extinction_continuation`	Flag. When set to 1, simulation of the monomorphic deterministic model continues after a species has gone extinct, otherwise simulation is aborted.
`extinction_init`	Vector of flags. When the element corresponding to species i is set to 0, this species is present initially, otherwise it is extinct.
`landscape_grid`	Vector of incremental steps determining the density of lines to be used in the two directions to depict the surface of the adaptive landscape.
`s_mindisplay`	Vector of lower bounds for s to be displayed.
`s_maxdisplay`	Vector of upper bounds for s to be displayed.
`monitor_level`	Flag controlling the extent of information written to `stdout` (can be 1, 2, 3 or 0; corresponding to basic, normal, detailed or no output).
`run_landscape`	Flag. When set to 1, the function `landscape()` is executed.

Output

To file `landscape.dat`. First column: trait values s_1, second column: trait values s_2, third column: heights. In addition, some information can be written to `stdout`.

Function `monosto()` Package `coevolve_sto.c`

Description

Implementation of the monomorphic stochastic model.

Input

`community_size`	Number N of species making up the coevolutionary community.
`birth_mono()`	Function providing the per capita birth rates in the community, see above.
`death_mono()`	Function providing the per capita death rates in the community, see above.
`m()`	Function providing the mutation distributions in the community, see above.
`mu`	Vector $\mu = (\mu_1, \ldots, \mu_N)$ of mutation ratios.
`s_init`	Vector $s = (s_1, \ldots, s_N)$ of adaptive trait values that are resident initially.
`t_end`	Time t at which simulation is to be aborted.

`monosto_samples`	Number of stochastic realization to be simulated. From these, a mean path is automatically constructed.
`monosto_logplot`	Flag. When set to 1, values $\log_{10} \lvert s_i(t) - \hat{s}_i \rvert$ instead of $s_i(t)$ are written to the file `monosto.dat`.
`s_fixedpoint`	Vector of trait values at a fixed point $\hat{s}$, only used when `monosto_logplot` is set to 1.
`monosto_grid`	Vector of incemental steps for the trait values s_1 to s_N according to which the master equation is discretized for the purpose of simulation.
`s_min`	Vector of lower bounds for s to be used for discretizing the master equation.
`s_max`	Vector of upper bounds for s to be used for discretizing the master equation.
`s_mindisplay`	Vector of lower bounds for s to be displayed.
`s_maxdisplay`	Vector of upper bounds for s to be displayed.
`random_seed`	Seed for the random number generator.
`monitor_level`	Flag controlling the extent of information written to `stdout` (can be 1, 2, 3 or 0; corresponding to basic, normal, detailed or no output).
`run_monosto`	Flag. When set to 1, the function `monosto()` is executed.

■ Output

To files `monosto.dat` and `monosto_mean.dat`. First column: time t; following columns: resident adaptive trait values $s_1(t)$ to $s_N(t)$. Subsequent simulations are separated by blank lines in `monosto.dat`. In addition, some information can be written to `stdout`.

Function `polysto()` Package `coevolve_sto.c`

■ Description

Implementation of the polymorphic stochastic model.

■ Input

`community_size`	Number N of species making up the coevolutionary community.
`birth_polysto()`	Function providing the per capita birth rates in the community, see above.
`death_polysto()`	Function providing the per capita death rates in the community, see above.
`m()`	Function providing the mutation distributions in the community, see above.
`mu`	Vector $\mu = (\mu_1, \ldots, \mu_N)$ of mutation ratios.
`s_init`	Vector $s = (s_1, \ldots, s_N)$ of adaptive trait values that are resident initially.
`t_end`	Time t at which simulation is to be aborted.
`polysto_samples`	Number of stochastic realization to be simulated. From these, a mean path is automatically constructed.
`polysto_update`	Number of birth or death events after which the birth and death rates of all individuals are updated.
`polysto_saveppm`	Flag. When set to 1, `.ppm` files are produced.
`ppm_color`	Flag. When set to 1, color `.ppm` files are produced, otherwise gray scaling is used.
`ppm_bins`	Number of discrete bins to be used to display in the `.ppm` files the distributions of individuals having continuous trait values.
`ppm_stretch`	Number of pixels in the `.ppm` files to be associated with each bin.
`ppm_margin`	Number of pixels in the `.ppm` files to be used as a margin for the picture.
`ppm_maxval`	Number contolling the color or gray scale resolution for the `.ppm` files. Normally set to 255.
`s_mindisplay`	Vector of lower bounds for s to be displayed.
`s_maxdisplay`	Vector of upper bounds for s to be displayed.
`random_seed`	Seed for the random number generator.
`monitor_level`	Flag controlling the extent of information written to `stdout` (can be 1, 2, 3 or 0; corresponding to basic, normal, detailed or no output).
`run_polysto`	Flag. When set to 1, the function `polysto()` is executed.

■ Output

To file `polysto_mean.dat`. First column: time t; following columns: populations sizes, mean values and standard deviations of the phenotypic distributions distributions p_1 to p_N at time t. Optionally, output is generated to `polysto1.ppm` to `polysto`N`.ppm`. These graphic files serve to display the time evolution of the phenotypic distributions p_1 to p_N. In addition, some information can be written to `stdout`.

Bibliography

[1] Abrams, P. A.: *Adaptive responses of predators to prey and prey to predators: the failure of the arms-race analogy.* Evolution 40, 1229–1247 (1986)

[2] Abrams, P. A.: *The importance of intraspecific frequency-dependent selection in modelling competitive coevolution.* Evol. Ecol. 3, 215–220 (1989)

[3] Abrams, P. A.: *Adaptive foreaging by predators as a cause of predator-prey cycles.* Evol. Ecol. 6, 56–72 (1992)

[4] Abrams, P. A., Matsuda, H., Harada, Y.: *Evolutionarily unstable fitness maxima and stable fitness minima of continuous traits.* Evol. Ecol. 7, 465–487 (1993)

[5] Akin, E.: *Cycling in simple genetic systems.* J. Math. Biol. 13, 305–324 (1981)

[6] Bailey, *The elements of stochastic processes.* New York: John Wiley and Sons 1964

[7] Baker, G. L., Gollub, J. P.: *Chaotic dynamics: an introduction.* Cambridge: Cambridge University Press 1990.

[8] Bakker, R. T.: *The deer flees, the wolf pursues: inconcruncies in predator-prey coevolution.* In: Futuyma, D. J., Slatkin, M. (eds.) *Coevolution*, pp. 350–382. Sunderland Massachusetts: Sinauer Associates 1983

[9] Bates, H. W.: *Contributions of an insect fauna of the Amazon Valley.* Trans. Linn. Soc. Lond. 23, 495–566 (1862)

[10] Brown, J. S., Vincent, T. L.: *Coevolution as an evolutionary game.* Evolution 41, 66–79 (1987a)

[11] Brown, J. S., Vincent, T. L.: *Predator-prey coevolution as an evolutionary game.* In: Cohen, Y. (ed.) *Applications of Control Theory in Ecology*, pp. 83–101. Lecture Notes in Biomathematics 73. Berlin: Springer Verlag 1987b

[12] Brown, J. S., Vincent, T. L.: *Organization of predator-prey communities as an evolutionary game.* Evolution 46, 1269–1283 (1992)

[13] Bulmer, M. G.: *The mathematical theory of quantitative genetics.* New York: Oxford University Press 1980

[14] Carroll, L.: *Through the looking glass and what Alice found there.* London: Macmillan 1871 (Harmondsworth Middlesex: Penguin Books 1970)

[15] Christiansen, F. B.: *On conditions for evolutionary stability for a continuously varying character.* Amer. Natur. 138, 37–50. (1991)

[16] Cohen, J. E., Pimm, S. L., Yodzis, P., Saldan, J.: *Body sizes of animal predators and animal prey in food webs.* J. Anim Ecol. 62, 67–78 (1993)

[17] Crawley, M. J. (ed.): *Natural enemies: the population biology of predators, parasites and diseases.* Oxford: Blackwell Scientific (1992)

[18] Darwin, C. R.: *The origin of species by means of natural selection.* John Murray 1859 (Harmondsworth Middlesex: Penguin Books 1968)

[19] Dawkins, R.: *The selfish gene.* Oxford: Oxford University Press 1976

[20] Dawkins, R., Krebs, J. R.: *Arms races between and within species.* Proc. R. Soc. Lond. B 205, 489–511 (1979)

[21] Dieckmann, U., Marrow, P., Law, R.: *Evolutionary cycles in predator-prey interactions.* Submitted for publication (1994)

[22] Dieckmann, U., Law, R.: *The dynamical theory of coevolution: a derivation from stochastic ecological processes.* Accepted for publication, J. Math. Biol. (1994)

[23] Ebeling,W., Feistel, R.: *Physik der Selbstorganisation und Evolution.* Berlin: Akademie-Verlag 1982

[24] Eckmann, J.-P., Ruelle, D.: *Ergodic theory of chaos and strange attractors.* Rev. Mod. Phys. 57, 617–656 (1985)

[25] Ehrlich, P. R., Raven, P. H.: *Butterflies and plants: a study in coevolution.* Evolution 18, 586–608 (1964)

[26] Eigen, M., Schuster, P.: *The hypercycle.* Berlin: Springer-Verlag 1979

[27] Eltringham, H.: *On specific and mimetic relationships in the genus Heliconius.* Trans. Ent. Soc. Lond., 101–155 (1916)

[28] Emlen, J. M.: *Evolutionary ecology and the optimality assumption.* In: Dupre, J. (ed.) *The latest on the best*, pp. 163–177. Cambridge: MIT Press 1987

[29] Eshel, I.: *Evolutionary and continuous stability.* J. theor. Biol. 103, 99–111 (1983)

[30] Eshel, I., Motro, U.: *Kin selection and strong stability of mutual help.* Theor. Pop. Biol. 19, 420–433 (1981)

[31] Falconer, D. S.: *Introduction to quantitative genetics.* 3rd Edition. Harlow: Longman 1989

[32] Feistel, R.: *Betrachtung der Realisierung stochastischer Prozesse aus automatentheoretischer Sicht.* Wiss. Z. WPU Rostock 26, 663–670 (1977)

[33] Fenner, F., Ratcliffe, F. N.: *Myxomatosis.* Cambridge: Cambridge University Press 1965

[34] Fenner, F., Ross, J.: *Myxomatosis.* In: Thompson, H. V., King, C. M. (eds.) *The European rabbit: history and biology of a successful colonizer*, pp. 205–239. Oxford: Oxford University Press 1994

[35] Fisher, R. A.: *The genetical theory of natural selection.* New York: Dover Publications 1958

[36] Frank, S. A., Slatkin, M.: Fisher’s fundamental theorem of natural selection. Trends Ecol. Evol. 7, 92–95 (1992)

[37] Fricke T., Schnakenberg J.: *Monte-Carlo simulation of an inhomogeneous reaction-diffusion system in the biophysics of receptor cells.* Z. Phys. B 83, 277 (1991)

[38] Futuyma, D. J.: *Evolutionary biology.* Sunderland Massachusetts: Sinauer Associates 1986

[39] Futuyma, D. J., Slatkin, M.: *Introduction.* In: Futuyma, D. J., Slatkin, M. (eds.) *Coevolution*, pp. 1–13. Sunderland Massachusetts: Sinauer Associates 1983

[40] Gardiner, C. W.: *Handbook of stochastic methods.* Berlin: Springer-Verlag 1985

[41] Gilbert, L. E.: *Coevolution and mimicry.* In: Futuyma, D. J., Slatkin, M. (eds.) *Coevolution*, pp. 263–281. Sunderland Massachusetts: Sinauer Associates 1983

[42] Gillespie, D. T.: *A general method for numerically simulating the stochastic time evolution of coupled chemical reactions.* J. Comp. Phys. 22, 403–434 (1976)

[43] Goel, N. S., Richter-Dyn, N.: *Stochastic models in biology.* New York: Academic Press 1974

[44] Hofbauer, J., Sigmund, K.: *Theory of evolution and dynamical systems.* New York: Cambridge University Press 1988

[45] Hofbauer, J., Sigmund, K.: *Adaptive dynamics and evolutionary stability.* Appl. Math. Lett. 3, 75–79 (1990)

[46] Hornby, A. S.: *Oxford advanced learner's dictionary of current English.* Oxford: Oxford University Press 1974

[47] Huang, K.: *Statistical mechanics.* New York: John Wiley and Sons 1987

[48] Iwasa, Y., Pomiankowski, A., Nee, S.: *The evolution of costly mate preferences. II. The "handicap" principle.* Evolution 45, 1431–1442 (1991)

[49] Janzen, D. H.: *When is it coevolution?* Evolution 34, 611–612 (1980)

[50] Kimura, M.: *The neutral theory of molecular evolution.* Cambridge: Cambridge University Press 1983

[51] Kubo, R., Matsuo, K., Kitahara, K.: *Fluctuation and relaxation of macrovariables.* J. Stat. Phys. 9, 51–96 (1973)

[52] Lande, R.: *Quantitative genetic analysis of multivariate evolution, applied to brain: body size allometry.* Evolution 33, 402–416 (1979)

[53] Lawlor, L. R., Maynard Smith, J.: *The coevolution and stability of competing species.* Amer. Natur. 110, 79–99 (1976)

[54] Levin, S. A.: *Some approaches to the modelling of coevolutionary interactions.* In: Nitecki, M. H. (ed.) *Coevolution*, pp. 21–65. University of Chicago Press 1983

[55] Lewontin, R. C.: *Fitness, survival, and optimality.* In: Horn, D. J., Stairs, G. R., Mitchell, R. D. (eds.) *Analysis of Ecological Systems*, pp. 3–21. Ohio State University Press 1979

[56] Lewontin, R. C.: *Gene, organism and environment.* In: Bendall, D. S. (ed.) *Evolution from molecules to men*, pp. 273–285. Cambridge: Cambridge University Press 1983

[57] Lewontin, R. C.: *The shape of optimality.* In: Dupre, J. (ed.) *The latest on the best*, pp. 151–159. Cambridge: MIT Press 1987

[58] Loeschke, V. (ed.): *Genetic constraints on adaptive evolution.* Berlin: Springer-Verlag 1987

[59] Mackay, T. F. C.: *Distribution of effects of new mutations affecting quantitative traits.* In: Hill, W. G., Thompson, R., Woolliams, J. A. (eds.) *Proc. 4th world congress on genetics applied to livestock production*, pp. 219–228. 1990

[60] Malthus, T. R.: *Essay on the principle of population.* 1798

[61] Marrow, P., Cannings, C.: *Evolutionary instability in predator-prey systems.* J. theor. Biol. 160, 135–150 (1993)

[62] Marrow, P., Dieckmann, U., Law, R.: *Evolutionary dynamics of predator-prey systems: an ecological perspective.* Accepted for publication, J. Math. Biol. (1994)

[63] Marrow, P., Law, R., Cannings, C.: *The coevolution of predator-prey interactions: ESSs and Red Queen dynamics.* Proc. R. Soc. Lond. B 250, 133–141 (1992)

[64] Maynard Smith, J.: *Evolution and the theory of games.* Cambridge: Cambridge University Press 1982

[65] Maynard Smith, J.: *Evolutionary genetics.* Oxford: Oxford University Press 1989

[66] Maynard Smith, J., Burian, R., Kauffman, S., Alberch, P., Campbell, J., Goodwin, B., Lande, R., Raup, D., Wolpert, L.: *Developmental constraints and evolution.* Q. Rev. Biol. 60, 265–287 (1985)

[67] Maynard Smith, J., Price, G. R.: *The logic of animal conflict.* Nature Lond. 246, 15–18 (1973)

[68] Metz, J. A. J., Nisbet, R. M., Geritz, S. A. H.: *How should we define "fitness" for general ecological scenarios?* Trends Ecol. Evol. 7, 198–202 (1992)

[69] Metz, J. A. J, Geritz, S. A. H., Iwasa, Y: *On the dynamical classification of evolutionarily singular strategies.* Submitted for publication, J. Math. Biol. (1994)

[70] Müller, F.: *Ituna and Tyridis: a remarkable case of mimicry in butterflies.* Proc. Ent. Soc. Lond., 20–29 (1879)

[71] Nicolis, J. S.: *Dynamics of hierarchical systems.* Berlin: Springer-Verlag 1986

[72] Nowak, M., Sigmund, K.: *Oscillations in the evolution of reciprocity.* J. theor. Biol. 137, 21–26 (1989)

[73] Oseledec, V. I.: Trudy Mosk, Mat. Obšč. 19, 179 (1968)

[74] Ott, E.: *Chaos in dynamical systems.* Cambridge: Cambridge University Press 1993

[75] Parker, G. A.: *Population consequences of evolutionarily stable strategies.* In: Sibly, R. M., Smith, R.H. (eds.) *Behavioural ecology: ecological consequences of adaptive behaviour,* pp. 35–58. Oxford: Blackwell Scientific 1985

[76] Pimentel, D.: *Population regulation and genetic feedback.* Science 159, 1432–1437 (1968)

[77] Prout, T.: *Sufficient conditions for multiple niche polymorphism.* Amer. Natur. 102, 493–496 (1968)

[78] Rand, D. A., Wilson, H. B.: *Evolutionary catastrophes, punctuated equilibria and gradualism in ecosystem evolution.* University of Warwick Preprint (1993)

[79] Rand, D. A., Wilson, H. B., McGlade, J. M.: *Dynamics and evolution: evolutionarily stable attractors, invasion exponents and phenotype dynamics.* Phil. Trans. Roy. Soc. B (1993)

[80] Reed, J., Stenseth, N. C.: *On evolutionarily stable strategies.* J. theor. Biol. 108, 491–508 (1984)

[81] Rosenzweig, M. L.: *Evolution of the predator isocline.* Evolution 27, 84–94 (1973)

[82] Rosenzweig, M. L., Brown, J. S., Vincent, T. L.: *Red Queens and ESS: the coevolution of evolutionary rates.* Evol. Ecol. 1, 59–94 (1987)

[83] Roughgarden, J.: *The theory of coevolution.* In: Futuyma, D. J., Slatkin, M. (eds.) *Coevolution*, pp. 33–64. Sunderland Massachusetts: Sinauer Associates 1983.

[84] Saloniemi, I.: *A coevolutionary predator-prey model with quantitative characters.* Amer. Natur. 141, 880–896 (1993)

[85] Sbordoni, V., Bullini, L., Scarpelli, G., Forestiero, S., Rampini, M.: *Mimicry in the burnet moth Zygaena ephialtes: population studies and evidencve of a Batesian-Müllerian situation.* Ecol. Entomol. 4, 83–93 (1979)

[86] Schnakenberg, J.: *Stochastische Prozesse.* Aachen: Lecture RWTH 1991

[87] Schnakenberg, J.: *Algorithmen in Quantenmechanik und statistischer Physik.* Aachen: Lecture RWTH 1993

[88] Schrödinger. E.: *What is life?* Cambridge: Cambridge University Press 1944

[89] Schuster, H. G.: *Deterministic chaos: an introduction.* Weinheim: VCH Verlagsgesellschaft 1989

[90] Schuster, P., Sigmund, K.: *Replicator dynamics.* J. theor. Biol. 100, 533–538 (1983)

[91] Seger, J.: *Evolution of exploiter-victim relationships.* In: Crawley, M. J. (ed.) *Natural enemies: the population biology of predators, parasites and diseases*, pp. 3–25. Oxford: Blackwell Scientific 1992

[92] Serra, R., Andretta, M., Compiani, M., Zanarini, G.: *Introduction to the physics of complex systems.* Oxford: Pergamon Press 1986

[93] Stearns, S. C.: *The evolution of life histories.* Oxford: Oxford University Press 1992

[94] Stenseth, N. C., Maynard Smith, J.: *Coevolution in ecosystems: Red Queen evolution or stasis?* Evolution 38, 870–880 (1984)

[95] Takada, T., Kigami, J.: *The dynamical attainability of ESS in evolutionary games.* J. Math. Biol. 29, 513–529 (1991)

[96] Taper, M. L., Case, T. J.: *Models of character displacement and the theoretical robustness of taxon cycles.* Evolution 46, 317–333 (1992)

[97] Taylor P. D.: *Evolutionary stability in one-parameter models under weak selection.* Theor. Pop. Biol. 36, 125–143 (1989)

[98] Taylor P. D., Jonker L. B.: *Evolutionarily stable strategies and game dynamics.* Math. Biosc. 40, 145–156 (1978)

[99] Tomita, T., Ohta, T., Tomita, H.: *Irreversible circulation and orbital revolution.* Prog. Theor. Phys. 52, 1744–1765 (1974)

[100] Turner J. R. G.: *Studies of Müllerian mimicry and its evolution in burnet moths and heliconid butterflies.* In: Creed, R. (ed.) *Ecological genetics and evolution*, Oxford: Blackwell Scientific 1971

[101] Turner, J. R. G., Johnson, M. S., Eanes, W. F.: *Contrasted modes of evolution in the same genome: allozymes and adaptive changes in Heliconius.* Proc. Nat. Acad. Sci. USA 76, 1924–1928 (1979)

[102] van Kampen, N. G.: *Fundamental problems in statistical mechanics of irreversible processes.* In: Cohen, E. G. D. (ed.) *Fundamental problems in statistical mechanics*, pp. 173–202. Amsterdam: North Holland 1962

[103] van Kampen, N. G.: *Stochastic processes in physics and chemistry.* Amsterdam: North Holland 1981

[104] Van Valen, L.: *A new evolutionary law.* Evol. Theory 1, 1–30 (1973)

[105] Vincent, T. L.: *Strategy dynamics and the ESS.* In: Vincent, T. L., Mees, A. I., Jennings, L. S. (eds.) *Dynamics of complex interconnected biological systems*, pp. 236–262. Basel: Birkhauser 1991

[106] Vincent, T. L., Cohen, Y., Brown, J. S.: *Evolution via strategy dynamics.* Theor. Pop. Biol. 44, 149–176 (1993)

[107] Wilson, D. S.: *The group selection controversy: history and current status.* Annu. Rev. Ecol. Syst. 14, 159–187 (1983)

[108] Wissel, C., Stöcker, S.: *Extinction of populations by random influences.* Theor. Pop. Biol. 39, 315–328 (1991)

[109] Wright, S.: *Evolution in Mendelian populations.* Genetics 16, 97–159 (1931)