The dynamical theory of coevolution: a derivation from stochastic ecological processes

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

Key words: Coevolution – Stochastic processes – Mutation-selection systems – Individual-based models – Population dynamics – Adaptive dynamics

1 Introduction

The self-organisation of systems of living organisms is elucidated most successfully by the concept of Darwinian evolution. The processes of multiplication, variation, inheritance and interaction are sufficient to enable organisms to adapt to their environments by means of natural selection (see e.g. Dawkins 1976). Yet, the development of a general and coherent mathematical theory of Darwinian evolution built from the underlying ecological processes is far from

complete. Progress on these ecological aspects of evolution will critically depend on properly addressing at least the following four requirements.

1. *The evolutionary process needs to be considered in a coevolutionary context.* This amounts to allowing feedbacks to occur between the evolutionary dynamics of a species and the dynamics of its environment (Lewontin 1983). In particular, the biotic environment of a species can be affected by adaptive change in other species (Futuyma and Slatkin 1983). Evolution in constant or externally driven environments thus are special cases within the broader coevolutionary perspective. Maximization concepts, already debatable in the former context, are insufficient in the context of coevolution (Emlen 1987; Lewontin 1979, 1987).

2. *A proper mathematical theory of evolution should be dynamical.* Although some insights can be gained by identifying the evolutionarily stable states or strategies (Maynard Smith 1982), there is an important distinction between non-invadability and dynamical attainability (Eshel and Motro 1981; Eshel 1983; Taylor 1989). It can be shown that in a coevolutionary community comprising more than a single species even the evolutionary attractors generally cannot be predicted without explicit knowledge of the dynamics (Marrow et al. 1996). Consequently, if the mutation structure has an impact on the evolutionary dynamics, it must not be ignored when determining evolutionary attractors. Furthermore, a dynamical perspective is required in order to deal with evolutionary transients or evolutionary attractors which are not simply fixed points.

3. *The coevolutionary dynamics ought to be underpinned by a microscopic theory.* Rather than postulating measures of fitness and assuming plausible adaptive dynamics, these should be rigorously derived. Only by accounting for the ecological foundations of the evolutionary process in terms of the underlying population dynamics, is it possible to incorporate properly both density and frequency dependent selection into the mathematical framework (Brown and Vincent 1987a; Abrams et al. 1989, 1993; Saloniemi 1993). Yet, there remain further problems to overcome. First, analyses of evolutionary change usually cannot cope with nonequilibrium population dynamics (but see Metz et al. 1992; Rand et al. 1993). Second, most investigations are aimed at the level of population dynamics rather than at the level of individuals within the populations at which natural selection takes place; in consequence, the ecological details between the two levels are bypassed.

4. *The evolutionary process has important stochastic elements.* The process of mutation, which introduces new phenotypic trait values at random into the population, acts as a first stochastic cause. Second, individuals are discrete entities and consequently mutants that arise initially as a single individual are liable to accidental extinction (Fisher 1958). A third factor would be demographic stochasticity of resident populations; however, in this paper we assume resident populations to be large, so that the effects of finite population size of the *residents* do not have to be considered (Wissel and Stöcker 1989). The importance of these stochastic impacts on the evolutionary process has been stressed by Kimura (1983) and Ebeling and Feistel (1982).

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

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

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

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

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

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

2 Formal framework

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

2.1 Conceptual background

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

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

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

Second, we apply the timescale argument together with an assumption of monostable population dynamics to achieve a *decoupling* of the population dynamics from the adaptive dynamics. In general, the population dynamics could be multistable, i.e. different attractors are attained depending on initial conditions in population size space. It will then be necessary to trace the population dynamics $\frac{d}{dt} n$ is size space $\hat{N}$ simultaneously with the adaptive

dynamics $\frac{d}{dt}s$ in trait space $\hat{S}$. This is no problem in principle but it makes the mathematical formulation more complicated; for simplicity we hence assume *monostability*. Due to the different timescales, the system of simultaneous equations can then be readily decomposed. The trait values s or functions thereof can be assumed constant as far as the population dynamics $\frac{d}{dt}n$ are concerned. The population sizes n or functions F thereof can be taken averaged when the adaptive dynamics $\frac{d}{dt}s$ are considered, i.e.

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

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

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

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

2.2 Specification of the coevolutionary community

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

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

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

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

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

Since we are mainly interested in the phenomenon of coevolution – an effect internal to the community – in the present paper we will not consider the extra

time-dependence in equations (2.4) which may be imposed on the environment by external effects.

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

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

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

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

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

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

$$\bar{f}_i(s'_i, s) = \tilde{f}_i(s'_i, s, \hat{n}(s)) \tag{2.7}$$

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

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

2.3 Application

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

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

$$\frac{d}{dt} n_1 = n_1 \cdot (r_1 - \alpha \cdot n_1 - \beta \cdot n_2) \, ,$$

$$\tag{2.8}$$

$$\frac{d}{dt} n_2 = n_2 \cdot (- r_2 + \gamma \cdot n_1)$$

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

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

$$\gamma(s_1, s_2)/u = c_1 \cdot \beta(s_1, s_2)$$
$$\beta(s_1, s_2)/u = \exp(-\delta_1^2 + 2c_2 \cdot \delta_1 \cdot \delta_2 - \delta_2^2), \qquad (2.9)$$
$$\alpha(s_1)/u = c_7 - c_8 \cdot s_1 + c_9 \cdot s_1^2$$

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

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

$$\tilde{b}_1(s_1', s, n) = r_1 \ ,$$
$$\tilde{d}_1(s_1', s, n) = \alpha(s_1') \cdot n_1 + \beta(s_1', s_2) \cdot n_2 \ ,$$
$$\tilde{b}_2(s_2', s, n) = \gamma(s_1, s_2') \cdot n_1 \ , \qquad (2.10)$$
$$\tilde{d}_2(s_2', s, n) = r_2 \ .$$

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

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

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

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

Although the coevolutionary community defined by (2.10) and (2.11) captures some features of predator–prey coevolution, other choices for the same purpose or for entirely different ecological scenarios could readily be made within the scope of our approach. Many features of the model presented

Table 1. The default parameter values for the coevolutionary predator–prey community

parameters affecting selection										
r_1	r_2	c_1	c_2	c_3	c_4	c_5	c_6	c_7	c_8	c_9
0.5	0.05	0.2	0.6	0.5	0.22	0.5	0.25	2.0	8.0	10.0
parameters affecting mutation										
σ_1		μ_1		σ_2		μ_2		u		
$5 \cdot 10^{-3}$		10^{-4}		$5 \cdot 10^{-3}$		10^{-3}		10^{-3}		

will be analyzed in the course of this paper; additional discussion is provided in Marrow et al. (1992, 1996) and Dieckmann et al. (1995).

3 Stochastic representation

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

3.1 Stochastic description of trait substitution sequences

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

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

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

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

Transition probabilities per unit time

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

$$w(s' \mid s) = \sum_{i=1}^{N} w_i(s'_i, s) \cdot \prod_{\substack{j=1 \\ j \neq i}}^{N} \delta(s'_j - s_j) \qquad (3.2)$$

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

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

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

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

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

    for the probability per unit time that the mutant enters the population.
3. The process of selection determines the mutant's probability $\mathcal{S}_i$ of escaping initial extinction. Since mutants enter as single individuals, the impact of

demographic stochasticity on their population dynamics must not be neglected (Fisher 1958). We assume, however, that the equilibrium population sizes $\hat{n}_i$ are large enough for there to be negligible risk of accidental extinction of the established resident population. Two consequences stem from this.

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

(b) The actual equilibrium size of the mutant after fixation is not important as long as it is large enough to exceed a certain threshold. Above this threshold the effect of demographic stochasticity is negligible (Wissel and Stöcker 1991).

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

$$\mathscr{S}_i(s'_i, s) = \begin{cases} 1 - \bar{d}_i(s'_i, s)/\bar{b}_i(s'_i, s) & \text{for } \bar{d}_i(s'_i, s)/\bar{b}_i(s'_i, s) < 1 \\ 0 & \text{for } \bar{d}_i(s'_i, s)/\bar{b}_i(s'_i, s) \geqq 1 \end{cases} \tag{3.5}$$

$$= \bar{b}_i^{-1}(s'_i, s) \cdot (\bar{f}_i(s'_i, s))_+$$

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

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

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

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

3.3 Applications

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

First, we can employ the *minimal process method* (Gillespie 1976) to obtain actual realizations of the stochastic mutation-selection process. We illustrate this method by means of our example of predator–prey coevolution. The two-dimensional trait space $\hat{S}$ of this system is depicted in Fig. 2a. The dashed line surrounds the region of coexistence $\hat{S}_c$. Within this region
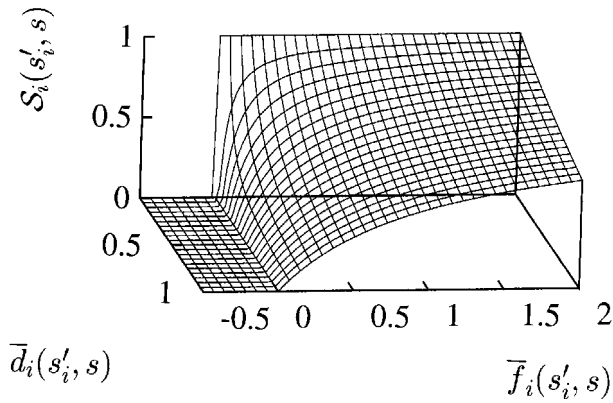
Fig. 1. Invasion success of a rare mutant. The probability $\mathscr{S}_i(s_i', s)$ of a mutant population initially of size 1 with adaptive trait value s_i' in a community of monomorphic resident populations with adaptive trait values s to grow in size such as to eventually overcome the threshold of accidental extinction is dependent on the per capita growth and death rates, $\bar{f}_i(s_i', s)$ and $\bar{d}_i(s_i', s)$, of individuals in the mutant population. Deleterious mutants with $\bar{f}_i(s_i', s) < 0$ go extinct with probability 1 but even advantageous mutants with $\bar{f}_i(s_i', s) > 0$ 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

different trait substitution sequences $(s_1(t), s_2(t))$ are displayed by continuous lines. Note that trait substitution sequences starting from the same initial states (indicated by asterisks) are not identical. This underlines the unique, historical nature of any evolutionary process. But, although these paths are driven apart by the process of mutation, they are kept together by the directional impact of selection.

Second, the latter observation underpins the introduction of a further concept from stochastic process theory. By imagining a large number r of trait substitution sequences $s^k(t) = (s_1^k(t), \ldots, s_N^k(t))$, with $k = 1, \ldots, r$, starting
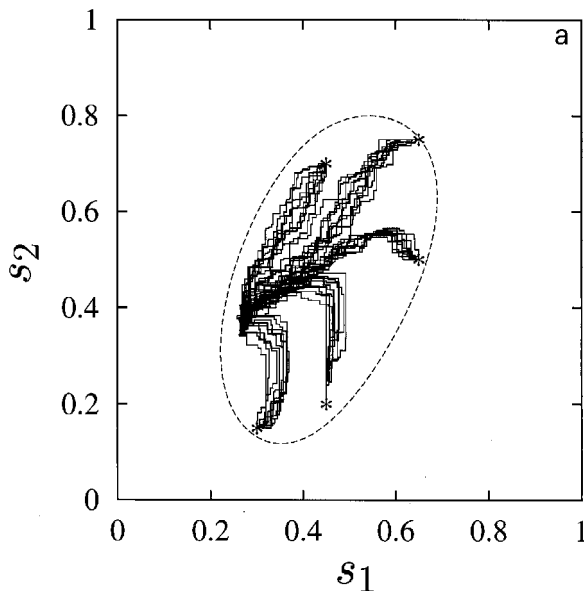
Fig. 2a. Stochastic representation of the adaptive dynamics: trait substitution sequences as defined by equations (3.1), (3.2) and (3.6). Ten directed random walks in trait space for each of five different initial conditions (indicated by asterisks) are depicted by continuous lines. The discontinuous oval curve is the boundary of the region of coexistence. The coevolution of both species drives the trait values towards a common equilibrium $\hat{s}$. The parameters of the coevolutionary predator–prey community are given in Table 1
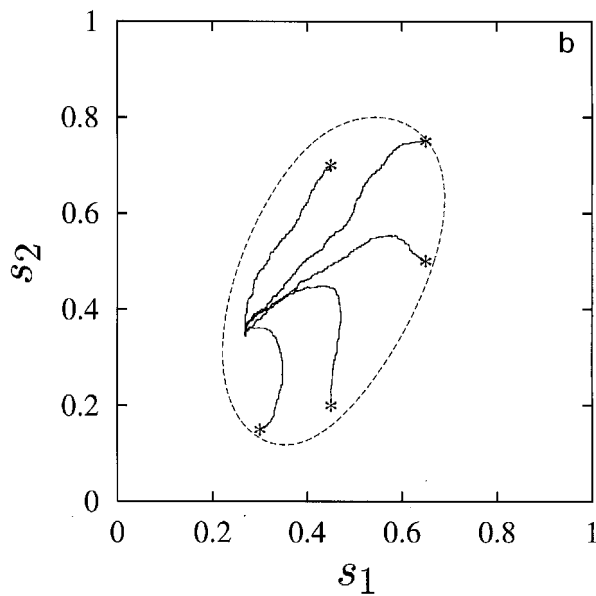
Fig. 2b. Stochastic representation of the adaptive dynamics: mean paths as defined by equation (3.7). Ten trait substitution sequences for each of the five different initial conditions (indicated by asterisks) are combined to obtain estimates for the mean paths, depicted by continuous lines. The jaggedness of the lines is caused by the finite number of ten trait substitution sequences. The discontinuous oval curve is the boundary of the region of coexistence. The parameters of the coevolutionary predator-prey community are as in Fig. 2a
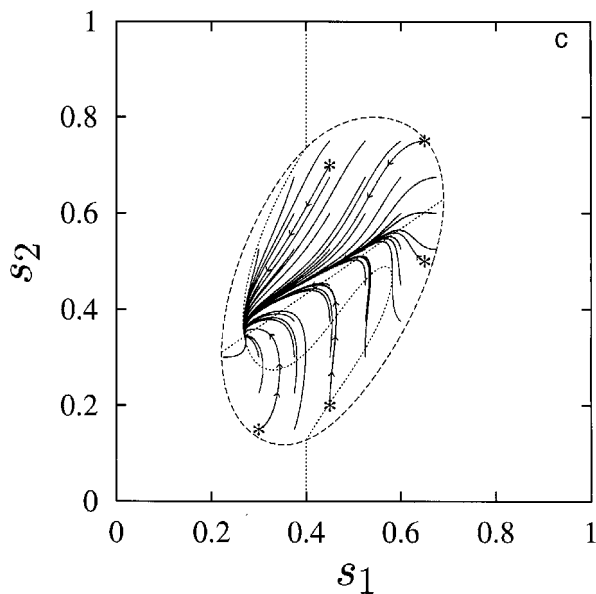
Fig. 2c. Deterministic approximation of the adaptive dynamics: phase portrait as defined by equations (4.12). The deterministic trajectories which correspond to the trait substitution sequences in Fig. 2a and to the mean paths in Fig. 2b are depicted by continuous lines (initial conditions are indicated by asterisks). Other trajectories have been added to supplement the phase portrait. The structure of the evolutionary flow in trait space thereby becomes visible. The discontinuous oval curve is the boundary of the region of coexistence. The dotted curves are the inner evolutionary isoclines of the two species (straight line: predator, curved line: prey). The parameters of the coevolutionary predator–prey community are as in Fig. 2a

from the same initial state, it is straightforward to apply an averaging process in order to obtain the *mean path* $\langle s \rangle (t)$ by

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

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

4 Deterministic approximation: first order

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

4.1 Determining the mean path

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

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

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

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

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

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

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

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

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

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

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

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

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

4.2 Deterministic approximation in first order

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

$$\frac{d}{dt}\, s_i = \mu_i(s_i)\cdot \bar{b}_i(s_i,s)\cdot \hat{n}_i(s)\cdot$$

$$\int_{R_i(s)} (s_i' - s_i)\cdot M_i(s_i, s_i' - s_i)\cdot \bar{b}_i^{-1}(s_i',s)\cdot \bar{f}_i(s_i',s)\,ds_i'\,, \qquad (4.7)$$

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

$$R_i(s) = \{s_i' \in \hat{S}_i \,|\, \bar{f}_i(s_i',s) > 0\}\,. \qquad (4.8)$$

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

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

and

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

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

apply the abbreviated notations

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

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

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

where

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

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

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

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

$$\partial_i' \bar{f}_i(s_i, s) = \frac{\partial}{\partial s_i'} \bar{f}_i(s_i', s) \bigg|_{s_i' = s_i}$$

$$= \lim_{\Delta s_i \to 0} \frac{1}{\Delta s_i} \cdot [\bar{f}_i(s_i + \Delta s_i, s) - \bar{f}_i(s_i, s)] \tag{4.14}$$

$$= \lim_{\Delta s_i \to 0} \frac{1}{\Delta s_i} \cdot \bar{f}_i(s_i + \Delta s_i, s)$$

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

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

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

4.3 Applications

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

However, some caveats are necessary for understanding the validity of any deterministic approximation of a stochastic process. First, if the adaptive dynamics turn out to be multistable (as in Fig. 3b), it will be possible for trait substitution sequences to exhibit jumps between the existing basins of attraction. This must be kept in mind while applying the deterministic approximation to initial states very close to the basin boundary. Figure 4a illustrates this point. In principle, large fluctuations between the multiple stable states themselves can happen. However, the latter will typically be associated with extremely small probabilities per unit time, which are negligible on ecological and even on evolutionary timescales; moreover, when the mutation distributions are bounded, such large jumps become impossible altogether. Second, if the flow of the dynamical system describing the deterministic path is expanding, i.e. trajectories are diverging (as in some regions of Fig. 3b), the deviations of the stochastic realizations from the mean path can grow too fast for the identification of the deterministic path with the mean path to be reliable (see Fig. 4b). Note that the construction of phase portraits based on the deterministic path is useful in any case, since these allow qualitative predictions of the stochastic dynamics by considering the combined process of movement along the trajectories accompanied by jumps between them. For illustration compare Figs. 2a and 2c, see also Fig. 4b. Third, if the attractors of
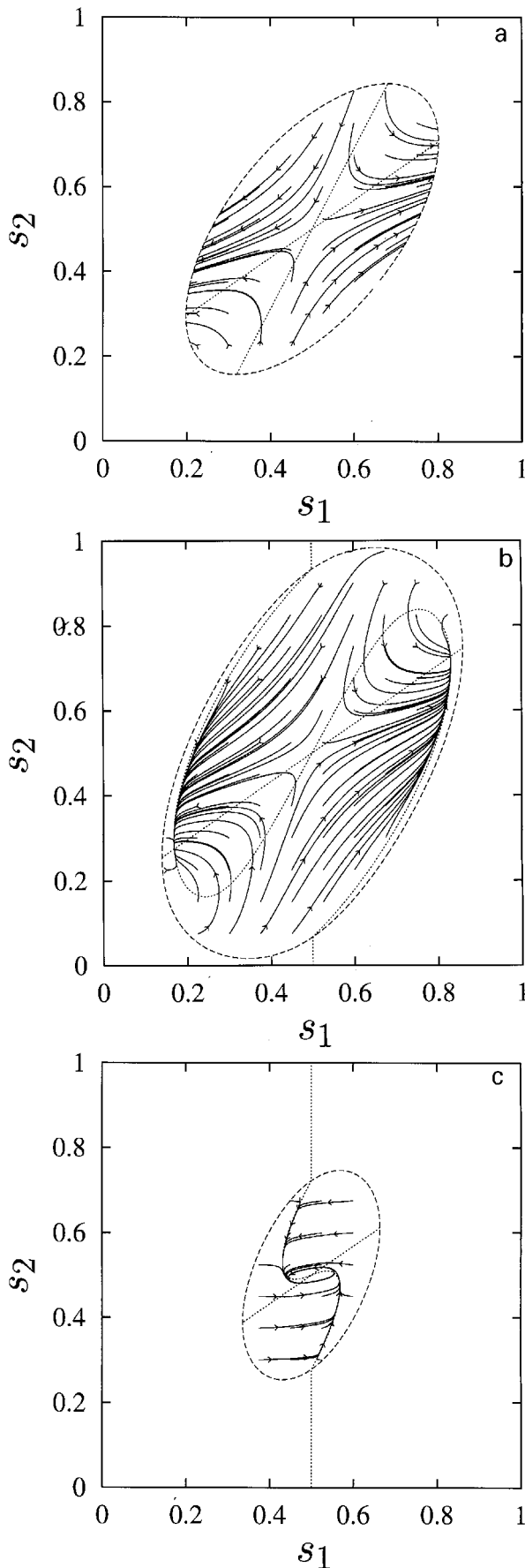
Fig. 3a–c. Deterministic approximation of the adaptive dynamics: phase portraits. The deterministic trajectories are depicted by continuous lines. Three qualitatively distinct outcomes of two-species coevolution are illustrated. **a** Evolutionary extinction (the coevolution of both species drives the trait values towards a boundary isocline where the predator becomes extinct). **b** Evolutionary multistability (depending on initial condition the coevolution of both species drives the trait values towards one of two equilibria which are separated by a saddle). **c** Evolutionary cycling (the coevolution of both species eventually forces the trait values to undergo sustained oscillatory change). The discontinuous oval curve in each figure is the boundary of the region of coexistence. The dotted curves are the inner evolutionary isoclines of the two species (straight lines: predator, curved lines: prey). The parameters of the coevolutionary predator–prey community are as in Table 1, except for: $c_1 = 1$, $c_7 = 3$, $c_8 = 0$, $c_9 = 0$ and $\mu_1 = 10^{-3}$ (Fig. 3a); $c_1 = 1$, $c_7 = 3$, $c_8 = 10$ and $\mu_1 = 10^{-3}$ (**b**); $c_1 = 0.11$, $c_7 = 3$, $c_8 = 10$ and $\mu_1 = 10^{-3}$ (**c**)
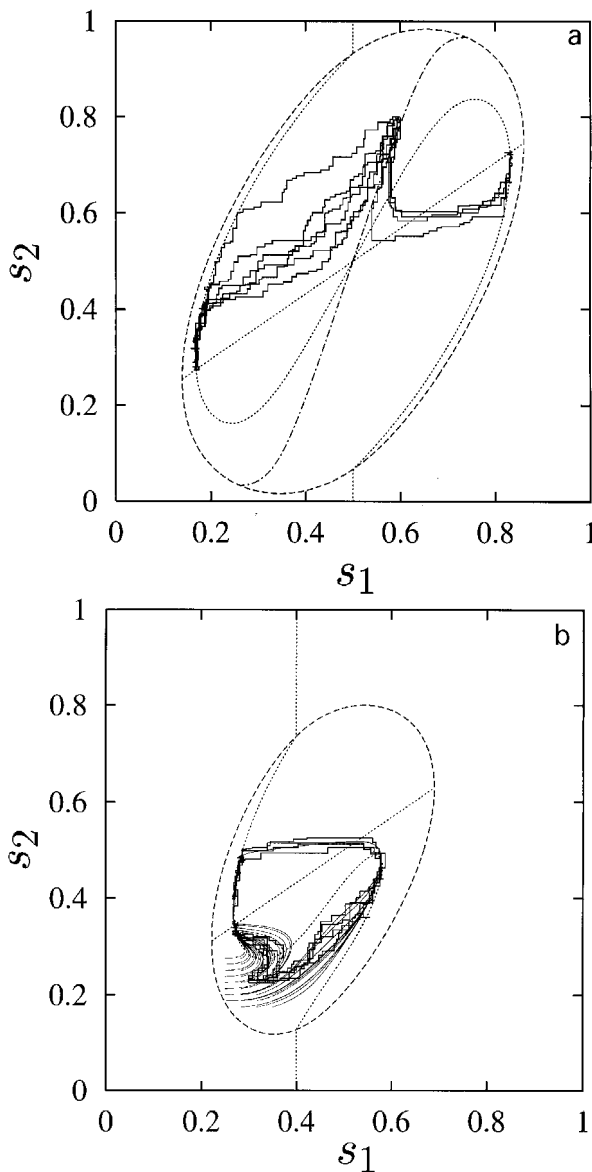
Fig. 4a, b. Descriptive capacity of the stochastic representation. Ten directed random walks in trait space with a common initial condition are depicted in each figure by continuous lines. **a** The set of trait substitution sequences splits permanently into two separate bundles as the initial condition is close to an existing basin boundary (depicted as a curve of dots and dashes). **b** The splitting of the set of trait substitution sequences into two separate bundles is only temporary and is caused by the existence of an expanding flow (shown as thin curves) in a region that contains the initial condition. Deterministic descriptions of the dynamics of the mean path cannot capture these features. The discontinuous oval curve in each figure is the boundary of the region of coexistence. The parameters of the coevolutionary predator–prey community for **a** are as in Fig. 3b, and for **b** as in Fig. 2c except for $\mu_1 = 10^{-3}$

the adaptive dynamics turn out to have dimensions other than 0 (as in Fig. 3c), the deterministic approximation in principle cannot predict aspects of the asymptotic mean dynamics of the stochastic process tangential to the attractor. The reason is that the tangential fluctuations are not balanced by counteracting forces. In consequence, for example, the asymptotic mean phase of stochastic limit cycle dynamics is not defined, though the asymptotic mean period is accurately described (Dieckmann et al. 1995).

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

5 Deterministic approximation: higher orders

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

5.1 Deterministic approximation in higher orders

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

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

and

$$\bar{b}_i^{-1}(s_i', s) \cdot \bar{f}_i(s_i', s) = \sum_{k=1}^{j} (s_i' - s_i)^k \cdot \frac{1}{k!} \cdot \sum_{l=1}^{k} \binom{k}{l} \cdot \partial_i'^l \bar{f}_i(s_i, s) \cdot \partial_i'^{k-l} \bar{b}_i^{-1}(s_i, s)$$

$$+ \mathcal{O}[(s_i' - s_i)^{j+1}] . \qquad (5.2)$$

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

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

with

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

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

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

The interpretation of the adaptive dynamics (5.3) is analogous to that given for (4.12) in Sect. 4.2. The $m_{ki}(s)$ are called the *kth mutation moments of the ith species*. They actually coincide with the *k*th moments of the mutation distribution M_i only if the range of integration $R_i(s)$ is $(-\infty, +\infty)$. However, as (5.5)

indicates, this is generically not the case. Even in the first order result the range of integration was restricted to either $(s_i, +\infty)$ or $(-\infty, s_i)$ and the situation gets more complicated now that higher orders are considered. Notice that in the derivation above we did not require any symmetry properties of the mutation process so the result (5.3) is independent of this assumption.

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

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

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

5.2 Shifting of evolutionary isoclines

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

The evolutionary s_i-isoclines are defined as those manifolds in trait space $\hat{S}$ on which $\frac{d}{dt}s_i = 0$ holds. The intersection of all isoclines coincides with the set of fixed points of the adaptive dynamics. In a first step we analyze the location of the evolutionary isoclines considering only infinitesimal mutational steps, in accordance with assumptions usually made in the literature (see e.g. Reed and Stenseth 1984; Taylor 1989). The result (4.12) is then exact, and we infer that the evolutionary s_i-isoclines are given by the union of manifolds on which either the selection derivative $\partial'_i \bar{f}_i(s_i, s)$ or the population size $\hat{n}_i(s)$

vanishes. We refer to the former as *inner isoclines* (these are subsets of $\hat{S}_c$) and call the latter *boundary isoclines* (as they are subsets of $\partial \hat{S}_c$). Since extinction of one species terminates the coevolutionary process of the N-species system, we concentrate on the inner isoclines. These can be classified as below (Metz et al. 1994).

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

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

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

This simple picture changes when we consider the adaptive dynamics in terms of the third and higher order results. We first examine the case of invadable evolutionary s_i-isoclines. Since in general the integration range is now no longer symmetric, the odd mutation moments do not vanish, and neither do the even mutation moments. Further, the second and higher order derivatives $\partial_i'^l \bar{f}_i(s_i, s)$ and the first and higher order derivatives $\partial_i'^{k-l} \bar{b}_i^{-1}(s_i, s)$ in equation (5.3) usually contribute. The third and higher order corrections therefore cause a displacement of the invadable inner evolutionary isoclines. These displacements are quantitative deviations from the first order result. But the higher order corrections can give rise even to qualitative discrepancies. Consider a manifold in trait space on which $\partial_i' \bar{f}_i(s_i, s) = \partial_i'^2 \bar{f}_i(s_i, s) = 0$ but $\partial_i'^3 \bar{f}_i(s_i, s) \neq 0$ hold. In terms of the first order result (4.12) this manifold

would be called an evolutionary s_i-isocline. In terms of the more general higher order result (5.3) we notice that this manifold is not an isocline at all, for the evolutionary rate $\frac{d}{dt}s_i$, though probably being small, does not vanish here. The deviations are not so dramatic for non-invadable s_i-isoclines. Here the range of integration cannot contain the resident trait value s_i. The displacement of the isocline thus will only be significant, if the mutation distribution $M_i(s_i, s_i' - s_i)$ extends considerably beyond that zero s_i' of $\bar{f}_i(s_i', s)$ 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 by the dotted curve in Fig. 5a. Note that not only the isoclines can be displaced, but in consequence also the fixed points themselves. Thus the shifting discussed here may affect the asymptotic stationary states of the coevolutionary system.

5.3 Conditions for evolutionary slowing down

For illustration, we consider the two dynamical systems $\frac{d}{dt}x_1 = -x_1$ and $\frac{d}{dt}x_2 = -x_2^3$. Both examples possess a locally stable fixed point at the origin. The time evolution of these systems is described by $x_1(t) = x_1(0) \cdot e^{-t}$ and
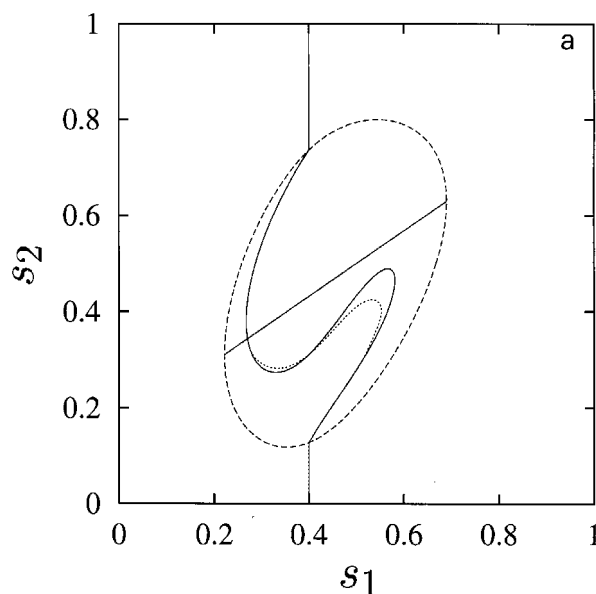
Fig. 5a. Shifting of evolutionary isoclines: the effect of finite mutation variance. The discontinuous oval curve is the boundary of the region of coexistence. The continuous curves are the inner evolutionary isoclines of the two species (straight line: predator, curved line: prey) for infinitesimal mutation variances $\sigma_1 \to 0$ and $\sigma_2 \to 0$. The dotted curve is the inner evolutionary isoclines of the predator for finite mutation variances, $\sigma_1 = 5 \cdot 10^{-2}$ and $\sigma_2 = 5 \cdot 10^{-2}$. The other parameters of the coevolutionary predator–prey community are as in Table 1
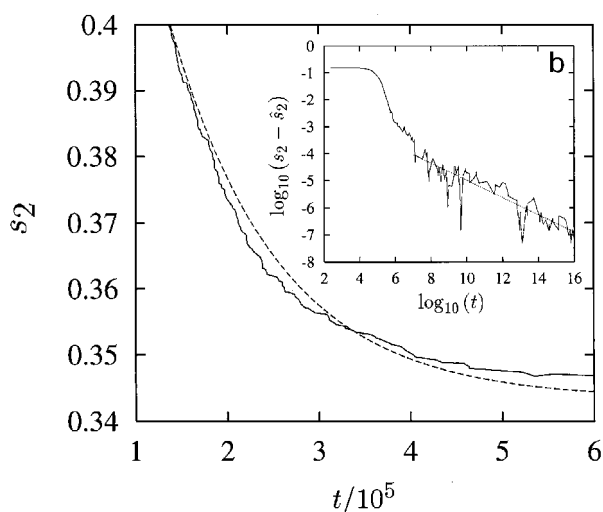
Fig. 5b. Evolutionary slowing down: algebraic approach towards a fixed point. The continuous curve shows the mean path dynamics of the predator's trait value close to the evolutionary equilibrium $\hat{s}$ in Fig. 2 (constructed from 20 trait substitution sequences). The fixed point $\hat{s}$ lies on a non-invadable predator isocline. In the figure the actual algebraically slow approach to $\hat{s}$ is compared to the exponentially fast one, depicted by the discontinuous curve, that is obtained from the first order result which cannot account for evolutionary slowing down. The inset confirms the derived power law $s_2(t) - \hat{s}_2 \propto t^{-1/3}$ by means of a double logarithmic plot, the jaggedness of the continuous curve stems from the extreme amplification of single trait substitutions due to the logarithmic scale. The dotted straight line resulting from a linear least square fit to the time series turns out to have a slope of -0.3154, close to the predicted value of $-1/3$. The parameters of the coevolutionary predator–prey community are as in Table 1

$x_2(t) = \pm [x_2^{-2}(0) + 2t]^{-1/2}$. 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 jth order slowing down at a fixed point $\hat{x}$ if $F(x) = \sum_{k=j}^{\infty} a_{k\pm} \cdot (x - \hat{x})^k$ around $x = \hat{x}$ with (i) $j > 1$ and with (ii) $\pm a_{j\pm} < 0$ for j even and $a_{j\pm} < 0$ for j odd. The distinction $\pm$ 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 $x(t) - \hat{x} \propto \pm (a_{j\pm} \cdot t)^{1/(1-j)}$.

The phenomenon of slowing down does arise in the context of coevolutionary dynamics. Before turning to the general case, for intuition we first utilize the second order result. We consider a locally stable fixed point of the adaptive dynamics which is situated on a non-invadable inner evolutionary s_i-isocline such that $\partial_i'^2 \bar{f}_i(s_i, s) < 0$ holds in the vicinity of this isocline. Thus the range of integration is given according to (5.5) by $R_i(s) = (s_i, s_i - 2 \cdot \partial_i' \bar{f}_i(s_i, s) / \partial_i'^2 \bar{f}_i(s_i, s))$ for $\partial_i' \bar{f}_i(s_i, s) > 0$ and by

$R_i(s) = (s_i - 2 \cdot \partial_i' \bar{f}_i(s_i, s)/\partial_i'^2 \bar{f}_i(s_i, s), s_i)$ for the other side of the isocline. Evidently, the range of integration in second order vanishes on the isocline itself. The ecological interpretation of this statement is intuitive: fewer and fewer mutants s_i' are advantageous while approaching the fixed point, until finally all possible mutants are deleterious. In order to prove formally that this process gives rise to evolutionary slowing down, we examine the coefficients $a_{j\pm}$ defined above in the case of the adaptive dynamics described by equation (4.7). For adaptation in a single species the results obtained are $a_{0\pm} = a_{1\pm} = a_{2\pm} = a_{3\pm} = 0$ whereas $a_{4+} = -a_{4-} < 0$. Thus we are confronted with slowing down of fourth order.

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

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

6 Extensions and open problems

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

6.1 Polymorphic coevolution

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

The theorem is as follows. Consider the population sizes n_i and n_i' of a resident trait value s_i and a sufficiently close mutant trait value s_i' respectively in an environment defined by trait values s_j and population sizes n_j with $j = 1, \ldots, N \neq i$. The dynamics of the population sizes are assumed to be of Lotka–Volterra type. When the mutant is absent we call the remaining dynamical system for the population sizes the *resident system*, when the resident is absent the *mutant system*, and when both are present the *combined*

system. Provided that, first, the selection derivative $\partial_i' \bar{f}_i(s_i, s)$ does not vanish, and that, second, the Lotka–Volterra interaction matrix is regular and varies smoothly with s_i', there exists no fixed point of the combined system in R_+^{N+1}. It can then be shown that the mutant will either go to fixation or to extinction. To our knowledge there exists no proof of the principle of mutual exclusion for coevolutionary communities not of Lotka–Volterra type, although even in such cases the principle has been tacitly assumed (e.g. Rand et al. 1993).

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

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

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

6.2 Multi-trait coevolution

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

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

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

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

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

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

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

as the first order result for the deterministic approximation of the multi-trait coevolutionary dynamics in S_C. Here $\nabla_i' \bar{f}_i(s_i, s)$ with $\nabla_i' = (\partial_{i1}', \ldots, \partial_{iv_i}')$

denotes the *selection gradient* for species i, a vector being composed of simple selection derivatives $\partial'_{il}\bar{f}_i(s_i, s)$ with $\partial'_{il} = \partial/\partial s'_{il}$ for the traits $l = 1, \ldots, v_i$ of species i. In the case of multi-trait coevolution σ_i^2 is the *variance-covariance matrix* of the multivariate mutation distribution M_i. The elements of this square matrix $\sigma_i^2 = (\sigma_{i,ll'}^2)$ are given by

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

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

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

6.3 Coevolution under nonequilibrium population dynamics

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

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

$$E_1(s'_i, s) = \lim_{T \to \infty} \frac{1}{T} \cdot \int_0^T \tilde{f}_i(s'_i, s, n(t))\, dt \; ,$$

$$E_2(s'_i, s) = \lim_{T \to \infty} \frac{1}{T} \cdot \log \frac{|\Delta n(T)|}{|\Delta n(0)|} \; , \tag{6.3}$$

$$E_3(s'_i, s) = \int_{A(s)} \tilde{f}_i(s'_i, s, n)\, dv(n) \; .$$

The first quantity E_1 is the *time average of the per capita growth rate* of the rare mutant along a trajectory $n(t)$ that starts on the attractor $A(s)$ of the resident system. This construct immediately follows from our formal framework set out in Sect. 2.1; in generalization of equation (2.7) we thus write $\bar{f}_i(s'_i, s) = E_1(s'_i, s)$. The second quantity E_2 (Metz et al. 1992) is the *Lyapunov*

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

In the literature, the condition for initial increase of the rare mutant is taken to be $E_k > 0$ with $k = 1, 2, 3$ (e.g. Metz et al. 1992; Rand et al. 1993). The equivalence of the three criteria can readily be established. First, the time average E_1 coincides with the phase average E_3 (Ott 1993) – there can be exceptional initial conditions $n(0)$ that do not satisfy this identity, but since the set of these has Lebesque measure zero they are irrelevant for realistic systems. Second, the time average E_1 equals the Lyapunov exponent E_2. To show this we linearize the dynamics of the combined system about the trajectory $n(t)$ and obtain $\frac{d}{dt} \Delta n(t) = J(n(t)) \cdot \Delta n(t)$ where $J(n)$ denotes the Jacobian matrix of the dynamics of the combined system evaluated at n. From the population dynamics of the combined system we get $\Delta n_i(0) = 0 \Rightarrow \Delta n_i(t) = 0$ (the left hand side holds since the initial displacement between $n(0)$ and $\tilde{n}(0)$ 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 impliction to the linearized dynamics yields $\frac{d}{dt} \Delta n_i'(t) = \tilde{f}_i(s_i', s, n)|_{n = n(t)} \cdot \Delta n_i'(t)$. From these equations we conclude $|\Delta n(T)|/|\Delta n(0)| = \exp \int_0^T \tilde{f}_i(s_i', s, n(t)) \, dt$ which completes the proof of $E_1 = E_2$.

We investigate whether or not we recover the condition $E_1 > 0$ for the initial increase of a rare mutant in the light of our stochastic approach.

Already in the case of a fixed point attractor in population size space we had to distinguish between the timescale τ_a of adaptive change and the timescale $\tau_f \ll \tau_a$ on which a mutant either goes extinct or reaches fixation while the population dynamics of the combined system attain its attractor. With population dynamics settling to a nonequilibrium attractor $A(s)$, an additional timescale τ_p for the motion on this attractor is introduced. We assume $\tau_a \gg \tau_f \gg \tau_p$. In this case the invasion of a successful mutant happens slowly compared to the dynamics on the attractor $A(s)$; this is typical for mutants whose trait values s_i' are sufficiently close to the resident trait values s_i. In generalizing equations (3.6) and (4.12) we obtain for the probabilities per unit time in the stochastic representation

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

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

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

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

We now turn to the invasion criteria. A rare mutant s_i' can successfully invade a community given by the resident trait values s provided that there is a positive transition probability per unit time for the trait substitution $s_i \rightarrow s_i'$, i.e. $w_i(s_i', s) > 0$. We easily draw the conclusion that our stochastic approach yields the criterion $E_1 > 0$ which is equivalent to those proposed previously. To see this, consider equation (6.4) together with the definitions of $(\ldots)_+$ and that of $\overline{f}_i(s_i', s) = E_1(s_i', s)$ in equation (6.3). However, our analysis not only yields these criteria for the initial increase of a rare mutant but provides us also with a full dynamical description of the adaptive process. We emphasize that the results above readily generalize to cover the issue of coevolution in slowly varying environments where the additional time dependence stems from external influences rather than from internal interactions.

7 Conclusions

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

To conclude, we briefly summarize these generalizations.

1. To obtain a dynamics like equation (1.1) from a mutation-selection process certain symmetry properties of the mutation distributions are needed, see Sect. 4.2. Both our deterministic approximation in higher order, see Sect. 5.1, and the stochastic representation in general remove this assumption.
2. Being a deterministic description of the coevolutionary dynamics, the canonical equation describes the mean path and thus does not cover the full richness of dynamical effects that can occur in stochastic mutation-selection systems, see e.g. the discussion in Sect. 4.3. We have provided a stochastic representation in Sects. 3.1 and 3.2 that accounts for these features. Two examples illustrating the difference are given in Figs. 4a and 4b.
3. We have recovered the canonical equation as an exact description of the coevolutionary deterministic path, provided that the mutational steps are considered to be infinitesimal. Although the canonical equation gives a good approximation for small finite mutation variance, the approximation becomes inaccurate as the variance increases and consideration of higher order correction terms is recommended, see the derivation in Sect. 5.1.
4. The canonical equation does not permit interdependencies between several traits within one species. In Sect. 6.2 we could show how the stochastic approach to the coevolutionary mutation-selection process in this case naturally leads to the introduction of the variance-covariance matrix for the mutation distributions. The latter can give rise to less direct pathways towards evolutionary attractors.
5. The scope of the canonical equation is confined to coevolutionary systems with equilibrium population dynamics and a constant external environment. We have demonstrated in Sect. 6.3 that this limitation can be overcome such that more general ecological scenarios may be tackled.

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

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