Three mechanisms of Red Queen dynamics

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SUMMARY

Models describing systems of coevolving populations often have asymptotically non-equilibrium dynamics (Red Queen dynamics (RQD)). We claim that if evolution is much slower than ecological changes, RQD arises due to either fast ecological processes, slow genetical processes, or to their interaction. The three corresponding generic types of RQD can be studied using singular perturbation theory and have very different properties and biological implications. We present simple examples of ecological, genetical, and ecogenetical RQD and describe how they may be recognized in natural populations. In particular, ecogenetical RQD often involve alternations of long epochs with radically different dynamics.

1. INTRODUCTION

Ecological and genetical changes are frequently considered separately, but in reality they occur simultaneously in systems of coevolving populations. According to the Red Queen hypothesis (Van Valen 1973), coevolution of interacting populations causes their ecological and genetical characteristics to vary forever, even when external conditions remain constant. This hypothesis has attracted considerable attention because such mode of coevolution may provide an advantage for sex (see Dybdahl & Lively 1995; Ebert & Hamilton 1996), lead to episodes of fast evolution separated by periods of stasis (punctuated equilibrium, Stenseth (1985) and Rand & Wilson (1993)) and significantly affect the assembly of ecological communities (Szathmary *et al.* 1990).

Various instances of Red Queen dynamics (RQD) were observed in coevolutionary models of rather differing natures (e.g. Rand & Wilson 1993; Van der Laan & Hogeweg 1995; Andreasen & Christiansen 1995), but so far no general classification of them is available. Here we propose a classification for the asymptotical properties of RQD, applicable when evolution is much slower than ecological changes. Slow evolution appears to be the common case (Diamond 1990; Vermeij 1994) although genetical changes based on pre-existing variability may occur on the same time scale as ecological changes. Many coevolutionary interactions, e.g. between leaf miners and trees (Labandeira *et al.* 1994), leaf beetles and various plants (Futuyma & Mitter 1996), figs and wasps (Anstett *et al.* 1997) and cuckoos and their hosts (Brooker & Brooker 1996) persist for millions of years. Asymptotic properties of such interactions are biologically relevant even if evolutionary changes are slow.

We will show that there exist three very different generic mechanisms that can cause asymptotically non-equilibrium dynamics in coevolving populations. Thus, several rather diverse phenomena, sometimes with opposing implications, can all be called RQD, and it is essential to understand which mechanism causes permanent coevolutionary fluctuations in a particular case. To illustrate how these mechanisms work, we will consider several simple models of coevolution between pairs of populations. Such models are directly applicable to some real biological problems because pairwise coevolutionary interactions occur in nature (Hougen-Eitzman & Rausher 1994; Nakajima & Kurihara 1994). The same classification of RQD is applicable to more complex situations, as long as evolution is slow.

2. THREE TYPES OF OSCILLATORY DYNAMICS IN FAST–SLOW SYSTEMS

Consider a general fast–slow system,

$$\frac{\mathrm{d}x_i}{\mathrm{d}t} = f_i(x_i, \alpha_j), \qquad (1\,\text{eco})$$

$$\frac{\mathrm{d}\alpha_j}{\mathrm{d}t} = \varepsilon g_j(x_i, \alpha_j), \qquad (1\,\text{gen})$$

where ε is small, $x = (x_1, \ldots, x_n)$ are fast variables, and $\alpha = (\alpha_1, \ldots, \alpha_m)$ are slow variables. In the context of this paper, we shall call fast and slow variables ecological and genetical, respectively. Two time scales have to be distinguished: fast ecological time scale (ETS) t, and slow genetical time scale (GTS) $\tau = \varepsilon t$. The singular perturbations theory (Mishchenko & Rozov 1980; Arnol'd *et al.* 1994) leads to a simple classification of possible asymptotically non-equilibrium dynamics in (1). Here we will describe this classification at the heuristic level; a more detailed treatment will be published separately. The proposed classification is based on the fact that non-equilibrium dynamics may be due to either non-equilibrium ecology (with quasi-stationary

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genetics on GTS), non-equilibrium genetics (with quasi-stationary ecology on ETS) or non-equilibrium ecology and genetics (with both changing rapidly on the corresponding time scale).

If $\varepsilon = 0$ ('frozen genetics'), system (1) reduces to its fast, ecological subsystem (1 eco). The motion in this subsystem eventually reaches one of its attractors (e.g. an equilibrium or a periodic motion; we will assume that the ecological variables do not grow unlimitedly). Genetical variables remain constant and their (initial) values can be treated as parameters of the ecological subsystem. Ecological subsystems corresponding to similar values of the genetical parameters will usually have similar attractors. Different ecological attractors corresponding to different values of genetical parameters and belonging to a continuous family (slow manifold, if the attractors are equilibria) will be regarded as the same attractor.

Now, suppose that $\varepsilon > 0$ but is still small, so that the genetical variables can change slowly, causing slow changes of the 'parameters' of the ecological subsystem. Usually, a motion in the ecological subsystem remains close to an instantaneous attractor corresponding to the current values of its parameters. One can say that most of the time the ecogenetical system (1) traces an ecological attractor in (1 eco) while this attractor changes slowly due to the evolution of the genetical variables. However, occasionally the ecological subsystem can abruptly switch between different attractors. Several modes of the asymptotical dynamics (at GTS) are possible.

(0) The ecological subsystem always remains close to the same attractor which is an equilibrium, while the genetical variables also evolve towards an equilibrium. Then, all changes in (1) eventually stop (no RQD).

(1) The ecological subsystem always remains close to the same attractor which is not an equilibrium, while the changes of the genetical variables do not show any systematic trend. Then, the changes in (1 eco) will occur forever. When the dynamics in (1 gen) depend on the ecological variables, small fluctuations of the genetical variables, 'induced' by the ecological changes, will also occur forever (*ecologically driven* RQD).

(2) The ecological subsystem always remains close to the same attractor which is an equilibrium, while the genetical variables keep changing permanently. When the dynamics in (1 eco) depend on the genetical variables, slow evolution in (1 gen) will forever cause slow changes of the ecological variables (*genetically driven* RQD).

(3*A*) The ecological subsytem always remains close to the same attractor which is not an equilibrium, while the genetical variables also undergo large-scale changes. Then, non-equilibrium dynamics in (1) represents the superposition of fast changes in (1 eco) and slow changes in (1 gen) (*ecogenetically driven* RQD, mode *A*).

(3*B*) The ecological subsystem keeps switching between two or more different attractors. Of course, this is only possible when evolution in (1 gen) also never

stops. Again, non-equilibrium dynamics in (1) represents the interaction of fast changes in (1 eco) and slow changes in (1 gen) (*ecogenetically driven* RQD, mode *B*).

Below we shall see that all these types of RQD occur naturally in simple models of coevolution.

3. A GENERAL MODEL OF COEVOLUTION

In the models of coevolution considered here, the only ecological characteristic of a population will be its size, while the genetical variability within it will be described by mean values of quantitative traits. Then, if distributions of the traits are Gaussian and/or selection is weak, the dynamics of n coevolving populations with $l(i)$ traits in the ith population are described by the ecogenetical system with gradient genetical equations (Slatkin & Maynard Smith 1979; Rummel & Roughgarden 1985; Saloniemi 1993; Taper & Case 1992; Abrams & Matsuda 1997):

$$\frac{\mathrm{d}x_i}{\mathrm{d}t} = x_i f_i(x_1, \ldots, x_n, \alpha_{11}, \ldots, \alpha_{nl(n)}), \qquad (2\,\mathrm{eco})$$

$$\frac{\mathrm{d}\alpha_{ij}}{\mathrm{d}t} = \varepsilon_{ij} \frac{\partial}{\partial \alpha_{ij}} f_i(x_1, \ldots, x_n, \alpha_{11}, \ldots, \alpha_{nl(n)}),$$
$$(2\,\mathrm{gen})$$

where x_i is the size of the ith population, f_i is its per capita growth rate, α_{ij} is the average value of the jth quantitative trait in the ith population, and ε_{ij} is additive genetic variance in the corresponding trait which determines its ability to respond to selection. We will assume that all ε_{ij} are constant and small (of order $\varepsilon \ll 1$), i.e. that the genetical changes are slow.

As usual, each f_i will be an algebraic sum of terms describing different ecological processes and quantitative traits will determine their rates. If a trait influences only one process whose rate is a monotonic function of the corresponding α_{ij}, this α_{ij} will increase or decrease indefinitely. Because indefinite changes of the phenotype are impossible (Rosenzweig *et al.* 1987), such dynamics are not interesting in the context of RQD. Thus, we will consider either traits which influence more than one process with negative trade offs (e.g. increase of α_{ij} reduces both the vulnerability of a population to competition and its growth rate without the competitor) and/or traits such that the optimal rate of a process they affect (maximal if the corresponding term in an f_i is positive and minimal otherwise) occurs under their intermediate values. For dependencies of the rates of ecological processes on quantitative traits, we will use simple functions with the appropriate behaviour.

4. EXAMPLES OF RQDS OF DIFFERENT NATURE

In this section we will present four examples of different types of RQDs. It can be shown that, under our assumptions, RQD in an isolated population ($n = 1$) with any number of traits is impossible. Thus, we will assume that $n > 1$. It suffices to study

only two coevolving populations with no more than one evolvable trait in each.

Two well-known models will be used as the ecological subsystem of (2). The first one is a predator–prey model with prey self-limitation and predator saturation:

$$\left.\begin{array}{l} f_1 = r_1 - r_2 x_1 - r_3 x_2/(1 + x_1), \\ f_2 = -r_4 + r_5 x_1/(1 + x_1), \end{array}\right\} \tag{3}$$

which is the simplest predator–prey model which has a stable limit cycle (see Bulmer 1994). Under given values of parameters, (3) has only one attractor, either an equilibrium or a limit cycle.

The second is the Lotka–Volterra competitor–competitor system:

$$\left.\begin{array}{l} f_1 = r_1 - r_2 x_1 - r_3 x_2, \\ f_2 = r_4 - r_5 x_2 - r_6 x_1. \end{array}\right\} \tag{4}$$

Here alternative stable equilibria may coexist (either species may win, depending on initial population sizes), while oscillations are impossible (Bulmer 1994).

To construct a coevolutionary model, (2), on the basis of either (3) or (4), we will treat some of the ecological parameters $r > 0$ as functions of the genetical variables, α. Asymptotically non-equilibrium dynamics in (2 gen) require, in the absence of multiple attractors in (2 eco), at least two genetical variables. Thus, for observing RQD of types 2 and 3A we will assume that each coevolving species has an evolvable trait. RQD of types 1 and 3B can appear with just one genetical variable.

(a) Ecologically driven RQD

When RQD in (2) are ecologically driven, ecological variables change with large amplitudes while genetical variables change only slightly even at long time intervals (GTS), although small ε does not automatically preclude large long-term changes. Such dynamics are inherited from the ecological subsystem, in the sense that non-equilibrium asymptotic behaviour occurs even when genetical variables are frozen, at least under some (now constant) modes of ecological interactions, f_i. Mathematically, this may correspond to a periodic orbit of the ecological subsystem persisting under singular perturbation. This requires that the genetical subsystem (averaged over periodic orbits of the ecological subsystem) has a stable equilibrium, near which all genetical oscillations occur.

Assume that in the ecological system, (3), the predator has one evolvable trait with the mean value α_2, which affects its mortality r_4 and its ability to capture prey r_5. With growing α_2, r_4 increases faster than r_5, while when r_5 is below some minimal value, no prey can be captured. Thus, there is a negative trade off which precludes unlimited changes of α_2. Let us choose the following functions:

$$\left.\begin{array}{l} r_4(\alpha_2) = a\alpha_2^2, \\ r_5(\alpha_2) = b\alpha_2 - c, \\ r_3(\alpha_2) = \gamma r_5(\alpha_2). \end{array}\right\} \tag{5}$$

With small $\varepsilon_2 > 0$ in (2), slow evolution of α_2 will eventually drive the ecological subsystem (3) either into the region of its parametric space where the attractor is an equilibrium or into the region where the attractor is a limit cycle. The second case results in ecologically driven periodic RQD (figure 1) and occurs if $b^2(r_1 - r_2) > 4ac(r_1 + r_2)$.

(b) Genetically driven RQD

When RQD in (2) are genetically driven, the changes of both ecological and genetical variables are small at ETS but large at GTS, although the former are capable of large fast changes. Such RQD are caused by slow non-equilibrium dynamics of the genetical variables only. Here the ecological subsystem with frozen genetics approaches the same stable equilibrium under all f possible within the range of αs. Because ecological variables respond quickly (asymptotically, i.e. with $\varepsilon \to 0$, instantly) to changes in genetical variables, xs can be found from algebraic expressions $f_i = 0$, $i = 1, \ldots, n$ relating them to αs and leading to equations of motion for αs only (these are called reduced equations on the slow manifold). If oscillations occur in the reduced system, arising, for example, via Andronov–Hopf bifurcation, they will persist for small ε, leading to a genetically driven RQD.

Assume that in (4) each competing population has one evolvable trait. The trait α_1 in the first population affects its growth rate r_1 and the intensity of interspecific competition r_3, but does not affect its self-limitation, r_2. In the same way, the trait α_2 in the second population affects r_4 and r_6 but not r_5. In each population, the growth of the corresponding α_i increases both its growth rate and its vulnerability to interspecific competition, thus providing negative trade offs. Growth of α_1 also increases the impact of interspecific competition on the second population, while growth of α_2 decreases the impact of interspecific competition on the first population. Thus, α_1 and α_2 can be interpreted as the traits involved in exploitation and interference (Crombie 1947) competition, respectively. Let us choose the following functions:

$$\left.\begin{array}{l} r_1(\alpha_1) = a\alpha_1^2 + b\alpha_1 + c, \\ r_3(\alpha_1, \alpha_2) = d\alpha_1^2/\alpha_2^2, \\ r_4(\alpha_2) = g\alpha_2^2/(\alpha_2^2 + h) + k, \\ r_6(\alpha_1, \alpha_2) = l\alpha_1^2\alpha_2. \end{array}\right\} \tag{6}$$

Because our two traits affect competition in very different ways, their interaction alone can lead to genetical cycling. In figure 2 we present an example of genetically driven periodic RQD in (4). Genetically driven RQD can also appear due to coevolution of predator and prey (Dieckmann *et al.* (1995) and the example below).

(c) Ecogenetically driven RQD

When RQD in equations (1) are ecogenetically driven, ecological variables change rapidly, either always or at least occasionally, at ETS (which is not
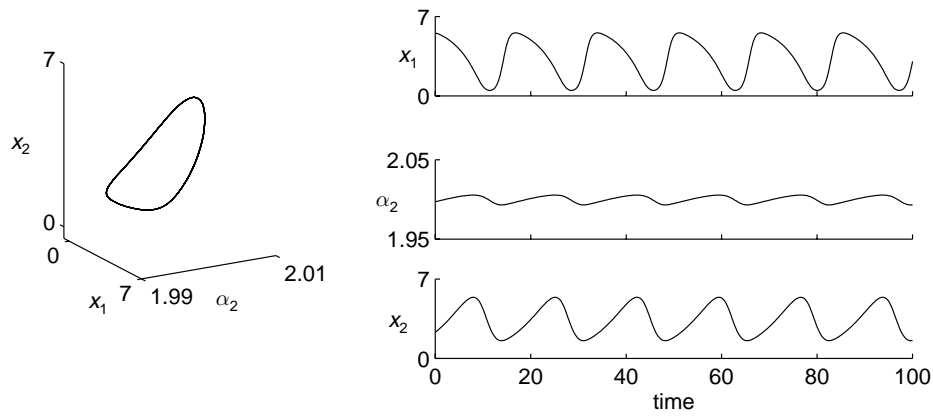
Figure 1. Ecologically driven RQD in (2) with the ecological subsystem, (3), and the genetical subsystem defined by (5) under $\varepsilon_2 = 0.01$, $r_1 = 2$, $r_2 = 0.3$, $a = 0.175$, $b = 1$, $c = 1$, $\gamma = 1$.
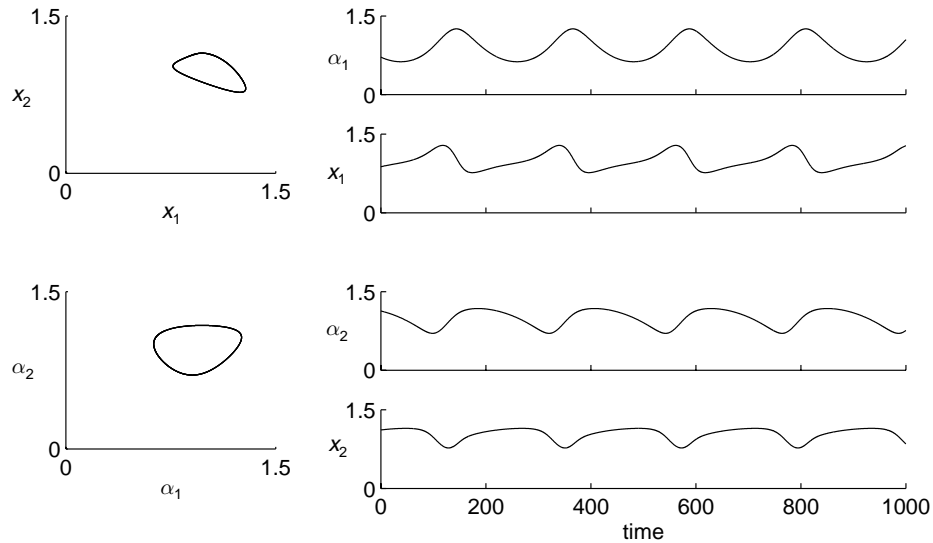

Figure 2. Genetically driven RQD in (2) with the ecological subsystem, (4), and the genetical subsystem defined by (6) under $\varepsilon_1 = \varepsilon_2 = 0.01$, $r_2 = 2$, $r_5 = 4$, $a = 0.75$, $b = 0.5$, $c = 1.75$, $d = 1$, $g = 5$, $h = 10$, $k = 4.5$, $l = 1$.

true with a genetically driven RQD), while genetical variables undergo substantial changes at GTS (which is not true with an ecologically driven RQD). We will consider two examples of ecogenetically driven RQD of mode B, which can arise due to several dynamical phenomena.

One possibility is that with 'frozen genetics' the ecological subsystem has multiple attractors (equilibria or more complex), while slow genetical changes permanently cause rare switches between them (analogous dynamics where some of the attractors are limit cycles are known in, e.g. neurobiology (Bertram *et al.* 1995) and ecology (Kuznetsov & Rinaldi 1996)). In the simplest case of two ecological equilibria, this leads to relaxation oscillations (Mishchenko & Rozov 1980), such that ecological changes are usually slow, but occasionally rapid. As an example, consider again the system, (4). Assume that only the 2nd population has an evolvable trait ($\varepsilon_1 = 0$) and choose parameter values such that interspecific competition is stronger than self-limitation, so that with 'frozen genetics' either species may win depending on the initial conditions (Bulmer 1994). When the second species wins, its slow evolution reduces its ability to

compete (while increasing its growth rate) and eventually allows the first species to take over. After this, slow evolution of the nearly extinct second species improves its competitive ability (at the expense of its growth rate) and eventually allows it to again increase in numbers (see figure 3). Qualitatively the same dynamics are possible when both competitors can evolve. Thus, in contrast with the opinion of Pimentel (1968), oscillations caused by the coevolution of competitors are not necessarily decaying.

Another option occurs when genetical variables have periodic or other asymptotically non-equilibrium behaviour, and slow genetical evolution drives the ecological subsystem through regions of its parametric space corresponding to different attractors, with smooth transitions between them. Consider again the predator–prey system, (3). Assume that each population has one evolvable trait. The prey's trait, α_1, affects its self-limitation coefficient, r_2, in such a way that an intermediate value ($\alpha_1 = 0$) leads to the lowest intensity of self-limitation. The intensity of predation is maximal when the value of the predator's trait, α_2, coincides with α_1, and declines when the difference between the values of these two
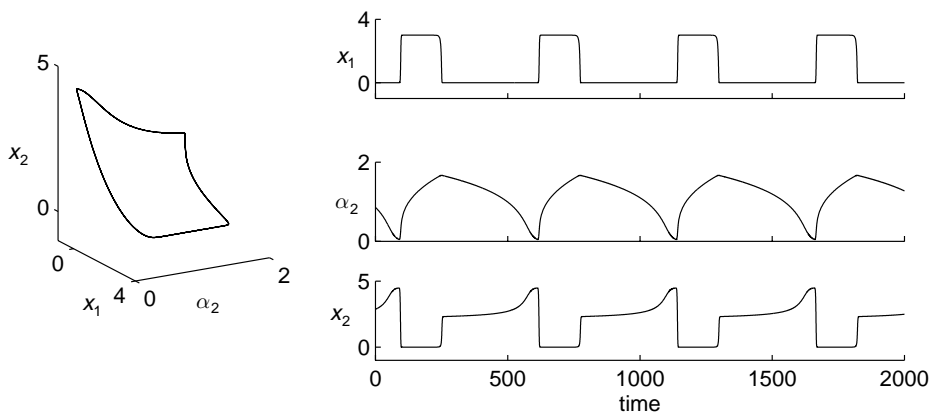
Figure 3. Ecogenetically driven RQD in (2) with the ecological subsystem, (4), and the genetical subsystem defined by (6) under $\varepsilon_1 = 0$, $\varepsilon_2 = 0.01$, $r_2 = 0.5$, $r_5 = 0.5$, $a = 0.75$, $b = 0.5$, $c = 0.25$, $d = 1$, $g = 0.5$, $h = 0.4$, $k = 1$, $l = 0.5$, $\alpha_1 = 1$.

traits increases. Let us choose the following functions:

$$\left.\begin{aligned}
r_2(\alpha_1) &= a\alpha_1^2 + b, \\
r_3(\alpha_1, \alpha_2) &= \exp(-c(\alpha_1 - \alpha_2)^2) + d, \\
r_5(\alpha_1, \alpha_2) &= \gamma r_3(\alpha_1, \alpha_2),
\end{aligned}\right\} \qquad (7)$$

Here, both the ecological and the genetical subsystems may oscillate. A slow genetical cycle may drive the ecological subsystem through the regions of equilibrium and oscillatory dynamics, leading to long bursts of oscillations alternating with long quiescent modes (figure 4).

Remarkably, small changes of parameters may convert the ecogenetically driven RQD of mode B into ecogenetically driven RQD of mode A, when the ecological subsystem always remains close to the limit cycle (e.g. if in figure 4, b is changed to 0.3), an ecologically driven RQD (e.g. if in figure 4, r_4 is changed to 0.7), a genetically driven one (e.g. if in figure 4, b is changed to 0.38) or even cause its transition to equilibrium dynamics (e.g. if in figure 4, r_1 is changed to 0.5).

5. DISCUSSION

Ecological interactions among genetically invariant populations easily lead to asymptotically non-equilibrium dynamics. In contrast, genetical processes considered alone usually tend to equilibrium, with cycling possible (Hastings 1981) but, apparently, rather rare. Simultaneous fast ecological and slow genetical changes often lead to asymptotically non-equilibrium dynamics (RQD) in one of the three different ways.

Ecologically driven RQD are simply an unavoidable implication of persistent fluctuations caused by ecological interactions alone, because fluctuating population sizes are bound to cause fluctuating selection and genetical changes. In contrast, slow genetically driven RQD (Dieckmann *et al.* 1995) are different from persistent fluctuations in either purely ecological or purely genetical models. Ecogenetically driven RQD are, not surprisingly, the most complex (Andreasen & Christiansen 1995; Van der Laan &

Hogeweg 1995). Ecologically driven RQD must be a common phenomenon. We do not know how common the other two mechanisms are, although they appear readily even in simple models. Still, coevolution can result in stasis (Stenseth & Maynard Smith 1984; Rand & Wilson 1993) as well as in RQD.

The ecological component of RQD causes fast ecological changes, either permanently (figure 1), or at least occasionally (figures 3 and 4), while genetically driven RQD lead to only slow ecological changes (figure 2). However, only the genetical component of RQD causes profound genetic changes of the coevolving species (figures 2–4), while ecologically driven RQD lead to only slight genetic changes (figure 1).

(a) *Implications of the three types of RQD*

Biological implications of the three modes of RQD are remarkably different. Due to slowness of the genetical response, the ecological component of RQD may cause the coevolving traits to lag far behind their current optima and, thus, leads to strong directional selection and high lag load (Stenseth 1985). In contrast, genetically driven RQD lead to weak selection with only small deviations of the mean values of the traits from their optima. The advantage of sex and recombination under fluctuating selection appears most naturally due to better responsiveness of sexual populations to strong effectively directional selection (see Kondrashov & Yampolsky 1996). Ecogenetically driven RQD are, perhaps, the most favourable for sex, since they may include long epochs of selection acting in the same direction (figure 3). In contrast, short-term ecological fluctuations will usually lead to frequent switches in the direction of selection under ecologically driven RQD. Such switches may provide an advantage to sexual reproduction due to non-responsiveness, but this is less likely (see Kondrashov & Yampolsky 1996). Genetically driven RQD probably do not lead to selection strong enough to maintain sex.

In contrast, profound, albeit slow, genetic changes during genetically driven RQD may significantly affect the outcome of community assembly (Rummel
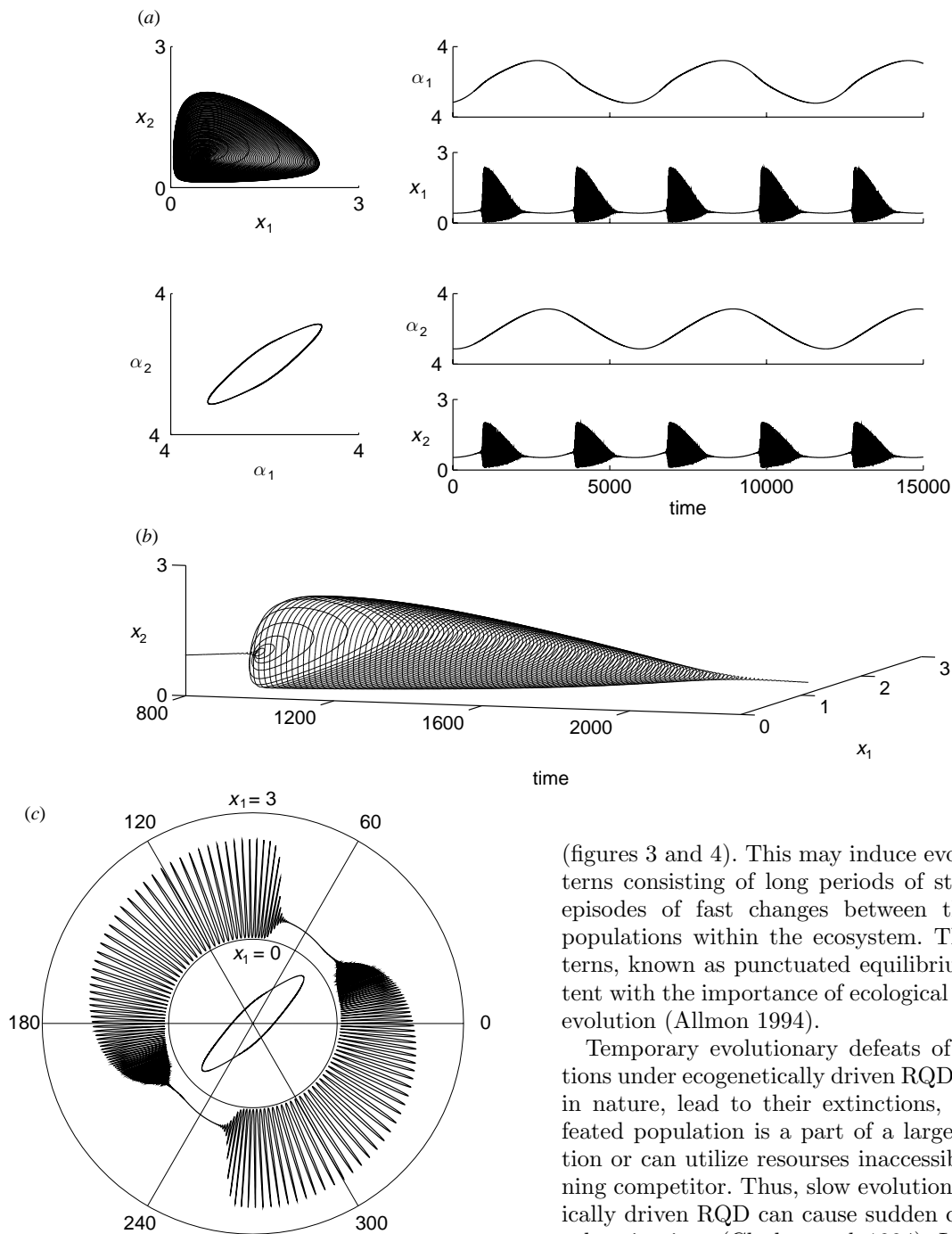
Figure 4. Ecogenetically driven RQD in (2) with the ecological subsystem, (3), and the genetical subsystem defined by (7). Parameters used are: $\varepsilon_1 = \varepsilon_2 = 0.01$, $r_1 = 1$, $r_4 = 0.59$, $a = 0.05$, $b = 0.32$, $c = 0.5$, $d = 1$, $\gamma = 1$. The polar plot at the bottom sketches the size of the prey population, measured along the polar radius, versus the polar angle ('phase') of the current position along the genetical cycle; the latter is reproduced in the smaller scale in the centre of the plot.

& Roughgarden 1985). The impact on this process of slight genetic changes caused by ecologically driven RQD must be much weaker. Ecogenetically driven RQD probably have the largest impact.

Only ecogenetically driven RQD can lead to alternations of long epochs of radically different states of the ecosystem with fast transitions between them

(figures 3 and 4). This may induce evolutionary patterns consisting of long periods of stasis and short episodes of fast changes between them in many populations within the ecosystem. Thus, such patterns, known as punctuated equilibrium, are consistent with the importance of ecological interactions in evolution (Allmon 1994).

Temporary evolutionary defeats of some populations under ecogenetically driven RQD (figure 3) can, in nature, lead to their extinctions, unless the defeated population is a part of a larger metapopulation or can utilize resourses inaccessible to the winning competitor. Thus, slow evolution and ecogenetically driven RQD can cause sudden complete or local extinctions (Clarke *et al.* 1994). Long-term data may be necessary to distinguish such events from the results of anthropogenic or other environmental changes (Pechmann *et al.* 1991).

Some models of coevolution assume indefinite changes of the traits in the same direction (Schaffer & Rosenzweig 1978). In nature, unidirectional coevolution can be rather long (West & Cohen 1994), but constraints and growing costs (Matsuda & Abrams 1994) must eventually stop it (Van Damme & Pickford 1995), leading to stasis (Brooker & Brooker 1996). During unidirectional evolution, increased evolvability, ε, is advantageous if not accompanied by extra deleterious mutations (Haraguchi & Sasaki 1996). In contrast, with ecogenetically driven RQD it is possible that the slower the currently winning species evolves, the longer it will persist (figure 3). Increased vulnerability of the ecosystem due to evolu-

tion of its dominant species may be at least partially responsible for successes of so many biological invasions (Rejmanek 1996). Of course, evolvability may be necessary for recovery of a losing species (Curry 1988).

(*b*) *Three types of RQD and data*

Short-term observations may be enough only to detect ecologically driven RQD, mostly by changes in population sizes. Long-term data are needed to distinguish genetically driven RQD from equilibrium, and ecogenetically driven RQD from either equilibrium or ecologically driven RQD. Abundances of competing species can undergo profound long-term fluctuations, e.g. in cladocerans (Mills & Forney 1988) and diatoms (Kilham *et al.* 1986) which may be caused by ecogenetically driven RQD (figure 3), even under uniform external environment.

Instead of long-term data on one population, short-term data on different populations may be used if RQD in different locations are asynchronous (see Travis 1996). Ecologically significant genetical differences between conspecific populations, if not caused by permanent differences in their environments, may indicate that they are engaged in RQD with the genetical component. In particular, short-term data may be informative if the populations which exchange migrants more frequently are not always more similar genetically and if spatial heterogeneity involves only some ecologically important loci. No unambiguous data of this kind are available on individual loci. However, different infectivety of several parasites to sympatric versus allopatric hosts was reported (see Dybdahl & Lively 1995; Morand *et al.* 1996). Profound differences among different local populations which are expected when RQD have a genetical component should lead to higher infectivity of parasites to sympatric hosts. With ecologically driven RQD, as well as if evolution is fast, there may be no clear-cut pattern (Morand *et al.* 1996).

(*c*) *The assumption of slow evolution*

As long as evolution is slow, our classification of RQD is still applicable if genetic variability is described by allele (Frank 1993), genotype (Andreasen & Christiansen 1995) or clone (Van der Laan & Hogeweg 1995) frequencies instead of mean values of the quantitative traits, if there are more than two interacting species, and if diffuse coevolution is considered instead of pairwise. Numerical experiments show that even with ε in (2) as high as *ca.* 0.1, the three mechanisms of RQD may still be recognizable. Small ε means either that allele frequencies and the mean values of the quantitative traits change slowly, or that they change rapidly but the ecological consequences of these changes are small. Fast evolution is possible only if alternative alleles, simultaneously present in the population with significant frequencies, have rather different ecological properties. This may be the case if fitness optimum fluctuates within

a narrow range. Some data are consistent with relatively fast changes in ecologically important traits (Lively 1993; Grosholz 1995; Henter 1995; Lively & Jokela 1996).

In contrast, response to long-term directional selection must be slow, because it requires incorporation of fresh mutations (Houle *et al.* 1996). If such selection persists, evolvability of a population, which was constant in our models, may decline due to exhaustion of genetic variability. Selection can hardly favour the increased mutation rate, because most new mutations are unconditionally deleterious (see Haraguchi & Sasaki 1996). Thus, the fast–slow framework must be suitable for description of many, although not all, coevolutionary interactions.

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