Can Initial Invasion Dynamics Correctly Predict Phenotypic Substitutions?

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1 Introduction

Adaptive dynamics are described as trait substitution sequences, where the states are formed by the attractors of the resident population dynamics and the jumps are driven by mutation, invasion and take-over. One of the fundamental assumptions made in adaptive dynamics states that if invasion is successful, and invasion under role reversal of resident and invader is not, then the invader replaces the resident. In this chapter we are going to challenge this assumption —which is actually very commonly made in evolutionary theory— by providing example models where successful invasion does not guarantee persistence of the mutant, let alone its fixation. To do this, we study invasibility and evolutionary stability in systems in which population dynamics do

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not lead to a steady state and several population dynamic attractors can coexist. These attractors, which can be periodic and/or chaotic, have different invasion properties. Moreover, successful invasion by a mutant strategy from one attractor can be followed by extinction of the former invader, caused by a switch of the resident system to another attractor. In other words, the resident strategy is *invasible, yet invincible.* We will discuss how this phenomenon of resilience relates to the theory of adaptive dynamics developed so far.

An *Evolutionarily Stable Strategy* [ESS; Maynard Smith & Price, 1973, Maynard Smith, 1982] is a non-invasible strategy (or trait value) in the sense that if the resident plays (has) it, any invasion by individuals with a different strategy (trait value) is bound to fail. A *local ESS* restricts invaders to playing only slightly different strategies. This concept is especially important if one assumes that mutant phenotypes originate with only slight deviations from the resident wild-type. Note that an ESS corresponds to a steady state of the adaptive dynamics, but that it is not built into the definition [Maynard Smith, 1982] that an ESS is an *attractor* of the adaptive dynamics. That which is defined by the classical definition of an ESS [Maynard Smith, 1982] could better be called a 'non-invasible strategy'. Therefore the definition of ESS's needs further classification [see Eshel, 1996, Metz *et al.*, 1996, Geritz *et al.*, 1998, Geritz & Kisdi, this volume].

If the initial exponential growth rate of a small mutant population in an established resident population is positive, the mutant has a positive probability to invade. This growth rate, which we refer to as invasion fitness, is generally defined as the dominant Lyapunov exponent [see Metz *et al.*, 1992, Rand *et al.*, 1994, Ferrière & Gatto, 1995, Metz & Ferrière, this volume]. If invasion is successful and the frequency of the mutant increases, its influence on the ecological environment, due to density dependence, will become more prominent. Consequently, the ecological environment will start to deviate from the original setting at the onset of invasion, which was determined exclusively by the resident phenotype. (As is common in evolutionary considerations like this, we focus on those components of the environment that are dynamically related to the trait under study.)

A successful invasion might be followed by an ongoing increase of the mutant frequency, ultimately leading to replacement of the resident by the mutant. However, there is a feedback loop: the mutant-induced environmental changes, in turn, influence the population dynamics of resident as well as mutant individuals. As a result, the combined influence of resident and mutant might also change the environment in such a way that the mutant frequency stops increasing, or even starts to decrease. If its increase only comes to a halt, a polymorphism is established by the mutant and the resident. If it starts decreasing and continues to do so, the mutant will ultimately find itself back in the insignificant position where it was when the invasion started. But will the resident population be in the same state as at the onset of invasion? If this is the case, the mutant will have a positive growth rate again. Then it will increase again and the sequence of events repeats indefinitely. In other words, its frequency may fluctuate, but the mutant can remain (in some long-term sense) in the population. In this chapter however, we will investigate some situations where, after ousting out the mutant, the resident population is in another state, from which it may not be possible for the mutant to invade again.

As it is extremely difficult to incorporate all relevant genetic and ecological factors which come into play in the transient phase between successive mutant invasions, and one wants an evolutionary framework with manageable proportions, restrictions have to be made. In adaptive dynamics, two assumptions are therefore standard. The first assumption postulates a separation of time-scales; one on which new mutations occur and one on which population dynamics converge to a new attractor [see Dieckmann & Metz, this volume]. This should rule out the possibility of a next successful mutation arising before the population dynamic transients triggered by a previous invasion have died out. The second assumption asserts that if invasion is successful, and invasion under role reversal of resident and invader is not [see the concepts of invasion functions and of pairwise invasibility; Geritz & Kisdi, this volume], then the invader replaces the resident. For a few special models, one can actually prove that such a competitive exclusion principle holds true [Dieckmann, 1995, Hans Metz pers. comm.]. These assumptions imply that the evolving system is mostly monomorphic in time, and that the evolutionary dynamics are mutation-limited.

It is the second, 'invasion implies fixation' assumption above that we are going to analyze in greater detail in our example models. The first example deals with a temporally structured population, and studies the timing of reproduction of semelparous individuals. The second one considers a spatially structured population, and studies the rate of dispersal in a metapopulation. To make (theory of) life simple, we neglect pair formation, sexual reproduction and genetic inheritance and pretend that reproduction is clonal.

2 First example: evolution of the age at reproduction in salmon

Pacific salmon (*Oncorhynchus* spp.) reproduce in upstream rivers. The fry migrate soon after birth to the ocean, and after a variable number of years the mature fish return to their natal river to spawn and die. We will consider competition between phenotypes with different ages at reproduction. To facilitate the description, we call individuals (populations, etc.) with a life-span of k years simply k-individuals (k-populations, etc.).

A paper by Kaitala & Getz [1995] inspired us to study this system. Readers who appreciate a more thorough analysis can consult Diekmann *et al.* [1999] and Mylius & Diekmann [2001].

Description of the population model and dynamics

Consider a population of salmon and assume that individuals reproduce either three or four years after birth. There are two fundamentally different mechanisms that can lead to the same population average (*i.e.*, the same probability that an arbitrarily chosen individual breeds at age 3 or 4). One mechanism is a so-called *pure strategy* formulation. This supposes that there are different types of individuals, each strictly adhering to a fixed life-span. Another possibility is a *mixed strategy* formulation, in which individuals can be characterized by the probability to return to the breeding water after three years, provided they are still alive. This could for example be the case if individuals experience environmental stochasticity, resulting in a distribution of life-spans. We will focus here on the pure-strategy formulation. In Diekmann *et al.* [1999] the mixed formulation is treated more elaborately. There we also consider competition between annual and biennial populations, which gives similar results as competition between 3-populations and 4-populations, but is more easy to deal with analytically.

As reproduction takes place at either three or four years, there are only two different types of individuals, and the population is *dimorphic* at most. Then we can presume that

$$\begin{aligned} x_t &= c_3\, x_{t-3}\, E_t \\ y_t &= c_4\, y_{t-4}\, E_t\ , \end{aligned} \tag{1}$$

where x_t and y_t measure the number of young entering the sea in year t, with a life-span of three and four years, respectively. The parameters c_k (with $k = 3, 4$) combine information about survival and reproductive potential k years after birth. The function E_t (E from *environment*) denotes the effect of intraspecific competition in the breeding spots up the river, given by the sum of the reproductive potentials of adult individuals (*i.e.*, $c_3\, x_{t-3} + c_4\, x_{t-4}$), and we take the relation

$$E_t = g(c_3\, x_{t-3} + c_4\, y_{t-4})\ , \tag{2}$$

where g is a positive decreasing function with $g(0) = 1$.

Box 1 Periodic patterns: good and bad years

When only one of the types is present, the attractors of the population numbers are described by

$$x_t = f(c\, x_{t-k})\ , \tag{3}$$

with $f(x) = x\, g(x)$ and $k = 3$ or $k = 4$. For the one-humped functions f that we consider, population dynamics lead to steady state for small c. If the hump is steep enough, and this can easily be the case for appropriate choices of g, this gives rise to non-equilibrium dynamics. Well-known examples include the logistic equation, the Ricker [1954] equation, Hassell's (1975) equation, and others. In this example, an increase of c will lead to a sequence of period-doubling bifurcations.

In Figure 1 we have depicted a bifurcation diagram of E for the case $g(x) = \exp(-x)$. When c increases beyond e^2 ($\approx$ 7.39), the equilibrium solution loses stability due to a period-doubling bifurcation and a stable period-two solution $E_G E_B E_G E_B \ldots$ comes into being. Here, years of E_G are referred to as *good* and years of E_B are referred to as *bad*. These indications reflect the viewpoint of an individual salmon: In good years the number of breeding salmon is low and, consequently, E is high, whereas in bad years the number of breeding salmon is high and E is low. The period-two solution loses stability at $c \approx 12.5$, where a period-four solution originates. In the remainder we will concentrate on the period-two solution. By convention, we always start with the good years being the even years and the bad years being the odd ones.

It is important to realize that for all $k = 1, 2, \ldots$, the bifurcation diagram is identical to the one depicted in Figure 1. When we

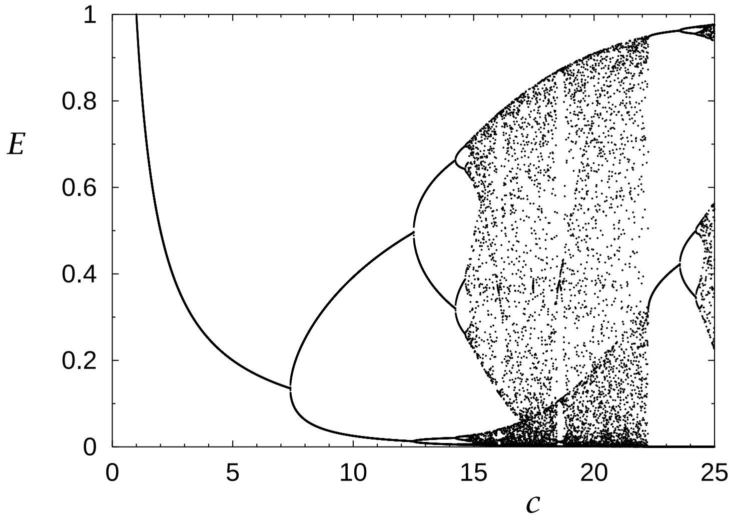

Figure 1: Bifurcation diagram of the environmental condition E from the delayed difference equation $x_t = c\,x_{t-k}\,E_t$, with $E_t = \exp(-c\,x_{t-k})$, and c ranging from 1 to 25.

look every k years in a delayed version ($k > 1$), E_G and E_B alternate in the same way as in a 'non-delayed' ($k = 1$) version when we look every year. Looking every year in a delayed version however, we see that each year corresponds to a different subpopulation or 'line', independently coexisting in time with the other $k - 1$ subpopulations. Together, these subpopulations form a metapopulation distributed in time, instead of in space, which is the usual situation (*cf.* the second example). The different attractors of the metapopulation correspond to different combinations of phase of the uncoupled subpopulations.

It turns out that the metapopulation shows, for small k, only a relatively small number of periodic patterns [see Diekmann *et al.*, 1999, Diekmann & van Gils, 2000]. For $k = 3$ the complete catalogue of possibilities consists of a period-two solution GB and a period-six solution $GGGBBB$, while for $k = 4$ it consists of the two period-eight solutions $GGBGBBGB$ and $GGGGBBBB$ (shown in Table 1).

The periodic solutions for each subpopulation are stable, since they are stable as solutions of the ordinary difference equation $x_t = f(c\,x_{t-1})$. Hence the periodic solutions of the metapopulation are also stable. The different attractors correspond to different combinations of phase of the uncoupled subpopulations.

Invasion leading to replacement or coexistence

In the pure-strategy formulation (equations 1 and 2) the state of a population is represented by a point in (x, y)-space and monomorphic populations are situated at one of the boundary planes $x \equiv 0$ and $y \equiv 0$. We will study the stability of the attractors in these reduced state spaces, in the direction of the

life-span 3	period 2	G	● ○ ○ ○ ○ ○ ○ ○ ○ ○ ○ ○
		B	● ○ ○ ○ ○ ○ ○ ○ ○ ○ ○ ○
	period 6	G	● ● ● ○ ○ ○ ○ ○ ○ ○ ○ ○
		B	● ● ● ○ ○ ○ ○ ○ ○ ○ ○ ○
life-span 4	period 8 (a)	G	● ● ● ● ○ ○ ○ ○ ○ ○ ○ ○
		B	● ● ● ● ○ ○ ○ ○ ○ ○ ○ ○
	period 8 (b)	G	● ● ● ● ○ ○ ○ ○ ○ ○ ○ ○
		B	● ● ● ● ○ ○ ○ ○ ○ ○ ○ ○

Table 1: Possible periodic patterns after the first period-doubling bifurcation of equation (3), for populations of individuals with a life-span (k) of three or four years. The elementary block that is repeated is indicated by solid dots.

interior of (x, y)-space. This is an example of an invasibility question: given a resident type, will an invader type grow when rare?

Under the assumption that the population dynamic attractor is a *fixed point* (*i.e.*, for low values of survival and/or reproduction, c), the situation is straightforward [see Diekmann *et al.*, 1999]: In the pure-strategy setting, breeding at age 3 is an ESS if $c_3 > c_4$ and breeding at age 4 is an ESS if $c_3 < c_4$. In other words, the ESS breeding strategy is at the age where age-dependent survival and/or reproduction are such that the expected offspring production is highest.

In the mixed-strategy setting we obtain, analogously to the pure-strategy situation, that breeding at age 3(4) is an ESS if $c_3 > (<)\, c_4$. Additionally, if $c_3 > (<)\, c_4$, then mutants with a higher (lower) probability to breed at age 3 than the resident can invade, so the trait substitution sequence exhibits a monotone movement to breeding at age 3 in the first case and to breeding at age 4 in the second case. In other words, in both settings the ESS is an attractor of the adaptive dynamics.

This result shows the other side of the coin of optimal adaptation to the environment: if density dependence acts by feedback to a one-dimensional environmental variable, then only the type that makes, as a resident, life as hard as possible is invulnerable to invasion [see also Mylius & Diekmann, 1995, Mylius & Metz, this volume]. In this example, density-dependent survival in the nursery attains a minimum at the ESS.

Things become more intricate if we assume that population dynamics show sustained *oscillations*. We first consider a (pure-strategy) population of 3-individuals, assuming that $c_3 > c_4$, and ask whether or not 4-individuals can invade. We now suppose c_3 is such that the fixed point is unstable and the 3-population will converge either to the period-two attractor or to the period-six attractor (see Box 1 and Table 1). These are both characterized by a pair of environmental values, a high E_G of good years and a low E_B of bad years. These E-values are such that

$$c_3^2\, E_G\, E_B \;=\; 1 \;, \tag{4}$$

since for successive generations of 3-individuals, good and bad years of reproduction alternate and on (geometric) average the number of offspring must be one.

Now imagine the resident 3-population has settled into the period-two pattern and look at the fate of an invading 4-individual that happens to be born in a good year. Then its offspring, and their offspring, will also be born in a good year. So the average number of offspring per generation is simply $c_4 E_G$ and we want to know whether or not this number exceeds one. To make the comparison with 3-individuals easier, we look two generations ahead and, using (4) in the first step, we write

$$y_t \;=\; \frac{c_4^2\, E_G^2}{c_3^2\, E_G\, E_B}\, y_{t-8} \;=\; \left(\frac{c_4}{c_3}\right)^2 \frac{E_G}{E_B}\; y_{t-8}\,, \tag{5}$$

which means that invasion is possible if

$$\frac{E_G}{E_B} \;>\; \left(\frac{c_3}{c_4}\right)^2 . \tag{6}$$

From this expression we see that the inherent disadvantage $c_4/c_3 < 1$ which we assumed, can, in principle, be overcome by systematic tuning to good years if the factor E_G/E_B is large enough. Right after the period-doubling bifurcation, where E_G and E_B do not yet differ very much (see Figure 1) the effect will not be strong enough. But once E_G/E_B exceeds $(c_3/c_4)^2$, 4-individuals tuned to the good years do increase in numbers when rare.

In the same way it follows that when a 4-individual is born in the first or the third good year, or in the middle bad year of the period-six solution, its descendants will experience two good environments and one bad environment out of every three reproduction events. Hence the invasibility condition becomes $c_4^3\, E_G^2\, E_B > 1$ which, by looking six generations ahead and, using (4) once again, we rewrite in the form

$$\frac{E_G}{E_B} \;>\; \left(\frac{c_3}{c_4}\right)^6 . \tag{7}$$

It is clear that the period-six attractor is more difficult to invade for the 4-individuals than the period-two attractor, since the synchronization with the good years is less perfect.

So we see that the invasion criterion is different for different attractors and as a consequence we cannot simply state that a population breeding at age 3 is (or is not) invasible by individuals breeding at age 4. The coexistence of attractors complicates the description of adaptive dynamics as trait substitution sequences.

We can also pose the question: what if survival and reproduction are such that the expected offspring production is higher when breeding at age 4 (*i.e.*, $c_4 > c_3$)? Then the fixed-point-, period-two- or period-six attractor of a 3-resident are all invasible by 4-individuals. Conversely, fixed-point attractors and both period-eight attractors of a 4-resident are uninvasible by 3-individuals. This is because 3 and 8 do not have a common factor, which makes tuning to good years impossible. So here there is no difference with invasibility as predicted by the steady-state situation.

In Figure 2 we introduce, for c-values above the first period-doubling bifurcation, mutants with a life-span of four years at low frequencies in a 'good year' of a fluctuating resident population with a life-span of three years and plot the

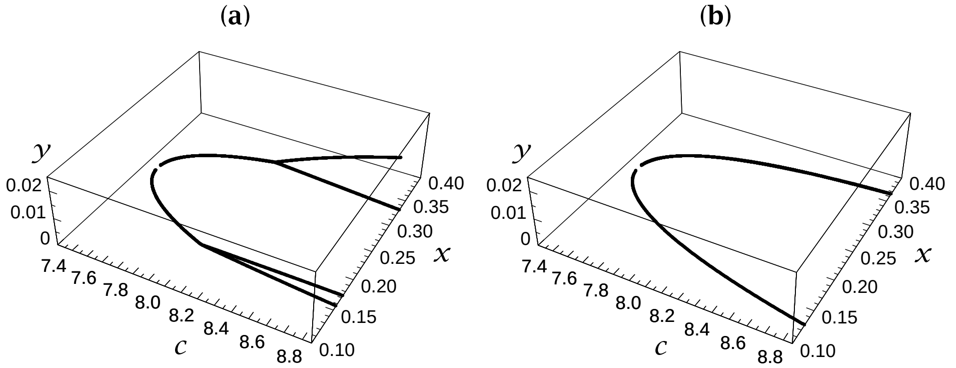

Figure 2: The attractor of population numbers x_t and y_t, of individuals with a life-span of three and four years, respectively, of the dimorphic system (1) with $g(x) = \exp(-x)$, $c_3 = c$ and $c_4 = 0.5\,c$, for c-values just above the first period-doubling bifurcation. The resident population with life-span three was fluctuating either on the period-two attractor (panel **a**) or on the period-six attractor (panel **b**) when life-span four mutants were introduced in small numbers.

resulting population dynamic attractor. (That is, we use c as a bifurcation parameter here and plot population numbers after the transients have disappeared. Also note that, because $c = c_3$, period-doubling bifurcations of the 3-resident population dynamics occur for the same values of c as in Figure 1.) We see that the period-two attractor (panel a) 'inherits' the uninvasibility from the fixed point at lower c-values, but can be invaded by 4-individuals if c is greater than approximately 8.0, whereas the period-six attractor (panel b) remains evolutionarily stable for c-values substantially greater than 8.0. The dimorphic system which results after successful invasion has a period-four attractor, still characterized by yearly alternations of 'good' and 'bad', but with two levels of each.

The resident strikes back: resilience in spite of invasibility

When c is increased further, beyond the above-mentioned value at which the period-two attractor becomes invasible, a particularly interesting phenomenon of resilience appears.

We start with a population of 3-individuals that oscillates with period two, the *good* years being the *even* years. Next, we introduce a small population of 4-individuals in an even year. After the 4-population has increased enough to constitute an appreciable part of the total population, a subtle interaction between the 3- and 4-subpopulations sets in. As a result of this interaction, the quality of even years deteriorates, while the quality of the odd years increases. After a certain period, the even years are even worse than the odd years. At this point the competitive advantage of 4-individuals turns into a competitive disadvantage, as now the reproduction of 4-individuals takes place in bad years. Therefore the 4-subpopulation is doomed to become extinct. In the end we have a population of 3-individuals that oscillates with period two, the *good* years being the *odd* years.

There is a sensitive dependence on initial conditions here since likewise it may happen, depending on the value of c, that the invasion of the period-two attractor leads, after a temporary phase of turmoil, to the period-six attractor

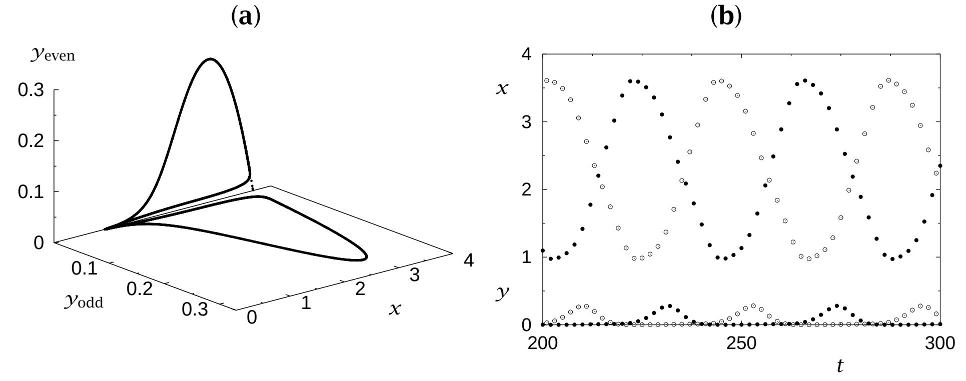

Figure 3: A numerical experiment with a variant of an annual-biennial system, in which biennials are introduced at low densities in an annual resident population in a period-two attractor, and 5 % of the biennials reproduces annually. Panel **a**: Phase plot; **b**: Time plot. Population densities in even and in odd years are plotted with • and ◦ symbols, respectively. System: $x_t = c_1\, x_{t-1}\, E_t$, $y_t = c_2\, y_{t-2}\, E_t$, with $E_t = g(c_1\, x_{t-1} + c_2\, y_{t-2})$. Parameters: $(c_1, c_2) = (10, 6)$. Initial condition: $(x_0, y_0^{\text{odd}}, y_0^{\text{even}}) = (3.67, 0.01, 0.01)$.

in a phase at which the 4-individuals are at a disadvantage.

Robustness of the results

The deterministic nature of the model at the individual level (reproduction at a strictly specified age) makes the model analyzed thus far rather degenerate. But the coexistence of attractors with different invasion properties is a robust phenomenon. To illustrate this, suppose that some proportion of individuals 'mistakes' and reproduces one year earlier or later. To what extent is the 'resident strikes back' scenario robust against this life-history noise?

In Figure 3 we show a numerical experiment of competition between annual and biennial lines, where 'inferior' biennials are introduced at low densities in an annual resident population that has converged to a period-two attractor [see Mylius & Diekmann, 2001, for details]. Parameter values are in the resident–strikes–back region, and each biennial individual is assumed to reproduce after one year already with a probability of 5 %. After the immediate rise and fall of the even-year biennial subpopulation, the odd-year line starts building up, triggered by the attractor switch caused by the even-line invasion. In this situation, the bad-year line is protected against extinction by individuals leaking out of the current good-year line. This leads to an infinitely ongoing situation of alternating favourable and unfavourable conditions, where each line will repeatedly have short periods of high abundance. The addition of other perturbations to this system, like demographic stochasticity or environmental noise, will only disturb the regularity of this pattern, provided that these perturbations are not too large. Successful invasion of one boundary attractor leading in the end to another attractor in the same boundary is a robust phenomenon as well.

3 Second example: evolution of dispersal in a metapopulation

The next example comes from metapopulation dynamics, and considers evolutionary competition between phenotypes with different dispersal rates in a two-patch system. In Doebeli [1998] one can find a more detailed treatment of this system, and in Doebeli & Ruxton [1997] a more general treatment of the evolution of dispersal rates in two-patch metapopulation models.

Box 2 Description of the basic model

We consider a discrete-time model of an annual species with two local populations that are coupled by dispersal. At every time step, or generation, there is density-dependent reproduction in each patch, followed by a dispersal phase. Reproduction is modeled by the difference equation

$$x_t = x_{t-1}\, g(x_{t-1}) \,, \tag{8}$$

where x_t is the local population density at time t, and $g(x)$ is the *per capita* reproductive output if the density in the patch is x. The form of the function g used in the numerical examples below is

$$g(x) = \frac{\lambda}{1 + (ax)^b} \tag{9}$$

[after Maynard Smith & Slatkin, 1973], but other functions yield the same results, as long as they permit non-equilibrium dynamics for system (8). In this particular form, λ, a and b are demographic parameters describing respectively the intrinsic growth rate, and the type and the strength of the intraspecific interactions that lead to density dependence [see Bellows, 1981]. Depending on these parameters, system (8) can exhibit various types of qualitative behaviour, including stable equilibrium dynamics, periodic dynamics and chaos.

We will assume that the two patches are ecologically identical, *i.e.*, the function g has the same parameters in the two patches.

Let x_t and y_t be the population densities in the two patches at time t. We define the dispersal rate d as the fraction of individuals that move to the other patch in the dispersal phase of each time step. Additionally, we assume that dispersing individuals survive only with a probability s (with $0 \le s \le 1$). With these assumptions, and the basic model description given in Box 2, the dynamics of the two-patch metapopulation are governed by the system of difference equations

$$\begin{aligned} x_t &= (1-d)\, x_{t-1}\, g(x_{t-1}) + s\, d\, y_{t-1}\, g(y_{t-1}) \\ y_t &= (1-d)\, y_{t-1}\, g(y_{t-1}) + s\, d\, x_{t-1}\, g(x_{t-1}) \,. \end{aligned} \tag{10}$$

Ecological dynamics

Either with or without a cost to dispersal ($s < 1$ or $s = 1$, respectively), the following metapopulation dynamics can occur. (See Hastings 1993, Gyllenberg *et al.* 1993, Doebeli 1995, and Lloyd 1995 for background information.) For intermediate dispersal rates d (around 0.3) and demographic parameters such that the local system (8) shows periodic or chaotic fluctuations, system (10) typically has two coexisting population dynamic attractors [see Doebeli, 1998, and the references therein]. One of them is an in–phase chaotic attractor, where the two local population densities are always identical to each other, and move on an aperiodic trajectory. The other is an out–of–phase period-two attractor, where the two local densities are always different from each other, and alternate between a higher and a lower value. The separatrix of the basins of attraction of these two attractors can have a very complicated shape [Hastings, 1993], which makes the dynamics of the system very sensitive to the initial conditions. As the dispersal rate increases, the basin of attraction of the in–phase chaotic attractor grows (until the 2-cycle has disappeared entirely).

So we see that the dispersal rate greatly influences the ecological dynamics of the metapopulation system.

Evolutionary dynamics

We can study evolution of dispersal in this metapopulation system (10) by analyzing the dynamics which result after introduction of an invader phenotype in low densities into a two-patch system governed by a resident phenotype. The resident and the invader differ only by their dispersal rates. That is, we study the system

$$\begin{aligned}
x_t^{\text{res}} &= (1-d^{\text{res}})\, x_{t+1}^{\text{res}}\, g(x_{t+1}) + s\, d^{\text{res}}\, y_{t+1}^{\text{res}}\, g(y_{t+1}) \\
y_t^{\text{res}} &= (1-d^{\text{res}})\, y_{t+1}^{\text{res}}\, g(y_{t+1}) + s\, d^{\text{res}}\, x_{t+1}^{\text{res}}\, g(x_{t+1}) \\
x_t^{\text{inv}} &= (1-d^{\text{inv}})\, x_{t+1}^{\text{inv}}\, g(x_{t+1}) + s\, d^{\text{inv}}\, y_{t+1}^{\text{inv}}\, g(y_{t+1}) \\
y_t^{\text{inv}} &= (1-d^{\text{inv}})\, y_{t+1}^{\text{inv}}\, g(y_{t+1}) + s\, d^{\text{inv}}\, x_{t+1}^{\text{inv}}\, g(x_{t+1})\ ,
\end{aligned} \tag{11}$$

where *res* stands for resident and *inv* for invader. The local densities of each phenotype in each patch at time t we denote by x_t^{res}, y_t^{res}, x_t^{inv} and y_t^{inv}, respectively, and the total local densities are denoted by $x_t = x_t^{\text{res}} + x_t^{\text{inv}}$, and $y_t = y_t^{\text{res}} + y_t^{\text{inv}}$ (*i.e.*, we assume that the two phenotypes are equally affected by each other's densities).

We study the dynamics of invading phenotypes numerically by initializing the system with some positive densities $(x_0^{\text{res}}, y_0^{\text{res}})$ of the resident type, running the system for T time steps to let the transients disappear, and then introducing the invader type in low densities $(x_T^{\text{inv}}, y_T^{\text{inv}})$.

If there is no cost to dispersal ($s = 1$), we can make some straightforward predictions. If the resident dynamics occur on the in–phase chaotic attractor, in each time step densities in both patches will be equal. In particular, the intraspecific competition due to density dependence in the two patches will be equal, and consequently dispersal will be a neutral trait. On the other hand, if the resident oscillates out of phase, on the 2-cycle, then any type with a higher dispersal rate than the resident can invade. (In Doebeli & Ruxton 1997 this is proved analytically.) Summarizing, if there is only temporal, but no spatial, variation in population density between the patches, then selection pressure on the dispersal rate is zero while if there is spatial as well as temporal variation then it pays to disperse more. Therefore, there is an interaction between the ecological and the adaptive dynamics of the metapopulation system: Selection

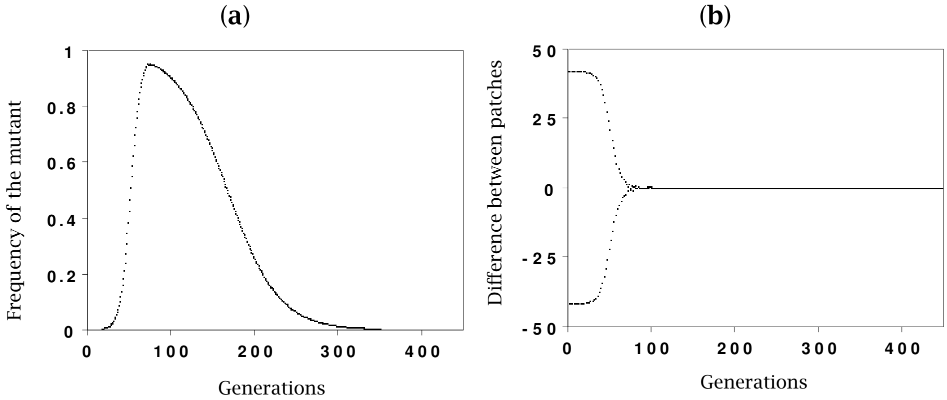

Figure 4: Invasion and extinction in a deterministic metapopulation system, of a mutant with a higher dispersal rate than the resident, accompanied by an attractor shift of the resident system. Frequency of the mutant phenotype (panel **a**) and difference of the total population densities x_t and y_t (panel **b**) as functions of time. The mutant's frequency is defined as $(x_t^{\text{inv}} + y_t^{\text{inv}})/(x_t + y_t)$. Parameters: dispersal rates $d^{\text{res}} = 0.33$ and $d^{\text{inv}} = 0.4$; survival rate for dispersers $s = 0.6$; demographic parameters in (9) $\lambda = 0.7$, $a = 0.1$, and $b = 5.83$.

pressures on dispersal rates depend on the ecological dynamics, and the ensuing evolutionary change in dispersal rates in turn may change the ecological dynamics, and hence the selection pressure on dispersal rates.

The situation becomes different if we introduce a cost to dispersal ($s < 1$). On the in–phase chaotic attractor, selective neutrality is now broken: it pays to disperse less, thus avoiding the mortality associated with dispersal. On the out–of–phase 2-cycle, however, mutants with a higher dispersal rate can still invade as long as the mutant dispersal rate and the cost to dispersal are not too high. (This can be checked numerically as well as analytically: see Doebeli & Ruxton 1997, and Doebeli 1998.)

The resident strikes back II

With a cost to dispersal, another 'resident strikes back' scenario is possible, which we illustrate with a typical numerical experiment in Figure 4. We start with a resident phenotype in a metapopulation with two coexisting attractors, as described above. The resident oscillates out of phase, on the 2-cycle. In Figure 4 a, we see a mutant phenotype with a higher dispersal rate first invade and increase in frequency. When the mutant really dominates the system it induces, due to its higher dispersal rate, an attractor shift from the out-of–phase 2-cycle to the in–phase chaotic attractor. But now, as soon as the in–phase attractor has been approached, the mutant frequency starts to decline, because the mutant suffers more from the dispersal-associated mortality than the resident. Moreover, as the system now moves near the in–phase attractor, where the resident with its lower dispersal rate is at an advantage, nothing can save the mutant from extinction. The phase of the dynamics is depicted in Figure 4 b. The difference between the local densities, $x_t - y_t$, is symmetric and non-zero at the onset of the invasion, and has changed to zero when the mutant frequency starts declining. Only a reverse attractor switch back to the out-of-phase attractor, could make conditions for the mutant favourable again. But there is no force present that causes this to happen, and the system remains in the basin of the in-phase attractor.

In the experiment described above, the dispersal rate of the mutant was high enough for the out-of-phase attractor to vanish if the mutant dominates the system. In other words, the resident and the mutant dispersal rates lie on opposite sides of the bifurcation point in phenotype space where the out-of-phase attractor vanishes. For mutant dispersal rates which differ only very little from the resident value, both attractors would be present, and there would be no attractor switch induced by the mutant. The result of such an invasion would be replacement of the resident by the mutant, while the system keeps oscillating on the (continuation of the) out-of-phase 2-cycle.

Adding stochasticity: cyclic evolutionary dynamics

Due to the deterministic nature of the systems considered so far in this section, an initial condition with equal densities in both subpopulations would keep the metapopulation system (4) on an in-phase trajectory forever. As the in-phase attractor of system (4) is locally asymptotically stable for the parameter values considered, small perturbations would bring the system back to the attractor again. So this deterministic nature is not the reason that the resident keeps in phase after it struck back.

But to what extent is the 'resident strikes back' scenario as depicted in Figure 4 robust against the effects of stochastic noise? To answer this question, we introduce stochasticity by replacing the next-generation local population densities $x_{t-1}^{\text{res}}\, g(x_{t-1})$, $y_{t-1}^{\text{res}}\, g(y_{t-1})$, $x_{t-1}^{\text{inv}}\, g(x_{t-1})$ and $y_{t-1}^{\text{inv}}\, g(y_{t-1})$ appearing in the right hand side of (11) by random variables. These variables are drawn from Gaussian distributions whose means are equal to the values generated by the deterministic recipe, and whose variances are some fixed proportion, say p, of the means. The Gaussian distributions are truncated so as to avoid negative population densities.

The stochastic version of (10) no longer has two separate attractors but a single stochastic attractor, which can be described as an invariant measure [Ruelle, 1989]. This invariant measure can be thought of as a probability distribution for the density of the population. It has two 'peaks', corresponding to the in-phase and the out-of-phase attractors of the deterministic system (10), and low but non-zero 'valleys', corresponding to the stochastic transitions between the basins of attraction of these two attractors.

If the noise level is low, the expected time until a stochastic jump to the other attractor component occurs is long, and consequently the orbit will move on each component for a long time. So if we now turn to the stochastic version of (11), a resident oscillating on the out-of-phase part typically remains there long enough to enable a more-dispersing mutant to invade. As soon as the invader frequency is high enough the system shifts to the approximate in-phase part, and remains there long enough to let the invader go extinct. A realization of this situation is shown in Figure 5. We see that, due to the noise, the shift to the (now approximate) in-phase dynamics occurs earlier than in the deterministic case, resulting in a lower maximum frequency for the mutant.

If the noise level is further increased, the mean times spent on each attractor

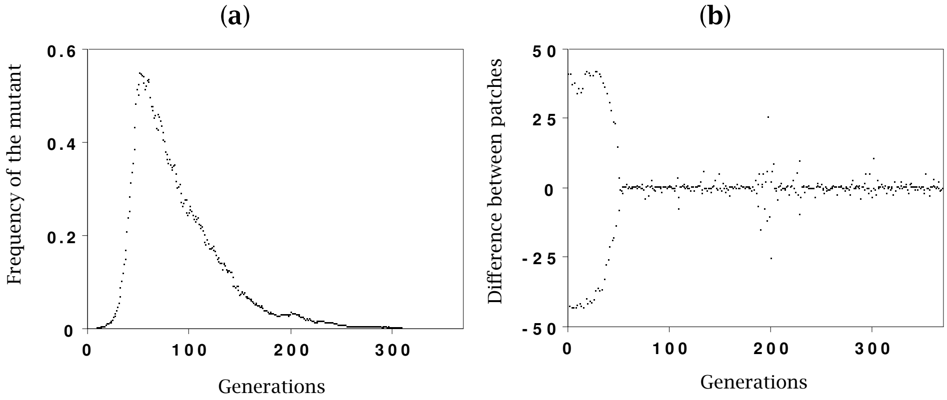

Figure 5: The same experiment as in Figure 4, with a low level of stochastic noise added. Frequency of the mutant phenotype (panel **a**) and difference of the total population densities x_t and y_t (panel **b**) as functions of time. Parameters: noise level $p = 0.05$; remaining parameters are the same as in Figure 4.

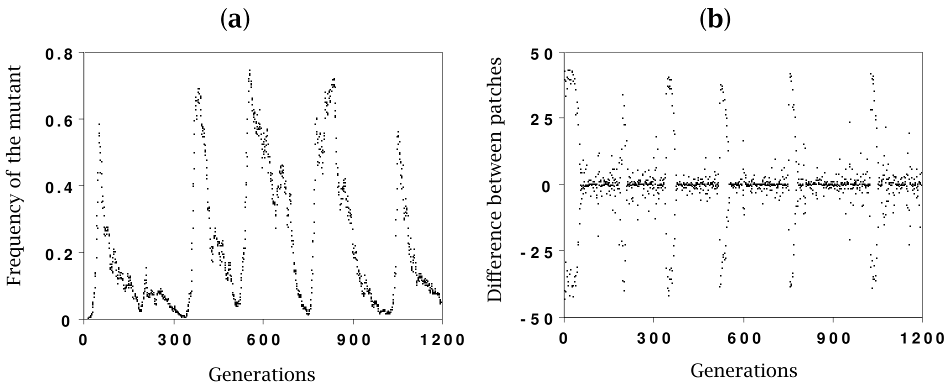

Figure 6: The same experiment as in Figure 5, with more stochastic noise added. Frequency of the mutant phenotype (panel **a**) and difference of the total population densities x_t and y_t (panel **b**) as functions of time. Parameters: noise level $p = 0.1$; remaining parameters are the same as in Figure 4.

component decrease. It is now very probable that the resident switches from the in–phase part, where the system was put on after the invader had penetrated, back to the out–of–phase part, while the mutant is still present in the population. In that case the mutant is once again at an advantage, whereupon it can increase in frequency again. This is likely to happen repeatedly, resulting in cyclic adaptive dynamics. A typical realization of this scenario is depicted in Figure 6.

4 Conclusions and discussion

In both examples, we saw that successful invasion in one attractor, with the invader population growing to an appreciable size, can be followed by extinction of the former invader, ultimately leading the resident to another attractor. We also found mutual invasibility of 'resident' and 'invader', yet without a protected polymorphism (*i.e.*, no internal attractor).

An important conclusion is that an evolutionary argument based on steady-state analysis, as is most frequently used [but see also Metz *et al.*, 1992, Gatto, 1993, Rand *et al.*, 1994, Ferrière & Gatto, 1995], may yield misleading conclusions when it is extended to parameter regions in which the population actually fluctuates. This is well known in the context of unpredictable environments caused by a fluctuating external driver, where risk aversion or ‘bet hedging’ gives advantages to strategies that would be inferior in a steady world [Tuljapurkar, 1990, 1994]. In contrast, in the examples presented here a more endogenous feedback mechanism is at work. Conditions first are favourable for the mutant to invade and increase in numbers, but by doing so the mutant changes the environment in a very unusual way, inducing a shift (or switch) in the population attractor(s) that favours the resident and enables the latter to take over again, after which the mutant is, as a rule, not able to persist. This resilience phenomenon has its roots in the coexistence of multiple population-dynamic attractors and the different population-dynamic feedback properties of different trait values, that cause a peculiar eco-evolutionary interaction. In the age–at–maturation context it is a matter of resonance and phase-tracking, with the invader taking advantage of its better synchronization with the good years, and in the dispersal context it is the interplay of spatio- and temporal inhomogeneity that gives the invader its temporary fitness advantage.

We emphasize that the resilience phenomenon is possible only when invasion exponents are multi-valued, as a result of coexisting attractors. The latter can in particular be expected whenever the population consists of subpopulations that interact only weakly or not at all before a mutant appears. That condition was clearly fulfilled in both examples presented here as well as in Van Dooren & Metz [1998], who show another case of multi-valued invasion functions, in the context of temporally structured populations.

It is well known that successful invasion of a mutant phenotype need not necessarily lead to replacement, as the mutant can lose its initial advantage, due to frequency- and density dependence incorporated in the population-dynamic feedback loop. For example, invasion of a mutant can transform a resident population at a stable equilibrium into a polymorphic population exhibiting intermittent chaos, in which the polymorphic population is again at a steady state for most of the time, but this state is interrupted by periods of wild fluctuations [Doebeli, 1994]. During these intermittent burst periods the mutant can reach very low frequencies and may be threatened by extinction due to chance events. Deterministically however, the mutant as well as the resident persist.

In the present examples, in contrast, successful invasion combined with uninvasibility under role reversal of invader and resident need not even lead to establishment of the mutant in a polymorphic population state. We have already argued that “ESS” is an awkward acronym for what it is supposed to cover. Our examples add another question about terminology in this respect. Should we call a strategy an ESS (or, more accurately, a non-invasible strategy) when it, as a resident, ultimately outcompetes every invader, even though the invader population may first reach a non-negligible size? We coin the term ‘invasible yet invincible’ for such strategies.

The invasion-oriented approach is a powerful tool that has increased our comprehension of phenotypic substitutions considerably. But the coexistence of attractors complicates the idea of representing the adaptive dynamics as a trait substitution sequence driven by successive mutant invasions. So the question is raised under what conditions initial invasion dynamics can successfully predict the fate of a rare mutant.

Will stochastic noise repair the predictive power of the invasion functions? With enough noise there will be no multiple attractors and consequently no attractor shifts. However, this sounds to us like defining the problem out of existence. Moreover, the addition of life-history noise in the salmon example, and of environmental noise in the metapopulation example, may restore the advantage of the mutant once it becomes rare again and lead to cyclic adaptive dynamics. In our view the cyclic dynamics with long periods of low mutant densities, that we observed in the experiments with noise, are just another manifestation of the mechanism that promotes exclusion of the initially successful invader.

Will the assumption that mutants originate from the wild-type resident only with small mutational steps rescue the trait substitution paradigm? In that case the phenomenon of sudden invasion-driven attractor shifts will be replaced by a resident phenotype-driven continuation of the attractor, and the resident can only strike back when the system is close to catastrophic population-dynamical events. With infinitely small step sizes, the probability that the latter will happen is infinitely small. However, one can argue that the restriction to small steps is not a biologically valid or meaningful assumption in many traits, such as the ones considered here.

In our opinion, this is a strong motivation to work with traits that allow for a mechanistic, rather than phenomenological, interpretation. For instance, it seems reasonable to assume that salmon base the irreversible transition to prepare for the return to fresh water on some indicator of their physi(ologi)cal condition, like size. In combination with a stochastic food supply, or a probabilistic description of growth, this then may easily lead to some returning at different ages than others.

Another related point is that the need to consider genetics [see also Eshel, this volume, Van Dooren, this volume, Doebeli & Dieckmann, this volume, Kisdi & Geritz, this volume] may be bigger when the trait relates to spatio-temporal inhomogeneity while population dynamics create fluctuations, since the resonance phenomenon as well as dispersal variability has assortative mating as a side effect. For the salmon case, Kaitala & Getz [1995] already noted that spatial heterogeneity may easily lead to assortative mating.

Of course it is important to find out how general these examples are. But they are at least theoretically possible, and if adaptive dynamics invasion functions are to be robust, their limitations should be evaluated in detail.

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