

Invasion of rare mutants does not imply their evolutionary success: a counterexample from metapopulation theory

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1. Introduction

It is common in evolutionary theory to assume that a mutant type which when rare has a long term growth rate that is larger than 1 can establish itself permanently in the resident population in which the mutant's growth rate is measured. The underlying argument goes roughly as follows. If the long term growth of the rare mutant is larger than 1, then the mutant initially increases in numbers as well as in frequency (the long term growth rate of the resident is equal to 1, because the resident is assumed to neither go extinct nor increase without bounds). As the mutant type becomes common, the ecological determinants of the mutant's growth rate may change due to frequency and density dependence, and the mutant's frequency in the population may decrease again. But every time the mutant is sufficiently rare, one is back in the original situation with a mutant growth rate that is larger than 1. Thus, once the mutant has appeared, its frequency may fluctuate, but it will never fall below a certain threshold, and the mutant will remain in the population. (Of course, the mutant may also just replace the resident.)

For this argument it is necessary to assume that the system always relaxes to the same state when the mutant is rare. Here I describe an example where this assumption is violated. In this example, an initially rare mutant invades a resident population, reaches very high frequencies, and then drops down to very low frequencies again. But instead of now increasing again as in the previous argument, the mutant has changed the system in such a way that when the mutant is rare again conditions are unfavourable for it, and it goes extinct. The resident population "remembers" the invasion of the mutant by being in a state that differs from the original one when the mutant becomes rare again. Thus, in a sense the mutant drives itself to extinction: when initially rare, it has a long term growth rate larger than 1, but invasion produces conditions that doom it to extinction.

The example is set in an ecological framework and comes from metapopulation dynamics, a field that has attracted a lot of attention in recent years (for an overview, see Hanski and Gilpin, 1997). I will consider evolutionary competition between phenotypes with different dispersal rates in a two patch metapopulation model. What follows is not an exhaustive treatment of the complex behaviour of this model. Rather, I want to illustrate the possibility of an interesting evolutionary phenomenon by means of a specific example coming from a widely used ecological theory.

2. The example

The ecological model is set in discrete time and describes a system of two local populations that are coupled by dispersal. In each generation, there is density dependent reproduction in each patch, followed by dispersal to the other patch. Reproduction is modeled by a difference equation

$$N_{t+1} = f(N_t) \cdot N_t, \quad (1)$$

where $f(N)$ is the reproductive output per individual if the (local) density in a patch is N . The particular form of the function $f(N)$ is not important for the results below as long as this function permits non-equilibrium dynamics for model (1). Here I use an equation from Maynard Smith and Slatkin (1973):

$$f(N) = \frac{\lambda}{1 + (aN)^b}, \quad (2)$$

but other equations such as the logistic equation, the Ricker equation (Ricker, 1954) or Hassell's equation (Hassell, 1975) would work equally well. The parameters λ , a , and b in (2) are demographic parameters describing the intrinsic growth rate and the type and the strength of the competitive interactions that lead to density dependence. Depending on these parameters, model (1) can exhibit various types of dynamics, including stable equilibrium dynamics, periodic dynamics, and chaos (May and Oster, 1976). For more detailed discussions of the ecological significance of the demographic parameters see e.g. Hassell et al. (1976) or Bellows (1981).

In the sequel, I assume that the two habitat patches of the metapopulation are ecologically identical, i.e., that the function $f(N)$ has the same parameters in the two patches. I further assume that the rate of dispersal between the two patches is given by a number d which describes the proportion of individuals that move from each patch to the other patch. Let N_t and M_t be the population densities in the two patches at time t . Then, according to what was said above, the dynamics of the metapopulation are given by

$$\begin{aligned} N_{t+1} &= (1-d) \cdot f(N_t) \cdot N_t + d \cdot f(M_t) \cdot M_t \\ M_{t+1} &= (1-d) \cdot f(M_t) \cdot M_t + d \cdot f(N_t) \cdot N_t. \end{aligned} \quad (3)$$

The dynamics of models of the form (3) have been studied quite extensively by various authors (Hastings, 1993; Gyllenberg et al., 1993; Doebeli, 1995; Lloyd, 1995). Here I concentrate on one particular phenomenon that occurs for intermediate dispersal rates d around 0.3 and for demographic parameters in eq. (2) that lead to complex local dynamics given by eq. (1). In this case, system (3) typically has two coexisting population dynamic attractors (Hastings, 1993). One of them is a chaotic in-phase attractor, on which the two local population densities are always identical to each other and move on an aperiodic trajectory. The other one is an out-of-phase 2-cycle, on which each of the local populations alternates between two densities with the two local populations being out of phase. The basins of attraction of the in-phase and of the out-of-phase attractors can have very complicated boundaries, which leads to sensitive dependence on initial population densities of the final state of the system (Hastings, 1993; Lloyd, 1995). As the dispersal rate d is increased the basin of attraction of the out-of-phase attractor gets smaller, and this attractor disappears entirely if dispersal rates are high enough. This influence of the dispersal rate on the ecological dynamics is important for the following evolutionary considerations.

Given the ecological scenario, evolutionary competition between two different dispersal phenotypes can be studied by assuming that the ecological conditions given by the parameters in eq. (2) are the same for both phenotypes, but that these phenotypes differ in their dispersal rate. I denote the two phenotypes by superscripts *res* for resident and *mut* for mutant. Thus the two phenotypes are given by two dispersal rates d^{res} and d^{mut} . Extending system (3) to a model for two phenotypes is straightforward and yields:

$$\begin{aligned}
 N_{t+1}^{res} &= (1 - d^{res}) \cdot f(N_t) \cdot N_t^{res} + d^{res} \cdot f(M_t) \cdot M_t^{res} \\
 M_{t+1}^{res} &= (1 - d^{res}) \cdot f(M_t) \cdot M_t^{res} + d^{res} \cdot f(N_t) \cdot N_t^{res}, \\
 N_{t+1}^{mut} &= (1 - d^{mut}) \cdot f(N_t) \cdot N_t^{mut} + d^{mut} \cdot f(M_t) \cdot M_t^{mut} \\
 M_{t+1}^{mut} &= (1 - d^{mut}) \cdot f(M_t) \cdot M_t^{mut} + d^{mut} \cdot f(N_t) \cdot N_t^{mut}.
 \end{aligned} \tag{4}$$

Here N_t^{res} , M_t^{res} denote the local densities of phenotype *res* at time t , N_t^{mut} , M_t^{mut} denote the local densities of phenotype *mut* in the two patches, and $N_t = N_t^{res} + N_t^{mut}$ and $M_t = M_t^{res} + M_t^{mut}$ are the sum of the densities of the two phenotypes in each patch. Thus, for model (4) I have assumed that the reproductive output $f(N)$ in the two patches depends on the sum of the densities of the two phenotypes, i.e., that as far as reproduction is concerned, the two phenotypes are equally affected by their own and by the other phenotype's density. The phenotypes only differ in their dispersal rates. To analyse evolution in this system, I assume that it first consists of the resident phenotype alone, and that the mutant phenotype appears in low frequency at some point in time. For numerical simulations of system (4) this means that one starts with some initial condition (N_0^{res} , M_0^{res} , $N_0^{mut} = 0$, $M_0^{mut} = 0$) at time 0, then runs the system for a number of generations, and then introduces a small amount of mutants ($N_T^{mut} = \epsilon$, $M_T^{mut} = \delta$) at some time T , where ϵ and δ are some small fraction of the resident densities N_T^{res} and M_T^{mut} in the two patches. One can then follow the fate of the mutant numerically.

However, some situations can be understood analytically. First of all, if the resident moves on the in-phase attractor described above, then the dispersal rate must be an evolutionarily neutral trait: since the densities in the two patches are identical at all times, the reproductive output is also the same in the two patches at all times, and hence it does not pay to either migrate less or more between the patches. Thus, if there is no spatial variation in population abundance between patches, then the selection pressure on dispersal rates is zero, even if there is temporal variation in each patch.

Second, it can be shown analytically that if the resident moves on the out-of-phase 2-cycle described earlier, then any mutant with a higher dispersal rate than that of the resident can invade (Doebeli and Ruxton, 1997). That is, the long term growth rate of any rare mutant with a higher dispersal rate than the resident is larger than 1. In particular, if there is temporal as well as spatial variation, it may pay to disperse more.

The two evolutionary scenarios described, selection for higher dispersal rates and neutrality, can lead to the following series of events in model (4): if we start out with a resident moving on an out-of-phase 2-cycle, a mutant with a higher dispersal rate can invade and increase in frequency. However, due to its higher dispersal rate, when the mutant reaches a high enough frequency, it induces an attractor shift onto the in-phase attractor. On the in-phase attractor, both the resident and the mutant have local densities that are equal in the two patches at all times. Therefore, the reproductive output in the two patches is the same at all times, and as a consequence there is no advantage anymore to either lower or higher dispersal, and evolution comes to a halt, i.e., the frequencies of the two types remain constant.

Thus, there is an interaction between ecological and evolutionary dynamics: when the resident is on the out-of-phase 2-cycle, a higher dispersal mutant can invade, and the higher dispersal rate shifts the dynamics onto the in-phase attractor. To get to the example I am driving at, we have to make this interaction a bit more interesting by introducing a cost of dispersal. For this I assume that dispersing individuals survive only with some probability $s < 1$, which is the same for *res* and for *mut*. This changes system (3) to

$$\begin{aligned} N_{t+1} &= (1-d) \cdot f(N_t) \cdot N_t + s \cdot d \cdot f(M_t) \cdot M_t \\ M_{t+1} &= (1-d) \cdot f(M_t) \cdot M_t + s \cdot d \cdot f(N_t) \cdot N_t \end{aligned} \quad (5)$$

and system (4) to

$$\begin{aligned} N_{t+1}^{res} &= (1-d^{res}) \cdot f(N_t) \cdot N_t^{res} + s \cdot d^{res} \cdot f(M_t) \cdot M_t^{res} \\ M_{t+1}^{res} &= (1-d^{res}) \cdot f(M_t) \cdot M_t^{res} + s \cdot d^{res} \cdot f(N_t) \cdot N_t^{res}, \\ N_{t+1}^{mut} &= (1-d^{mut}) \cdot f(N_t) \cdot N_t^{mut} + s \cdot d^{mut} \cdot f(M_t) \cdot M_t^{mut} \\ M_{t+1}^{mut} &= (1-d^{mut}) \cdot f(M_t) \cdot M_t^{mut} + s \cdot d^{mut} \cdot f(N_t) \cdot N_t^{mut}. \end{aligned} \quad (6)$$

For a single phenotype given by system (5) it is still true that for intermediate dispersal rates a chaotic in-phase attractor coexists with an out-of-phase 2-cycle.

But now the evolutionary stage set by system (6) is different, because higher dispersal rates have an inherent disadvantage due to the cost of dispersal.

On the one hand, selective neutrality on the in-phase attractor is now broken: if the local densities are synchronous and hence reproductive outputs identical in the two patches at all times, it clearly pays to disperse less, because this leads to lower mortality due to dispersal. On the other hand, even with a cost to dispersal a resident on the out-of-phase 2-cycle can be invaded by a mutant with a higher dispersal rate as long as the cost to dispersal and the mutant dispersal rate are not too high. This can be checked numerically as well as analytically.

This new setup can now lead to the following evolutionary scenario. We start out with a resident on the out-of-phase cycle. Despite the cost, a mutant with a higher dispersal rate can invade. As before, invasion shifts the metapopulation onto the in-phase attractor. But now, as soon as the system moves on this attractor, the frequency of the mutant starts to decrease as described above, because the mortality due to dispersal is higher for the mutant. Thus the mutant becomes rare again. But as it does so, nothing saves it from extinction, because the system remains on the in-phase attractor: there is nothing that would push the resident back on the out-of-phase cycle and make conditions favourable again for the mutant. In this scenario, the mutant can invade, but it cannot establish itself permanently in the population, because invasion changes the state of the resident such that the mutant becomes rare again, and when it does reinvasion is no longer possible. The invasion attempt has left a trace in the resident population in the form of a switch from the out-of-phase attractor, on which the long term growth rate of the mutant is larger than 1 when rare, to the in-phase attractor, on which the long term growth rate of the mutant is smaller than 1.

Figure 1 illustrates a realization of this eco-evolutionary scenario which is typical for a range of parameters in model (6). Figure 1a shows the frequency of the mutant as a function of time. After it is introduced, its frequency reaches very high values close to 1. At this point, the mutant dominates the system, and its high dispersal rate induces synchronous, in-phase metapopulation dynamics. The synchrony of the dynamics is depicted in Figure 1b, which shows the difference of the population densities in the two patches, $N_t - M_t$, as a function of time. This difference is non-zero at the beginning, and the point where it becomes zero marks the onset of in-phase dynamics and of the downfall of the mutant. Thereafter, the mutant goes extinct, because the resident remains on the in-phase attractor.

The phenotypes used for Figure 1 were chosen such that the dispersal rate of the resident allows for two coexisting population dynamic attractors, namely the out-of-phase two cycle and the in-phase chaotic attractor, whereas the dispersal rate of the mutant is high enough for the out-of-phase attractor to have vanished, so that if the mutant dispersal rate were used for the single phenotype model (5), only the chaotic in-phase attractor would be present. In other words, the resident and mutant dispersal rates lie on opposite sides of the bifurcation point in phenotype space at which the out-of-phase 2-cycle disappears. This is not a coincidence: if both the resident and the mutant dispersal rates would allow the in-phase and the out-of-phase attractors to coexist (i.e. if the mutant dispersal rate would be low

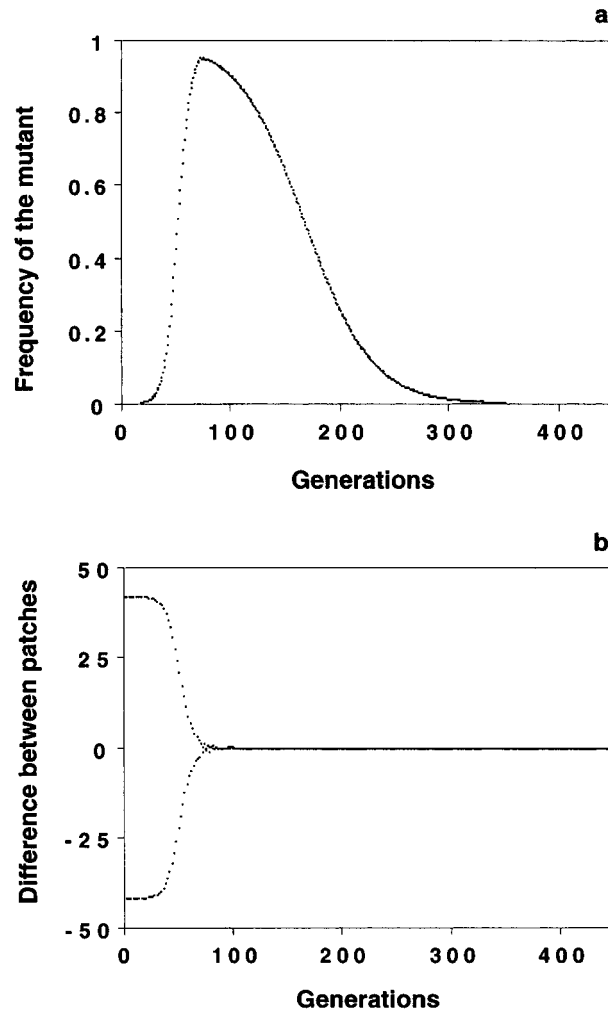


Fig. 1. Invasion of a mutant leads to its extinction. 1a shows the frequency of the mutant in successive generations after it has been introduced into a resident population that moves on an out-of-phase 2-cycle, which is seen in 1b as symmetric non-zero density differences in the two patches. On this attractor, the long term growth rate of the mutant is larger than 1 when the mutant is rare, and hence the mutant can invade. It reaches a frequency close to 1, at which point the system switches to in-phase dynamics, seen in 1b as zero density difference between the two patches. On the in-phase attractor, the mutant has a disadvantage due to the cost of dispersal. Because there is no switch back to the out-of-phase attractor as the mutant gets rare, the mutant goes extinct. The parameters for the figure were $\lambda = 7$, $a = 0.1$ and $b = 5.83$ in eq. (2); the dispersal rate of the resident was $d^{res} = 0.33$, and that of the mutant was $d^{mut} = 0.4$; the survival rate of dispersers, was $s = 0.6$; the mutant was assumed extinct, and the simulation stopped, when its frequency fell below 10^{-4} .

enough to lie on the same side of the bifurcation point as the resident dispersal rate), then the trait substitution from resident to mutant would not induce an attractor switch from the out-of-phase to the in-phase attractor, at least not if the difference between the resident and the mutant were small. In this case, the higher dispersal mutant would still be able to invade a resident on the out-of-phase attractor, but because the perturbation to the system that is caused by the appearance of the mutant is small, the system would remain on the out-of-phase attractor. That is, the mutant would simply replace the resident and then move itself on the out-of-phase 2-cycle.

Thus, the phenomenon shown in Figure 1 can only be observed if the mutant dispersal rate bridges the gap across the bifurcation point where the out-of-phase cycle disappears. In this case, once the mutant becomes common the only dynamic possibility for the population is to move on the in-phase attractor, and hence a switch to this attractor occurs. For this to happen the difference between the resident and the mutant dispersal rates may be small (as e.g. in Fig. 1), but to reiterate, the phenotypes must be such that the resident dispersal rate is low enough to allow for two coexisting attractors, whereas the mutant dispersal rate is high enough to lie above the bifurcation point where one of these attractors, the out-of-phase cycle, disappears.

If one starts the single phenotype system (5) with identical initial densities in the two patches, $N_0 = M_0$, then the system remains in phase for all times, even if the corresponding trajectory is not an attractor (i.e., even if the system would never reach in-phase dynamics if started from unequal initial local densities). Therefore, in principle results as those shown in Figure 1 might be an artifact that is due to the deterministic nature of system (6): as the mutant gets rare again after it has induced synchronous dynamics in the system, the resident might only remain in phase because there is no noise in the system. With noise, the resident would be thrown off the in-phase dynamics when the mutant becomes rare, and if the in-phase dynamics are not attracting, the resident would move back to the attracting out-of-phase 2-cycle, thus reinstalling the conditions under which the mutant can invade. This would lead to oscillatory dynamics for the frequency of the mutant.

However, as mentioned, for the parameters used for Figure 1 the in-phase dynamics of the resident are indeed an attractor. Therefore, the evolutionary scenario of Fig. 1 is robust against noise, at least to some extent. There are several ways to introduce noise in system (6), one of the easiest being to replace the quantities $f(N_t) \cdot N_t^{res}$, $f(N_t) \cdot N_t^{mut}$, $f(M_t) \cdot M_t^{res}$, and $f(M_t) \cdot M_t^{mut}$ appearing on the right hand side in these equations (i.e., the local densities of the phenotypes after reproduction) by random variables that are drawn from Gaussian distributions whose means are equal to the replaced deterministic quantities, and whose variances are some fixed proportion p of these means. If the proportion p is not too large, say $<20\%$, the chance of getting nonsensical negative values through this procedure is very small, and if a negative value results nevertheless, the randomizing procedure is simply repeated until a positive value is obtained. If noise is introduced in this way, the two deterministic attractors in the resident population corresponding to the in-phase and the out-of-phase dynamics merge to a single

stochastic attractor. This stochastic attractor has two components that correspond to the two deterministic attractors in the noise-free system, one part on which the metapopulation exhibits approximate out-of-phase dynamics, and one part on which it exhibits approximate in-phase dynamics. Due to the noise, the system can jump back and forth between these two parts of the stochastic attractor, because in the presence of noise, the system will eventually cross the boundaries of attraction corresponding to the two attractors in the deterministic system.

However, if the noise level is low, the mean time between such a passage and the next, i.e. the mean time spent on the different parts of the stochastic attractor, is typically long. For example, a resident population that moves on the out-of-phase part typically remains there long enough for a higher dispersal mutant to invade. This is shown in Figure 2. Invasion of higher dispersal mutants is still possible due to the out-of-phase character of the resident dynamics, and as in the deterministic case, invasion of the mutant causes a switch in the metapopulation to approximate in-phase dynamics. Due to the noise, this switch actually occurs earlier than in the deterministic system. With approximate in-phase dynamics, the mutant has a disadvantage due to the cost of dispersal as before, and its frequency decreases, leaving the resident on the in-phase part of the stochastic attractor. Due to the noise, the resident will eventually switch back to the out-of-phase part of the attractor, but if the noise level is low, this takes a long time, during which the mutant has gone effectively extinct. This is also shown in Figure 2, for which I assumed the mutant to be extinct if its frequency has fallen below 10^{-4} . In the run shown in Figure 2, this happened before the resident left the in-phase part of the stochastic attractor, so that overall, a very similar scenario as in the deterministic case resulted, a scenario in which the mutant invades, induces a switch to in-phase dynamics, and therefore goes extinct again.

If the noise level is higher, the mean time spent on the in-phase part of the stochastic resident attractor before passage to the out-of-phase component becomes smaller. As a consequence, the resident can switch from the in-phase part, on which it is left as the mutant gets rare again, back to the out-of-phase part before the mutant falls below the threshold frequency for extinction. This resets the system to the initial conditions under which the mutant could invade in the first place. Thus, the switch from out-of-phase to in-phase dynamics that is caused by the invasion of the mutant is reversed by stochasticity once the mutant is rare, whereupon the mutant's frequency increases again due to the out-of-phase dynamics of the resident. The result are cyclic evolutionary dynamics, an example of which is shown in Figure 3.

3. Conclusions

The evolutionary scenario described, in which a positive initial growth rate of a rare mutant does not imply the permanent establishment of the mutant, rests on the existence of multiple population dynamic attractors for the resident population, and on the ecological consequences of the evolving traits. When the mutant is rare, its

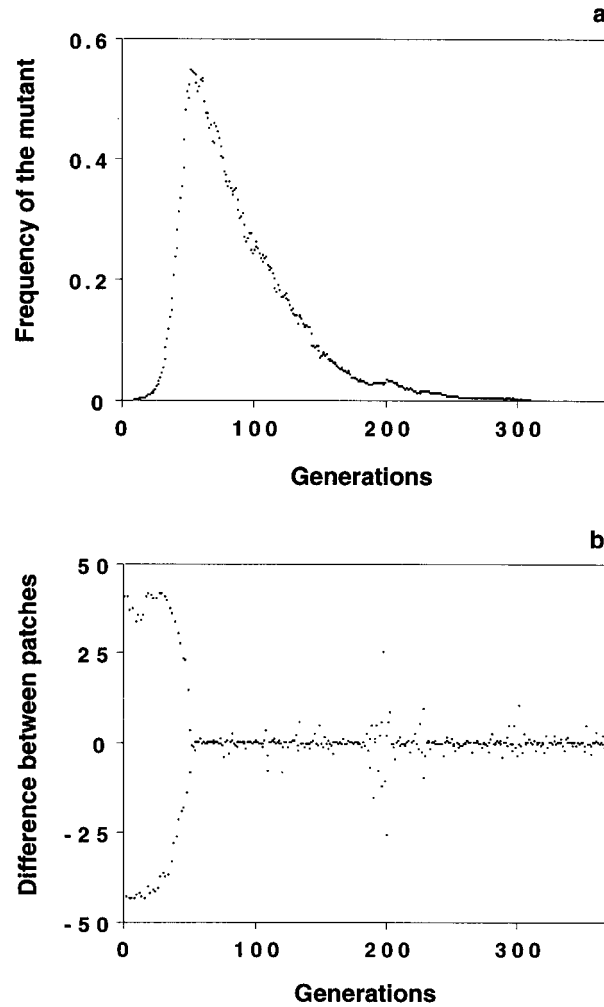


Fig. 2. Same as Figure 1, but with noise in the system. The noise level parameter was set to $p = 0.05$ (see text). The mutant's invasion comes to a halt at lower mutant frequencies than in Fig. 1, because the noise facilitates the switch to in-phase dynamics. After this switch, the system remains close to being synchronous long enough for the mutant's frequency to drop below 10^{-4} , which is when the mutant was assumed to be extinct.

long term growth rate is larger than 1 on one of the resident attractors, implying invasion, while its growth rate when rare is smaller than 1 on the other resident attractor, implying extinction. The crucial point is that because of the dependence of the ecological dynamics on phenotypic properties, here dispersal rates, invasion of the mutant phenotype leads to a switch from the ecological attractor permitting

invasion to the attractor on which the mutant phenotype cannot persist. Because of this interaction between ecological and evolutionary dynamics, invasion ability is not a good criterion for evolutionary persistence in the example presented here.

The reversal from favourable to unfavourable conditions has nothing to do with a change in the external environment of the population, since the demographic

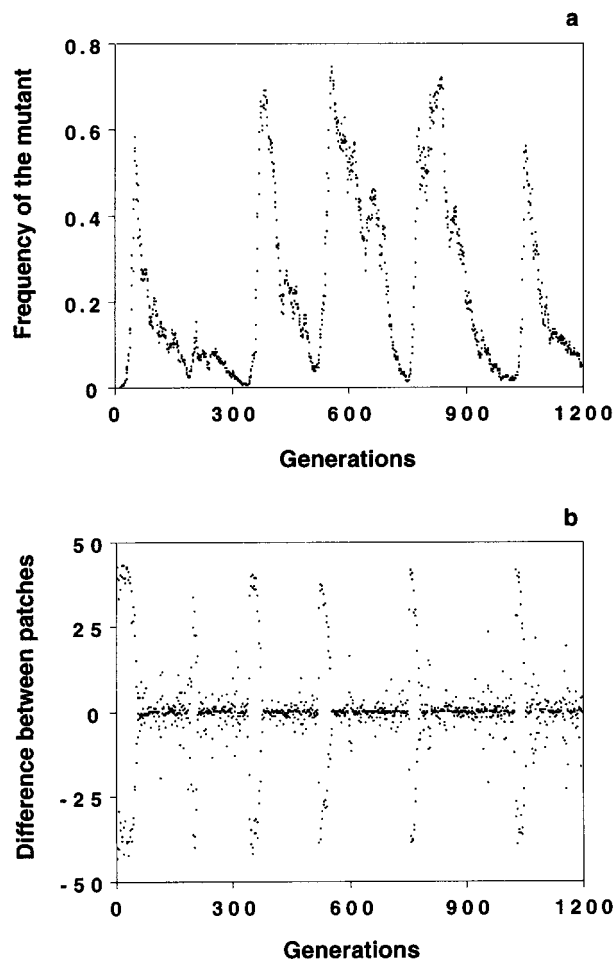


Fig. 3. Same as Figure 2, but with a higher noise level, $p = 0.1$. As long as the mutant is common, the in-phase dynamics are stable against noise because of the mutant's high dispersal rate. However, when the mutant gets rare due to in-phase dynamics, noise induces a switch from the in-phase part of the stochastic resident attractor back to the out-of-phase part. This reinstalls the advantage of the mutant phenotype, and the process starts anew. Cyclic frequency dynamics are the consequence. The switches between the different components of the stochastic attractors can be seen in 3b as intermittent dynamics for the density difference between the two patches.

parameters incorporating these external factors remain constant all along. Rather, this reversal is caused by a change in the "internal environment" that is due to density dependence and is determined by the population dynamic attractors. It is known, albeit not widely, that different population dynamic environments set by the resident can lead to different invasion conditions for a given mutant, i.e., that when there are multiple resident attractors, then the long term growth rate of a rare mutant can vary depending on these attractors. For example, Van Dooren and Metz (1998) studied models of temporally structured populations in which the long term growth rate of a rare mutant may depend on the resident attractor. Moreover, in their models invasion success of a rare mutant may also depend on the point in time at which the mutant appears. For example, if the mutant has a strategy of delaying maturation for one year, and hence only breeds every second year, and if the resident is, say, on a 2-cycle, then the growth rate of the mutant may depend on the point of the resident 2-cycle at which the mutant first appears. This can happen even if there is only one resident attractor.

In addition, it could happen that due to the invasion of the mutant the temporal order of the 2-cycle in the resident population is reversed, leading to unfavourable conditions for the mutant. Before the present paper was written, Diekmann et al. (in press) have worked out such a case in a model for temporally structured salmon populations. In their example, a delaying mutant can invade a resident moving on a 2-cycle if the mutant enters in an even year, and therefore only experiences the even year densities of the resident, but not if it enters the resident population in an odd year. However, as a consequence of the invasion of the mutant, the temporal ordering of the resident densities is reversed, so that the previous odd year resident densities now occur in even years, and vice versa. Since the mutant is still only reproducing in even years, the conditions then become unfavourable, and the mutant goes extinct, because the temporal ordering of the resident 2-cycle does not switch back as the mutant becomes rare. Thus, invasion of the mutant leads to a temporal rearrangement within the resident attractor, which in turn causes the extinction of the mutant because of the mutant's particular spatial structure.

Moreover, Diekmann et al. (in press) also observed that invasion can lead to a switch from the resident 2-cycle permitting invasion to an entirely different attractor on which the mutant again has a disadvantage due to its temporal structure. As in the scenarios described in the present article, this switch leads to the extinction of an initially successful mutant type. The examples of Diekmann et al. (in press) are special in the sense that they are only possible with temporal structure due to delayed maturation. In the examples given here the phenomenon that invasion does not lead to persistence is independent of the temporal structure of the population trajectories and of the point in time at which the mutant appears.

Probably the most common assumption made in evolutionary modeling about invasion scenarios is that "invasion implies fixation" i.e., that if conditions are favourable for a rare mutant, then the mutant phenotype remains advantageous as its frequency increases, and hence drives the resident phenotype to extinction. For example, such an assumption is implicitly made in all evolutionary optimality

models. Of course, it is well known that the presence of the mutant in the population can change the conditions in such a way that an initially favoured phenotype loses its advantage as it becomes common. For example, such negative frequency dependence can occur in game theory models and can lead to polymorphisms with complicated frequency dynamics. Thus, invasion may not imply fixation, and in general models of frequency and density dependent evolution, it is instead often implicitly and less restrictively assumed that invasion only implies permanent establishment of the mutant, at least until further mutations occur (Metz et al., 1996). While the mutant's fate may change temporarily, one then still makes the assumption that whenever the mutant is rare, the resident population is back in the same state that allowed initial invasion of the mutant. The examples given here, as well as those of Diekmann et al. (in press), show that this is not necessarily the case, and that a mutant's invasion may create conditions which lead to its extinction. This may not be a very common phenomenon, but it seems worthwhile to point out that it may occur at least in theory, particularly since the examples described here are in the realm of a very widely used ecological theory.

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References

- Bellows, T. S. Jr. 1981. The descriptive properties of some models for density dependence. *J. Anim. Ecol.* 50: 139–156.
- Diekmann, O., S. D. Mylius and J. R. ten Donkelaar. 1997. Saumon à la Kaitala et Getz, sauce hollandaise. *Evol. Ecol.* (in press).
- Doebeli, M. 1995. Dispersal and dynamics. *Theor. Pop. Biol.* 47: 82–106.
- Doebeli, M. and G. D. Ruxton. 1997. Evolution of dispersal rates in metapopulation models: branching and cyclic dynamics in phenotype space. *Evolution* 51: 1730–1741.
- Gyllenberg, M., G. Söderbacka and S. Ericsson. 1993. Does migration stabilize local population dynamics? Analysis of a discrete metapopulation model. *Math. Biosci.* 118: 25–49.
- Hanski, I.A. and M. E. Gilpin (Eds.) 1997. *Metapopulation Biology: Ecology, Genetics, and Evolution*. Academic Press, San Diego.
- Hassell, M. P. 1975. Density-dependence in single-species models. *J. Anim. Ecol.* 44: 283–296.
- Hassell, M. P., J. H. Lawton and R. M. May. 1976. Patterns of dynamical behaviour in single-species populations. *J. Anim. Ecol.* 45: 471–486.
- Hastings, A. 1993. Complex interactions between dispersal and dynamics: lessons from coupled logistic equations. *Ecology* 74: 1362–1372.
- Lloyd, A. L. 1995. The coupled Logistic map – a simple model for the effects of spatial heterogeneity on population dynamics. *J. Theor. Biol.* 173: 217–230.
- May, R. M. and G. F. Oster. 1976. Bifurcations and dynamic complexity in simple ecological models. *Am. Nat.* 110: 573–599.
- Maynard Smith, J. and M. Slatkin. 1973. The stability of predator-prey systems. *Ecology* 54: 384–391.

- Metz J. A. J., S. A. H. Geritz, G. Meszéna, F. J. A. Jacobs and J. S. van Heerwaarden. 1996. Adaptive dynamics: a geometrical study of the consequences of nearly faithful reproduction, pp 183–231. *In* S. J. van Strien and S. M. Verduyn Lunel (Eds.), *Stochastic and Spatial Structures of Dynamical Systems*. North Holland, Amsterdam.
- Ricker, W. E. 1954. Stock and recruitment. *J. Fish. Res. Bd. Can.* 11: 559–623.
- Van Dooren, T. and J. A. J. Metz. 1998. Delayed maturation in temporally structured populations with non-equilibrium dynamics. *J. evol. biol.* 11: 41–62.

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