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Evolutionary suicide in a discrete-time metapopulation model

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ABSTRACT

Question: Can the Allee effect promote evolutionary suicide by dispersal evolution in a discrete-time metapopulation model?

Mathematical methods: Adaptive dynamics.

Features of model: Metapopulation consisting of infinitely many patches. Local dynamics, dispersal, and catastrophe events defined in discrete time.

Results: Fitness-based calculations show that evolutionary suicide can happen in the model. Evolutionary simulations support the result. After evolutionary branching, dimorphic evolutionary suicide does not occur.

Keywords: adaptive dynamics, Allee effect, dispersal, evolutionary suicide, migration, structured metapopulation.

INTRODUCTION

Many species are known to have gone extinct. These extinctions are often explained by invoking changes in the environment, to which the species has been unable to adapt. An alternative explanation is that the species itself is initially viable, but changes its behaviour because of natural selection in such a way that it can no longer persist. This phenomenon is called 'evolutionary suicide' (Ferrière, 2000), but is also known as Darwinian extinction (Webb, 2003) and evolution to extinction (Dieckmann *et al.*, 1995). [For recent reviews of the phenomenon, see Parvinen (2005) and Rankin and López-Sepulcre (2005).]

For the theoretical analysis of evolutionary suicide in this article, I use the framework of adaptive dynamics (Metz *et al.*, 1992, 1996; Dieckmann and Law, 1996; Geritz *et al.*, 1997, 1998). It is a single mathematical framework for modelling the dynamics of long-term phenotypic evolution in ecologically realistic models. After the introduction of the original concept of an evolutionarily stable strategy (Maynard Smith, 1976), ESS theory has been applied to a wide variety of models, and has resulted in various concepts and techniques of modern ESS theory (e.g. Eshel, 1983; Matsuda, 1985; Van Tienderen and De Jong, 1986; Taylor, 1989; Christiansen, 1991). Such concepts and techniques have been integrated and extended into the adaptive dynamics framework.

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Evolutionary suicide (Ferrière, 2000) means that there exists a trait substitution sequence driven by mutation and selection taking a population toward and across a boundary in the population's trait space beyond which the population cannot persist. Evolutionary suicide has been found in several contexts, including:

- consumer search effort in a resource–consumer model (Matsuda and Abrams, 1994b; Parvinen, 2005);
- an asymmetric competition model (Gyllenberg and Parvinen, 2001);
- dispersal in metapopulation models (Cadet, 1998; Gyllenberg *et al.*, 2002).

It is also possible that the evolving population is viable for all finite strategies, but the evolving strategy tends to infinity, while population size approaches zero, and extinction by chance becomes more and more likely (Matsuda and Abrams, 1994a). Following Parvinen (2005), I will call this phenomenon 'demographically stochastic evolutionary suicide'.

Richard Levins (1969, 1970) introduced the concept of a metapopulation. In general, it is a population of local populations living in habitat patches (Hanski and Gilpin, 1997; Hanski, 1999). Studying adaptive dynamics in the Levins metapopulation as such is difficult, because it is not defined on the individual level. In particular, local population sizes and local population dynamics are not defined. However, they are incorporated in size-structured metapopulation models (Gyllenberg and Metz, 2001; Metz and Gyllenberg, 2001; Parvinen, 2006).

Gyllenberg *et al.* (2002) found evolutionary suicide in a continuous-time metapopulation model (Gyllenberg and Metz, 2001; Metz and Gyllenberg, 2001) under two ecological scenarios. In the first, the catastrophe rate decreases with local population size. In the second, there is an Allee effect in local growth. In this article, I show that the second scenario can result in evolutionary suicide also in the corresponding discrete-time model (Parvinen, 2006). Extinction occurs because the population evolves to disperse too little to be able to colonize empty patches. To determine whether a mutant can invade or not, one has to calculate how it performs in different patches over a long period, because the differences in local population sizes are maintained by catastrophes. The proxy for invasion fitness (basic reproduction ratio) can be efficiently used to discern the invasion ability, but calculating it directly from metapopulation dynamics (either discrete-time or continuous-time) requires very many generations. Therefore, if the calculation of local dynamics is slow, such as the numerical integration of differential equations in the continuous-time model, running evolutionary simulations is not feasible. In the discrete-time metapopulation model, local dynamics can be computed fast. Therefore, one can run evolutionary simulations which support the fitness-based results.

In this article, I show that the bifurcation to evolutionary suicide can happen with respect to many parameters, such as the probability to survive dispersal, the catastrophe probability, and a parameter contributing to fecundity in local growth. Evolutionary branching is possible in this model when fecundity is large enough. In principle, the dimorphic population could evolve towards and across an extinction boundary, like the monomorphic population does in evolutionary suicide. However, I illustrate that a low-dispersal strategy can co-exist with a more frequently dispersing strategy in an unprotected dimorphism, and the extinction boundaries of the dimorphic population are evolutionarily repelling. Therefore, a dimorphic metapopulation will not experience evolutionary suicide after evolutionary branching.

MODEL PRESENTATION AND THEORY OF EVOLUTIONARY SUICIDE

Metapopulation dynamics

Parvinen (2006) presented a discrete-time metapopulation model that consists of an infinite number of different habitat patches. For simplicity, I assume here that there is only one patch type. Patches thus differ in the size and composition of the local populations, but are otherwise equal. In each season, first reproduction occurs. In a patch with a local population of size x, the expected number of offspring each individual gets is $f(x)$. After that, a fraction s of the offspring disperses and enters the disperser pool. Without immigration, the population size in this patch would be $(1 - s)xf(x)$, because I assume that all adults die at the end of the season.

The newly emigrated offspring are not yet able to immigrate into the patches. They will survive to the next season in the disperser pool with probability F, otherwise they die. All other dispersers in the disperser pool will immigrate into a habitat patch. Immigrants choose their patch at random, independently of the local population size. Therefore, the amount of immigrants I_t each patch will receive is equal to the disperser pool size D_t. Alternatively, it could be assumed that dispersers could remain in the dispersal pool for longer. However, Parvinen (2006) showed that metapopulation dynamical equilibria and invasion fitness depend on the events in the dispersal pool only through the probability to survive dispersal, which in this case is equal to F.

Catastrophes occur randomly. I assume that the probability μ that a catastrophe occurs is independent of the local population size. A catastrophe will kill all individuals in the patch, thus setting the local population size to zero. This patch remains habitable, and can be re-colonized by dispersers from the disperser pool. If a catastrophe has not occurred, the local population size of a patch with population size x in the next season is

$$x_{t+1} = (1 - s)f(x_t)x_t + I_t, \tag{1}$$

where I_t is the amount of immigrants each patch will receive.

The disperser pool D consists of emigrants from all patches. To account for all emigrated individuals, it is necessary to know the state of the metapopulation at time t, which is the population size distribution n_t. The quantity $\int_{[x_1,x_2]} n_t(dx)$ is the probability that the local population size is between x_1 and x_2 at time t. Furthermore, $\int_{[0,\infty]} n_t(dx) = 1$. The disperser pool size in the next season will therefore be

$$D_{t+1} = F\int sf(x)xn_t(dx) = I_{t+1}, \tag{2}$$

and is equal to the amount of immigrants I_{t+1} each patch will receive at time $t + 1$.

Adaptive dynamics

Invasion fitness (Metz *et al.*, 1992) is the long-term exponential growth rate $r(s_{\mathrm{mut}}, E_{\mathrm{res}})$ of a rare mutant s_{mut} in an environment E_{res} set by the resident. In the metapopulation setting, it is more convenient to study the basic reproduction ratio R of dispersal generations: Consider a mutant disperser that has just immigrated into a patch. This mutant will experience the environment set by the resident population, and produce offspring accordingly. This mutant and its descendants in the patch will form a clan, which will send dispersers to the disperser pool until a catastrophe wipes out the local population. The expected number of these dispersers is the basic reproduction ratio R of dispersal generations (Gyllenberg and Metz, 2001; Metz and Gyllenberg, 2001). Parvinen (2006) presented this fitness proxy and a fast algorithm to compute it for the corresponding discrete-time metapopulation model.

The basic reproduction ratio $R(s_{\text{mut}}, E_{\text{res}}) > 1$ if and only if the invasion fitness $r(s_{\text{mut}}, E_{\text{res}}) > 0$. This means that the mutant can invade and possibly replace the old resident and become the new resident itself. These mutation–invasion events result in the change of the strategy of the individuals constituting the population.

If no mutant can invade the resident, then the strategy s_{res} of the resident is unbeatable, and it is called an evolutionarily stable strategy (ESS) (Maynard Smith, 1976). When a resident population has reached an evolutionarily stable strategy, all mutants necessarily have lower fitness than the resident, i.e. $r(s_{\text{mut}}, E(s_{\text{res}})) < 0$ for all $s_{\text{mut}} \neq s_{\text{res}}$. Therefore, the resident strategy is a (local) fitness maximum and the selection gradient (i.e. the derivative of invasion fitness with respect to the strategy of the mutant) vanishes at such points,

$$\frac{\partial}{\partial s_{\text{mut}}} r(s_{\text{mut}}, E_{\text{res}}) \bigg|_{s_{\text{mut}} = s_{\text{res}}} = 0. \tag{3}$$

More generally, strategies for which the selection gradient is zero are called evolutionarily singular strategies (Geritz *et al.*, 1998).

A useful graphical tool in the analysis of evolutionary dynamics is a pairwise invasibility plot (Van Tienderen and De Jong, 1986). In these plots, the sign of the invasion fitness $r(s_{\text{mut}}, E(s_{\text{res}}))$ is displayed in dependence on resident and mutant strategies. As the resident population is on an attractor, necessarily the equality $r(s_{\text{res}}, E(s_{\text{res}})) = 0$ holds. Therefore, the diagonal $s_{\text{mut}} = s_{\text{res}}$ is a zero-contour line of the invasion fitness. Singular strategies lie at those points, where other zero-contour curves cross the diagonal. In the pairwise invasibility plots in this article, dark grey regions correspond to combinations of resident and mutant dispersal strategies, s_{res} and s_{mut}, that allow for mutant invasion. For these combinations, the invasion fitness $r(s_{\text{mut}}, E(s_{\text{res}}))$ is positive. In contrast, light grey regions correspond to negative signs and therefore to deleterious mutants.

Evolutionary suicide and ecological bifurcations

In evolutionary suicide, consecutive mutation and invasion events first take the strategy of the evolving population near an extinction boundary (which is a bifurcation point) in the population's trait space (Fig. 1a). Then a mutant which is not viable alone invades, and moves the dynamics out of the resident attractor, which results in the extinction of the whole population (Fig. 1b). There are two general properties in the illustration in Fig. 1 that require specific attention. The first is that the invasion event illustrated in Fig. 1b is possible only near an ecological bifurcation point. The second is that this bifurcation has to be a discontinuous transition to extinction. Both properties are based on theory, and I will discuss them in turn.

When there are several population-dynamical attractors, initial invasion dynamics alone is not sufficient to determine the success of a mutant (Doebeli, 1998; Mylius and Diekmann, 2001). For example, assume that the mutant can invade the resident on a specific attractor and the resident cannot invade the mutant on the corresponding attractor. Initially, the mutant population is small, and therefore the resident–mutant population is inside a narrow tube in the resident–mutant population state space where the sum of the population densities of the

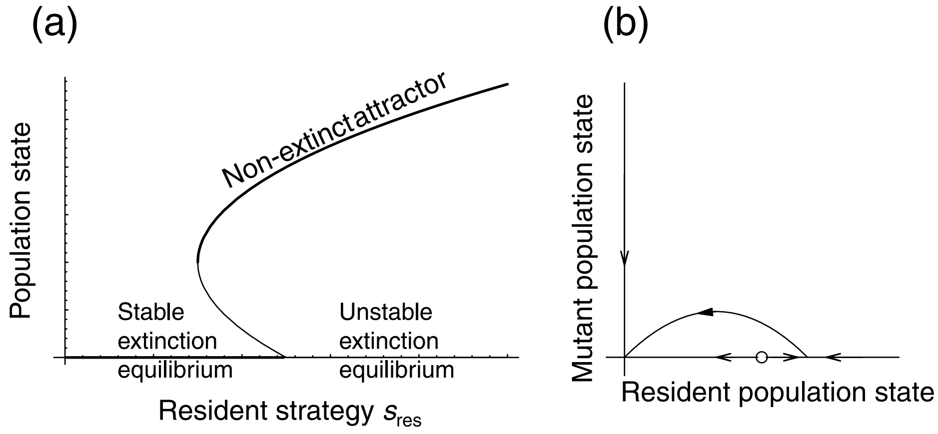
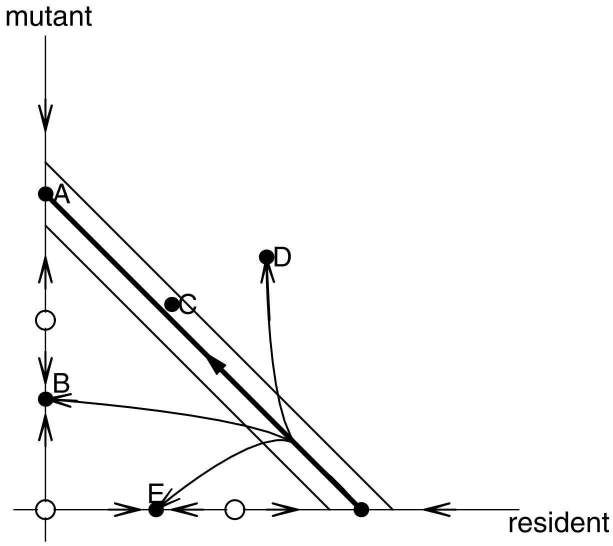


Fig. 1. Illustration of evolutionary suicide.



A: Attractor inheritance

B: Attractor switching

C: Co-existence inside tube

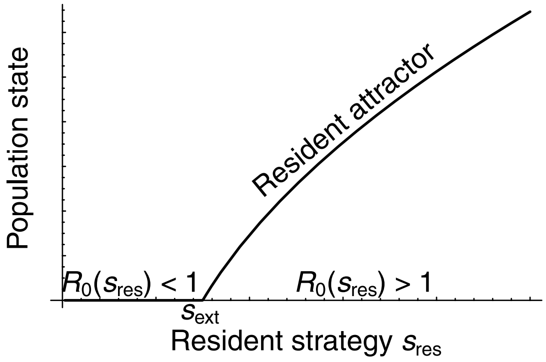
D: Co-existence outside tube

E: Resident strikes back scenario
(Mylius and Diekmann, 2001)

Fig. 2. Possible events after the initial increase of the mutant population in the case of several attractors. Solid circles illustrate attractors and open circles repellors of population dynamics.

resident and the mutant are close to the resident densities of the monomorphic resident attractor. Various events which may occur after the initial increase of the mutant population are illustrated in Fig. 2.

Assume that $A(s)$ is a population dynamical attractor for all $s \in S$, where S is a compact subset of the strategy space. For each s, $A(s)$ is thus a subset of the population state space. $A(s)$ is called an *attractor family*, if $A(s)$ varies continuously as a function of s on S [see definition 3.2 of Geritz *et al.* (2002) for a precise definition]. The type of the attractor need not to be the same for all values of s on S. For example, the period-doubling bifurcation in discrete-time models happens in such a way that $A(s)$ varies continuously. The Tube



Theorem (Gyllenberg *et al.*, 2002): If the resident attractor goes continuously to zero when the resident strategy approaches the extinction boundary, then this extinction boundary is evolutionarily repelling, and evolutionary suicide is not possible.

Fig. 3. Continuous transition to extinction.

Theorem (Geritz *et al.*, 2002) shows that, under rather general conditions, if $s_{\mathrm{mut}} \approx s_{\mathrm{res}}$, the mutant will remain in the same attractor family, and thus attractor inheritance occurs.

This result leaves open two options for evolutionary suicide. The first is as illustrated in Fig. 1, where attractor switching occurs at an extinction boundary, which is a discontinuous transition to extinction. The second option is that the resident attractor goes continuously to zero when the resident strategy approaches the extinction boundary (Fig. 3), because technically this does not require attractor switching. However, evolutionary suicide is not possible for other reasons, as shown by Gyllenberg *et al.* (2002).

In a continuous transition to extinction, when the strategy s approaches s_{ext}, the population size of the resident goes continuously to zero. In well-constructed models, the effect of the resident population on the environment also goes to zero. For this reason, if the resident is at an extinction boundary, the mutant population will grow as if it were in a virgin environment. Therefore, the mutant's fitness is the same as the fitness in the virgin environment. That means that exactly those mutants that are viable in the absence of the resident can invade. Mutants that are not viable cannot invade. In other words, selection pressure keeps the population away from the extinction boundary, thus evolutionary suicide is not possible (Gyllenberg *et al.*, 2002). A discontinuous transition to extinction (Fig. 1a) is therefore a necessary, but not a sufficient, condition for evolutionary suicide.

A weaker phenomenon than what I have called evolutionary suicide (Parvinen, 2005) is demographically stochastic evolutionary suicide. In this phenomenon, evolution leads to smaller and smaller population size that extinction by chance becomes more and more likely. Typically, however, the stochasticity needed to cause extinction is not explicitly included in the model. Webb (2003) called this phenomenon gradual Darwinian extinction. Matsuda and Abrams (1994a) were the first to observe this phenomenon in a mathematical model. Note that in evolutionary suicide, no demographic stochasticity is required, extinction is deterministic.

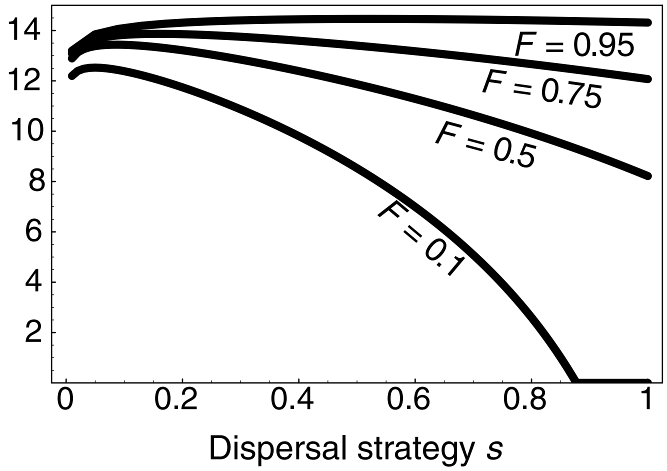
RESULTS

Ecological bifurcations in the metapopulation model

Since a discontinuous transition to extinction is a necessary condition to evolutionary suicide, I will now illustrate what kind of bifurcations occur in the discrete-time metapopulation model with respect to the dispersal strategy. Parvinen (2006) proved that one of the following three cases applies:

1. The extinction equilibrium is unstable for all dispersal strategies $0 < s \leq 1$ (Fig. 4a with $F = 0.5$, 0.75 and 0.95).
2. The extinction equilibrium is unstable for dispersal strategies $0 < s < \tilde{s}$ (Fig. 4a with $F = 0.1$).
3. The extinction equilibrium is stable for all dispersal strategies $0 < s \leq 1$ (Fig. 4b).

(a) Ricker model



(b) Allee effect

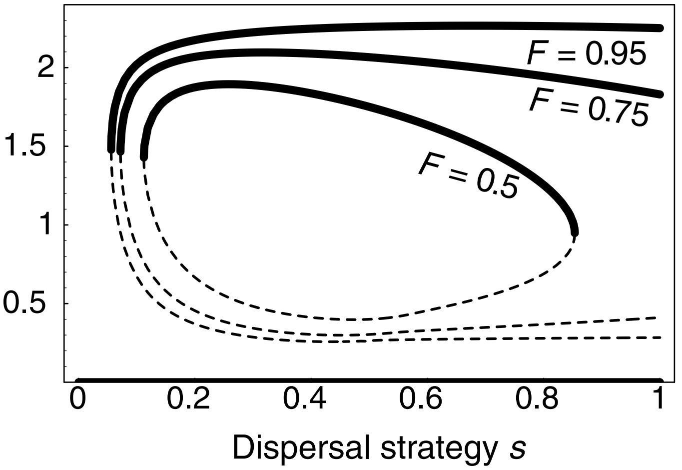


Fig. 4. Average local population size in a metapopulation equilibrium with respect to the dispersal strategy s. Stable equilibria are plotted with a continuous curve, unstable equilibria with a dotted curve. Local growth occurs according to (a) the Ricker model and (b) a model with an Allee effect described in equation (4) with $r = 5$ and $k = 1$. Other parameters: $\mu = 0.05$.

Figure 4a illustrates the case that local population growth occurs according to the Ricker (1954) model with $f(x_t) = re^{-x_t/K}$. This is also the model that Parvinen (2006) used in numerical explorations. Either case (1) or (2) listed above occurs; and in case (2) the transition to extinction is continuous ($F = 0.1$). Because no discontinuous transition to extinction appears, evolutionary suicide cannot occur. This is consistent with the numerical results of Parvinen (2006): exactly one evolutionarily attracting singular strategy was always found. Depending on parameter values, it was either an evolutionarily stable strategy (ESS) or a branching point.

The Allee effect – that is, increasing per capita growth at low densities (Allee *et al.*, 1949) – is a natural mechanism to provide ecological bistability, and discontinuous transitions to extinction. This effect is present in the local growth model with

$$f(x_t) = rx_t e^{-kx_t}. \tag{4}$$

It is easy to find functions with that property. However, obtaining such a model from mechanisms on the individual level is more desirable. Recently, Geritz and Kisdi (2004) presented a mechanistic underpinning of various discrete-time population models including the Ricker (1954) model. Their work was based on a continuous-time resource–consumer model for the dynamics within a year, from which they derived a discrete-time model for the between-year dynamics. However, their underpinning does not give models with an Allee effect. They assumed that individuals, and thus also the population size, affect the reproduction rate of other individuals only through the availability of resources. However, if two individuals are required for reproduction, individuals have problems in mate finding when the population size is low. Using this mechanistic underpinning, Eskola and Parvinen (2007) have presented several discrete-time population models with an Allee effect, including the one I have used here (equation 4).

Figure 4b illustrates that an Allee effect on the local patch dynamics results in an Allee effect on the metapopulation level. After a catastrophe has occurred, the local population size in this patch is zero. If there is too little immigration, the local population size cannot grow beyond the local Allee threshold. Since all patches will eventually encounter a catastrophe, the metapopulation is not viable for too small dispersal strategies, and the extinction equilibrium is stable. Figure 4b also shows that, if the dispersal risk is high ($F = 0.5$), the metapopulation is not viable for too large dispersal strategies either. These transitions from viability to extinction in Fig. 4b are clearly discontinuous.

Evolutionary bifurcation to evolutionary suicide

A discontinuous transition to extinction is only a necessary condition for evolutionary suicide. In Fig. 5a ($F = 0.75$), the boundary of viability is repelling, although Fig. 4b shows that the transition to extinction is discontinuous. In this case, there exists an intermediate singular strategy $s^* \approx 0.106$ that is convergence stable and evolutionarily stable. It is thus the expected evolutionary endpoint.

When the dispersal survival probability is decreased, the boundary of viability becomes evolutionarily attracting, and another singular strategy $\hat{s}$ appears that is not convergence stable (Fig. 5b with $F = 0.713$). Evolutionary suicide can already happen if the initial strategy of the metapopulation is between the extinction boundary $s_{\text{ext}} \approx 0.076$ and $\hat{s} \approx 0.078$. However, the domain of initial conditions leading to evolutionary suicide is very small compared with the domain of viable strategies.

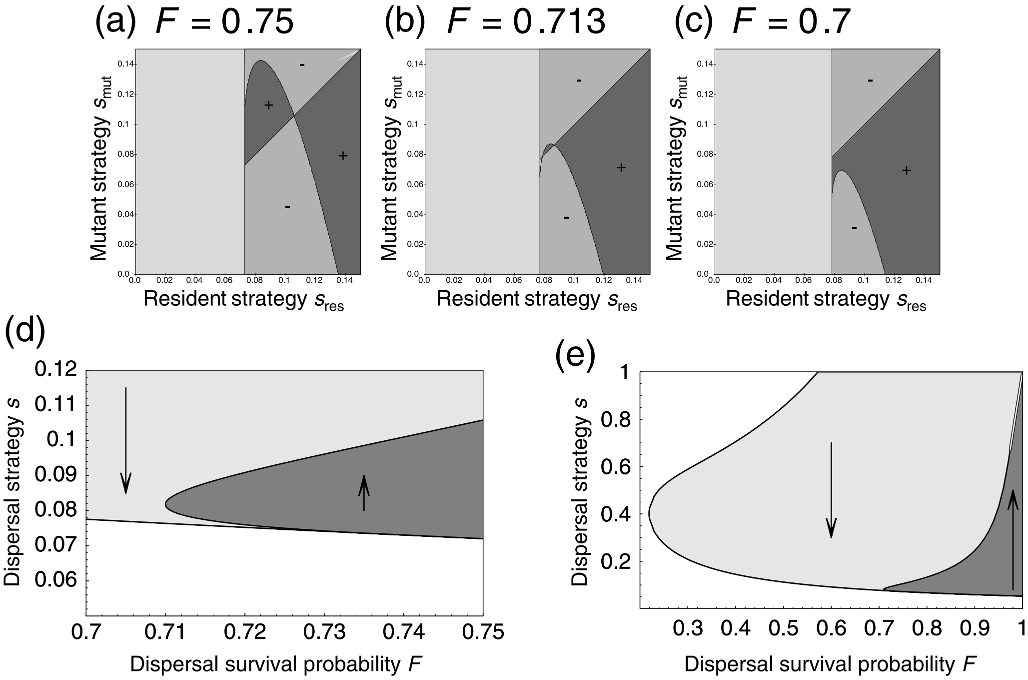


Fig. 5. Illustration of the evolutionary bifurcation from an evolutionary attractor (convergence stable ESS) to evolutionary suicide. (a–c) Pairwise invasibility plots. The light grey rectangle depicts those resident strategies for which the resident is not viable. (d, e) Direction of evolution as a function of the dispersal survival probability *F*. Local growth occurs according to equation (4) with $r = 5$ and $k = 1$. Other parameters: $\mu = 0.05$.

When the dispersal survival probability is decreased further, the two singular strategies collide and disappear (Fig. 5c). For $F \leq 0.71$, the fitness gradient is negative for all resident strategies (Fig. 5d). Therefore, no matter what the strategy of the resident is, a mutant with a slightly smaller dispersal strategy has positive fitness and can invade. The dispersal strategy will eventually reach the boundary of viability s_{ext}. In such a situation, a mutant with an even smaller strategy has positive fitness, and can initially increase in population size. However, the mutant is not viable alone (the light grey rectangles in Figs. 5a, b, c depict non-viable strategies). The only remaining attractor is the extinction equilibrium, and thus the initial invasion of the 'kamikaze' mutant will take the whole metapopulation to extinction, as illustrated in Fig. 1. Thus evolutionary suicide will occur.

Gyllenberg *et al.* (2002) found a similar evolutionary bifurcation in a metapopulation model defined in continuous time (see their Figure 5). However, to make an evolutionary simulation in that model demands too much computation time to be feasible. In contrast, in the model in this article, making such an evolutionary simulation is relatively easy. In practice, one has to choose a large number of patches (in this article I used 1000). After that, ecological dynamics is straightforward: calculate the local population sizes in each patch using equations (1) and (2), and then set the local population size of a patch to zero with probability μ independently in each patch. An evolutionary simulation (Fig. 6) consists of several evolutionary time steps:

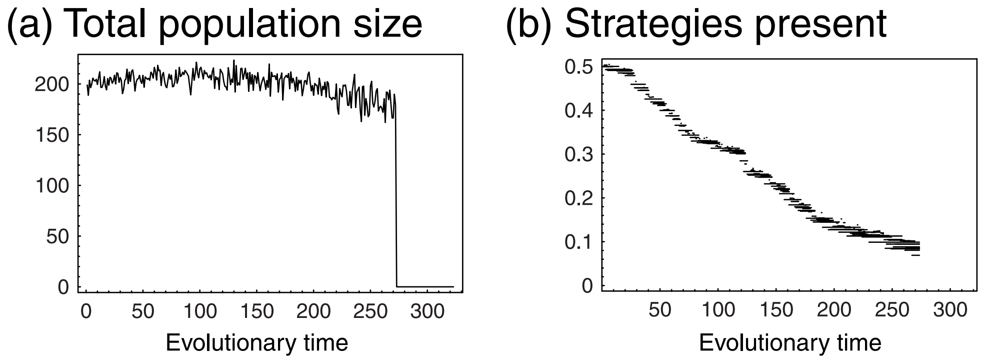


Fig. 6. Evolutionary simulation resulting in evolutionary suicide. Parameters as in Fig. 5c.

- *Mutation*: Select a resident randomly according to the resident population size distribution. Add a mutant with very low population size to the metapopulation. The strategy of the mutant is the sum of the strategy of the chosen resident and a random Gaussian variable with zero mean and standard deviation $\sigma = 0.01$.
- *Metapopulation dynamics*: Repeat the ecological dynamics 1000 times.
- *Removal*: Remove the strategies with population size practically zero from the metapopulation.

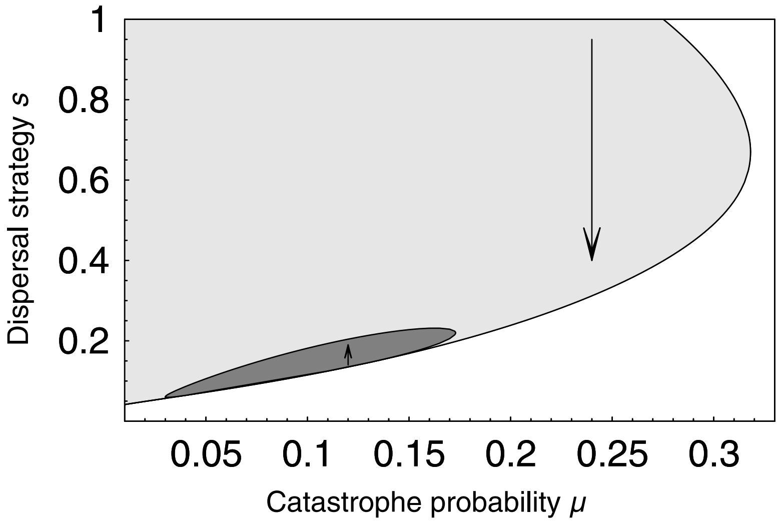
Figure 6 illustrates an evolutionary simulation for the parameter values as in Fig. 5c, when evolutionary suicide is expected. Indeed, the dispersal strategy will decrease until the boundary of extinction is reached at evolutionary time $t \approx 270$, and the whole metapopulation goes extinct.

The effect of various parameters

Figure 5 illustrates the evolutionary bifurcation of two colliding singular strategies resulting in evolutionary suicide with respect to the dispersal survival probability F. I next address the question of how general this phenomenon is in terms of other parameters.

Figure 7a illustrates the non-monotonous effect of the catastrophe probability μ on the evolution of dispersal: an evolutionary attracting ESS exists for intermediate catastrophe probabilities μ, but when μ is either increased or decreased, the above-mentioned evolutionary bifurcation occurs [see also Figure 8b of Gyllenberg *et al.* (2002)]. Figure 7b illustrates the effect of the growth parameter r: the evolutionary bifurcation resulting in evolutionary suicide occurs when r becomes too small. Elsewhere, evolutionarily singular dispersal strategies increase as a function of r, and for large r these singular strategies are evolutionary branching points. Singular strategies are branching points also when the dispersal survival probability F is large enough (Fig. 5e). The effect of the parameter k on the evolution of dispersal is not illustrated, because with a change of variables $y_t = kx_t$, reproduction with equation (4) becomes $y_{t+1} = y_t f(y_t) = \frac{r}{k} y_t e^{-y_t}$. Thus results with parameter $k \neq 1$ can be obtained with $k = 1$ by adjusting the growth parameter r accordingly. Figures 5e and 7 illustrate that when there is an Allee effect present, making the environment less favourable

(a) Catastrophe probability μ



(b) Growth parameter r

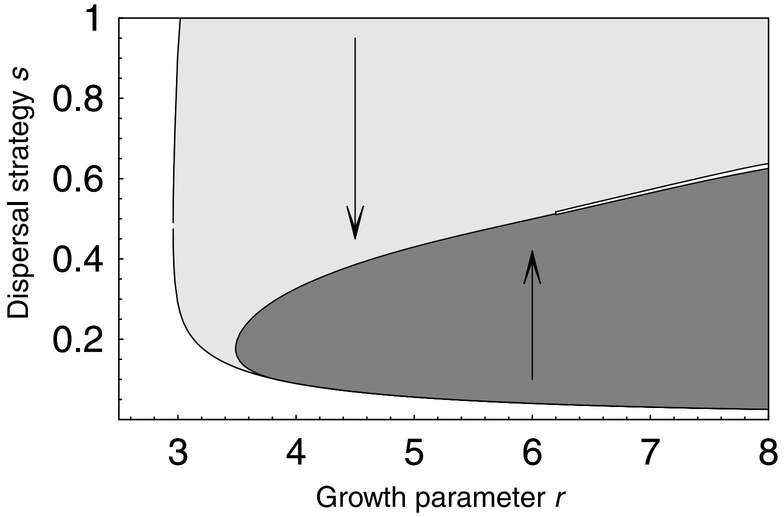


Fig. 7. Direction of evolution as a function of various parameters. Local growth occurs according to equation (4) with $k = 1$. Uninvadable singular strategies are drawn with black curves, evolutionary branching points with white curves with a black border. Parameters: (a) $F = 0.75$ and $r = 5$, (b) $\mu = 0.05$ and $F = 0.95$.

(by increasing μ or decreasing F or r) will cause an evolutionarily viable population to experience evolutionary suicide. Surprisingly, also making the environment more favourable by decreasing μ can cause evolutionary suicide (Gyllenberg *et al.*, 2002).

Dimorphic evolution

The presence of evolutionary branching points (Fig. 8a) raises the question of what happens after the population has become dimorphic (consisting of two strategies). The expected course of evolution can be analysed by plotting the direction of the selection

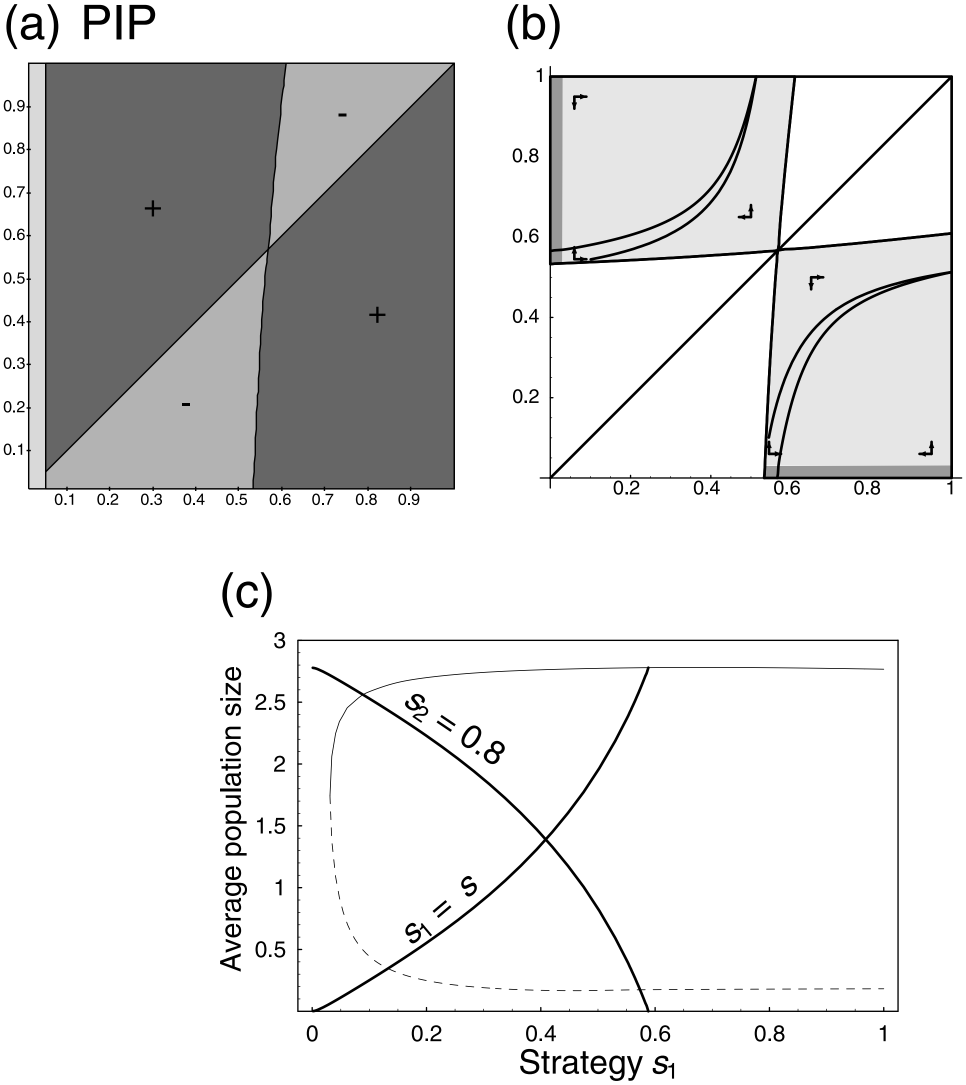


Fig. 8. (a) Pairwise invasibility plot with a branching point. (b) Direction of the selection gradient in a dimorphic population. Light grey areas depict protected co-existence, and dark grey areas unprotected co-existence. (c) Average population sizes of strategies s_1 and $s_2 = 0.8$ in a dimorphic equilibrium as a function of s_1 (bold curves), and the average population size of strategy s_1 alone in a monomorphic stable equilibrium (continuous thin curve) and unstable equilibrium (dotted thin curve). Parameters: $F = 0.95$, $\mu = 0.05$. Local growth occurs according to equation (4) with $r = 7$ and $k = 1$.

gradient $\{s_1', s_2'\}$ (Fig. 8b), where $s_i' = \frac{\partial}{\partial s_{\text{mut}}} r^{\text{mut}} \Big|_{s_{\text{mut}} = s_i}$, for those values of $\{s_1, s_2\}$ for which s_1 and s_2 can co-exist. In principle, the dimorphic population could evolve towards a boundary where either one or both branches would go extinct. The first option would result in branching–extinction cycles (Kisdi *et al.*, 2001; Dercole, 2003), and the second one would mean dimorphic evolutionary suicide.

Figures 8b and c illustrate that in addition to protected co-existence, a rarely dispersing strategy can co-exist together with a frequent disperser, although the rarely dispersing strategy cannot persist alone ($s_1 < 0.031$). [Co-existence is called protected, if strategy s_2 can invade strategy s_1, when strategy s_1 is on a positive monomorphic attractor, and vice versa, thus $r(s_1, E(s_2)) > 0$ and $r(s_2, E(s_1)) > 0$.] Figure 8c also illustrates that the (dimorphic) population size of s_1 goes continuously to zero as s_1 goes to zero. Similarly, when s_1 approaches 0.59, the (dimorphic) population size of s_2 goes continuously to zero. Thus for the parameter values in Fig. 8, the transitions to extinction are continuous, and selection pressure will prevent evolutionary suicide (Gyllenberg *et al.*, 2002). Figure 8b shows that the dimorphic population is expected to reach eventually the strategy coalition $\{0.514, 1\}$, and no evolutionary suicide will occur. Further numerical studies suggest that dimorphic evolutionary suicide does not happen in this metapopulation model for other parameter values either (not illustrated).

SUMMARY

One could naively think that evolution, survival of the fittest, would always improve the viability of the population. The question of which mutants can invade depends only on how mutants perform in the environment set by the resident population. The environmental conditions may, however, become worse once these successful mutants become common. It is well known that selection does not maximize the population size, when selection is frequency-dependent. Selection-driven extinction (evolutionary suicide) is an extreme example of that.

Evolutionary suicide is related to the tragedy of the commons (Hardin, 1968). There selfish individuals decide to increase their use of a common resource, because they get all the benefit from this increase, and the cost of decreased resource quality is shared among all users. This will lead to heavy overgrazing and possibly even ruin of the common resource. In some examples of evolutionary suicide (Parvinen, 2005), the evolving strategy changes into the direction which can clearly be interpreted as an increase of selfishness. In contrast, dispersal contains both selfish and altruistic components: On the one hand, dispersal can be seen as an altruistic act, since there are more resources left for the individuals who remain. On the other hand, if the native patch of an individual is resource-poor, dispersing to a resource-rich target patch is clearly selfish. Based on earlier work (Gyllenberg *et al.*, 2002) and results in this article, it seems that evolutionary suicide in the evolution of dispersal may occur only due to selection for too low dispersal. To my knowledge, extinction due to selection for too frequent dispersal has not been observed.

Previous findings of evolutionary suicide in dispersal evolution have been based solely on fitness calculations. In this article, I have presented the first evolutionary simulation, which supports the fitness-based results, that evolutionary suicide can occur in dispersal evolution, when there is an Allee effect in local growth. Evolutionary branching of dispersal has been observed in many models (Holt and McPeek, 1996; Doebeli and Ruxton, 1997; Johst *et al.*, 1999; Parvinen, 1999, 2002, 2006; Mathias *et al.*, 2001; Kisdi, 2002). In the presence of the Allee effect, there is a discontinuous transition to extinction and too low dispersal strategies are not viable alone. Therefore, evolutionary branching could result in the extinction of one branch [branching–extinction cycles (Kisdi *et al.*, 2001; Dercole, 2003)] or both branches (dimorphic evolutionary suicide). However, I have illustrated that low-dispersal strategies can co-exist with higher dispersal strategies in an unprotected polymorphism. Although the non-dispersing strategy is not viable, the transition to extinction is continuous, and this extinction boundary is evolutionarily repelling. Therefore, I did not find selection-driven extinction in a dimorphic metapopulation after evolutionary branching.

REFERENCES

Allee, W.C., Emerson, A., Park, T. and Schmidt, K. 1949. *Principles of Animal Ecology*. Philadelphia, PA: W.B. Saunders.

Cadet, C. 1998. *Dynamique adaptative de la dispersion dans une métapopulation: modèles stochastiques densité-dépendants*. Master's thesis, University of Paris VI.

Christiansen, F.B. 1991. On conditions for evolutionary stability for a continuously varying character. *Am. Nat.*, **138**: 37–50.

Dercole, F. 2003. Remarks on branching–extinction evolutionary cycles. *J. Math. Biol.*, **47**: 569–580.

Dieckmann, U. and Law, R. 1996. The dynamical theory of coevolution: a derivation from stochastic ecological processes. *J. Math. Biol.*, **34**: 579–612.

Dieckmann, U., Marrow, P. and Law, R. 1995. Evolutionary cycling in predator–prey interactions: population dynamics and the Red Queen. *J. Theor. Biol.*, **176**: 91–102.

Doebeli, M. 1998. Invasion of rare mutants does not imply their evolutionary success: a counter-example from metapopulation theory. *J. Evol. Biol.*, **11**: 389–401.

Doebeli, M. and Ruxton, G.D. 1997. Evolution of dispersal rates in metapopulation models: branching and cyclic dynamics in phenotype space. *Evolution*, **51**: 1730–1741.

Eshel, I. 1983. Evolutionary and continuous stability. *J. Theor. Biol.*, **103**: 99–111.

Eskola, H. and Parvinen, K. 2007. On the mechanistic underpinning of discrete-time population models with Allee effect. *Theor. Popul. Biol.* (DOI: 10.1016/j.tpb.2007.03.004).

Ferrière, R. 2000. Adaptive responses to environmental threats: evolutionary suicide, insurance, and rescue. *Options*, Spring, pp. 12–16. Laxenburg, Austria: IIASA.

Geritz, S.A.H. and Kisdi, É. 2004. On the mechanistic underpinning of discrete-time population models with complex dynamics. *J. Theor. Biol.*, **228**: 261–269.

Geritz, S.A.H., Metz, J.A.J., Kisdi, É. and Meszéna, G. 1997. Dynamics of adaptation and evolutionary branching. *Phys. Rev. Lett.*, **78**: 2024–2027.

Geritz, S.A.H., Kisdi, É., Meszéna, G. and Metz, J.A.J. 1998. Evolutionary singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol. Ecol.*, **12**: 35–57.

Geritz, S.A.H., Gyllenberg, M., Jacobs, F.J.A. and Parvinen, K. 2002. Invasion dynamics and attractor inheritance. *J. Math. Biol.*, **44**: 548–560.

Gyllenberg, M. and Metz, J.A.J. 2001. On fitness in structured metapopulations. *J. Math. Biol.*, **43**: 545–560.

Gyllenberg, M. and Parvinen, K. 2001. Necessary and sufficient conditions for evolutionary suicide. *Bull. Math. Biol.*, **63**: 981–993.

Gyllenberg, M., Parvinen, K. and Dieckmann, U. 2002. Evolutionary suicide and evolution of dispersal in structured metapopulations. *J. Math. Biol.*, **45**: 79–105.

Hanski, I.A. 1999. *Metapopulation Ecology*. Oxford: Oxford University Press.

Hanski, I.A. and Gilpin, M.E., eds. 1997. *Metapopulation Biology: Ecology, Genetics, and Evolution*. San Diego, CA: Academic Press.

Hardin, G. 1968. The tragedy of the commons. *Science*, **162**: 1243–1248.

Holt, R.D. and McPeek, M. 1996. Chaotic population dynamics favors the evolution of dispersal. *Am. Nat.*, **148**: 709–718.

Johst, K., Doebeli, M. and Brandl, R. 1999. Evolution of complex dynamics in spatially structured populations. *Proc. R. Soc. Lond. B*, **266**: 1147–1154.

Kisdi, É. 2002. Dispersal: risk spreading versus local adaptation. *Am. Nat.*, **159**: 579–596.

Kisdi, É. Jacobs, F.J.A. and Geritz, S.A.H. 2001. Red Queen evolution by cycles of evolutionary branching and extinction. *Selection*, **2**: 161–176.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Entomol. Soc. Am.*, **15**: 237–240.

Levins, R. 1970. Extinction. In *Some Mathematical Problems in Biology* (M. Gerstenhaber, ed.), pp. 77–107. Providence, RI: American Mathematical Society.

Mathias, A., Kisdi, É. and Olivieri, I. 2001. Divergent evolution of dispersal in a heterogeneous landscape. *Evolution*, **55**: 246–259.

Matsuda, H. 1985. Evolutionarily stable strategies for predator switching. *J. Theor. Biol.*, **115**: 351–366.

Matsuda, H. and Abrams, P.A. 1994a. Runaway evolution to self-extinction under asymmetrical competition. *Evolution*, **48**: 1764–1772.

Matsuda, H. and Abrams, P.A. 1994b. Timid consumers: self-extinction due to adaptive change in foraging and anti-predator effort. *Theor. Popul. Biol.*, **45**: 76–91.

Maynard Smith, J. 1976. Evolution and the theory of games. *Am. Sci.*, **64**: 41–45.

Metz, J.A.J. and Gyllenberg, M. 2001. How should we define fitness in structured metapopulation models? Including an application to the calculation of ES dispersal strategies. *Proc. R. Soc. Lond. B*, **268**: 499–508.

Metz, J.A.J., Nisbet, R.M. and Geritz, S.A.H. 1992. How should we define ‘fitness’ for general ecological scenarios? *Trends Ecol. Evol.*, **7**: 198–202.

Metz, J.A.J., Geritz, S.A.H., Meszéna, G., Jacobs, F.J.A. and van Heerwaarden, J.S. 1996. Adaptive dynamics, a geometrical study of the consequences of nearly faithful reproduction. In *Stochastic and Spatial Structures of Dynamical Systems* (S.J. van Strien and S.M. Verduyn Lunel, eds.), pp. 183–231. Amsterdam: North-Holland.

Mylius, S.D. and Diekmann, O. 2001. The resident strikes back: invader-induced switching of resident attractor. *J. Theor. Biol.*, **211**: 297–311.

Parvinen, K. 1999. Evolution of migration in a metapopulation. *Bull. Math. Biol.*, **61**: 531–550.

Parvinen, K. 2002. Evolutionary branching of dispersal strategies in structured metapopulations. *J. Math. Biol.*, **45**: 106–124.

Parvinen, K. 2005. Evolutionary suicide. *Acta Biotheor.*, **53**: 241–264.

Parvinen, K. 2006. Evolution of dispersal in a structured metapopulation model in discrete time. *Bull. Math. Biol.*, **68**: 655–678.

Rankin, D.J. and López-Sepulcre, A. 2005. Can adaptation lead to extinction? *Oikos*, **111**: 616–619.

Ricker, W.E. 1954. Stock and recruitment. *J. Fish. Res. Board Can.*, **11**: 559–623.

Taylor, P.D. 1989. Evolutionary stability in one-parameter models under weak selection. *Theor. Popul. Biol.*, **36**: 125–143.

Van Tienderen, P.H. and De Jong, G. 1986. Sex ratio under the haystack model: polymorphism may occur. *J. Theor. Biol.*, **122**: 69–81.

Webb, C. 2003. A complete classification of Darwinian extinction in ecological interactions. *Am. Nat.*, **161**: 181–205.