

Mats Gyllenberg · Kalle Parvinen · Ulf Dieckmann

Evolutionary suicide and evolution of dispersal in structured metapopulations

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Abstract. We study the evolution of dispersal in a structured metapopulation model. The metapopulation consists of a large (infinite) number of local populations living in patches of habitable environment. Dispersal between patches is modelled by a disperser pool and individuals in transit between patches are exposed to a risk of mortality. Occasionally, local catastrophes eradicate a local population: all individuals in the affected patch die, yet the patch remains habitable. We prove that, in the absence of catastrophes, the strategy not to migrate is evolutionarily stable. Under a given set of environmental conditions, a metapopulation may be viable and yet selection may favor dispersal rates that drive the metapopulation to extinction. This phenomenon is known as evolutionary suicide. We show that in our model evolutionary suicide can occur for catastrophe rates that increase with decreasing local population size. Evolutionary suicide can also happen for constant catastrophe rates, if local growth within patches shows an Allee effect. We study the evolutionary bifurcation towards evolutionary suicide and show that a discontinuous transition to extinction is a necessary condition for evolutionary suicide to occur. In other words, if population size smoothly approaches zero at a boundary of viability in parameter space, this boundary is evolutionarily repelling and no suicide can occur.

1. Introduction

In “The Origin of Species” Darwin (1859) explained the unexpectedly wide geographical distribution of certain fresh-water species, by “...their having become fitted, in a manner highly useful to them, to short frequent migrations from pond to pond, or from stream to stream.” It is clear from this quote that Darwin realized that dispersal is a life-history trait which is under selection and the change of which may have profound ecological implications. He also came very close to a verbal description of what is today known as a *metapopulation* – at least the

M. Gyllenberg, K. Parvinen: Department of Mathematics, FIN-20014 University of Turku, Finland

M. Gyllenberg: Turku Centre for Computer Science, FIN-20014 University of Turku, Finland

U. Dieckmann, K. Parvinen: Adaptive Dynamics Network, International Institute for Applied Systems Analysis, A-2361 Laxenburg, Austria

Correspondence to: Kalle Parvinen, e-mail: kalle.parvinen@utu.fi

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discreteness of habitat patches was made explicit. Presently, many researchers agree that the metapopulation concept provides a suitable framework for studying evolution of dispersal, both theoretically (Gyllenberg and Metz 2001) and experimentally (Clobert *et al.* 2001).

Today, habitat loss is the worst threat to endangered species in most parts of the world (Barbault and Sastrapradja 1995). For instance, habitat loss has been acknowledged as a significant cause of increased extinction risk in 82% of endangered bird species (Temple 1986), and, in Finland, habitat loss or alteration is the primary threat to 73% of the red-listed species (Rassi *et al.* 2000). In such changing environments, an individual's fitness depends of its ability either to rapidly adapt to local conditions or to move to other habitats (Ferrière 2000). This dependence is one of the main reasons for the renewed interest in the evolution of dispersal which started about three decades ago. The literature on the subject is vast; here we give only a few references to key papers in which mathematical modelling plays a prominent role (Cohen 1967; Van Valen 1971; Hamilton and May 1977; Comins *et al.* 1980; Hastings 1983; Levin *et al.* 1984; Cohen and Motro 1989; Doebeli 1995; Doebeli and Ruxton 1997; Cadet 1998; Dieckmann *et al.* 1999; Gandon 1999; Gandon and Michalakis 1999; Parvinen 1999; Gyllenberg and Metz 2001; Gyllenberg and Parvinen 2001; Heino and Hanski 2001; Metz and Gyllenberg 2001; Parvinen 2001). For a review of mathematical models describing the evolution of dispersal and of empirical tests that have appeared before 1990, we refer to the paper by Johnson and Gaines (1990).

It is a well-known fact, observed already by Darwin (1859, 1871) and later discussed in detail by Haldane (1932), that natural selection may favour traits that eventually, through environmental change, turn out to be harmful to the individuals. Darwin (1859) even pointed out that this may lead to the species becoming extinct. The observation that what is advantageous for the individual may ultimately be disastrous for the species raises the question as to the conditions under which natural selection is expected to drive species to extinction. It is the purpose of this paper to investigate this question in the context of structured metapopulation models (Gyllenberg *et al.* 1997; Gyllenberg and Hanski 1992, 1997; Hanski and Gyllenberg 1993, 1997) when the trait under selection is an individual's tendency to migrate from one patch to another.

This work utilizes the framework of *adaptive dynamics* (Metz *et al.* 1992, 1996; Dieckmann and Law 1996; Geritz *et al.* 1997, 1998), which explicitly relates evolution to population dynamics. We assume that individuals are characterized by a one-dimensional trait (or strategy) that determines the dispersal rate of an organism, and therefore the *strategy space* (that is, the set of all feasible strategies) is a subset of the real numbers. A given trait value, together with the *environmental input*, determines the life history of an individual expressing that trait. The *viability set* is the set of all traits to which there corresponds at least one nonzero population dynamical attractor.

A possible scenario in which evolution drives a species to extinction by small mutational steps is as follows. Consider a resident population with a strategy in the viability set and assume that it can be invaded and outcompeted by a mutant strategy lying slightly closer to the boundary of the viability set (the so-called *extinction*

boundary). If the new resident can in turn be invaded and outcompeted by a strategy lying still closer to the extinction boundary, then evolution will eventually lead to the emergence of trait values lying on or very close to the extinction boundary. If the fitness gradient calculated at such a trait value points towards the outside of the viability set, then selection will lead to extinction. Following Ferrière (2000) we call this phenomenon *evolutionary suicide*. In this paper we give a mathematical formalization of evolutionary suicide and we also give necessary conditions for an adapting population to undergo such an event.

The loss of metapopulation viability occurs through a bifurcation (Gyllenberg *et al.* 2002). In the Levins (1969, 1970) model there is always a continuous transition to extinction as the value of the bifurcation parameter crosses the boundary between the viability and extinction regions. On the other hand, as shown by Gyllenberg and Hanski (1992), structured metapopulations may well exhibit catastrophic bifurcations so that at the bifurcation point there exists a gap between the stable branch on which the metapopulation is viable and the stable branch corresponding to metapopulation extinction. Phrased differently, this allows for discontinuous transitions to extinction to occur as the value of the bifurcation parameter crosses the boundary between the viability and extinction regions.

One of the main results presented in this paper is that a discontinuous transition to extinction is a necessary (but not sufficient) condition for evolutionary suicide. It is therefore possible that structured metapopulation models, which explicitly take local dynamics into account, exhibit evolutionary suicide. In this paper we give examples of mechanisms at the local level that lead to evolutionary suicide at the metapopulation level. One of these involve catastrophe rates that increase with decreasing local population size: this can be thought of as reflecting a greater sensitivity of small local populations to demographic and environmental stochasticity. The other is the Allee effect, that is, the assumption that small local populations have a negative intrinsic growth rate and thus can only persist (or be rescued) by immigration.

2. Model description

We consider a metapopulation with a large number of identical habitat patches. This number is assumed to be large enough for the metapopulation dynamics to be well approximated by a metapopulation with infinitely many patches. Each patch can support a local population. The metapopulation is structured by the size $x \in \mathbf{R}$ of local populations. The state of the metapopulation is thus given by the distribution n of local population sizes (Gyllenberg *et al.* 1997).

The size x of local populations grows or decreases due to birth and death events according to local density regulation with a per capita growth rate $g(x)$. Patches are connected by dispersal: individuals leave their patch at a rate $k(x)$ and enter a disperser pool. $k(x)$ is the emigration rate or dispersal rate. The density of dispersers is denoted by D . Individuals in the disperser pool experience mortality at a per capita rate ν and they leave the pool and immigrate into a patch at a per capita rate α . The quantity

$$I = \alpha D \tag{1}$$

is the immigration rate to each patch, which for simplicity we from now on call immigration rate. The quantity

$$\pi = \frac{\alpha}{\alpha + \nu} \quad (2)$$

is the probability that a disperser survives migration. Correspondingly, $\rho = 1 - \pi = \nu/(\alpha + \nu)$ is the probability that a disperser dies during migration. We therefore refer to ρ as the dispersal risk.

Local populations may go extinct as a result of catastrophes, which are assumed to occur at a size-specific rate $\mu(x)$. After a catastrophe, the patch remains habitable, and is immediately recolonized by migrants from the disperser pool, provided $I > 0$. We assume that the rates g , k , and μ are continuous functions of local population size.

In the following subsections, we first investigate the dynamics of a metapopulation of resident individuals with dispersal rate $k(x)$, and then analyze how the resident metapopulation responds to the arrival of mutants with a different dispersal rate $k_{\text{mut}}(x)$. All theorems apply for size-dependent dispersal strategies, but in the examples dispersal is assumed to be constant $k(x) = k$.

2.1. Resident dynamics

As our basic metapopulation model we use the one introduced by Gyllenberg and Metz (2001). The local population growth, including emigration and immigration, is given by

$$\frac{dx}{dt} = f(x, I(t)), \quad (3)$$

with

$$f(x, I) = g(x)x - k(x)x + I. \quad (4)$$

At the metapopulation level, we study the density $n(t, x)$ of local population sizes x . The dynamics of this density can be described by the partial differential equation,

$$\frac{\partial}{\partial t} n(t, x) + \frac{\partial}{\partial x} [f(x, I(t))n(t, x)] = -\mu(x)n(t, x), \quad (5a)$$

which has to obey the following side condition at $x = 0$:

$$I(t)n(t, 0) = \int_0^{\infty} \mu(x)n(t, x)dx. \quad (5b)$$

The dynamics of the immigration rate is given by

$$\frac{d}{dt} I(t) = -(\alpha + \nu)I(t) + \alpha \int_0^{\infty} k(x)xn(t, x)dx. \quad (5c)$$

As a matter of fact, we consider the model (5a)–(5c) as a shorthand notation for a mathematically precise model in the so-called cumulative formulation (Diekmann *et al.* 1998, 2001; Gyllenberg *et al.* 1997).

One of the reasons for this is that the metapopulation state corresponding to metapopulation extinction is the point mass concentrated at the origin and this cannot be represented by a density n . Another reason is that we shall consider the situation of no catastrophes ($\mu = 0$), in which case the boundary condition (5b) becomes meaningless. And last but not least, it follows from the results by Diekmann *et al.* (2001) that the model in the cumulative formulation is well-posed. Diekmann *et al.* (2000) gave examples of innocent looking hyperbolic systems very similar to (5a)–(5c), that lack unique solutions. We refer to Gyllenberg and Metz (2001) for a complete cumulative model formulation. In the Appendix A we derive expressions for the steady states in the cases $\mu = 0$ and $I = 0$, which require the cumulative formulation.

2.2. Resident equilibria

For a given constant value $I > 0$ of the input, we infer from (5a)–(5b) that the unique distribution of local population sizes satisfying $\frac{\partial}{\partial t}n(t, x) = 0$ is

$$n(x, I) = \begin{cases} \frac{1}{l(I)} \frac{\Pi(x, I)}{f(x, I)} & \text{if } x < \tilde{x}(I) \\ 0 & \text{otherwise,} \end{cases} \quad (6)$$

where

$$\tilde{x}(I) = \inf \{x > 0 \mid f(x, I) = 0\} \quad (7)$$

is the supremum of attainable sizes. Two other functions are used in (6). First,

$$\Pi(x, I) = \exp \left[- \int_0^x \frac{\mu(\xi)}{f(\xi, I)} d\xi \right] \quad (8)$$

is the probability that a local population will survive at least to size x . Second,

$$l(I) = \int_0^{\tilde{x}(I)} \frac{1}{f(x, I)} \Pi(x, I) dx \quad (9)$$

is the expected lifetime of a local population. From (5c) we see that the equilibrium immigration rate must satisfy the balance equation

$$I = \pi \int_0^{\tilde{x}(I)} k(x)x n(x, I) dx = \pi \frac{E(I)}{l(I)}, \quad (10)$$

where

$$E(I) = \int_0^{\tilde{x}(I)} \frac{k(x)x}{f(x, I)} \Pi(x, I) dx \quad (11)$$

denotes the expected number of dispersers produced by a local population during its entire life. Equation (10) therefore has the natural interpretation that, at equilibrium,

the immigration rate equals the emigration rate times the probability of surviving migration. We denote equilibrium inputs, that is, solutions of (10), by I^* . The equilibrium local population size distribution corresponding to I^* is

$$n^*(x) = n(x, I^*). \quad (12)$$

2.3. Basic reproduction ratio of the resident

We define the basic reproduction ratio R as the mean number of arriving offspring produced over the lifetime of a local population divided by the mean number of arrivals. When the input I is constant, the mean number of arrivals equals $l(I)I$. Thus we obtain

$$R^{\text{res}}(I) = \pi \frac{E(I)}{l(I)I}. \quad (13)$$

Observe that the steady-state condition (10) reduces to $R^{\text{res}}(I) = 1$, which means that every arriving disperser exactly replaces itself. For a more abstract way of defining $R^{\text{res}}(I)$ as the spectral radius of the next-generation operator we refer to Diekmann *et al.* (1998), Gyllenberg *et al.* (1997) and Gyllenberg and Metz 2001.

The number

$$R_0^{\text{res}} := \lim_{I \rightarrow 0} R^{\text{res}}(I) \quad (14)$$

determines whether the resident population can spread in a virgin environment.

Theorem 1. *The number R_0^{res} equals*

$$R_0^{\text{res}} = \begin{cases} \pi \frac{k(0)}{\mu(0) - g(0) + k(0)} & \text{if } \mu(0) - g(0) + k(0) > 0 \\ \infty & \text{if } \mu(0) - g(0) + k(0) \leq 0 \text{ and } k(0) > 0. \end{cases} \quad (15)$$

Proof. Consider the quantity

$$\bar{E}(I) = \frac{E(I)}{I} = \int_0^{\bar{x}(I)} \frac{k(x)x}{lf(x, I)} \Pi(x, I) dx. \quad (16)$$

By a change of variables, $z = x/I$, we obtain

$$\bar{E}(I) = \int_0^{\bar{x}(I)/I} \frac{k(zI)z}{[g(zI) - k(zI)]z + 1} \exp \left[- \int_0^z \frac{\mu(\eta I)}{[g(\eta I) - k(\eta I)]\eta + 1} d\eta \right] dz. \quad (17)$$

Let $I \rightarrow 0$ to get

$$\begin{aligned} \lim_{I \rightarrow 0} \bar{E}(I) &= \int_0^\infty \frac{k(0)z}{[g(0) - k(0)]z + 1} \exp \left[- \int_0^z \frac{\mu(0)}{[g(0) - k(0)]\eta + 1} d\eta \right] dz \\ &= \frac{k(0)}{\mu(0)[\mu(0) - g(0) + k(0)]}. \end{aligned} \quad (18)$$

The result (15) follows from this, from equation (13), and from the fact that $\lim_{I \rightarrow 0} l(I) = 1/\mu(0)$. \square

If $R_0^{\text{res}} > 1$, the metapopulation is viable. The model can have multiple equilibria, as can be seen in Figs. 1b and 1c. This was already noted by Gyllenberg and Hanski (1992) for a very similar model with a different colonization rule. Therefore, $R_0^{\text{res}} < 1$ does not necessarily imply extinction.

2.4. Invasion fitness of the mutant

When a mutant arrives in a patch where the resident population has size x_{res}^0 , it feels the local population size $X_I(t, x_{\text{res}}^0)$, where $X_I(t, x_{\text{res}}^0)$ is the solution of (3) with

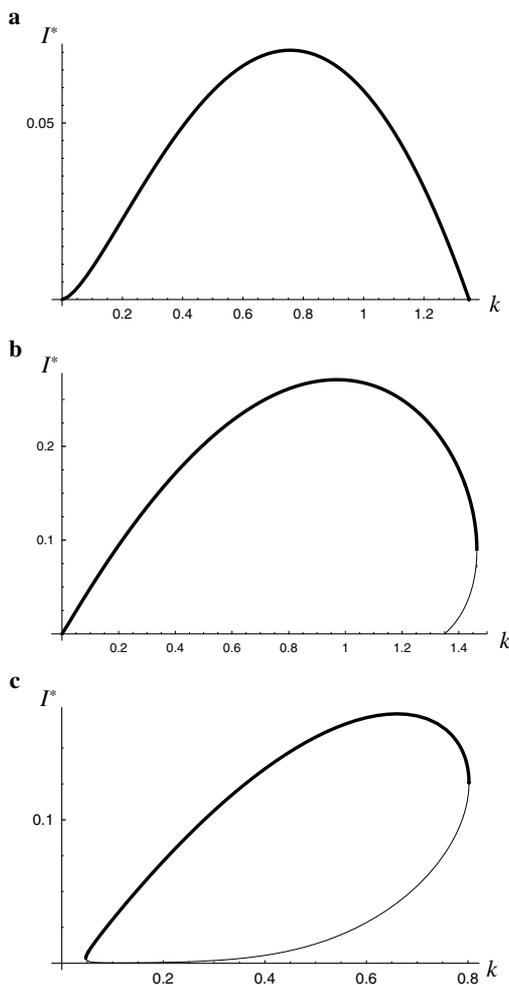


Fig. 1. Dependence of the equilibrium immigration rate I^* on the dispersal rate k in different settings. (a) Constant catastrophes $\mu(x) = 0.4$. (b) & (c) Catastrophe rate μ decreases with local population size x according to (34) with $\mu(0) = 0.4$ in (b) and $\mu(0) = 1.2$ in (c). Stable and unstable equilibria I^* are shown as thick and thin curves, respectively. Local growth is logistic with $g(x) = 1 - x$. Parameters: $\alpha = 0.5$, $\nu = 0.4$.

$x(0) = x_{\text{res}}^0$. As shown by Gyllenberg and Metz (2001), the expected number of dispersers per individual produced by a mutant population can be written as

$$\begin{aligned} E^{\text{mut}}(x_{\text{res}}^0, I) &= \int_0^\infty k_{\text{mut}}(X_I(t, x_{\text{res}}^0)) \exp \left[\int_0^t g(X_I(\tau, x_{\text{res}}^0)) \right. \\ &\quad \left. - k_{\text{mut}}(X_I(\tau, x_{\text{res}}^0)) - \mu(X_I(\tau, x_{\text{res}}^0)) d\tau \right] dt \\ &= \int_{x_{\text{res}}^0}^{\tilde{x}(I)} \frac{k_{\text{mut}}(x)}{f(x, I)} \exp \left[\int_{x_{\text{res}}^0}^x \frac{g(\xi) - k_{\text{mut}}(\xi) - \mu(\xi)}{f(\xi, I)} d\xi \right] dx. \end{aligned} \quad (19)$$

The fitness of the mutant is given by

$$\begin{aligned} R^{\text{mut}}(I^*) &= \pi \int_0^{\tilde{x}(I^*)} E^{\text{mut}}(x_{\text{res}}, I^*) n^*(x_{\text{res}}) dx_{\text{res}} \\ &= \frac{\pi}{l(I^*)} \int_0^\infty E^{\text{mut}}(X_{I^*}(t, 0), I^*) \Pi(X_{I^*}(t, 0), I^*) dt. \end{aligned} \quad (20)$$

See also Parvinen (2002). Based on this invasion fitness, which was derived by Gyllenberg and Metz (2001), we can use the framework of adaptive dynamics (Metz *et al.* 1992, 1996; Dieckmann and Law 1996; Geritz *et al.* 1997, 1998) to analyze the evolutionary dynamics of the metapopulation.

A strategy k^* is an *evolutionarily stable strategy* (ESS) if it cannot be invaded by other strategies (Maynard Smith and Price 1973, Maynard Smith 1982). A strategy k^* is *convergence stable* or an evolutionary attractor if the repeated invasion of nearby mutant strategies into nearby resident strategies will lead to the convergence of resident strategies towards k^* (Christiansen 1991). A strategy that is both convergence stable and evolutionarily stable is called a *continuously stable strategy* or CSS (Eshel 1983). For the distinction between evolutionary and convergence stability see also Taylor (1989). This terminology might not be ideal, but has nevertheless become established in the literature.

3. Without catastrophes the strategy not to disperse is an ESS

If there are no catastrophes, populations in all patches will grow towards the supremum size $\tilde{x}(I^*)$. It is therefore intuitively clear that the equilibrium local population size distribution will be $\delta_{\tilde{x}(I^*)}$, a unit mass concentrated at $\tilde{x}(I^*)$, a fact that will be proved in Lemma 1. At a demographic equilibrium there is no advantage to dispersal; a dispersing individual will arrive at a patch that has the same conditions as the one it has left. In fact, we shall prove that the strategy not to disperse is evolutionarily stable in the absence of catastrophes. Furthermore, we shall prove that it is a continuously stable strategy (CSS) if, in the absence of catastrophes, there is positive dispersal risk: $\rho > 0$.

The equilibrium distribution n^* of local population sizes found in (12) is a density, that is, an element of $L^1(\mathbb{R}_+)$. By the usual (Radon-Nikodym) embedding of L^1 into M (the space of all Borel measures), densities can be regarded as absolutely continuous measures. In particular, it makes sense to speak about weak*-convergence of densities.

Lemma 1. Assume $\mu(x) = \mu \geq 0$ is independent of x . If $\mu = 0$, then $n^* = \delta_{\tilde{x}(I^*)}$. Moreover, n^* tends to $\delta_{\tilde{x}(I)}$ in the weak*-topology as $\mu \rightarrow 0$.

Proof. That $\mu = 0$ implies $n^* = \delta_{\tilde{x}(I)}$ is proved in the Appendix A.

When $\mu(x) = \mu \neq 0$ then $l(I) = 1/\mu$. Let $H(x)$ be continuously differentiable. Integrating by parts, we obtain

$$\begin{aligned} G(\mu, H) &= \int_0^{\tilde{x}(I)} H(x)n^*(x)dx = \int_0^{\tilde{x}(I)} H(x)\frac{\mu}{f(x, I)}\Pi(x, I)dx \\ &= H(0) + \int_0^{\tilde{x}(I)} H'(x)\Pi(x, I)dx. \end{aligned} \quad (21)$$

The integral is bounded and $\Pi(x, I) \rightarrow 1$ for $x < \tilde{x}(I)$ when $\mu \rightarrow 0$. By Lebesgue's dominated convergence theorem we have

$$\lim_{\mu \rightarrow 0} G(\mu, H) = H(0) + \int_0^{\tilde{x}(I)} H'(x)dx = H(\tilde{x}(I)). \quad (22)$$

Since continuously differentiable functions are dense in the set of continuous functions, the claim $\lim_{\mu \rightarrow 0} G(\mu, H) = H(\tilde{x}(I))$ holds also when H is only continuous. \square

Using the weak*-convergence of the local population size distribution we can evaluate explicitly the fitness of rare mutants and conduct the evolutionary analysis in the absence of catastrophes.

Theorem 2. If $\mu = 0$, the non-dispersing strategy $k(x) = 0$ is evolutionarily stable; it is also an evolutionary attractor (convergence stable) if $v > 0$.

Proof. According to Lemma 1, the fitness of the mutant is

$$\begin{aligned} R^{\text{mut}}(I^*) &= \pi E^{\text{mut}}(\tilde{x}(I^*), I^*) \\ &= \pi \int_0^\infty k_{\text{mut}}(\tilde{x}(I^*)) \exp \left[\int_0^t g(\tilde{x}(I^*)) - k_{\text{mut}}(\tilde{x}(I^*))d\tau \right] dt \\ &= \begin{cases} \pi \frac{k_{\text{mut}}(\tilde{x}(I^*))}{k_{\text{mut}}(\tilde{x}(I^*)) - g(\tilde{x}(I^*))} & \text{if } k_{\text{mut}}(\tilde{x}(I^*)) - g(\tilde{x}(I^*)) > 0 \\ \infty & \text{if } k_{\text{mut}}(\tilde{x}(I^*)) - g(\tilde{x}(I^*)) < 0. \end{cases} \end{aligned} \quad (23)$$

As proved in the Appendix A, $I^* = \pi k(\tilde{x}(I^*))\tilde{x}(I^*)$. Therefore, from $f(\tilde{x}(I^*), I^*) = 0$,

$$g(\tilde{x}(I^*)) = k(\tilde{x}(I^*)) - \frac{I^*}{\tilde{x}(I^*)} = \rho k(\tilde{x}(I^*)). \quad (24)$$

Therefore, when $k_{\text{mut}}(\tilde{x}(I^*)) > \rho k(\tilde{x}(I^*))$, we have

$$R_0^{\text{mut}}(I^*) = \frac{\alpha k_{\text{mut}}(\tilde{x}(I^*))}{\alpha k_{\text{mut}}(\tilde{x}(I^*)) + v[k_{\text{mut}}(\tilde{x}(I^*)) - k_{\text{res}}(\tilde{x}(I^*))]}. \quad (25)$$

The case $\nu = 0$ is neutral, since then $R_0^{\text{mut}}(I^*) = 1$. If $\nu > 0$ we easily see

$$R_0^{\text{mut}}(I^*) \begin{cases} = 1 & \text{if } k_{\text{mut}}(\tilde{x}(I^*)) = k_{\text{res}}(\tilde{x}(I^*)) \\ > 1 & \text{if } k_{\text{mut}}(\tilde{x}(I^*)) < k_{\text{res}}(\tilde{x}(I^*)) \\ < 1 & \text{if } k_{\text{mut}}(\tilde{x}(I^*)) > k_{\text{res}}(\tilde{x}(I^*)) \end{cases} \quad (26)$$

and $R_0^{\text{mut}}(I^*) = \pi = \frac{\alpha}{\alpha + \nu} < 1$ if $k_{\text{res}}(\tilde{x}(I^*)) = 0$. Therefore, the strategy not to disperse is continuously stable. \square

The evolutionary stability of zero dispersal in the absence of catastrophes has been studied before. Hastings (1983) found this in a continuous-time model with a finite number of patches. Parvinen (1999) investigated a discrete-time metapopulation model with a finite number of patches without catastrophes and proved that within the model the strategy not to migrate is a CSS, if the resident is at a fixed point equilibrium and there is mortality during dispersal.

4. Continuous transition to extinction

The metapopulation is not viable for all parameter values. In general, the viability region V is defined as the set of strategies for which there exists a nonzero population dynamical attractor. The extinction boundary ∂V is simply the boundary of the viability region V . The change from viability to extinction at the boundary ∂V can happen through several different bifurcations. In this section we study transitions to extinction, for which the equilibrium immigration rate goes to zero continuously as the dispersal rate k varies. A typical example is the situation in which the solution corresponding to metapopulation extinction ($I^* = 0$) loses its stability through a supercritical bifurcation (see Fig. 2a).

4.1. Limit patch size distribution

If the immigration rate I becomes zero, patches will not be recolonized after a catastrophe has occurred. Accordingly, the corresponding equilibrium size distribution n^* is the trivial one, δ_0 , with all patches being empty. Our next lemma shows that n^* continuously depends on I at δ_0 with respect to the weak*-topology.

Lemma 2. $I = 0$ implies $n^* = \delta_0$. Furthermore $n^* \rightarrow \delta_0$ in the weak*-topology as $I^* \rightarrow 0$.

Proof. That $I = 0$ implies $n^* = \delta_0$ is proven in the Appendix A.

Let $H(x)$ be a continuously differentiable function. Integrating by parts, we get

$$\int_0^{\tilde{x}(I)} H(x) \frac{\Pi(x, I)}{f(x, I)} dx = \frac{H(0)}{\mu(0)} + \int_0^{\tilde{x}(I)} \frac{d}{dx} \left[\frac{H(x)}{\mu(x)} \right] \Pi(x, I) dx. \quad (27)$$

The last integral is bounded, therefore Lebesgues dominated convergence theorem can be used. Since $\Pi(0, I) = 1$ and $\lim_{I \rightarrow 0} \Pi(x, I) = 0$ when $x > 0$, the last integral tends to zero for $I \rightarrow 0$. The integral

$$\int_0^{\tilde{x}(I)} H(x) \frac{\Pi(x, I)}{f(x, I)} dx \rightarrow \frac{H(0)}{\mu(0)} \quad (28)$$

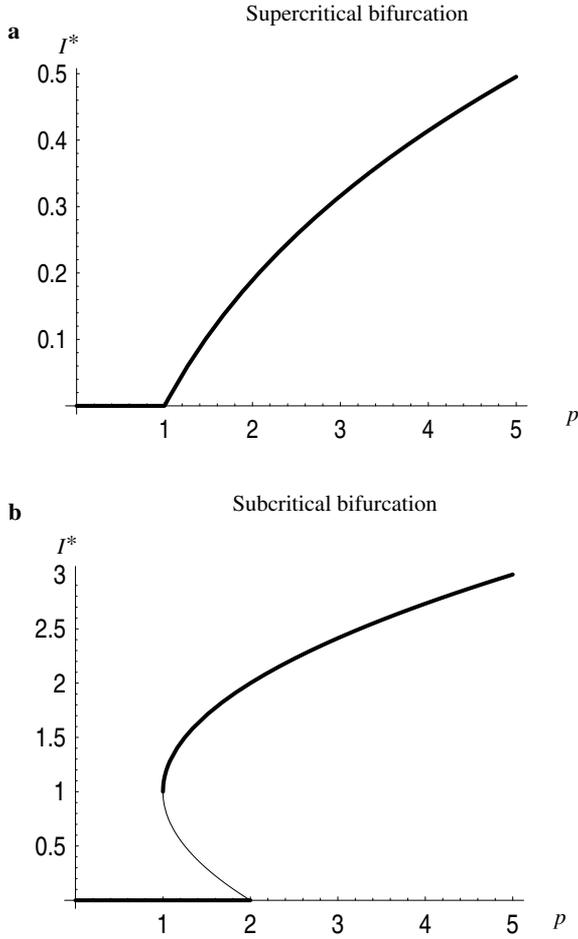


Fig. 2. Typical examples of (a) continuous and (b) discontinuous transitions to extinction. The equilibrium immigration rate I^* is plotted against some parameter p . Stable equilibria lie on the thick curve, unstable ones on the thin curve.

for $I \rightarrow 0$, if H/μ is bounded. Take $H(x) = 1$ to obtain $\lim_{I \rightarrow 0} l(I) = 1/\mu(0)$. Therefore

$$\int_0^{\bar{x}(I)} H(x)n^*(x)dx = \int_0^{\bar{x}(I)} H(x) \frac{\Pi(x, I)}{l(I)f(x, I)} dx \rightarrow H(0) \quad (29)$$

for $I \rightarrow 0$. As in the proof of Lemma 1, the claim holds also when H is only continuous, since continuously differentiable functions are dense in the set of continuous functions. \square

4.2. Evolutionary repulsion of the extinction boundary

When the resident population size is low, the mutant metapopulation will grow and produce dispersers as if it were in a virgin environment. Therefore the mutant's fitness equals R_0^{res} . This is proven in the following lemma.

Lemma 3.

$$\lim_{I \rightarrow 0} R^{\text{mut}}(I) = R_0^{\text{res}} \Big|_{k_{\text{res}}=k_{\text{mut}}}. \quad (30)$$

Proof. According to Lemma 2

$$\lim_{I \rightarrow 0} R^{\text{mut}}(I) = \pi \lim_{I \rightarrow 0} E^{\text{mut}}(0, I). \quad (31)$$

The result (30) follows from

$$\begin{aligned} E^{\text{mut}}(0, 0) &= \int_0^\infty k_{\text{mut}}(0) \exp \left[\int_0^t [g(0) - k_{\text{mut}}(0) - \mu(0)] d\tau \right] dt \\ &= \begin{cases} \frac{k_{\text{mut}}(0)}{k_{\text{mut}}(0) + \mu(0) - g(0)}, & \text{if } k_{\text{mut}}(0) + \mu(0) - g(0) > 0 \\ \infty & \text{otherwise.} \end{cases} \end{aligned} \quad (32)$$

□

For those readers interested in adaptive dynamics theory we mention that Lemma 3 is very closely related to the assumption S3 in section 6.3.3 of Metz *et al.* (1996).

Because the transition to extinction is assumed to be continuous, the resident population size is zero at the boundary ∂V of the viability region V . Therefore, if the value of an evolving parameter p is at the boundary ∂V of the viability region V , then mutants that are viable in the absence of the resident can invade. Mutants that are not viable cannot invade. This proves the following theorem.

Theorem 3. *Let p be an evolving parameter, V the viability region and $I^*(p)$ a branch of stable nontrivial equilibria corresponding to p . If $\lim_{p \rightarrow \partial V} I^*(p) = 0$, then ∂V is evolutionarily repelling.*

Theorem 3 says that if the immigration rate goes continuously to zero when the viability boundary is approached, then this boundary is evolutionarily repelling; thus selection will move the dispersal strategy into the interior of the viability region. This means that evolutionary suicide is not possible.

4.3. First example: Constant catastrophe rate

We now study an example, in which the metapopulation exhibits a transcritical bifurcation, i.e., a continuous transition to extinction. We assume that neither the catastrophe rate nor the dispersal rate depend on local population size; the local growth rate is chosen as being logistic, $g(x) = a(1 - x/K)$.

In this case the basic reproduction ratio is given by

$$R^{\text{res}}(I) = \pi \int_0^1 \frac{2k[1 - y^{\frac{S(I)}{\mu}}]}{S(I) + k - a + y^{\frac{S(I)}{\mu}} [S(I) - k + a]} dy, \quad (33)$$

with $S(I) = \sqrt{(k - a)^2 + 4aI/K}$. Tedious but straightforward calculations show that $\frac{d}{dI} R^{\text{res}}(I) \leq 0$, so the function $R^{\text{res}}(I)$ is monotonically nonincreasing. Therefore, if $R_0^{\text{res}} > 1$, there exists a unique positive equilibrium, which is stable. If $R_0^{\text{res}} < 1$, the extinct state is the only equilibrium. At the boundary of viability $R_0^{\text{res}} = 1$ and the immigration rate goes continuously to zero. We thus have a transcritical bifurcation at $k = (a - \mu)/\rho$ and at $k = 0$. See Fig. 1a for an example. According to Theorem 3 the boundaries are evolutionarily repelling.

Figure 3a shows how the evolutionarily stable dispersal rate changes with respect to the catastrophe rate μ_0 and dispersal risk ρ . In Figure 3a there is always a continuously stable strategy in the viability region $0 \leq \mu < 1$. As shown by Parvinen *et al.* (in press), the CSS dispersal rate exhibits an intermediate maximum with respect to the catastrophe rate μ . Increasing dispersal risk ρ decreases the dispersal rate.

As Parvinen *et al.* (in press) pointed out, an increase in the catastrophe rate while it is low is expected to select for higher dispersal rates, because local extinctions result in empty or thinly populated patches, the existence of which makes dispersal profitable. However, for high rates of local extinction, adapted dispersal rates decrease again when extinctions become more frequent. Parvinen *et al.* (in press) suggested the following explanation for this. An increased rate of local extinction also affects the size structure of the metapopulation by decreasing the average population size and increasing the fraction of small local populations. The per capita growth rate is highest in patches with a small population, which are therefore the most advantageous to be in. With the rate of local extinction increasing, more and more individuals thus reside in advantageous patches, which in turn decreases the benefit of dispersal. An intermediate maximum of dispersal rates has been earlier observed also by Ronce *et al.* (2000).

5. Discontinuous transition to extinction

In this section we study the case of discontinuous transition to extinction: here the equilibrium immigration rate first changes continuously, but then suddenly drops to zero as the dispersal rate k varies. As a typical example we mention the case in which the equilibrium corresponding to $I^* = 0$ loses its stability in a subcritical bifurcation (see Fig. 2b).

5.1. A discontinuous transition to extinction is necessary for evolutionary suicide

Evolutionary suicide is an evolutionary process, during which an initially viable metapopulation adapts in such a way that it can no longer persist, see Ferrière (1999, 2000, in prep.). See also Matsuda and Abrams (1994), as well as Cadet (1998).

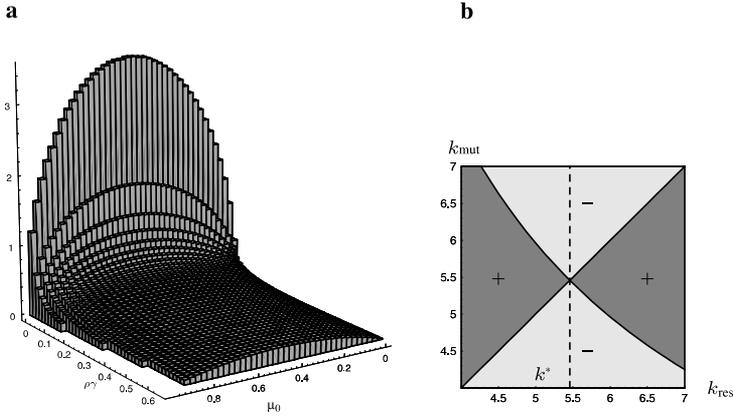


Fig. 3. (a) Dependence of CSS dispersal rate k^* on catastrophe rate μ_0 and dispersal risk ρ for the first example. Parameters: $a = 1$, $K = 1$, $\alpha = 0.5$. (b) Pairwise invasibility plot for $\mu_0 = 0.8$ and $\rho = 0.005$. The CSS dispersal rate is located at $k^* \approx 5.5$.

Theorem 3 shows that, in the case of a continuous transition to extinction, the boundaries of viability are evolutionarily repelling. Therefore, a discontinuous transition to extinction is a necessary condition for evolutionary suicide. It is, however, not a sufficient condition, as we will see from our second and third example below. We refer to the paper by Gyllenberg and Parvinen (2001) for a further discussion on conditions for evolutionary suicide. In the following section we analyze how the phenomenon of evolutionary suicide can occur in the metapopulation model studied in this paper.

5.2. Second example: Size-dependent catastrophe rate

If the catastrophe rate is a decreasing function of the local population size and $R_0^{\text{res}} < 1$, we can observe a special type of evolutionary bifurcation when increasing the dispersal risk ρ . In the following examples we use the catastrophe function

$$\mu(x) = \mu_0 \left[1 - (1 - p) \frac{1 - \exp(-zx/K)}{1 - \exp(-z)} \right]. \quad (34)$$

This specific choice is used for illustration only. See Fig. 4 for an example. The number $\mu(0) = \mu_0$ describes the level of the catastrophe functions, it does not change its shape. The number K is chosen to be the carrying capacity of the local growth function $g(x)$ and p is the fraction of the catastrophe rate at the carrying capacity K relative to μ_0 , thus $\mu(K) = p\mu_0$. The parameter z describes the steepness of decrease.

With low dispersal risk ρ , there exists one CSS (Fig. 5a). When the risk increases, the viable region decreases and the CSS dispersal rate approaches the lower boundary of viability. When the risk is high enough, there appears another evolutionarily stable strategy that, however, is not convergence stable, i.e., it is an

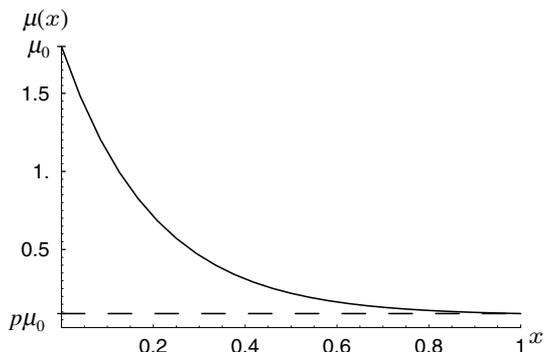


Fig. 4. The catastrophe function $\mu(x)$ as described by (34) for $\mu_0 = 1.8$, $p = 0.05$, $K = 1$, $z = 5$.

evolutionary repeller (Fig. 5b). When the dispersal risk increases even more, these two singular strategies collide (Fig. 5c) and thereby disappear (Fig. 5d).

Once the regime depicted in Fig. 5d has been reached, residents with a viable dispersal rate can always be invaded by some mutants with a lower dispersal rate. The dispersal rate will therefore decrease and will move closer and closer towards the lower boundary of viability. Once a resident at the lower boundary has become established, again a mutant with even lower dispersal rate can increase in population size. The mutant is not viable alone and therefore it cannot replace the resident. It will, however, move the resident population size away from its original attractor into the basin of attraction of the equilibrium that corresponds to extinction. Thus, the metapopulation will go extinct.

Figure 6a shows the interplay of dispersal risk ρ and catastrophe rate μ_0 in setting the stage for evolutionary suicide. For low dispersal risks and catastrophe rates the viability boundaries are repelling and there is a continuously stable dispersal rate. When either dispersal risk or catastrophe rate is increased enough an evolutionary bifurcation to evolutionary suicide occurs as described above. Beyond that point, the viability region shrinks and finally disappears, leading to extinction of the metapopulation. Figure 6b illustrates this bifurcation structure along a cross-section at $\mu_0 = 1.8$.

5.3. Third example: Allee effect

Another ecological scenario for which we would expect a discontinuous transition to extinction arises from local population growth functions with an Allee effect, i.e., with a negative per capita growth rate at low population sizes (Allee *et al.* 1949).

The resulting bifurcation structure is similar to that in the second example: intermediate dispersal risks and catastrophe rates result in a CSS dispersal rate. When either dispersal risk or catastrophe rate is increased enough, a bifurcation to evolutionary suicide occurs. See Fig. 8.

For low catastrophe rates, however, the situation is different. Selection towards low dispersal then leads to evolutionary suicide. This is remarkable: one would

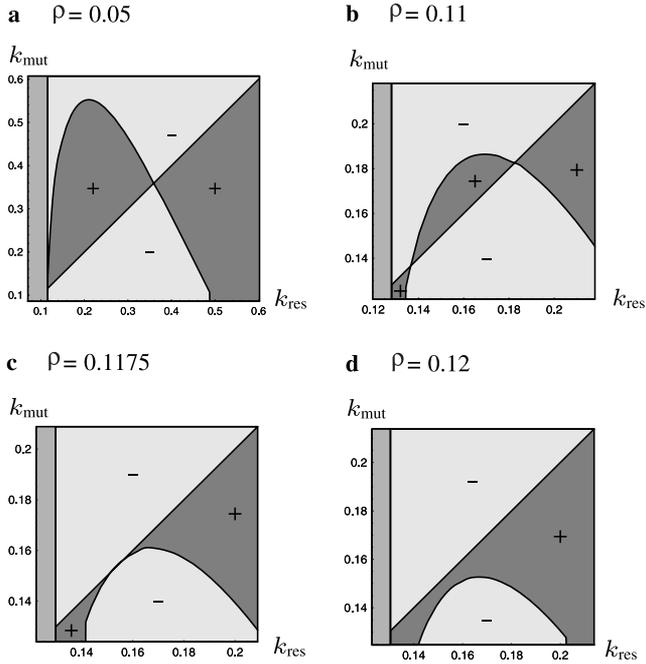


Fig. 5. Pairwise invasibility plots illustrating the route to evolutionary suicide. The medium gray rectangle on the left side of each panel corresponds to values of the resident strategy k for which the metapopulation is not viable. Local growth is logistic with $g(x) = a(1 - x/K)$. Parameters: $\alpha = 0.5$, $a = 1$, $K = 1$. The catastrophe function $\mu(x)$ is given by (34) with $\mu_0 = 1.8$, $p = 0.05$, $z = 5$.

naively expect that only too high catastrophe rates may cause a metapopulation to go extinct. Yet in this example extinction also happens if there are too few catastrophes.

Is this finding compatible with Theorem 2, which states that without catastrophes the strategy not to disperse is a CSS? It is indeed compatible, as the remainder of this paragraph explains. When there are no catastrophes, all patches will reach the maximum population size \tilde{x} , therefore the average population size is \tilde{x} . Selection will favor low dispersal: after adaptation is completed, we have $k = 0$. Therefore \tilde{x} equals the carrying capacity of the growth function. Patches with very small population size would become empty if an Allee effect were present, but this is not a problem to the metapopulation since all local populations are large and no catastrophes occur. However, as soon as we introduce a little amount of catastrophes, the situation changes drastically. Catastrophes are so infrequent that low dispersal is still favored by selection. Yet, when dispersal becomes too low, a patch cannot be rescued after its population has been eradicated by a catastrophe. Since all patches will eventually experience a catastrophe, the metapopulation goes extinct.

Figure 9 illustrates this situation. In the absence of catastrophes, the metapopulation is viable for any dispersal rate that is not too large. With positive catastrophe rate, the range of viable dispersal rates shrinks at both ends. In particular, the

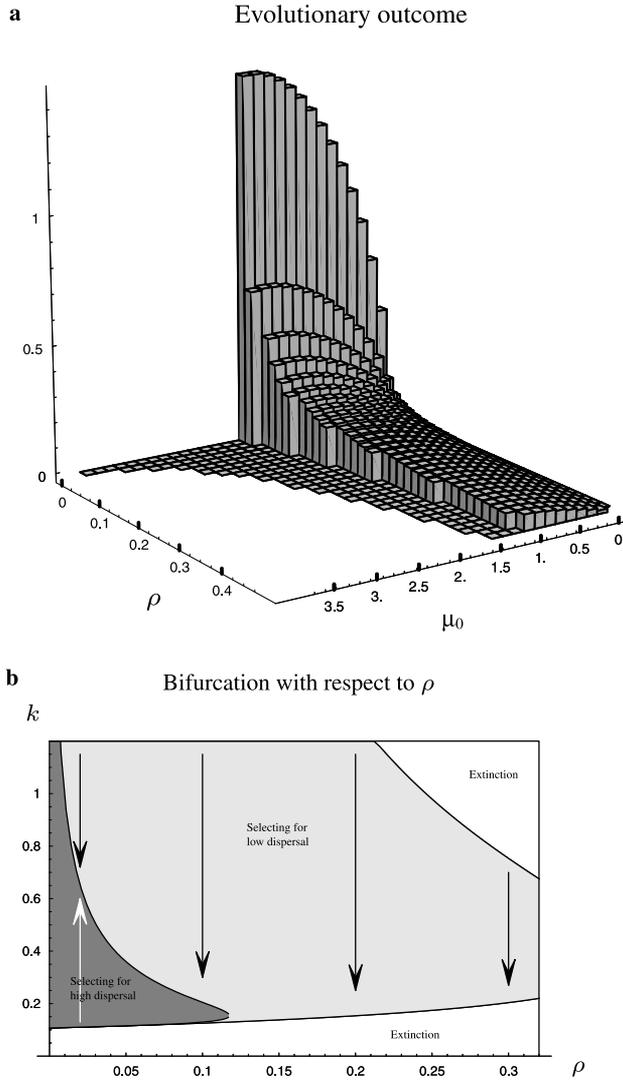


Fig. 6. (a) Dependence of CSS dispersal rate k^* on catastrophe rate μ_0 and dispersal risk ρ for the second example. For small dispersal risk and catastrophe rate there exists a CSS dispersal rate. When either dispersal risk or catastrophe rate is increased enough, an evolutionary bifurcation to evolutionary suicide occurs (gray part of bottom plane). The white part of the bottom plane corresponds to parameter combinations for which the metapopulation is not viable. (b) Bifurcation diagram with respect to ρ for a cross-section at $\mu_0 = 1.8$. Dispersal rates at which selection favors lower dispersal rates are plotted in light gray; selection for higher dispersal rates is indicated by dark gray. In the white area the metapopulation is not viable. For low dispersal risk, a CSS dispersal rate exists. When the dispersal risk is increased, the domain in which selection favors higher dispersal rates shrinks and finally disappears. After that point, selection for lower dispersal rates leads to evolutionary suicide. Local growth is logistic, $g(x) = a(1 - x/K)$. The catastrophe function is given by (34) with $z = 5$, $p = 0.05$. Other parameters: $\alpha = 0.5$, $a = 1$, $K = 1$.

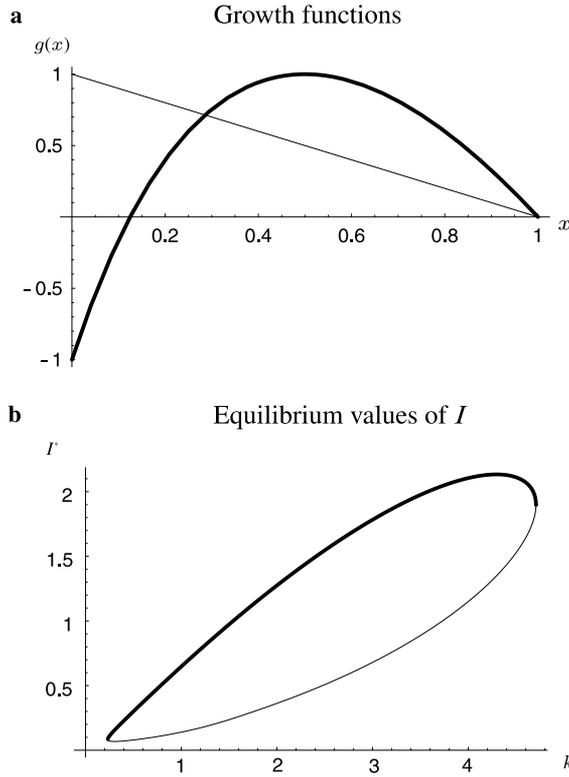


Fig. 7. (a) Logistic growth function $g(x) = 1 - x$ (thin curve) and a growth function with Allee effect (thick curve) $g(x) = a \frac{x}{1+x} - b - cx$ with $a = 18$, $b = 1$, $c = 8$. (b) Equilibrium values for the immigration rate I in the case of an Allee effect. Stable equilibria lie on the thick curve, unstable ones on the thin curve. Parameters: $\alpha = 0.5$, $\mu = 0.2$, $\nu = 0.1$.

metapopulation is not viable for sufficiently small dispersal rates and a discontinuous transition to extinction arises that allows for evolutionary suicide.

5.4. A discontinuous transition to extinction is not sufficient for evolutionary suicide

According to Theorem 3, no evolutionary suicide can occur when the transition to extinction is continuous. As stated in Section 5.1, a discontinuous transition to extinction is therefore a necessary condition for evolutionary suicide. Nevertheless, the boundaries of the viability region can be repelling also in this case. Both our second and third example allow for some parameter values that bring about a discontinuous transition to extinction without resulting in evolutionary suicide.

In the second example the catastrophe rate $\mu(x)$ is a decreasing function of the local population size x . If $\mu(0) > g(0)$, the basic reproduction ratio R_0^{res} is less than 1 for any dispersal rate. Therefore, either a discontinuous transition to extinction occurs (as in Fig. 1c) or the metapopulation is not viable for any dispersal rate

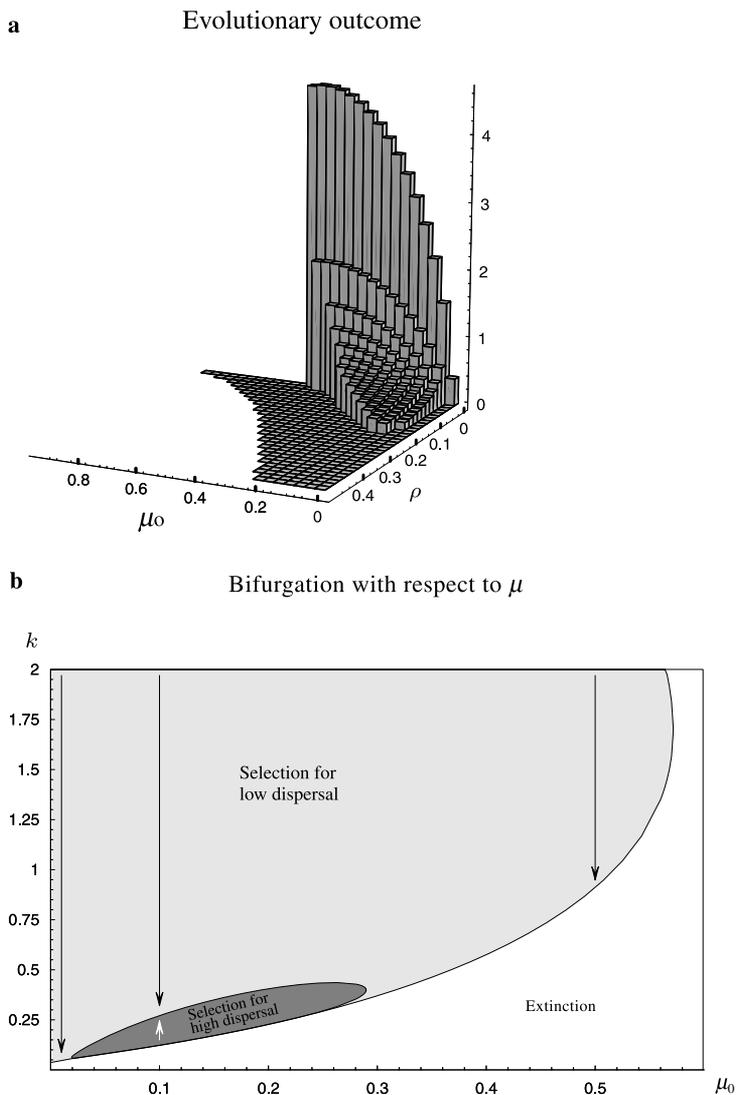


Fig. 8. (a) Dependence of CSS dispersal rate k^* on catastrophe rate μ_0 and dispersal risk ρ for the third example. For high dispersal risk and catastrophe rate we observe the same pattern as in Fig. 6: the range for which selection favors higher dispersal rates decreases and eventually disappears, leading to evolutionary suicide. For low catastrophe rates the situation is completely different: evolutionary suicide can result from an improvement of environmental conditions by decreasing μ_0 . (b) Bifurcation diagram with respect to μ_0 for a cross-section at $\rho = 0.15$. The region of parameter values where lower dispersal is selected for is plotted in light gray, and selection for higher dispersal occurs for the region plotted in dark gray. In the white area the metapopulation is not viable. Local growth exhibits an Allee effect according to Fig. 7a. Parameters: $\alpha = 0.5$, $\mu(x) = \mu_0$.

k . When the dispersal risk ρ is low enough, a CSS dispersal rate exists and no evolutionary suicide occurs (see Figs. 5a and 6).

In the third example we have $g(0) < 0$ and the basic reproduction ratio R_0^{res} is less than 1 for any catastrophe rate μ and dispersal rate k . Like in the second example, there is either a discontinuous transition to extinction (Fig. 7b) or certain extinction. Also in this example there are parameter combinations of μ and ρ that allow for a CSS dispersal rate (see Fig. 8).

6. Discussion

In this paper we have studied the evolution of dispersal and the potential for evolutionary suicide in a structured metapopulation model. We have proved that, in the absence of local catastrophes, selection favours decreased dispersal rates: the strategy not to disperse is an ESS. In the presence of catastrophes, we have studied bifurcations that result from the dispersal rate crossing the boundary between regions of viability and extinction. We proved that if the bifurcation is such that the metapopulation size goes continuously to zero as the dispersal rate approaches the extinction boundary, then the extinction boundary is evolutionarily repelling and no evolutionary suicide can occur. This means that a discontinuous transition to extinction (a positive metapopulation size going to zero abruptly as the dispersal rate crosses the boundary) is a necessary but not a sufficient condition for evolutionary suicide. These findings are summarized in Fig. 10.

In general, the mechanisms by which evolutionary suicide can occur are related to the tragedy of the commons (Hardin 1968), that is, a situation in which selfish individual behaviour leads to worsening of the living conditions. The invasion fitness of a rare mutant depends on the mutant's phenotype and the environment set by the resident's phenotype. It provides a criterion for invasion but does not tell anything about how the environmental conditions change in case the mutant in-

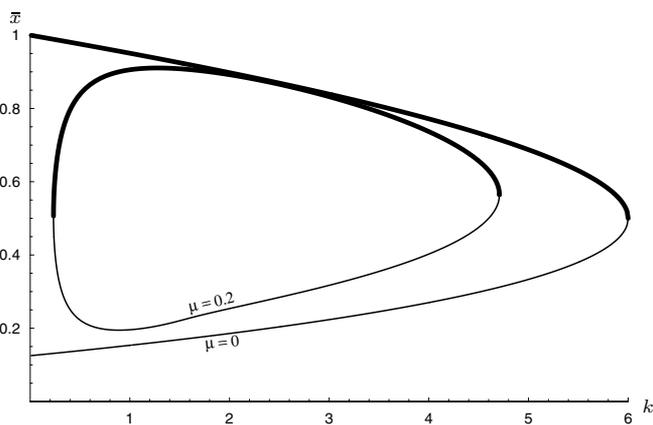


Fig. 9. Average population size \bar{x} at equilibrium for $\mu = 0$ and $\mu = 0.2$ when the growth function exhibits an Allee effect. Population sizes corresponding to stable equilibria lie on the thick curve, unstable ones on the thin curve. Parameters: $\alpha = 0.5$, $\nu = 0.1$.

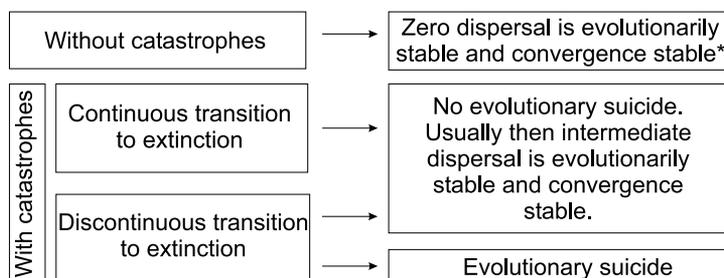


Fig. 10. Summary of the different cases investigated in this paper. *: convergence stability applies if dispersal risk is positive.

vades and becomes the new resident. It is therefore perfectly possible that evolution leads to a gradual, and self-inflicted deterioration of the conditions experienced by the evolving population, potentially up to a point at which the population's viability is jeopardized. In this paper we have given specific examples of this general phenomenon in the context of evolution of dispersal in metapopulations.

Figure 5 describes a typical route to evolutionary suicide in which two singular strategies come closer and closer to each other and finally collide and disappear. Similar evolutionary patterns in metapopulations involving colliding and disappearing singular strategies have been described by Jansen and Mulder (1999) and De Mazancourt and Loreau (2000).

Our basic population dynamical model is based on the assumption of infinitely many patches with infinitely large local populations. As a consequence of the latter assumption, a single individual and in particular, a disperser, is of infinitesimal size relative to the local populations. This simplification leads to a tractable deterministic model, but has three biologically relevant implications.

Firstly, it means that the model does not allow for empty patches in an extant metapopulation; after a local population has been wiped out by a catastrophe, the patch will immediately be recolonized by a continuous "rain" of dispersers arriving from other patches.

Secondly, being deterministic the model does not explicitly take demographic stochasticity into account. However, letting the local catastrophe rate be a decreasing function of local population size one can model the consequences of demographic stochasticity: small populations are subject to a higher risk of extinction than larger ones.

The third consequence, which is most important in the present context, is that the fitness of a mutant is not affected by its relatedness to other individuals in the same patch. The reason is that mutants are initially infinitesimally rare, both at the local and the metapopulation level. Therefore a mutant is unrelated to practically all other individuals in the patch. This is in glaring contrast to models with finite local populations and immigration modelled as a discrete event. In such models a local population will after colonization but before the next immigration event consist of individuals which are all related. As a matter of fact, the evolution of dispersal has often been interpreted in the context of altruism and kin selection (Hamilton and

May 1977). We point out that our model cannot capture the evolutionary consequences of relatedness.

As a matter of fact, the three consequences of our basic assumption highlighted above have less impact on the predicated evolutionary outcomes of dispersal evolution than one might naïvely think: it can be shown (Parvinen *et al.* in press) that dispersal rates in a metapopulation model with finite local population sizes largely evolve in the same way as in the model studied here, as long as local population sizes are not too small and catastrophe rates are not zero.

As rarity is the precursor of extinction, a problem related to the study of evolutionary suicide is to understand the mechanisms by which natural selection may lead to low population densities. Once a species has become rare, demographic stochasticity is likely to wipe it out. Matsuda and Abrams (1994) considered a model in which evolution continually reduced a population's carrying capacity; they called the resulting phenomenon *runaway evolution to self-extinction*. Their model described a population under asymmetric intraspecific competition, in which, under certain circumstances, individuals with larger body size were always favoured by selection. Since individuals were also assumed to possess a carrying capacity that decreased with their body size, evolution towards larger body sizes implied a ceaseless reduction of carrying capacity. Yet, carrying capacity always remained positive and therefore no evolutionary suicide was possible in the deterministic version of Matsuda and Abrams's model. In particular, the authors correctly emphasized that it would be left to demographic stochasticity to finish off a dwindling population and that, if the population's carrying capacity would actually jump to zero at a finite body size, self-extinction could not occur. In this sense, our model, and the one described by Ferrière (2000) may thus be the first to demonstrate the existence of an evolutionarily attracting extinction boundary.

Yet, the study by Matsuda and Abrams (1994) makes another important point: whenever adaptation takes a population into or through regions of trait space that imply small carrying capacities, the evolving population can go extinct. Evidently, evolutionary suicide therefore occurs more easily under stochastic population dynamics than under deterministic ones. While conditions for the deterministic form of evolutionary suicide have been analyzed in this paper, we do not expect that similarly systematic conditions exist for forms of evolutionary suicide that require populations of finite size.

We defined evolutionary suicide as evolution towards a point of the extinction boundary at which the fitness gradient points outwards from the viability set. A possibly similar process of evolution towards an extinction boundary has been found before by Rand *et al.* (1995). These authors studied the evolution of transmissibility in an individual-based spatial host-pathogen system on a square lattice with next-neighbor interactions. They found that there exists a critical transmissibility above which the pathogen dies out (by "burning out" local clusters of susceptible hosts). If the transmissibility is allowed to mutate, it evolves to this critical value, but unlike in the case of evolutionary suicide, the pathogen does not appear to go extinct. Rand *et al.* (1995) called this alternative phenomenon self-evolved criticality. Their study, however, does not contain an explanation of the selection mechanisms that would prevent evolutionary suicide and ultimate extinction at the

critical state. Two reasons for this at first sight paradoxical situation can be considered. One option is that pathogen extinction in this model involves a continuous transition, implying, as shown in the present paper, that the pathogen's extinction boundary is evolutionarily repelling. In this case it might be that there actually exists an evolutionary attractor very close to the extinction boundary, which, however, went unnoticed in the numerical explorations reported in Rand *et al.* (1995). The described phenomenon would then not amount to self-evolved criticality but, rather, to self-evolved "near-criticality". An alternative explanation would be required if the extinction boundary was indeed attracting as claimed by the authors, and thus involved a discontinuous transition to pathogen extinction. This explanation is concerned with the tools by which the authors dealt with the stochastic nature of their model. While the pathogen goes extinct with probability one in any finite version of the model, the time required for such stochastic extinction grows very long for systems of increased size. Following a standard procedure for studying stochastic models of finite populations, Rand *et al.* (1995) therefore conditioned their analysis on the non-extinction of the pathogen and thus might have excluded evolutionary suicide from the investigation.

There is a striking repercussion of evolutionary suicide that deserves to be highlighted because of its much surprising implications for conservation biology. We are generally accustomed to the phenomenon that, if the living conditions of a population become too unfavorable, the population will go extinct. In our model, such environmental deterioration could be reflected either by an increasing catastrophe rate or an increasing dispersal risk. For low catastrophe rates in the presence of an Allee effect, selection actually favors individuals that disperse too little to recolonize patches emptied by catastrophes. As shown on the left side of Figure 8b, making an environment more favorable by reducing the catastrophe rate from some intermediate value to very low levels can therefore have drastic and undesired consequences for metapopulation viability: the *improving* environmental conditions can send the metapopulation to extinction through evolutionary suicide.

A. Cumulative formulation of the model

In this appendix we derive the expressions for the metapopulation steady states in the cases $\mu = 0$ and $I = 0$, which could not be dealt with using the shorthand notation (5a)–(5c) of the model. The nonlinear theory of general structured population models was presented by Diekmann *et al.* (2001) and adapted to structured metapopulation models by Gyllenberg *et al.* (1997). The specific model treated in this paper was formulated by Gyllenberg and Metz (2001).

Because we are only dealing with steady states, we can replace equation (5c) by its quasi-steady approximation,

$$I(t) = \pi \int_0^\infty k(x)xn(t, dx). \quad (35)$$

This approximation leads, of course, to precisely the same metapopulation steady states as the full model incorporating a disperser pool. In (35) the metapopulation

state $n(t, \cdot)$ at time t is a measure. If $n(t, \cdot)$ has a density, as in Section 2, we write (abusing notation) $n(t, x)dx$ instead of $n(t, dx)$.

Local population growth is modelled as a Markov process with local extinction as an absorbing state by specifying the transition probabilities $u_I(t, x)$, that is, $u_I(t, x)(\omega)$ is the probability that a local population which had size x at time 0 is still extant at time t and has size in the set ω . Reproduction (the formation of new local populations) is modelled by prescribing the reproduction kernel Λ : $\Lambda_I(t, x)(\omega)$ is the expected number of new local populations with “size-at-birth” in the set ω , produced in the time interval $[0, t)$ by a local population which had size x at time 0. Our notation here differs slightly from the one used by Diekmann *et al.* (2001).

We define $X_I(t, x_0)$ as the solution of (3) with $x(0) = x_0$. A local population, which at time 0 had size x , will at time t have size $X_I(t, x)$, provided it has not been wiped out by a local catastrophe. The probability that the population is still extant at time t is

$$\mathcal{F}_I(t, x) = \exp \left[- \int_0^t \mu(X_I(s, x)) ds \right]. \quad (36)$$

Note that if $\mu = 0$ (there are no catastrophes), $\mathcal{F}_I \equiv 1$. The transition probability of the local population size is given by the measure

$$u_I(t, x) = \mathcal{F}_I(t, x) \delta_{X_I(t, x)}. \quad (37)$$

When a local population is destroyed by a catastrophe, the patch it inhabited will immediately be recolonized by migrants arriving from other patches provided $I > 0$. We consider this event as the simultaneous death of the local population and the birth of a new local population with size 0. If $I = 0$, there are no dispersers and there will still be death but no birth of a new population. The expected number of new local populations produced in the time interval $[0, t)$ by a local population having size x at time 0 and subject to the input I is therefore

$$1 - \mathcal{F}_I(t, x) \quad (38)$$

and the reproduction kernel is

$$\Lambda_I(t, x) = \begin{cases} (1 - \mathcal{F}_I(t, x)) \delta_0 & \text{if } I > 0 \\ 0 & \text{if } I = 0. \end{cases} \quad (39)$$

Let us first consider the case $\mu = 0$. Then there are neither births nor deaths of local populations, that is, $\Lambda_I \equiv 0$. The system is therefore at equilibrium if and only if the local dynamics given by u_I is at equilibrium, that is

$$n = \int_{[0, \infty)} u_I(t, x) n(dx) \quad (40)$$

for all $t \geq 0$. Inserting (37) (with $\mathcal{F}_I \equiv 1$) into (40) one gets

$$n = \int_{[0, \infty)} \delta_{X_I(t, x)} n(dx) \quad (41)$$

for $t \geq 0$, from which it follows that $n = \delta_{\tilde{x}(I)}$, where $\tilde{x}(I)$, given by (7), is the supremum of attainable sizes. We have now shown that $\delta_{\tilde{x}(I)}$ is the steady state, where I is solved from

$$I = \pi \int k(x)x\delta_{\tilde{x}(I)}(dx), \quad (42)$$

that is, from

$$I = \pi k(\tilde{x}(I))\tilde{x}(I). \quad (43)$$

Finally, let us turn to the case $I = 0$. In this case we still have $\Lambda_I \equiv 0$. Because the value of the function f , defined by (4), is $f(0, 0) = 0$, we have $X_I(t, 0) = 0$ for all t . Therefore $u_I(t, 0) = \delta_0$ for $I = 0$ and consequently (40) can be satisfied by $n = \delta_0$ only. Thus $I = 0$ implies $n = \delta_0$.

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