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On diploid versus clonal ESSes in metapopulations

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Abstract

Most studies of evolutionarily stable strategies (ESSes) assume clonal reproduction. At least in the simplest cases, more realistic genetic models yield results compatible with the clonal results. In this paper we study a case where the diploid and clonal results are not expected to be similar: evolution in a metapopulation with small local population sizes. It turns out, that although there are differences between the clonal and diploid ESS dispersal rates, the trait under consideration, the discrepancy is irrelevant for all practical purposes (less than 2%).

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1   Introduction

For many years ESS theory (Maynard Smith and Price, 1973; Maynard Smith, 1976; Lawlor and Maynard Smith, 1976) and its more recent dynamic extension adaptive dynamics (Metz et al., 1996; Dieckmann and Law, 1996; Geritz et al., 1997, 1998) has been used as a general tool for studying evolution in realistic ecological models with environmental feedback. ESS and adaptive dynamics studies generally assume clonal reproduction. However, there are many results showing that, at least in the simplest cases, more realistic genetic models yield results compatible with the clonal ones (Eshel and Feldman, 1984; Eshel, 1996; Hammerstein, 1996). However, the situation may be expected to differ when we consider trait evolution in metapopulations with small local population sizes, or haystack models for that matter, as there mutants may form an appreciable fraction of the inhabitants of any patches containing them, even when the mutant population is still globally small. So we cannot just neglect mutant homozygotes, while it is the feasibility of this approximation that lies at the basis of the correspondence of the clonal and diploid ESSs. In this paper we study the size of the resulting discrepancies for a set of metapopulation models in continuous time for which we have available a relatively easily calculated measure of invasion fitness (Metz et al., 1992; Rand et al., 1994) based on first principles, both for the clonal (Metz and Gyllenberg, 2001) and the diploid case (developed in this paper). The particular metapopulation model under study was presented in clonal form by Parvinen et al. (2002). The, to us, surprising conclusion is that although there indeed are differences between the calculated clonal and diploid ESS dispersal rates, for this model at least the discrepancy is so minor as to be irrelevant for all practical purposes.

2   The population model

The model that we use consists of an infinite number of patches. Each patch can support a local population, subject to the events illustrated in Figure 1.

Given a local population size of n individuals within a patch, the per capita birth and death rates are given by b_n and d_n, respectively. At carrying capacity k, birth and death rates are equal, $b_k = d_k$. The maximum population size within a patch is K. Individuals migrate out of their patches at a rate m, entering the disperser pool of the metapopulation. Below this dispersal rate is assumed to be the parameter under evolutionary control. While in the disperser pool, individuals experience mortality at rate $\tilde{d}$. They leave the disperser pool by settling into a new patch at rate s. An individual thus has the probability $\rho = \tilde{d}/(s + \tilde{d})$ of dying during dispersal. The probability to survive dispersal is $\pi = 1 - \rho$. Occasionally a local catastrophe kills the local population. The patch remains habitable
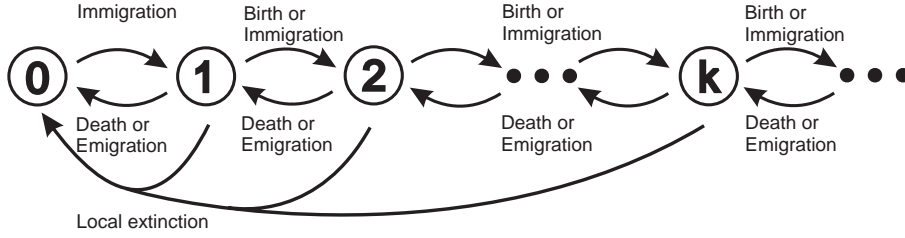
Figure 1: Transition diagram for a single patch. Arrows describe the possible transitions in the state of the patch. Local population size is increased by one by birth and immigration events and decreases by one when a death or emigration event occurs. Local extinction events can kill all individuals in a patch, thus resetting its population size to zero. At carrying capacity k, birth and death rates are equal. (Source: Parvinen *et al.* 2002)

and can be recolonized by dispersers from the disperser pool. These extinctions of a local population due to external disturbances occur at rate e.

At the metapopulation level we study the local population size distribution p_n, where p_n is the probability that a randomly selected patch has a local population with population size n. The combination of local population size distribution p_n and the size of the dispersal pool D experience the following dynamics:

$$
\begin{aligned}
\frac{d}{dt}p_0 &= -sDp_0 + (d_1 + m)p_1 + e(1 - p_0) , \\
\frac{d}{dt}p_n &= [sD + (n - 1)b_{n-1}]p_{n-1} - [n(b_n + m + d_n) + sD + e]p_n \\
&\quad + (n + 1)(d_{n+1} + m)p_{n+1} \text{ for } n > 0 , \\
\frac{d}{dt}D &= -sD + m\sum_{n=1}^{\infty} np_n - \tilde{d}D .
\end{aligned}
\tag{1}
$$

2.1 Clonal fitness

The calculation of fitness in the clonal model has been explained in Metz and Gyllenberg (2001) and Parvinen et al. (2002). For the sake of completeness, we give a brief summary, as it forms the basis for the fitness calculation in the diploid case.

The method for determining values of invasion fitness is based on first solving for the equilibrium $\hat{p}_n$ of (1) for a given resident strategy. A mutant disperser has probability $\hat{p}_n s/(s + \tilde{d})$ to end up in an $(n, 0)$-patch, turning it into an $(n, 1)$-patch. The newly founded colony then undergoes a Markovian stochastic population process until extinction (See Fig. 2a). Extinction of such a colony can result from a catastrophe killing the whole local population, or from demographic stochasticity bringing the number of mutants to zero. The rate at which a patch with size (n, n') becomes a patch with size $(n, n' + 1)$ we denote as $c_{n,n'}^{0,+}$ etc. The subscript (n, n') refers to a patch that initially has n resident and n' mutant individuals, while the superscript $(0, -)$ indicates that the number of resident individuals resulting from the considered type of event remains unchanged whereas the number of mutant individuals is decreased by 1. For $n \geqslant 0$ and $n' \geqslant 1$, because a mutant colony has at least one mutant, we have

$$
\begin{aligned}
c_{n,n'}^{0,+} &= n'b_{n+n'} \\
c_{n,n'}^{0,-} &= n'(d_{n+n'} + m') \\
c_{n,n'}^{+,0} &= sD + nb_{n+n'} \\
c_{n,n'}^{-,0} &= n(d_{n+n'} + m)
\end{aligned}
\tag{2}
$$

In addition we define

$$
\begin{aligned}
c_{n,n'}^{0,0} &= c_{n,n'}^{0,+} + c_{n,n'}^{0,-} + c_{n,n'}^{+,0} + c_{n,n'}^{-,0} + e \\
&= (n+n')d_{n+n'} + nm + n'm' + sD + (n+n')b_{n+n'} + e
\end{aligned}
\tag{3}
$$

Let $\hat{v}_{n,n'}$ be the average number of times that a local mutant colony passes trough state (n,n') before going extinct. By combining results from Markov chain theory (Kemeny and Snell, 1960) and techniques for numerical mathematics (Faddeev and Faddeeva, 1963) it can be shown that $\hat{v}_{n,n'}$ can be calculated as the limit $v_{n,n'}(\infty)$ from the recurrence

$$
\begin{aligned}
v_{n,n'}(t+1) &= \frac{c_{n,n'+1}^{0,-}}{c_{n,n'+1}^{0,0}} v_{n,n'+1}(t) + \frac{c_{n-1,n'}^{+,0}}{c_{n-1,n'}^{0,0}} v_{n-1,n'}(t) \\
&+ \frac{c_{n+1,n'}^{-,0}}{c_{n+1,n'}^{0,0}} v_{n+1,n'}(t) + \frac{c_{n,n'-1}^{0,+}}{c_{n,n'-1}^{0,0}} v_{n,n'-1}(t)
\end{aligned}
\tag{4}
$$

for $n \geqslant 0$, $n' \geqslant 1$, $n + n' \leqslant K$ with the boundary conditions $v_{n,0} = \hat{p}_n s/(s+\tilde{d})$, $v_{-1,n'} = 0$ and $v_{i,K+1-i} = 0$, together with the convention $c_{n,0}^{0,+} = 1$ and $c_{n,0}^{0,0} = 1$, for any initial condition. We used the Gauss-Seidel version (Faddeev and Faddeeva, 1963) of the above Jacobi iteration to speed up the computation.

The quantity $c_{n,n'}^{0,0}$ is the rate at which the colony leaves the state n, n'. Therefore the average time spent there each time is $1/c_{n,n'}^{0,0}$, and the average total time that a mutant colony will spend in state (n, n') is $\hat{v}_{n,n'}/c_{n,n'}^{0,0}$. The expected number of mutant dispersers sent out when the colony is in state (n, n') is $m'n'\hat{v}_{n,n'}/c_{n,n'}^{0,0}$. When we sum over all possible states for the colony, we get the expected number of mutant dispersers

$$
R_0' = m' \sum_{n=0}^{K-1} \sum_{n'=1}^{K-n} \frac{n'\hat{v}_{n,n'}}{c_{n,n'}^{0,0}},
\tag{5}
$$

which is the metapopulation-equivalent of the basic reproduction ratio of the mutant, as it is familiar from ordinary population dynamics. Notice, however, that R_0' measures the increase in the mutant population size between dispersal events, as opposed to between birth events. If, as usual, we define the invasion fitness as the average long-term per capita growth rate of the small mutant population in the fixed biotic environment set by the resident, then, for given dispersal rates of resident and mutant, m and m', the invasion fitness $s_m(m')$ is sign-equivalent with $\log R_0'$.

2.2 Diploid fitness

In the diploid version of the model, a mutant can be either a heterozygote or a homozygote. This applies both to mutant dispersers and the mutants inside a patch. We denote as (n, n', n^*) a situation with n resident homozygotes, n' heterozygotes and n^* mutant homozygotes (See Fig. 2b). When a mutant arrives in a patch with a resident population size n, denoted as $(n, 0, 0)$ this population is turned either to $(n, 1, 0)$ or $(n, 0, 1)$, depending on the type of the mutant.

As in the clonal case, the newly founded mutant colony undergoes a Markovian stochastic population process until extinction. The corresponding rates are, for the special case where inheritance is intermediate, that is, the phenotype of a heterozygote is the average of the phenotypes of a resident homozygote and a mutant homozygote,
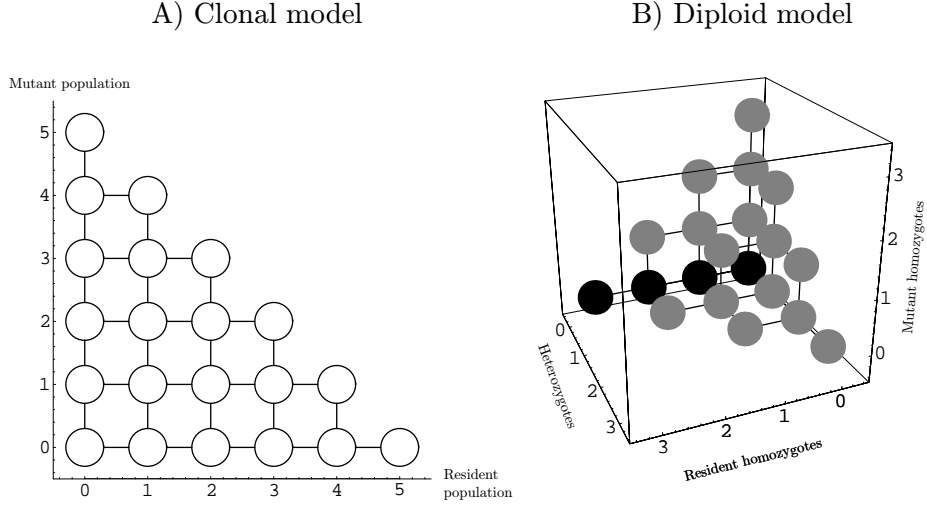
3

Figure 2: Sketch of the possible states of a mutant colony in the (A) clonal model and (B) diploid model.

$$
\begin{aligned}
c_{n,n',n^*}^{+,0,0} &= sD + \left(\frac{n+0.5n'}{N}n + \frac{0.5n+0.25n'}{N}n' \right) b_{n+n'+n^*} \\
c_{n,n',n^*}^{0,+,0} &= \left(\frac{0.5n'+n^*}{N}n + \frac{0.5n+0.5n'+0.5n^*}{N}n' + \frac{n+0.5n'}{N}n^* \right) b_{n+n'+n^*} \\
c_{n,n',n^*}^{0,0,+} &= \left(\frac{0.25n'+0.5n^*}{N}n' + \frac{0.5n'+n^*}{N}n^* \right) b_{n+n'+n^*} \\
c_{n,n',n^*}^{-,0,0} &= n(d_{n+n'+n^*} + m) \\
c_{n,n',n^*}^{0,-,0} &= n'(d_{n+n'+n^*} + \frac{m+m'}{2}) \\
c_{n,n',n^*}^{0,0,-} &= n^*(d_{n+n'+n^*} + m') \\
c_{n,n',n^*}^{0,0,0} &= (n + n' + n^*)d_{n+n'+n^*} + nm + n'\frac{m+m'}{2} + n^*m' \\
&\quad + sD + (n + n' + n^*)b_{n+n'} + e
\end{aligned}
\tag{6}
$$

The birth rates take account of the possible genetic combinations produced with the assumption of random mating, and otherwise these quantities are analogous to the clonal case. Take as an example the case when a resident is born, the rate of which is in the quantity $c_{n,n',n^*}^{+,0,0}$. A resident homozygote mates with a resident homozygote with probability n/N, in which case the offspring is a resident homozygote. It mates with a heterozygote with probability n'/N, in which case the offspring is a resident homozygote with probability $1/2$. A resident homozygote and mutant homozygote cannot get a resident homozygote offspring. This results in the term $\frac{n+0.5n'}{N}nb_{n+n'+n^*}$. Other birth rates are obtained in a similar way.

In the clonal version of the model, the basic reproduction ratio was simply the expected number of dispersers produced by one disperser. In the diploid model, we have to take into account that there are two types of dispersers. The diploid version of the recurrence is

$$
\begin{aligned}
v_{n,n',n^*}(t+1) \quad &= \frac{c^{-,0,0}_{n+1,n',n^*}}{c^{0,0,0}_{n+1,n',n^*}} v_{n+1,n',n^*}(t) + \frac{c^{+,0,0}_{n-1,n',n^*}}{c^{0,0,0}_{n-1,n',n^*}} v_{n-1,n',n^*}(t) \\
&+ \frac{c^{0,-,0}_{n,n'+1,n^*}}{c^{0,0,0}_{n,n'+1,n^*}} v_{n,n'+1,n^*}(t) + \frac{c^{0,+,0}_{n,n'-1,n^*}}{c^{0,0,0}_{n,n'-1,n^*}} v_{n,n'-1,n^*}(t) \\
&+ \frac{c^{0,0,-}_{n,n',n^*+1}}{c^{0,0,0}_{n,n',n^*+1}} v_{n,n',n^*+1}(t) + \frac{c^{0,0,+}_{n,n',n^*-1}}{c^{0,0,0}_{n,n',n^*-1}} v_{n,n',n^*-1}(t)
\end{aligned}
\tag{7}
$$

for $n \geqslant 0$, $n' \geqslant 0$, $n^* \geqslant 0$, $n' + n^* \geqslant 1$, $n + n' + n^* \leqslant K$ with the boundary conditions $v_{n,0,0} = \hat{p}_n s/(s+\tilde{d})$, $v_{-1,n',n^*} = v_{n,-1,n^*} = v_{n,n',-1} = 0$ and $v_{i,j,K+1-i-j} = 0$, together with the convention $c^{0,+,0}_{n,0,0} = p_{\text{hetero}}$, $c^{0,0,+}_{n,0,0} = 1 - p_{\text{hetero}}$ and $c^{0,0}_{n,0,0} = 1$.

Using this recurrence method, we compute the number of times $\hat{v}^{\text{hetero}}_{n,n',n^*}$ that a colony spends in state (n, n', n^*) when all arriving mutants are heterozygotes by setting $p_{\text{hetero}} = 1$. Correspondingly, by setting $p_{\text{hetero}} = 0$ we compute the number of times $\hat{v}^{\text{mutant}}_{n,n',n^*}$ that a colony spends in state (n, n', n^*) when all arriving mutants are homozygotes. The expected number of heterozygote dispersers produced by a colony initiated by a mutant homozygote is

$$
a_{\text{hetero mutant}} = \frac{m + m'}{2} \sum_{n,n',n^*} \frac{n' \hat{v}^{\text{mutant}}_{n,n',n^*}}{c^{0,0,0}_{n,n',n^*}},
\tag{8}
$$

and the other quantities $a_{\text{hetero hetero}}$, $a_{\text{mutant hetero}}$ and $a_{\text{mutant mutant}}$ are defined analogously. Now define the matrix M as

$$
M = \begin{pmatrix} a_{\text{hetero hetero}} & a_{\text{hetero mutant}} \\ a_{\text{mutant hetero}} & a_{\text{mutant mutant}} \end{pmatrix}.
\tag{9}
$$

The average number of heterozygotes n^t_{hetero} and mutant homozygotes n^t_{mutant} in the disperser generation t will be obtained from

$$
\begin{pmatrix} n^t_{\text{hetero}} \\ n^t_{\text{mutant}} \end{pmatrix} = M^t \begin{pmatrix} n^0_{\text{hetero}} \\ n^0_{\text{mutant}} \end{pmatrix}
\tag{10}
$$

So the mutant population will increase over the generations if and only if the dominant eigenvalue of the matrix M is greater than one. Therefore, for the fitness in the form of a basic reproduction ratio (Diekmann et al., 1990, 1998) we may take the dominant eigenvalue of the matrix M. The fraction of heterozygotes and mutant homozygotes is obtained from the normalized eigenvector corresponding to the dominant eigenvalue.

3 Results

In order to evaluate the difference between the diploid and clonal evolutionarily stable strategies, we did a variety of numerical explorations. For simplicity, we assume that per capita birth rates are unaffected by density, $b_n = r$, while per capita death rates increase linearly with local population size, $d_n = rn/k$, where r is the intrinsic growth rate of local populations and k determines the local carrying capacity of patches. Consequently local growth is logistic, $f_n = b_n - d_n = r(1 - n/k)$.
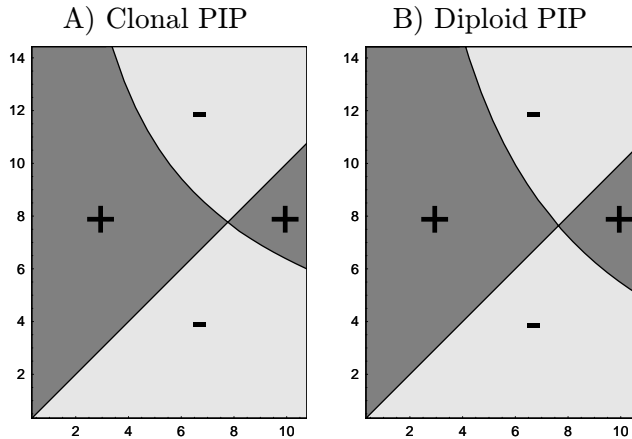
Figure 3: A) Clonal and B) diploid pairwise invasibility plots (PIP). Parameters: $\pi = 0.995$, $\mu = 0.1$, $r = 1$, $k = 2.5$, $K = 5$.

The general impression from our exploration is that there is some difference in the resulting evolutionarily stable strategies, but the difference is quite small (See Fig. 3). We shall further illustrate this by considering the dependence of the ESS on the carrying capacity k. The natural intuition is that the difference will be largest for small k, as then the probability that mutant come as homozygotes is largest. The clonal and diploid model give us the same qualitative result that increasing the carrying capacity decreases dispersal (Fig. 4a). Even better, as Figure 4b shows, the difference between the two cases turn out to be minor on the full range of parameter values. However, contrary to naive expectation, no clear pattern appears for the effect of the carrying capacity on the difference between the diploid and clonal model. The appearance of both heterozygotes and mutant homozygotes seems to be one force that makes the evolutionarily stable strategies different.

As another comparison we look at the dependence of the ESS on the catastrophe rate e. Parvinen et al. (2002) found that increasing the catastrophe rate can result in several responses in the clonal model: Dispersal can be monotonically increasing or decreasing, or there may be an intermediate minimum or maximum. In Figure 5a dispersal rate increases with the catastrophe rate both in the clonal and diploid model. Again the difference between the two cases is very small, and becomes even smaller for large catastrophe rates (Fig. 5b). Our heuristic explanation for this is that increasing the catastrophe rate decreases the resident population size and increases the amount of empty patches. In such a situation, mutants and residents rarely see each other and the situation is close to the clonal case. One sign of this is that the probability of being a heterozygote disperser decreases with increasing catastrophe rate: dispersing mutant homozygotes can find empty patches and produce mutant homozygotes for a long time before the first resident disperser arrives.

4 Discussion

In most studies of evolutionarily stable strategies clonal reproduction is assumed. More realistic genetic models, at least in the simplest cases, have been shown to yield results compatible with the clonal results. The clonal and diploid results are expected to differ in models for viscous populations, or in the case of metapopulation models, where the local population sizes are small. However, luckily the situation seems less dire than might
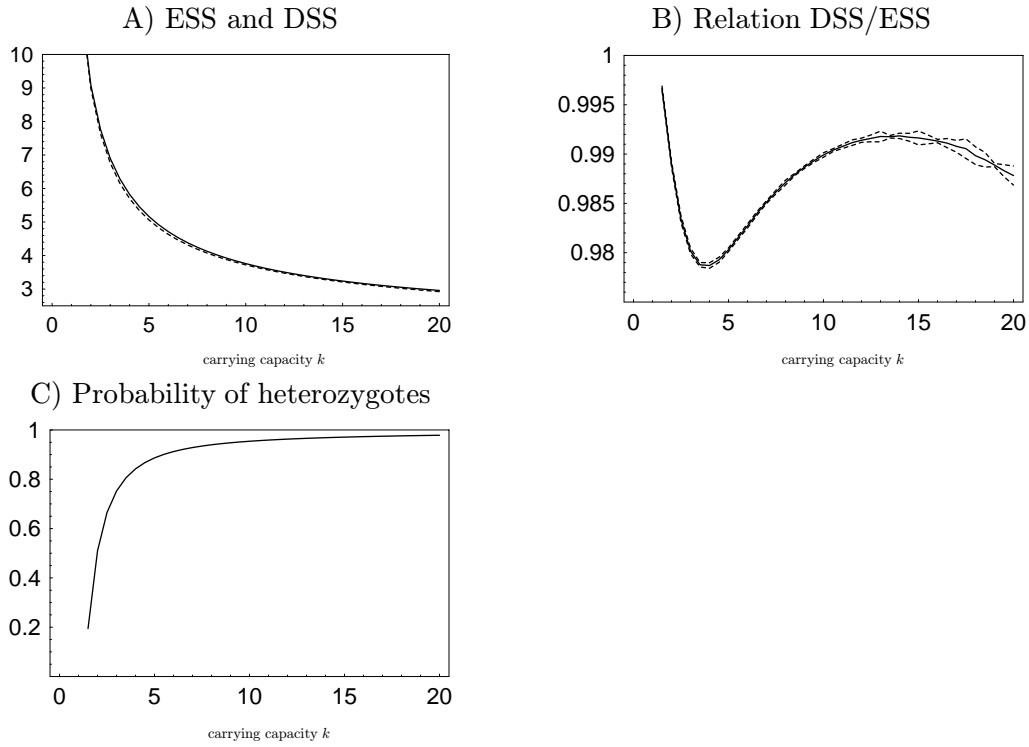
Figure 4: Effect of the carrying capacity k. A) Clonal ESS plotted with a solid curve and diploid ESS (DSS) with a dotted curve. B) The fraction DSS/ESS. The domain of uncertainty is plotted with dotted curves. C) The probability that a mutant disperser is a heterozygote. The metapopulation is not viable for $k < 1.5$. Parameters: $\pi = 0.995$, $e = 0.1$, $r = 1$, $K = 2k$.

be expected, at least for the demographic variable studied by us, namely dispersal rates. Here we found that the difference in ESS is actually so small as to be irrelevant for all practical purposes (less than 2%).
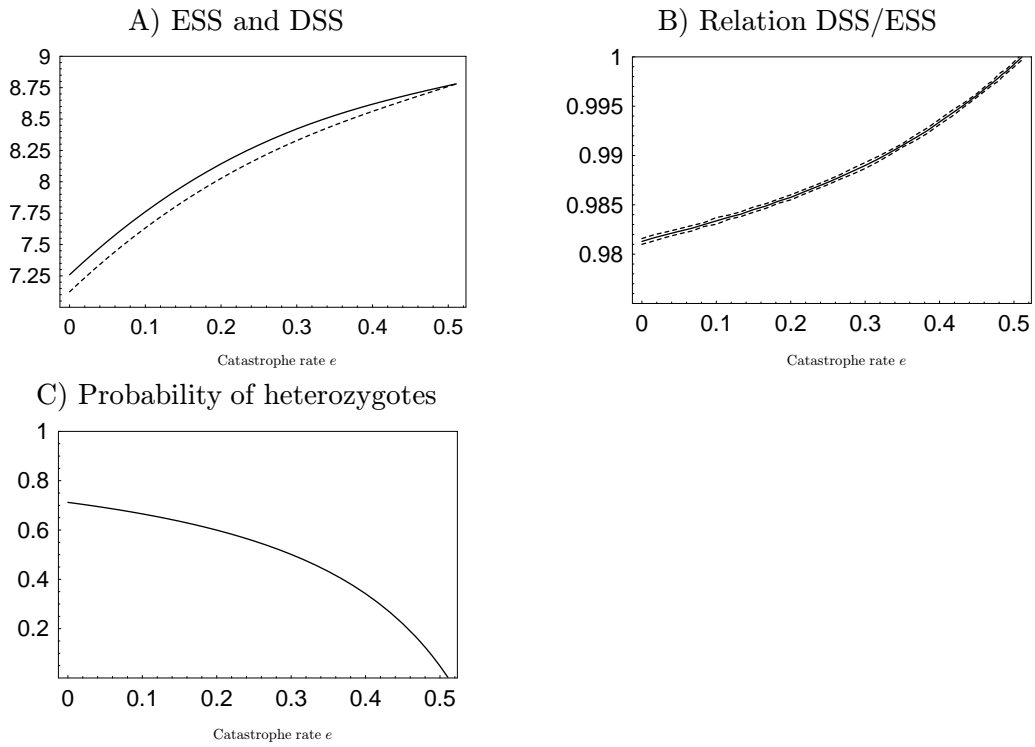
A) ESS and DSS

B) Relation DSS/ESS

C) Probability of heterozygotes

Figure 5: Effect of the catastrophe rate. A) Clonal ESS plotted with a solid curve and diploid ESS (DSS) with a dotted curve. B) The fraction ESS/DSS. The domain of uncertainty is plotted with dotted curves. C) The probability that a mutant disperser is a heterozygote. The metapopulation is not viable for catastrophe rates larger than $e_{ext} \approx 0.5$. Parameters: $\pi = 0.995$, $r = 1$, $k = 2.5$, $K = 5$.

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