

# A novel fitness proxy in structured locally finite metapopulations with diploid genetics, with an application to dispersal evolution

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Received 29 October 2007

Available online 3 February 2008

## Abstract

Many studies of evolutionarily stable strategies (ESS) for technical reasons make the simplification that reproduction is clonal. A post-hoc justification is that in the simplest eco-evolutionary models more realistic genetic assumptions, such as haploid sexual or diploid sexual cases, yield results compatible with the clonal ones. For metapopulations the technical reasons were even more poignant thanks to the lack of accessible fitness proxies for the diploid case. However, metapopulations are also precisely the sort of ecological backdrop for which one expects discrepancies between the evolutionary outcomes derived from clonal reproduction and diploid genetics, because substantially many mutant homozygotes appear locally even though the mutant is rare globally. In this paper we devise a fitness proxy applicable to the haploid sexual and diploid sexual case, in the style of Metz and Gyllenberg [Metz, J.A.J., 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], that can cope with local population fluctuations due to environmental and demographic stochasticity. With the use of this fitness proxy we find that in dispersal evolution the studied clonal model is equivalent with the haploid sexual model, and that there are indeed many differences between clonal and diploid ESS dispersal rates. In a homogenous landscape the discrepancy is but minor (less than 2%), but the situation is different in a heterogeneous landscape: Not only is the quantitative discrepancy between the two types of ESSs appreciable (around 10%–20%), but more importantly, at the same parameter values, evolutionary stability properties may differ. It is possible, that the singular strategy is evolutionarily stable in the clonal case but not in the diploid case, and vice versa.

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**Keywords:** Evolutionarily stable strategy; Clonal; Diploid; Fitness; Structured metapopulation

## 1. Introduction

The concept of an evolutionarily stable strategy (ESS; Maynard Smith and Price, 1973; Maynard Smith, 1976; Lawlor and Maynard Smith, 1976) is an essential concept of modern evolutionary biology. When such strategy is adopted by a resident population, no rare mutant population is able to invade the resident population, and thus such a strategy can be called uninvadable or unbeatable. ESS-theory has been applied to a wide variety of models, and has resulted in various derived concepts and

techniques (e.g. Eshel (1983), Matsuda (1985), Van Tienderen and De Jong (1986), Taylor (1989) and Christiansen (1991)). For technical reasons, many ESS studies assume that but for mutations the offspring is phenotypically identical to the parent. This is the case when reproduction is clonal. This assumption is also generally made in developing the adaptive dynamics toolbox (e.g. Metz et al. (1992), Metz et al. (1996), Dieckmann and Law (1996), Geritz et al. (1997) and Geritz et al. (1998)).

A post-hoc justification for the assumption of clonal reproduction is that if evolution stays mutation limited, rare mutants in a well-mixed population mate practically only with residents. Therefore in the one-locus sexual haploid case, the offspring of a mutant are either mutants identical to the parent or residents. In the one-locus sexual diploid case with a monomorphic resident, mutant offspring are either

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heterozygotes or residents. Therefore in the diploid case, the question whether a mutant population can invade the resident or not, does not depend on the properties of mutant homozygotes. In both cases all mutants are identical. This is the reason why usually in the simplest eco-evolutionary models more realistic genetic assumptions yield results compatible with the clonal ones. More precisely, the value of the singular strategies and their evolutionary stability and convergence stability properties do not change between clonal and diploid cases. This has been shown under many different genetic scenarios in the past and more recently (Maynard Smith, 1981; Eshel and Feldman, 1984; Eshel, 1996; Hammerstein, 1996; Geritz and Kisdi, 2000).

A practical reason for the simplifying assumption of clonal reproduction in locally finite metapopulation models with density-dependent demographic stochasticity is that no fitness proxy to the diploid case has been available so far (but see Roze and Rousset (2005) and Ravigne et al. (2006)). In this paper we devise such a fitness proxy based on first principles, in the style of Metz and Gyllenberg (2001), for a set of metapopulation models defined in continuous time. This fitness proxy can cope with local population fluctuations due to environmental and demographic stochasticity. We are motivated also by the fact that metapopulations are also precisely the sort of ecological backdrop for which one expect discrepancies between the evolutionary outcomes derived from clonal reproduction and more realistic genetics. Namely, in metapopulation models and in haystack models (Maynard Smith, 1964; Bulmer and Taylor, 1980; Charnov, 1982; Van Tienderen and De Jong, 1986) where local populations are small, mutants may form an appreciable fraction of the inhabitants of any patches containing them, even when the mutant population is still globally small.

In general, invasion fitness (Metz et al., 1992; Rand et al., 1994) is the long-term exponential growth rate  $r(\text{strategy}_{\text{mutant}}, E_{\text{resident}})$  of a rare mutant in an environment  $E_{\text{res}}$  set by the resident. A positive invasion fitness implies that the mutant is able to grow in population size, and possibly replace the old resident and itself become the resident. These mutation-invasion events result in long-term changes of the strategy of the individuals constituting the population (Eshel and Feldman, 1984). With invasion fitness one can study the evolution of various traits in detail. Especially, one can calculate the selection gradient, i.e. the derivative of invasion fitness with respect to the strategy of the mutant. Strategies, for which the selection gradient is zero, are called singular (Geritz et al., 1997, 1998). A singular strategy  $m^*$  is convergence stable or an evolutionary attractor if the repeated invasion of nearby mutant strategies into resident strategies will lead to the convergence of resident strategies towards  $m^*$  (Eshel, 1983; Taylor, 1989; Christiansen, 1991; Metz et al., 1996; Eshel et al., 1997; Geritz et al., 1998). If the invasion fitness is negative for all mutant strategies different from the resident strategy, this singular strategy is unbeatable, and thus an evolutionarily stable strategy (ESS) (Maynard Smith, 1976).

How can one extend the above-mentioned toolbox to handle diploid genetics, more in particular, how can one define invasion fitness? Invasion fitness describes growth in real

time, and is rather complicated to calculate in structured metapopulations. Instead, we can use a fitness proxy, which was presented by Metz and Gyllenberg (2001) for the clonal case, namely the clan reproduction ratio between dispersal generations. It is the metapopulation-equivalent of the basic reproduction ratio of the mutant, familiar from ordinary population dynamics. It is the expected number of mutant dispersers produced by a local mutant population initiated by one mutant disperser. The mutant population will grow, has positive fitness, if and only if each local mutant clan begets on average more than one successful disperser. Here we extend this calculation to cover the haploid sexual case, and notice that it is equivalent with the clonal model, if birth rates do not evolve. This calculation is relatively simple in the clonal and haploid sexual cases because there is only one type of disperser or “clan birth state”. However, in the diploid case mutant dispersers are either heterozygotes or homozygotes, meaning that there are two “birth” states.

The idea of calculating the basic reproduction ratio in ordinary population models in case of several birth states is the following: calculate the expected number of offspring  $M_{ij}$  of type  $i$  produced by an individual with birth state  $j$ , and collect these numbers into the matrix  $M$ . Let  $x$  denote the vector of initial population sizes. After  $n$  generations, the expected population size is obtained with matrix multiplication,  $M^n x$ . The population is expected to grow, if the dominant eigenvalue of matrix  $M$  is greater than one. Therefore, it is the basic reproduction ratio and can be used as a fitness proxy. Analogously in the metapopulation model, the matrix  $M$  consists of the expected number of different mutant dispersers produced by a local mutant population initiated by different mutant dispersers, and the clan reproduction ratio is its dominant eigenvalue.

The details of the fitness proxy calculation according to the above-described principle in the metapopulation model are presented in Section 2. In short, each local population consists of two types (resident and mutant) in the clonal and haploid sexual cases, and three types (resident homozygote, heterozygote, and mutant homozygote) in the diploid case. Because of demographic stochasticity, the population sizes in each local population change according to a Markov chain, and we can calculate the lifetime disperser production of a local population using the stationary distribution of a Markov chain.

Since a fitness proxy is now available for the metapopulation model with small local population sizes both in the clonal case (Metz and Gyllenberg, 2001) and in the diploid case (developed in this paper), we are able to compare the evolutionary outcomes in these two cases. The particular metapopulation model under study was presented in clonal form by Parvinen et al. (2003). The results are expected to differ, because mutant homozygotes cannot be neglected, while it is the feasibility of this approximation that lies at the basis of the correspondence of the clonal and diploid ESSs. Metz and Gyllenberg (2001) and Parvinen et al. (2003) assumed that the ecological properties are equal in all patches, although population sizes are different. Our numerical explorations for such a homogeneous landscape suggest that although there indeed are quantitative differences

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