



Evolutionary branching in deme-structured populations



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ABSTRACT

Adaptive dynamics shows that a continuous trait under frequency dependent selection may first converge to a singular point followed by spontaneous transition from a unimodal trait distribution into a bimodal one, which is called “evolutionary branching”. Here, we study evolutionary branching in a deme-structured population by constructing a quantitative genetic model for the trait variance dynamics, which allows us to obtain an analytic condition for evolutionary branching. This is first shown to agree with previous conditions for branching expressed in terms of relatedness between interacting individuals within demes and obtained from mutant-resident systems. We then show this branching condition can be markedly simplified when the evolving trait affect fecundity and/or survival, as opposed to affecting population structure, which would occur in the case of the evolution of dispersal. As an application of our model, we evaluate the threshold migration rate below which evolutionary branching cannot occur in a pairwise interaction game. This agrees very well with the individual-based simulation results.

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1. Introduction

In evolutionary game theory, individuals are allowed to interact with each other and selection will be frequency-dependent. Even in a constant environment, a population may then show intriguing temporal dynamics. For example, if a trait evolves by the accumulation of small mutations and if disruptive selection stemming from frequency-dependent selection is at work, a continuous trait may show convergence to a singular point followed by spontaneous splitting of a unimodal trait distribution into a bimodal (or multimodal) one, referred to as “evolutionary branching” (Metz et al., 1992, 1996; Geritz et al., 1997). Evolutionary branching is predicted to occur at an evolutionarily singular point that is approaching stable (or convergence stable, CS, Eshel, 1983) but not evolutionarily stable (ES), and it is actually observed in individual-based simulations in many models for the evolution of ecological traits (Doebeli et al., 2004; Brännström et al., 2011).

One important contribution of evolutionary game theory and adaptive dynamics is the analytically tractable prediction of the criteria of evolutionary branching, i.e., the CS and non-ES condition (e.g., Eshel, 1983; Geritz et al., 1997), which generally agrees

well with individual-based simulations. This has been applied to a large spectrum of ecological scenarios involving both inter- and intra-specific interactions. However, the standard application of the recipe assumes an infinite and well-mixed population to obtain the stability criteria. Since real populations are always finite and usually have a spatial structure (dispersal is localized and organisms are likely to interact with neighbors), extending the criteria of stability to more realistic models is biologically relevant.

One important contribution of evolutionary game theory and inclusive fitness theory is an analytically tractable measure of selection (or mutant invasion fitness) for deme-structured populations (e.g., Taylor, 1988; Frank, 1998; Rousset, 2004), which provides a condition for convergence stability (Rousset, 2004). Owing to the smallness of local deme size, any analytic measure of selection needs to take into account local fluctuations of allele frequencies induced by genetic drift. This generates positive correlations of mutant frequencies among individuals in the same deme, making mutant-mutant interactions unavoidable. The concept of relatedness plays a crucial role here, as it allows to reduce the problem of computing the full local distribution of mutants (and thus accounting for their interactions) to the simpler problem of computing the probability that two genes sampled from different individuals are identical-by-descent, thereby making tractable the evaluation of invasion fitness. This has been applied to a large number of different social scenarios (e.g., Frank, 1998), and agrees generally well with individual-based simulations (e.g., Bulmer, 1986; Pen, 2000;

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Leturque and Rousset, 2002; Rousset and Ronce, 2004; Guillaume and Perrin, 2006). However, the standard application of the recipe usually ignores the possibility of branching.

Evolution of continuous traits under a wide variety of different biological situations has been studied using adaptive dynamics and inclusive fitness (e.g., Metz et al., 1992; Dieckmann and Law, 1996; Geritz et al., 1997, 1998; Frank, 1998; Rousset, 2004; Wenseleers et al., 2010). Branching condition in structured populations has been studied using the number of successful emigrants descended from a mutant immigrant, R_m , as invasion fitness measure (e.g., Metz and Gyllenberg, 2001; Parvinen and Metz, 2008; Ajar, 2003). The 2nd-order derivative R_m^* being positive is the non-ES condition in this approach. Day (2001) takes a slightly different approach and calculates the expected fitness of a carrier of the mutant allele under a probability distribution of the number of mutant alleles in the same deme.

It is relevant to mention that the previous approaches compute invasion fitness under the assumption that there are only two types (or alleles), the mutant and the resident, present in the population. From a stochastic process point of view, this is obtained in the asymptotic of rare mutations, where adaptive evolution is described as a monomorphic jump process that gives rise to the so-called canonical equation of adaptive dynamics (Dieckmann and Law, 1996; Champagnat et al., 2006a,b). Strictly speaking, branching is impossible unless at least three alleles segregate in the population (e.g., Wakano and Lehmann, 2012). Thus, the mutant-resident approach based on a two-allele system does not directly deal with evolutionary branching, but only provides an ad-hoc measure of disruptive selection, which matches very well with results from simulations.

There is, however, another approach to describe the adaptive dynamics. This is to model the trait distribution dynamics in quantitative genetics. Some studies directly deal with the evolution of the full phenotypic distribution (e.g., Sasaki and Ellner, 1995; Jabin and Raoul, 2011; Mirrahimi et al., 2012), while other studies focus only on some important moments of the distribution such as the mean or the variance (Iwasa et al., 1991; Abrams et al., 1993; Day and Taylor, 1996; Sasaki and Dieckmann, 2011). The dynamics of these moments can be derived under some assumptions on the trait distribution, which is called the moment closure. In this distributional context, which is generally applied to panmictic populations, evolutionary branching is characterized by the increase of the variance in the trait distribution (Sasaki and Dieckmann, 2011). This approach can also be extended to finite and well-mixed population models, in which case the trait variance dynamics provides the branching condition in finite populations (Wakano and Iwasa, 2013).

Here, we aim to construct a model to obtain the condition for evolutionary branching from the variance in the trait distribution in a population subdivided into demes of finite size. To that end, we derive moment dynamics to the 2nd-order of selection and study the 1st (mean) and 2nd (variance) moments. In doing so, we combine elements of inclusive fitness theory, adaptive dynamics, and quantitative genetics to obtain the condition of evolutionary branching in deme structured populations. Using a Gaussian moment closure approximation, the condition for disruptive selection will be expressed analytically. To describe the effect of population structure on selection, we will extend standard coalescence arguments to a quantitative genetics framework.

This paper is organized as follows. We first describe the biological framework of our deme-structured population model and present results of our individual-based simulations as motivating examples. When the migration rate is low, mutant-mutant interactions are more likely to occur and the evolutionary dynamics can be different from that in well-mixed population. By simulation, we first find the threshold migration rate below

which evolutionary branching does not occur, illustrating the importance of spatial structure for branching. We then present our mathematical analysis of the condition for evolutionary branching and we finally perform a detailed comparison between simulation results and analytic predictions.

2. Model and analysis

2.1. Main assumptions

We consider a spatially structured population consisting of N_d islands (demes), each of size N , thus summing up to $N_T = N_d N$ adult haploid individuals in total. Each individual i in deme k has a genetically determined continuous trait value z_{ki} . Individuals play games and the payoffs determine their fecundity. We assume that a large number of juveniles are produced by each adult, and that a fraction of them disperses randomly to another deme. Adults die with a constant probability and juveniles compete on each deme for the vacated spots so that exactly N individuals in each deme form the next generations of adults. No other exact assumption about social interactions, reproduction, competition, and dispersal is done at this stage (but later for applications). The model can thus take independent demic extinction (or catastrophes) into account so as to capture meta-population processes.

2.2. A preliminary simulation result

Before carrying out our derivation of moment dynamics, we present a motivational example satisfying our assumptions and illustrating the role of spatial structure for branching. We run individual-based simulations of a pairwise non-linear public goods game (Doebeli et al., 2004) played within demes under a Wright–Fisher updating scheme with standard infinite island model of dispersal assumptions, where the migration rate is m (Fig. 1; for simulation details see Section 4). When the migration rate is relatively large ($m = 0.6$), the evolutionary dynamics was similar to that in a well-mixed population, and branching occurred as soon as the trait evolved to reach the convergence stable (CS) value z^* (Fig. 1a). For $m = 0.4$, branching still occurred but the dynamics was more stochastic (Fig. 1b). For $m = 0.2$, branching was never observed (Fig. 1c). These simulation results clearly illustrate the importance of spatial structure, implying the existence of a threshold migration rate, m^* , below which evolutionary branching does not occur. One practical goal of our analysis is to give an analytical prediction on this threshold migration rate. We will now derive approximations for the dynamics of the mean and variance in trait value under our population assumptions.

2.3. Mean trait dynamics to the 1st-order effect of selection

We write the fitness of individual i in deme k (expected number of adult offspring produced) as a function $w_{ki}(\mathbf{z})$ of the full trait distribution $\mathbf{z} := (z_{11}, z_{12}, \dots, z_{N_d N})$ in the population (see below for examples). The expectation of the mean trait value in the next generation is given by

$$E[\bar{z}_{t+1} | \mathbf{z}_t = \mathbf{z}] = \frac{1}{N_T} \sum_{k=1}^{N_d} \sum_{i=1}^N z_{ki} w_{ki}(\mathbf{z}) \quad (1)$$

When the trait distribution is narrow around the mean $\bar{z} := (1/N_T) \sum_k \sum_i z_{ki}$, the deviation $\delta_{ki} := z_{ki} - \bar{z}$ is small and the fitness function can be approximated by a 1st-order Taylor expansion about the mean:

$$w_{ki}(\mathbf{z}) = w_{ki}(\bar{\mathbf{z}}) + w_{ki,ki} \delta_{ki} + \sum_{j \neq i} w_{ki,kj} \delta_{kj} + \sum_{l \neq k} \sum_j w_{ki,lj} \delta_{lj} \quad (2)$$

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