



Evolutionary dynamics of a quantitative trait in a finite asexual population



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ABSTRACT

In finite populations, mutation limitation and genetic drift can hinder evolutionary diversification. We consider the evolution of a quantitative trait in an asexual population whose size can vary and depends explicitly on the trait. Previous work showed that evolutionary branching is certain (“deterministic branching”) above a threshold population size, but uncertain (“stochastic branching”) below it. Using the stationary distribution of the population’s trait variance, we identify three qualitatively different subdomains of “stochastic branching” and illustrate our results using a model of social evolution. We find that in very small populations, branching will almost never be observed; in intermediate populations, branching is intermittent, arising and disappearing over time; in larger populations, finally, branching is expected to occur and persist for substantial periods of time. Our study provides a clearer picture of the ecological conditions that facilitate the appearance and persistence of novel evolutionary lineages in the face of genetic drift.

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1. Introduction

Speciation is said to be “ecological” when reproductive isolation has resulted from divergent natural selection driving subpopulations into different ecological niches (Schluter and Conte, 2009). When this divergence occurs in sympatry, the initial differentiation of phenotypic traits requires multiple fitness peaks in the adaptive landscape (Calsbeek et al., 2012), with selection favoring different phenotypes given the current composition of the population. Divergent natural selection, however, does not always lead to phenotypic divergence – i.e., evolutionary branching – if there is not enough variation for selection to act upon or when genetic drift is too strong relative to selection, even when the populations are asexual.

Historically, most quantitative genetic models were developed under the assumption that selection is frequency-independent with a single optimum, i.e., that fitness landscapes are constant and

single-peaked. That said, the potential importance of frequency-dependent selection as a source of quantitative genetic variation was recognized early on (Clarke and O’Donald, 1964; Cockerham et al., 1972), and some quantitative genetic models have included frequency-dependent selection (e.g., Bulmer, 1980; Lande, 1976; Slatkin, 1979; Bürger and Gimelfarb, 2004). Social interactions between individuals of the same species, whether competitive, spiteful or altruistic, as well as interspecific interactions, such as interactions between predators and their preys or hosts and parasites, often result in frequency-dependent selection (Doebeli and Dieckmann, 2000). It is therefore crucial to understand how frequency-dependent selection affects the evolution of quantitative traits, under both stabilizing or diversifying selection, since the former seems to be neither more prevalent nor stronger than the latter in nature (Kingsolver et al., 2001). Particularly needed are models that incorporate both frequency-dependent selection and drift.

After the pioneering works of I. Eshel (Eshel and Feldman, 1984; Eshel, 1996), the desire to understand the long-term implications of frequency-dependence led to the development of the adaptive dynamics framework (Geritz et al., 1998; Doebeli, 2011). The method requires the assumption that mutations are rare, so that evolution proceeds as a series of competitive displacements of resident genotypes by mutant genotypes; mutations are also

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assumed to be of small phenotypic effect and population sizes are typically assumed to be large. Central to the framework is the concept of invasion fitness (Metz et al., 1992), which corresponds to the initial growth rate of a rare mutant in a population of very large size.

The assumption that the population size is large is a central one in the adaptive dynamics framework, but computer simulations have helped investigate the consequences of stochasticity in populations of smaller size (e.g., Dieckmann and Doebeli, 1999; van Doorn and Weissing, 2002). Because population size affects the fate of mutations, the outcome of an adaptive dynamics process can change in small populations. Claessen et al. (2007) for instance observed that evolutionary branching was much harder to obtain in individual-based simulations with small population sizes. Claessen et al. proposed two explanations for this phenomenon: first, because of random drift, the trait mean in the population changes over time and may wander away from the area where branching can happen. Second, even if branching is initiated, the incipient branches may go extinct by chance.

In populations of small size, Proulx and Day (2002) showed that the probability of fixation is a better predictor of the course of evolution in stochastic environments than invasion fitness. Similarly, the “canonical diffusion of adaptive dynamics” (Champagnat et al., 2006; Champagnat and Lambert, 2007), which describes the evolution of a quantitative trait in a finite asexual population, involved gradients of fixation probability (instead of invasion fitness). Although they allow the consideration of the effect of genetic drift, these two approaches dealt with directional selection only and did not account for the creation and maintenance of quantitative genetic diversity due to frequency-dependent selection. Obviously, as a probability of fixation refers to the fixation of one genotype and the loss of another, this measure of evolutionary success does not naturally describe the maintenance of diversity (Rousset, 2004; Allen et al., 2013). In other words, a method based on a trait substitution sequence, which assumes that the fate of a mutation is either loss or fixation, is not suited to account for evolutionary diversification, where different types coexist.

In this article, we study the evolution of a quantitative trait under frequency-dependent selection, in an asexual population of finite, but not fixed, size. We use a moment-based approach, because it bridges the gap between quantitative genetic and adaptive dynamic frameworks (Abrams et al., 1993; Abrams, 2001; Débarre et al., 2013, 2014). We illustrate our results with a model of social evolution in a well-mixed population (i.e., in the absence of any spatial or social structure), where the quantitative trait Z under selection corresponds to investment in social behavior (Doebeli et al., 2004; Lehmann, 2012; Wakano and Lehmann, 2012; Wakano and Iwasa, 2013).

Our study builds upon the work of Wakano and Iwasa (2013). In their model, Wakano and Iwasa (2013) assume asexual reproduction, discrete, non-overlapping generations and a potentially small but constant population size (using a Wright–Fisher model). The authors explore models where branching is expected in infinite populations but may fail to occur within finite populations. They identify two major parameter regimes involving diversifying selection: where branching is expected deterministically and continues to be observed in finite populations even if mutations have small effects (termed “deterministic branching”) and where branching is expected deterministically but will only occur in finite populations occasionally, when mutations are of large enough size to overwhelm drift (termed “stochastic branching”).

Here, we extend the framework of Wakano and Iwasa (2013) to populations whose size is finite but not fixed and to a life-cycle with overlapping generations (a birth–death process). We derive expressions for the stationary distribution of the total population size, trait mean, and trait variance under stabilizing selection, and

we show how these distributions can help us refine the conditions for evolutionary diversification when selection is diversifying. In particular, we show that the “stochastic branching” regime identified by Wakano and Iwasa can be sub-divided further into (i) a “no branching” regime in which branching will either never occur or be so seldom and collapse so rapidly that the population is very unlikely to be observed in a diversified state; (ii) an “intermittent branching” regime in which branching arises and collapses over biologically reasonable time frames; and finally (iii) a regime akin to the “deterministic branching” regime, in which branching is so likely and collapses so rarely that the system maintains multiple species almost always, with populations likely to remain branched for long enough to accumulate further speciation barriers.

2. Model and methods

2.1. Model

We describe the evolution of a trait Z in a population of asexual individuals. Each individual in the population is characterized by its genotype z_i , which we also refer to as phenotype in the absence of environmental effects; in the remainder of the article, we refer to z_i as “type” or simply “trait”. At a given time t , we denote the current size of the population by $N(t)$, while a vector $\mathbf{z}(t)$ summarizes all the types present in the population. The trait mean (first moment of the distribution) is $\bar{z}(t) = \sum_{i=1}^{N(t)} z_i/N(t)$ and the variance (second central moment of the distribution) is $v(t) = (z - \bar{z}(t))^2$. For each of these variables, we may drop the time dependency for simplicity. Each time step, either one individual reproduces (producing exactly one offspring) or one individual dies.

We use the term “fecundity” to refer to the reproductive potential of an individual, which is proportional to the chance that this individual will reproduce in a time step. We assume that individual fecundity F_i depends on both the type of each individual and the distribution of types in the population; we denote by \bar{F} the mean fecundity in the population. When it does reproduce, a parent of type z_i produces an offspring with phenotype $z_i + \delta$, where δ follows a distribution u (called a mutation kernel) with mean $m_u = 0$ and variance σ_u^2 assumed to be small. Mutation is therefore a source of variation in the population, and multiple types can coexist at any time point even though the population is finite and potentially small.

Individual survival, on the other hand, is type- and frequency-independent, but it is density-dependent: individual survival decreases as the size of the population increases. The *per capita* death rate per time step, D_i , is defined as $D_i = dN$. We denote by \bar{D} the mean death rate in the population.

In the next time step, both the size of the population and the distribution of types have changed; our aim is to find expressions for their stationary distributions. Key to our derivation is the assumption that populations that have not diversified have a trait distribution that is Gaussian (at any time), with a small variance v . Hence, we only need to follow the mean \bar{z} and variance v of the distribution of types. By contrast, populations undergoing evolutionary branching are characterized by a substantial increase of trait variance. Thus, we determine whether or not evolutionary branching is likely to be observed by determining when the steady state distribution for the trait variance does not or does have substantial density at small values of v .

Illustration: social evolution

We illustrate our results using the specific example where Z is a social trait that represents individual investment into social behavior; the trait can take any value between 0 (no investment) and 1 (maximum investment). Initially analyzed by Doebeli et al. (2004) under the assumption that population size was infinite,

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