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Evolutionary branching under slow directional evolution

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HIGHLIGHTS

- We derive conditions for evolutionary branching in directionally evolving populations.
- The derived conditions extend those for univariate trait spaces to bivariate trait spaces.
- Numerical analyses demonstrate their robustness.
- Our conditions are further extended to multivariate trait spaces.

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ABSTRACT

Evolutionary branching is the process by which ecological interactions induce evolutionary diversification. In asexual populations with sufficiently rare mutations, evolutionary branching occurs through trait-substitution sequences caused by the sequential invasion of successful mutants. A necessary and sufficient condition for evolutionary branching of univariate traits is the existence of a convergence stable trait value at which selection is locally disruptive. Real populations, however, undergo simultaneous evolution in multiple traits. Here we extend conditions for evolutionary branching to bivariate trait spaces in which the response to disruptive selection on one trait can be suppressed by directional selection on another trait. To obtain analytical results, we study trait-substitution sequences formed by invasions that possess maximum likelihood. By deriving a sufficient condition for evolutionary branching of bivariate traits along such maximum-likelihood-invasion paths (MLIPs), we demonstrate the existence of a threshold ratio specifying how much disruptive selection in one trait direction is needed to overcome the obstruction of evolutionary branching caused by directional selection in the other trait direction. Generalizing this finding, we show that evolutionary branching of bivariate traits can occur along evolutionary-branching lines on which residual directional selection is sufficiently weak. We then present numerical analyses showing that our generalized condition for evolutionary branching is a good indicator of branching likelihood even when trait-substitution sequences do not follow MLIPs and when mutations are not rare. Finally, we extend the derived conditions for evolutionary branching to multivariate trait spaces.

1. Introduction

Real populations have undergone evolution in many quantitative traits. Even when such populations experience contemporary selection pressures, their selection response will usually be highly multivariate. However, not all responding adaptive traits evolve at the same speed: in nature, such evolutionary speeds exhibit a large variation (Hendry and Kinnison, 1999; Kinnison and Hendry, 2001). Past speciation processes may have been driven mainly by traits undergoing fast evolution (Schluter, 1996), while gradual evolutionary differentiation among species, genera, and families may derive from traits undergoing slow evolution. These differences in evolutionary speed can have two fundamentally different causes. First, they may be due to less genetic variation being available for evolution to act on: in asexual populations this occurs when mutation rates and/or magnitudes are smaller in some traits than in others, while in sexual populations this occurs when standing genetic variation is smaller in some traits than in others. Second, differences in evolutionary speed are also expected when fitness is much less sensitive to changes in some traits than to changes in others.

For brevity we refer to the slowly evolving and the rapidly evolving traits as slow traits and fast traits, respectively. If the slow traits are sufficiently slow, it is tempting to neglect their effects on the evolution of the fast traits. As far as evolutionary responses to directional selection are concerned, this simplification is usually

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unproblematic: the directional trend of evolution (Rice et al., 2011) resulting from such selection, which we can refer to as directional evolution, is described effectively by ordinary differential equations or difference equations focusing only on those fast traits (Price, 1970; Lande, 1979; Dieckmann and Law, 1996; Rice et al., 2011).

On the other hand, such a simplification may not be safe where more complex evolutionary dynamics are involved. A typical example is adaptive speciation, i.e., evolutionary diversification driven by ecological interactions (Dieckmann et al., 2004; Rundle and Nosil, 2004). Ito and Dieckmann (2007) have shown numerically that when populations undergo disruptive selection in a fast trait, their evolutionary diversification can be suppressed by directional evolution of another trait, even if the latter is slow. Conversely, if the slow directional evolution is sufficiently slow, disruptive selection in the fast trait can drive evolutionary diversification, both in asexual populations and in sexual populations (Ito and Dieckmann, 2007). The suppression of evolutionary diversification can occur even when the slow and fast traits are mutationally and ecologically independent of each other. Thus, in a multivariate trait space, evolutionary diversification in one trait can be suppressed by slow directional evolution in just one of the many other traits. Moreover, such slow directional evolution may never cease, as the environments of populations are always changing, at least slowly, due to changes in abiotic components (e.g., climatic change) or biotic components (i.e., evolution in other species of the considered biological community). It is therefore important to improve the theoretical understanding of this phenomenon by deriving conditions for evolutionary diversification under slow directional evolution.

As a starting point to this end, we can consider the special situation in which there is only a single fast trait, while all other traits of the considered population are evolving extremely slowly, such that they are completely negligible. In this case, the question whether the selection on the fast trait favors its evolutionary diversification can be examined through conditions that have been derived for the evolutionary branching of univariate traits (Metz et al., 1992; Geritz et al., 1997, 1998). In general, evolutionary branching is the process through which a unimodal phenotype distribution of a population becomes bimodal in response to frequency-dependent disruptive selection (Metz et al., 1992; Geritz et al., 1997, 1998; Dieckmann et al., 2004), which can occur through all fundamental types of ecological interaction, including competition, exploitation, mutualism, and cooperation (Doebeli and Dieckmann, 2000; Doebeli et al., 2004). This kind of diversifying evolution provides ecological underpinning for the sympatric or parapatric speciation of sexual populations (e.g., Doebeli, 1996; Dieckmann and Doebeli, 1999; Kisdi and Geritz, 1999; Doebeli and Dieckmann, 2003; Dieckmann et al., 2004; Claessen et al., 2008; Durinx and Van Dooren, 2009; Heinz et al., 2009; Payne et al., 2011). Moreover, evolutionary branching may lead to selection pressures that favor further evolutionary branching, inducing recurrent adaptive radiations and extinctions (e.g., Ito and Dieckmann, 2007), and thus community assembly (e.g., Jansen and Mulder, 1999; Bonsall et al., 2004; Johansson and Dieckmann, 2009; Brännström et al., 2012) and food-web formation (e.g., Loeuille and Loreau, 2005; Ito et al., 2009; Brännström et al., 2010; Takahashi et al., 2014). Therefore, evolutionary branching may be one of the important mechanisms underlying the evolutionary diversification of biological communities.

Conditions for the evolutionary branching of univariate traits can be extended to bivariate trait spaces, if all traits considered evolve at comparable speeds (Bolnick and Doebeli, 2003; Vukics et al., 2003; Ackermann and Doebeli, 2004; Van Dooren et al., 2004; Egas et al., 2005; Leimar, 2005; Van Dooren, 2006; Ito and Shimada, 2007; Ravigné et al., 2009). However, if their evolutionary speeds are significantly different, the resultant conditions for bivariate traits can fail to predict evolutionary branching observed in numerical analyses (Ito and Dieckmann, 2007, 2012; Ito et al., 2009). In the present study, we therefore derive conditions for a population′s evolutionary branching in a fast trait when, at the same time, such a population is directionally evolving in one or more slow traits. The resultant conditions reveal when slow directional evolution either prevents or permits evolutionary branching.

This paper is structured as follows. Section 2 explains heuristically how the likelihood of evolutionary branching in asexual populations depends on selection pressures and mutational step sizes. Section 3 derives a normal form for strong disruptive selection and weak directional selection in a bivariate trait space and explains when arbitrary bivariate fitness functions can be mapped onto this normal form. Section 4 introduces the concept of maximum-likelihood-invasion paths, formed by mutants with maximum likelihood of invasion. On that basis, Section 5 derives sufficient conditions for evolutionary branching. Section 6 numerically examines the robustness of these conditions when the simplifying assumptions underlying our derivation are relaxed. Section 7 summarizes all conditions needed for identifying evolutionary-branching lines and extends these conditions to multivariate trait spaces. Section 8 discusses how our results generalize previously derived conditions for evolutionary branching that ignored slow directional evolution, and how our maximum-likelihood-invasion paths are related to existing methods for determining evolutionary dynamics or reconstructing evolutionary histories.

2. Heuristics

We start by describing, in a heuristic way, how disruptive selection in one direction, directional selection in another direction, and mutational step sizes may affect the likelihood of evolutionary branching. We then explain the analyses required for deriving the conditions for evolutionary branching, which are conducted in the subsequent sections.

When a population undergoes disruptive selection in trait x, as well as directional selection in trait y, its fitness landscape resembles that illustrated in Fig. 1a. The strength of disruptive selection in x is given by the fitness landscape′s curvature (i.e., second derivative) along x, denoted by D_{xx}, while the strength of directional selection in y is given by the fitness landscape′s slope (i.e., first derivative) along y, denoted by G_{y}. For simplicity, we assume that the population is monomorphic with a resident phenotype (x, y), indicated by a small black circle in Fig. 1a, and that mutational step sizes are identical in all directions. In this case, possible mutants are located on a circle around the resident phenotype, as shown in Fig. 1b–g. Then, small G_{y} means slow evolution in y. Roughly speaking, the direction of evolution favored by selection is indicated by the mutants possessing maximum fitness (small white circles in Fig. 1b–g). These mutants are located where the circle of considered mutants is tangential to the fitness contours.

From this simple setting, we can already draw the following geometrically evident conclusions. If G_{y} is large compared to D_{xx}, which results in low curvatures for the fitness contours (Fig. 1b), the mutant having the maximum y has maximum fitness, in which case directional evolution along y is expected. On the other hand, if G_{y} is sufficiently small compared to D_{xx} (Fig. 1c and d), the high curvatures mean that two different mutants are sharing the same maximum fitness. In this case, evolutionary diversification in x may be expected. In addition, we can easily see (Fig. 1e–g) that the smaller the mutational step size, the smaller the G_{y} and/or larger the D_{xx} required for two different mutants jointly having maximum fitness (Fig. 1e–g).