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A general condition for adaptive genetic polymorphism in temporally and spatially heterogeneous environments

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ABSTRACT

Both evolution and ecology have long been concerned with the impact of variable environmental conditions on observed levels of genetic diversity within and between species. We model the evolution of a quantitative trait under selection that fluctuates in space and time, and derive an analytical condition for when these fluctuations promote genetic diversification. As ecological scenario we use a generalized island model with soft selection within patches in which we incorporate generation overlap. We allow for arbitrary fluctuations in the environment including spatio-temporal correlations and any functional form of selection on the trait. Using the concepts of invasion fitness and evolutionary branching, we derive a simple and transparent condition for the adaptive evolution and maintenance of genetic diversity. This condition relates the strength of selection within patches to expectations and variances in the environmental conditions across space and time. Our results unify, clarify, and extend a number of previous results on the evolution and maintenance of genetic variation under fluctuating selection. Individual-based simulations show that our results are independent of the details of the genetic architecture and whether reproduction is clonal or sexual. The onset of increased genetic variance is predicted accurately also in small populations in which alleles can go extinct due to environmental stochasticity.

1. Introduction

Explaining observed levels of genetic variation within natural populations is one of the major challenges in the study of evolution. One can distinguish adaptive explanations from non-adaptive explanations, with neutral variation and mutation–selection balance being the prime examples for the latter. Amongst adaptive explanations we can distinguish those based on genetic constraints such as over-dominance, where only heterozygote individuals can realize highest fitness, from those that do not rely on such constraints and consequently also apply to haploid species. In the latter case, genetic diversity is an adaptive response to the environment. Our aim is to characterize the conditions that select for adaptive diversity in this sense.

Both temporal and spatial fluctuations are omnipresent in natural populations. From early on there has been a perception in evolutionary research that such fluctuations should be favorable for the evolution and maintenance of genetic diversity. Modeling efforts to support this claim started in the second half of the 20th century (reviewed in Felsenstein, 1976 and Hedrick et al., 1976). Spatial heterogeneity was soon identified as a potent factor to maintain diversity, even if individuals move freely among patches. The pioneering model here is the Levene model (Levene, 1953; Gliddon and Strobeck, 1975), an island model (Wright, 1943) with different selective pressures among islands (or patches) and random dispersal of all individuals in each generation. As pointed out by Dempster (1955), a crucial feature of the Levene model is that density regulation takes place locally within patches. This “soft-selection” regime (Wallace, 1975; Christiansen, 1975) can adaptively maintain a protected genetic polymorphism. If only a part of the population disperses, this further aids the maintenance of genetic variation as sub-populations can become locally adapted (Deakin, 1966, 1968; Spichtig and Kawecki, 2004).

In the absence of genetic constraints, it was initially thought that purely temporal fluctuations in selection are not sufficient

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to maintain genetic polymorphism, but would generally favor the genotype with the highest geometric mean fitness (Gillespie, 1973b, 1974; Felsenstein, 1976). It was therefore concluded that temporal fluctuations can only account for a limited amount of the observed genetic variance in diploid populations (Dempster, 1955) and that there is no tendency to maintain polymorphism in haploid populations (Cook and Hartl, 1974). However, two mechanisms were subsequently identified that can maintain genetic polymorphism under temporal fluctuations, named the "storage effect of generation overlap" (Chesson and Warner, 1981; Chesson, 1984) and the "effect of relative non-linearity" (Chesson, 1994; Szilágyi and Meszéna, 2010). In both cases, selection is no longer a function of time alone: With the storage effect, selection acts only on a short-lived stage of the life cycle (e.g., juveniles), while a long-lived stage (e.g., adults or persistent dormant stages) is not affected by the fluctuations. With the non-linearity effect, temporal fluctuations lead to fluctuations in the population density and polymorphism is maintained by an additional density-dependent selection component.

Environmental heterogeneities simultaneously occurring in space and time have also been studied. After an early attempt by Levins (1962), it was mainly Gillespie (1974, 1975, 1976; but see also Hedrick, 1978) who treated this topic. He considered fluctuations in an island model, in which the distribution of environmental conditions is identical across all patches, but in which the realized environment at any given point in time may differ among patches. Gillespie's main conclusion was that these transient spatial differences can be sufficient to maintain genetic diversity.

Adaptive maintenance of genetic diversity can also be addressed from an ecological perspective, where species coexistence is a classical research focus (see Chesson 2000b for a review). Models and methods are closely related to their genetic counterparts, although this connection is often not made explicit. For clonal inheritance, it is only a matter of semantics whether maintenance of polymorphism within species (population genetics) or species diversity (ecology) is considered. Conditions for species coexistence in temporally and spatially fluctuating environments have been studied by Chesson (1985, 2000a) and Comins and Noble (1985). Both combine an island model with environmental fluctuations in time and space (similar to Gillespie's model) with Chesson's lottery model introducing generation overlap. They find that in such a scenario both temporal and spatial environmental fluctuations can promote species coexistence.

Most models described above focus on the maintenance of diversity among two discrete and immutable alleles or types. Thus, stability of the polymorphism is considered from the short-term evolutionary perspective of the dynamics of allele (or phenotype) frequencies. From a long-term evolutionary perspective, one can further ask whether a polymorphism remains stable also in the presence of mutations leading to gradual adaptive changes in the allelic values or phenotypes. In particular, evolutionary stability in this sense should also guarantee that the polymorphism cannot be lost due to the appearance of a single superior (generalist) type. This long-term evolutionary stability has increasingly gained attention with the development of adaptive dynamics and the discovery of evolutionary branching points (Metz et al., 1992, 1996; Dieckmann and Law, 1996; Geritz et al., 1998). Evolutionary branching points are trait values that are attractors of the evolutionary dynamics, but once the population has evolved sufficiently close to such trait values, selection turns disruptive and alternative alleles can invade and coexist. In short, evolutionary branching indicates that the emergence and maintenance of genetic polymorphism is an adaptive process. Several recent studies have used this approach to ask how environmental heterogeneity affects the existence of evolutionary branching points. This has been done for purely spatial heterogeneity (Meszéna et al., 1997; Geritz et al., 1998; Day, 2000; Nilsson and Ripa, 2010a,b), under purely temporal variation (Ellner and Hairston, 1994; Svardal et al., 2011; Abrams et al., 2013) and for a combination of the two (Kisdi, 2002; Parvinen and Egas, 2004; Nurmi and Parvinen, 2008, 2011). Note that the latter studies by Parvinen and coworkers are meta-population models in which temporal variation is introduced through catastrophes wiping out local populations. The general conclusion from the above studies is that in spatially heterogeneous environments low migration and large spatial differences favor evolutionary branching, while under purely temporal fluctuations a sufficiently large generation overlap is necessary for branching.

In this article, we follow the recent line of research and ask how environmental heterogeneity affects the scope for the adaptive evolution and maintenance of genetic polymorphism. We consider a modified island model with local population regulation resulting in constant patch occupancies (soft selection), which combines features from the approaches above and extends them in several directions. We follow the evolution of a quantitative trait with a continuum of alleles. The strength and direction of selection within a patch depends on the realized environmental condition. In particular, we allow for an arbitrary distribution of environmental conditions across space and time, including spatial and temporal correlations. The functional dependence of fitness on the trait is also arbitrary. For example, selection can be stabilizing with the optimal trait value depending on the realized local environment, or directional with the direction fluctuating in space and time. We analytically derive a condition for the existence of an evolutionary branching point and investigate the robustness our finding with individual-based simulations.

2. Model

2.1. Population structure and life cycle

Consider the classical island model of population genetics (Wright, 1943). A population occupies n patches that are connected by dispersal. We assume that the population dynamics is regulated locally by a limiting resource (e.g., space) so that the adult population size within each patch is at a stable equilibrium and stays constant over time. For our analytical treatment, we assume that local populations are sufficiently large so that stochastic effects due to drift can be ignored. This assumption is relaxed in Section 3.6, where we present simulation results for small populations. For large populations, our results are independent of the total population size and it is sufficient to follow relative population sizes in the following.

The life cycle is shown in Fig. 1 and an overview of our notation can be found in Table 1. The relative carrying capacity for adults may depend on the patch, with a fraction of k_i adults living in the ith patch, i.e., $\sum_{i=1}^{n} k_i = 1$. Adults reproduce within their patch and a fraction $1 - \gamma$ dies after reproduction. The remaining fraction γ survives to the next reproductive season. Hence, we allow for overlapping generations and the parameter γ will be called "generation overlap" in the following. The case $\gamma = 0$ corresponds to the classical island model with non-overlapping generations and for $\gamma \to 1$ the individuals approach immortality. Note that the long-lived life-stage could also be a dormant stage such as resting eggs or a seed bank (Ellner and Hairston, 1994).

Juveniles are subject to local viability selection, which depends on their phenotype and the realized environmental condition in the patch. After selection, trait-independent local density regulation further decreases offspring to a patch specific relative juvenile carrying capacity c_i, where $\sum_{i=1}^{n} c_i = 1$. A fraction m of the surviving offspring disperses globally so that the probability of arriving in a certain patch is independent of the patch of origin.