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Separation of time scales, fixation probabilities and convergence to evolutionarily stable states under isolation by distance

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Abstract

To a first order of approximation, selection is frequency independent in a wide range of family structured models and in populations following an island model of dispersal, provided the number of families or demes is large and the population is haploid or diploid but allelic effects on phenotype are semidominant. This result underlies the way the evolutionary stability of traits is computed in games with continuous strategy sets. In this paper similar results are derived under isolation by distance. The first-order effect on expected change in allele frequency is given in terms of a measure of local genetic diversity, and of measures of genetic structure which are almost independent of allele frequency in the total population when the number of demes is large. Hence, when the number of demes increases the response to selection becomes of constant sign. This result holds because the relevant neutral measures of population structure converge to equilibrium at a rate faster than the rate of allele frequency changes in the total population. In the same conditions and in the absence of demographic fluctuations, the results also provide a simple way to compute the fixation probability of mutants affecting various ecological traits, such as sex ratio, dispersal, life-history, or cooperation, under isolation by distance. This result is illustrated and tested against simulations for mutants affecting the dispersal probability under a stepping-stone model.

Keywords: Coalescence; Diffusion; Inclusive fitness; Quasi equilibrium

1. Introduction

An initial aim of this work has been to establish some population genetic underpinnings of game theory under isolation by distance, but the results will go beyond a restrictive conception of game theory. A motivation of early work on game theory was to emphasize the important factors involved in the evolution of behavioral contests (Maynard Smith and Price, 1973), and thereby to address issues in the group selection debate. To this effect, the basic idea of game theory is to find stable strategies and to analyze fitness effects on rare mutants deviating from these stable states, in order to understand the selection pressures acting on the trait. The approach is defended as easier than a more complete analysis of a population genetic model of the same biological scenario, yet yielding the most important information that can be provided by a fast, simplified approach (Maynard Smith, 1982; Eshel, 1996). In this respect, the brand of game theory I will consider here is only a variant of population genetics that seeks useful approximations for the long term evolution of ecological traits, in particular when frequency dependence is expected.

A strategy x^* may be recognized as an evolutionarily stable strategy (ESS) if deviant strategies $x^* + \delta$ are less fit when rare, whether δ is positive or negative. This implies that the first derivative of mutant fitness vanishes in x^*, and that the first nonzero derivative is of even order and negative. A candidate ESS may thus be defined as a point where the first derivative of mutant fitness vanishes. When it is not null, the first derivative determines the direction of selection on mutants with small phenotypic effect. A mutant favored when rare may either go to fixation, in particular if selection is not frequency dependent so that the mutant is also favored when common, or it may reach a stable polymorphism, in particular when selection is negatively frequency dependent. Thus what happens at

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intermediate frequencies is determinant, though it can often be read from what happens close to fixation of either allele, so that the usual approach of measuring selection on rare deviants is justified.

This logic forms the basis of the convergence and ESS criteria for continuous traits (Maynard Smith, 1982; Eshel, 1983). First order effects are used to determine whether the population will evolve by allelic substitutions toward x^* (convergence stability), and at this point the second order effects are used to determine whether deviants will be selected against (evolutionary stability). Obviously in nature mutants may have large effects, so the derivatives in x^* may not be enough to determine the dynamics of the system, and it is not always easy to see when they will be enough. But stable strategies have to be stable against invasion by mutants with small effects.

In most applications, the fitness effects are computed for "rare" deviants. Here the (often implicit) assumption is that the sign of the first order effect is not frequency dependent, otherwise this concept of rare deviant is often ambiguous, in its definition or in its practical application. It should be clear by now that fitness effects over one generation on a single deviant are not determinant: they may be informative only to the extent that they inform us on fitness effects when the deviant is not unique. Indeed, if selection is not strong a negative fitness effect on a unique deviant is easily overcome by drift, even in an infinite population, and the fitness effects when there are several copies of the deviant allele become determinant.

In a spatially subdivided population, one thus has to take into account that an allele may be locally common even if it is globally rare. This is usually accomplished by some separation of time scales argument, by which the local distribution of a deviant allele reaches some type of quasi-equilibrium much faster than the deviant allele frequency changes in the total population. For example, Motro (1982) computed quasi-equilibrium distributions to obtain ESS dispersal rates. One may aim to compute only the minimal features of the distribution that are relevant for the computation of first order effects: this is what is achieved by inclusive fitness arguments as first developed by Hamilton (1964, 1970). Likewise one may compute those terms relevant for the second order effects (Ajar, 2003). Multilocus quasi-equilibrium techniques are based on similar ideas, though here the genetic structure under consideration is the statistical association between alleles at different loci (e.g. Barton and Turelli, 1991; Kirkpatrick et al., 2002). The spatial and multilocus quasi-equilibrium techniques can be combined (Roze and Rousset, 2005).

For rare mutants in an infinite island model, a variant of this argument considers the descendants of a single immigrant in a deme, and follows the number of such descendants until the local extinction of the family descended from this immigrant (Metz and Gyllenberg, 2001). Several deviant descendants may thus be interacting, and this accounts for the fact that the allele may be locally common. The assumption that the allele is globally rare enters into the computation through ignoring the immigration of other deviant individuals in the deme. Clearly the probability of such immigration depends on the allele frequency p, and when p vanishes the overall fitness effect on the descendants of an ancestor connects smoothly with the fitness effect when the single deviant ancestor is the single deviant in the total population, so the computation ignoring deviant immigrants is informative about the fitness of individuals over a range of values of p.

Under localized dispersal, where immigrants preferentially come from adjacent demes, one cannot neglect the immigration of deviant individuals simply on the ground that the allele is globally rare. There is still some concept of quasi-equilibrium (as will be shown below), but attempts to compute a quasi-equilibrium distribution have focused on models involving demographic stochasticity. These attempts are confronted with an infinite system of equations. So-called pair approximations have been used to reduce this to a finite system, with results of variable accuracy (Matsuda et al., 1992; van Baalen and Rand, 1998). The simpler case without demographic stochasticity seems unexplored by these techniques.

An alternative approach that turns out to be feasible in the latter case is to obtain results for fixation probability without knowing the exact relation between deviant fitness and p (Rousset and Billiard, 2000). Such results should be consistent with quasi-equilibrium arguments when a stable polymorphism is not maintained by selection. More precisely, for mutants with small phenotypic effect, the latter condition means that first order effects of selection should be of constant sign over all values of p, except perhaps for a few configurations of the population, as when there is a single deviant individual, since as noted above these occasional opposite effects of selection may be overcome by drift. That the first order selection is of constant sign is known in island models when the number of demes is large (Rousset, 2004, pp. 109, 207) and this paper will show that this also occurs under isolation by distance.

Further, fixation probabilities provide a meaningful, even if incomplete, way of measuring the effects of finite size on the direction of selection, which alternative approaches have not addressed. This idea has attracted a recent surge of interest, with applications to so-called linear games in unstructured populations (Nowak et al., 2004; Wild and Taylor, 2004; Lessard, 2005). Diffusion approximations have long provided an efficient tool to analyze evolution in finite unstructured populations, and this paper will consider the extension of a diffusion result for fixation probability in populations with localized dispersal. I will generalize an elegant argument due to Maruyama (1983), showing how fixation probabilities can be computed despite the exact form of the first order effect not being known.