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François Rousset: Genetic Structure and Selection in Subdivided Populations

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CHAPTER ONE

Introduction

GENETIC STRUCTURE IN RELATION TO SELECTION

Initial interest in spatial genetic structure came out of the idea that dispersal prevents genetic differentiation of populations. To some extent, it may prevent adaptation to the local environment. More efficiently, it limits the random genetic divergence of populations and thus the first step of allopatric speciation. In most species, however, dispersal is spatially restricted, and individuals interact and compete preferentially with their neighbors.

According to Wright, limited dispersal was important for adaptation. He considered that adaptation occurred mainly through the evolution of coadapted gene complexes, that is, of alleles at different loci, which would be deleterious when combined with alleles of another coadapted gene complex. These deleterious effects would prevent adaptive evolution from one coadapted complex to another in a large, randomly mixing population. The selection against deleterious intermediates would be more easily overcome by random effects in small populations.

Thus, to explain adaptation, Wright proposed what he called the “shifting-balance” theory (e.g., Wright 1931b; Provine 1986). According to this theory, limited exchanges between local populations allowed local allele frequencies to randomly fluctuate (the phenomenon of genetic drift), and thus different coadapted gene complexes could be fixed in different populations. The better adapted gene complexes made populations more fecund, and a small amount of dispersal allowed them to spread in the total population (a step that Wright called interdeme selection). These multilocus processes were and still are difficult to quantify, so Wright mainly developed one-locus models quantifying

the extent of local differentiation due to drift. Later works have quantified the probability of fixation of various kinds of mutants in a single deme, and various approximations have been suggested for subdivided populations. It is clear that limited dispersal may slow, but not prevent, the spread of advantageous mutants, so the main output of such models concerns the extent to which spatial structure affects the selective advantage experienced by a mutant, particularly when this advantage depends on its local frequency.

Today, there is little evidence supporting Wright's shifting-balance theory and the idea that population structure is essential for adaptation (Coyne et al. 1997). However, the question remains of how demography, including the extent of dispersal or the regulation of population sizes, can affect selection, and this question has been addressed by population geneticists using the concepts developed by Wright. For example, there have been renewed attempts to compute fixation probabilities of mutants, their fixation times, and allele frequency distributions by way of diffusion approximations, an approach also largely initiated by Wright.

However, the demographic factors, such as dispersal rates, which may affect adaptation in natural populations, are difficult to estimate by demographic methods. To overcome this difficulty, the genetic structure itself has been used to infer dispersal and other demographic events in natural populations. Such studies were initiated by Dobzhansky and Wright (1941), and their number exploded after electrophoresis was developed to measure enzyme polymorphisms in natural populations, and more recently with microsatellite genotyping.

Out of such studies has grown a belief (e.g., Lewontin 1974; Slatkin 1987; Whitlock and McCauley 1999) that observed genetic structure is often not consistent with the expectations of the simple models developed by Wright, Malécot, and their followers. Various explanations have been proposed for these discrepancies, including selection on the genetic markers used and past demographic processes such as range expansions. At lower spatial and temporal scales, increased attention has also been given to "metapopulation" processes of extinction and recolonization and to their consequences on genetic differentiation.

These factors undoubtedly have an effect on the genetic structure of natural populations. With respect to selection, although statistical analyses of molecular polymorphisms have often been inconclusive (Kre-

itman and Akashi 1995), enzyme polymorphisms often appear subject to selection when they are studied using a combination of biochemical studies and field experiments (e.g. Feder et al. 1997; Eanes 1999). Comparable studies have not yet been conducted for microsatellites. Likewise, range expansions and contractions are parts of a species' history as a result of, for example, climate changes or changing interactions with competitors and parasites. Together, these factors put into question our ability to estimate demographic parameters from studies of population structure.

Another concern that has generated much speculation about population structure is the occurrence of supposedly altruistic behaviors. By altruistic we mean behaviors that increase some group's production of offspring to the detriment of the fitness of the individuals expressing them. The occurrence of altruism in natural populations was little questioned and attracted little interest until some authors, including Hamilton (1963, 1964), Maynard Smith (1964), and Williams (1966) felt that altruism needed a special explanation. What needed a special explanation was how genes increasing the expression of a behavior that supposedly decreases the fitness of altruists could spread into the population.

To define conditions under which cooperative or altruistic behaviors would be selected for or against, Hamilton (1964 and later works) developed the theory of inclusive fitness. This theory accounts for the fact that individuals who make altruistic fitness gifts may also be the main recipients of such gifts. This will occur when interactions occur between individuals more genetically similar than those who do not interact, so that an individual who bears genes increasing the expression of a fitness gift behavior interacts with individuals who tend to make fitness gifts to it. Then the individual fitness of altruists may on average be higher than that of nonaltruists.

Although inclusive fitness theory did not initially focus on spatially localized dispersal, it was recognized that such limited dispersal results in a genetic structure by which spatially close individuals are more genetically similar than spatially distant individuals. Thus, population structure has often been suggested as an explanation for the evolution of altruistic behaviors.

Whether many behaviors once viewed as altruistic are actually so has been repeatedly questioned. But inclusive fitness is a conceptual

framework that applies identically, in principle, to behaviors that are altruistic or not, and to a wide diversity of life history traits, such as sex ratios, and parental investment. Any behavior that affects the fitness of neighbors, that is, essentially all behaviors in spatially subdivided populations, will be affected by spatial genetic structure. Limited dispersal adds a new dimension, as dispersal is itself a selected trait, and it interacts with many other traits of ecological importance. Selfing or outcrossing, the evolution of sex ratios when dispersal is sex biased, and the investment in reproduction versus survival when only juveniles disperse are only a few examples. Further analysis is required to assess when the consequences of these traits on dispersal will have important implications on their evolution.

To say that neighbors are genetically more similar than distant individuals is essentially the same as saying that there are fluctuations of allele frequencies among different populations. Hence, Hamilton saw a connection between inclusive fitness and Wright's measures of population structure, and the idea has been put to work in some models. However, application of the inclusive fitness framework to spatially subdivided populations has had a checkered history and no consistent development until recently. While inclusive fitness theory has recently benefited from important methodological insights, allowing a wide range of selection processes to be analyzed using a few well-defined tools, its basic concepts remain commonly misunderstood.

Inclusive fitness is used mostly to determine the direction of phenotypic evolution in a game theoretical perspective that seeks what will be the "unbeatable strategies" to which a population will evolve. Evolutionary game theory grew out of the works of, for example, Hamilton (1967), Maynard Smith (e.g., 1982), and Eshel (1983), and recent developments have been publicized as "adaptive dynamics." However, the relationship of inclusive fitness to adaptive dynamics has also been questioned (e.g., Doebeli 1999). Indeed, it has been hard to find both general and consistent arguments for the use of inclusive fitness measures in game theory.

These difficulties with inclusive fitness are illustrative of a more general problem, in which different schools of thought address the same question with different languages and may each ignore results easily obtained by another approach. In contrast, reliable science is possible only when scientists base their work on widely shared con-

cepts. A major objective of this book is to show how the different approaches mentioned above relate to the theory of genetic structure and complement each other.

Therefore, this book presents a synthesis of the different approaches that have been developed to understand evolution in subdivided populations. This book:

- reviews models of genetic differentiation in subdivided populations. These form the basis for appreciating the potential for random differentiation under different circumstances. What can or cannot be reliably concluded from statistical analyses of population structure will be highlighted based on these models.
- shows how the selection process can be analyzed in terms of measures of spatial structure. I will show how this can be done with minimal effort under a variety of population structures, what it implies in terms of social evolution, and how it relates to game theoretical approaches. Unambiguous and widely applicable concepts of genetic similarity will come out of these analyses.
- shows, in a nontechnical way, how the same methods and the concept of effective size can be used for a finer description of the selection process, focusing for illustration on the question of fixation probabilities in subdivided populations.

This book also contains some new results. In particular, it discusses simple methods to construct better diffusion approximations for subdivided populations. Most of the results for effective size in metapopulations, and their derivations, also depart from earlier work.

PLAN OF THE BOOK

Chapter 2 illustrates basic concepts used by Wright and Hamilton to quantify evolutionary processes. It provides a more formal exposition of the ideas presented in this introduction and sets a statistical framework in which the concepts will be developed.

Chapter 3 develops some basic models of population structure: the finite island model and models of isolation by distance. It provides both a self-contained presentation of unusual and often poorly accessible algebra and a less technical discussion of the broad implications of the models for the interpretation of patterns observed in natural populations.

Chapter 4 reviews the biological significance and properties of the different measures of identity and of population structure in the context of coalescence theory. It emphasizes a distinction between models that have a hierarchical structure with two time scales and those that do not. This chapter departs from some tradition in emphasizing definitions and interpretations that apply equally under different dispersal models and to finite and infinite populations, that is, to the full range of scenarios considered in applications of the measures of population structure, rather than simply the infinite island model.

Chapter 5 introduces the different measures of evolutionary convergence and evolutionary stability of a phenotype (or “behavior” or “strategy”) used in game theory and discusses how they can be computed in subdivided populations.

Chapter 6 demonstrates a mathematically and conceptually minimal way of determining convergence to evolutionarily stable strategies in a subdivided population, and illustrates its application in the example of dispersal rates.

Using simple models of cooperative or altruistic interactions in a subdivided population, chapter 7 shows how these results relate to the concepts of inclusive fitness theory, such as costs, benefits, and altruism.

The following chapters detail the application and generalization of these ideas to progressively more complex models.

Chapter 8 deals with the specifics of diploid populations. It analyzes patterns of genetic structure in plant populations with selfing, and shows how to measure fitness effects, whether the trait selected is under parent or offspring control in sexual diploid populations.

Chapter 9 develops concepts of effective size. It compares the different definitions of effective size used in the literature. It shows how effective size can be used, together with the techniques developed in previous chapters to quantify selection, to obtain better approximations of allele frequency dynamics in subdivided populations. It emphasizes the interpretation of effective size in terms of elementary events affecting gene lineages, an interpretation that easily generates a number of formulas for effective size, as illustrated in particular for populations with different classes of individuals.

Chapter 10 extends the analysis of effective size to populations with demographic fluctuations, in particular to metapopulations with local

extinctions and recolonization, for which some new results and new interpretations are presented.

Chapter 11 shows how selection can be measured in class-structured populations or metapopulations by the same concepts developed in previous chapters.

Much of the book is based on highly simplified models. The concluding chapter considers possible developments and discusses what conclusions can and cannot safely be drawn from the models. In particular, it highlights a number of common misconceptions of analyses of genetic diversity in natural populations. There is currently much interest in “coalescent” methods, and this chapter explains the logic of these methods. I have refrained from an extensive review of these methods, because their practical reliability is unknown, so little can be safely concluded at present.

In summary, this book aims to show how a range of questions can be efficiently addressed using a limited number of concepts and technical tools, and to provide a self-contained account of the basic models of the genetic structure of populations. There are two alternative paths through this book. One path temporarily ignores much of the neutral theory of population structure, jumping from chapter 2 to chapter 5 and later chapters on selection. On the other hand, the readers who want to make themselves more familiar with the computation and interpretation of measures of population structure may read chapters 3 and 4 before chapter 5.