CHAPTER ONE

Introduction

Evolution occurs when organisms reproduce so that their offspring inherit certain characteristics, or traits. Variation in heritable traits, together with variation in reproductive success, generates evolutionary change in trait distributions. If the correlation between heritable variation and reproductive variation is (close to) zero, evolutionary change is neutral, and the trait distribution performs an evolutionary random walk. In contrast, evolution is adaptive if the correlation between heritable variation and reproductive variation is significantly different from zero.

Adaptive evolution is generally thought to be of central importance for the history of life on earth. The process of adaptation, whereby types that are better adapted to the prevalent circumstances leave more offspring than types that are less well adapted, is, for example, believed to have been the main driving force generating major evolutionary transitions (Szathmáry & Maynard Smith, 1995). By far the most widespread view of adaptation, both among experts and laymen, is that of an optimization process: Given a set of environmental conditions, the type that is best adapted to these conditions prevails. Determining the optimal type in a given situation, and understanding how genetic and developmental constraints impinge on the evolutionary trajectory toward such optimal types, have been among the main objectives in evolutionary theory.

One of the problems with viewing evolution as an optimization process is that this perspective leaves little room for diversity: the optimally adapted type has more offspring than all other types, and so eventually, all other types will go extinct, leaving the optimal type as the single type present. Of course, recurring mutations may constantly introduce genetic variation into a population, but optimization essentially generates uniformity. In particular, evolution of distinct ecological types out of a uniform ancestral lineage at the same physical location is precluded under the tenet of evolutionary optimization.

Yet understanding the evolution of diversity is one of the central and most fundamental problems in biology. To explain the evolution of diversity in the realm of the traditional optimization perspective, one needs to

invoke geographical heterogeneity: if environmental conditions differ between different geographical locations, then different optimization problems must be solved, and hence different adaptations evolve in different locations. The process of diversification due to local adaptation to different environments is usually called ecological speciation (Schluter, 2000, 2009), but different local adaptations can also be generated by sexual selection (e.g., Lande, 1981). After their formation in separate geographical areas, different types may migrate to and coexist at the same location due to a plethora of genetic and ecological mechanisms, which have been the subject of intense study. However, physical separation, and hence an intrinsically nonbiological ingredient, is necessary to explain the emergence of diverse life forms if one views evolution primarily as an optimization process. Note that geographical isolation is also necessary for diversity to arise due to neutral evolution, but such a neutral theory of diversification has become less popular among evolutionary biologists (e.g., Hendry, 2009; Schluter, 2009), partly because it runs contrary to the generally accepted notion that diversity is paramount in nonneutral traits (i.e., in traits in which heritable variation and variation in reproductive success are significantly correlated).

Optimization theory has proved to be useful for gaining many evolutionary insights. However, it misses out on a class of ecological and evolutionary mechanisms that are intuitively appealing, and that opens up a whole new perspective on the problem of the evolution of diversity. These mechanisms operate whenever the relevant components of the environment determining selection pressures on a given focal type not only consist of abiotic, physical ingredients that may remain constant over evolutionary time, but also comprise other organisms that may be present in the environment. Whether these other organisms are individuals of the focal type's species, or part of other species with which the focal type interacts, it is often obvious that an individual's survival and fecundity generally depend on the ecological impact of other organisms. For example, if organisms with different traits eat different types of food, then whether a given trait confers a high food intake will depend on the traits of the other organisms currently present in the population (with food intake low if the other organisms have similar traits, and hence eat similar food). Moreover, the food intake of a given organism may change as the distribution of traits in the population changes. As a consequence, adaptation to constant conditions may rarely occur: as the population evolves, the biological environment changes, and hence the optimization problem changes as evolution unfolds.

The phenomenon that the evolving population is part of the changing environment determining the evolutionary trajectory is usually referred to as

frequency-dependent selection. In the language of correlations used above, selection is frequency-dependent if the sign and magnitude of the correlations between heritable variation and reproductive variation change as a consequence of changes in the trait distribution that are themselves generated by such correlations. From an anthropocentric perspective, frequency dependence is of course very familiar, as it is obvious to us that in many of our enterprises, what is "good" for us depends very much on what everyone else is doing. In principle, applying such anthropocentric insights to evolutionary theory is deeply problematic, but it works in the context of frequency dependence, as it seems obvious that whether a trait or a behavioral strategy of an organism confers a fitness advantage may very much depend on the traits or strategies of other organisms.

In fact, from the perspective of mathematical modeling, the realm of frequency dependence in evolution is larger than the realm of situations in which selection is not frequency-dependent, because the absence of frequency dependence in a mathematical model of evolution essentially means that some parameters describing certain types of biological interactions are set to zero (or almost zero). Thus, in a suitable parameter space, frequency independence corresponds to the region around zero, while everything else corresponds to frequency dependence. In this way, frequency independence can be seen as a special case of frequency dependence, much like neutral evolution is a special case of adaptive evolution (with neutral evolution corresponding to certain correlations being near zero, see earlier). From a theoretical point of view, frequency-dependent selection should therefore be considered the norm, not the exception, for evolutionary processes.

Using the metaphor of a fitness landscape for evolutionary optimization problems, frequency dependence implies that the fitness landscape is changing as a consequence of evolutionary change. Thus, frequency dependence generates a kind of evolutionary feedback mechanism. In line with general dynamical systems theory, where feedback mechanisms can lead to many complicated scenarios, frequency dependence can lead to very interesting evolutionary dynamics. This is true in particular in models for the evolution of diversity. For example, it has long been known that frequency dependence can mediate the coexistence of different types without geographical isolation. This is most easily seen using the mathematical framework of evolutionary game theory, where frequency dependence can allow for coexistence between different strategies already in very simple games such as the Hawk-Dove game (Doebeli & Hauert, 2005). However, in evolutionary game theory, coexistence typically requires the a priori presence of different types. Moreover, game theory is limited in that it typically assumes payoff functions that are linear

functions of the strategy distribution. These restrictions imply that traditional game theory cannot explain the origin of diversity out of uniform ancestral populations.

However, such explanations can be provided by an extension of game theory to nonlinear payoff functions that depend on continuously varying strategy traits. This extension is known as *adaptive dynamics*, a mathematical framework that has been developed by Hans Metz and others (Dercole & Rinaldi, 2008; Dieckmann et al., 2004; Dieckmann & Law, 1996; Geritz et al., 1998, 1997; Metz et al., 1996), and that has proved to be a very convenient and useful tool for studying many different aspects of long-term evolutionary dynamics of quantitative traits under frequency-dependent selection. In particular, using the concepts of evolutionarily singular points and evolutionary branching, adaptive dynamics has allowed to generally identify and classify adaptive processes that are conducive to evolutionary diversification. Evolutionary branching points are points in phenotype space that have, roughly speaking, two characteristic properties: they are attractors for the evolutionary dynamics, and they are fitness minima. Points with these properties can only exist if fitness landscapes change as the population evolves, that is, if selection is frequency-dependent. Evolutionary branching occurs if a fitness minimum is "catching up" with the evolving population: As long as the population is away from the evolutionary branching point, it sits on one side of the fitness minimum, but as it is moving up that side of the disruptive landscape, the landscape changes so that the population comes to lie closer and closer to the trough of the landscape until eventually it reaches the singular point, which coincides with the fitness minimum. At this point, the population experiences disruptive selection, and hence is prone to splitting into two diverging lineages.

If diversification occurs due to evolutionary branching, it is adaptive in the sense that when the population is sitting at the evolutionary branching point, being different from the population mean confers an adaptive advantage. Thus, the splitting of the population into different phenotypic branches is itself an adaptive process that is driven by frequency-dependent biological interactions. Such diversification due to frequency-dependent selection is called *adaptive diversification* (Dieckmann et al., 2004). In contrast to diversification scenarios unfolding due to geographical isolation, adaptive diversification requires ecological contact between the diverging lineages. Using traditional terminology, adaptive diversification can occur in sympatry or parapatry, but not in strict allopatry. Thus, adaptive diversification is in some sense the antithesis to allopatric speciation.

I am of course well aware that diversification under conditions of sympatry continues to have a rather tainted reputation in evolutionary biology. The

prevalent skepticism is perhaps best reflected in treatments in which authors present a whole catalog of conditions that presumably need to be satisfied for "true" sympatric speciation to occur (Bolnick & Fitzpatrick, 2007; Coyne & Orr, 2004). Such lists often contain circular elements, for example, when one purported requirement is the presence of gene flow in sympatric speciation, even though it is clear that any form of speciation, whether sympatric or not, requires the eventual disruption of gene flow. To me, such discussions are reminiscent of medieval scholarly disputes about how many angels can dance on the head of a pin. In fact, I think that placing the geographic context at the center of the speciation problem detracts from the more important question about the actual biological mechanisms that lead to diversification and speciation. For example, Schluter (2009) provides an interesting discussion of speciation mechanisms, arguing that mutation order speciation, which occurs when different mutations are fixed in separate populations adapting to similar selection pressures, is generally less likely than ecological speciation, which subsumes all speciation processes that are driven by adaptation to divergent environmental conditions. Nevertheless, this discussion does not distinguish between different mechanisms for ecological speciation, and in particular does not mention the possibility that ecological speciation can be driven by frequency-dependent selection.

More generally, frequency-dependent selection does not really seem to be on the radar of mainstream evolutionary biology as a potential mechanism for generating major evolutionary patterns. For example, Estes & Arnold (2007) conducted an extensive study to test the feasibility of various population genetic models to explain the mechanisms generating evolutionary data series on many different time scales. Estes & Arnold (2007) had no qualms about using optimization models, but frequency-dependent selection was not even mentioned in their article, nor was it mentioned in a subsequent discussion of their work (Hendry, 2007).

Perhaps this book will serve the purpose of generating more awareness of frequency-dependent selection as a potentially powerful evolutionary mechanism, so that evolutionary biologists at least think twice before dismissing this perspective from their approach. After all, when studying a particular problem, the outcome of the analysis is often partly determined by the perspectives one has in mind at the outset. It is therefore important to keep an open mind, and this seems particularly true when studying the evolution of diversity, a field that seems to have been dominated by established doctrine for quite some time. That said, this book is of course itself biased toward demonstrating the potential role of frequency dependence for evolutionary diversification. However, the book is not about making any claims

about the ubiquity of such adaptive diversification in real empirical systems (except to say that it does seem to occur in one particular microbial system, see Chapter 10), and it is not my intention to advocate adaptive diversification and speciation as the predominant mode of evolutionary diversification. Determining the mechanisms generating biological diversity is ultimately an empirical, not a theoretical, question. However, what I do indeed want to say with this book is that from a theoretical point of view, adaptive diversification, that is, diversification as a response to disruptive selection caused by frequency-dependent selection, is, after all, little more enigmatic than alternative explanations of diversification based on geographical isolation or neutral evolution. Thus, hopefully, this book will contribute to paving the way for a more parsimonious approach than currently often used when it comes to assessing the causes and mechanisms of diversification in natural systems.

One insight gained from modeling adaptive diversification is that convergence toward points in phenotype space at which selection turns disruptive does not require fine tuning of parameters. Instead, evolutionary branching is a structurally stable and robust dynamical process, and the conditions for its occurrence can be readily assessed using the theory of adaptive dynamics. Moreover, the basic insights about adaptive diversification obtained from studying adaptive dynamics and evolutionary branching can be corroborated using other methods, most notably stochastic, individual-based models and partial differential equation models, with which one can investigate the dynamics of pattern formation in polymorphic phenotype distributions. These frameworks confirm the basic results obtained from the theory of evolutionary branching and show that adaptive diversification into distinct phenotypic clusters is a generic outcome of frequency-dependent selection, and hence a theoretically plausible evolutionary process. It should be noted that this does not imply that this process should continually occur and that we should see it in operation at all times in a given lineage. On the one hand, diversification in the form of lineage splitting is but one possible evolutionary consequence of frequency-dependent selection, which can also cause other forms of increased phenotypic variation, such as sexual dimorphism or phenotypic plasticity (Rueffler et al., 2006b). On the other hand, once a lineage has diversified, the conditions for further evolutionary branching are often harder or impossible to satisfy, leading to a saturation of diversity much like that envisaged in adaptive radiations (Schluter, 2000).

But here I concentrate on the primary process of adaptive diversification, and the goal of this book is to make the theory and principles of adaptive diversification accessible to a wide audience by providing an overview of different types of models from a diverse range of ecological settings (including cultural evolution, see Chapter 8). In populations in which sexual reproduction leads to a reshuffling of phenotypes, the emergence of distinct lineages through adaptive diversification requires assortative mating mechanisms, which I will discuss fairly extensively in Chapter 4. In the presence of prezygotic isolating mechanisms due to assortative mating, adaptive diversification leads to adaptive speciation (Dieckmann et al., 2004), that is, to reproductive isolation between the emerging lineages. However, I want to emphasize that the main purpose of this book is not to address the various genetic mechanisms of assortment enabling adaptive speciation once the ecological conditions for diversification are satisfied, but to show that there are many different ecological scenarios that are conducive to diversification in the first place. Perhaps heretically, I view the evolution of assortative mating mechanisms as a secondary problem for diversification. The primary problem is to identify the circumstances that lead to selection for diversification, that is, to disruptive selection due to frequency-dependent ecological interactions. Once there is selection for diversification, evolution will seek a solution to the problem of allowing diversification to happen, and in particular to the problem of allowing assortative mating mechanisms to induce speciation in sexual populations. Although relying on more elaborate assumptions, this perspective is similar to the one traditionally taken when modeling evolution as an optimization problem: there the task is to find the evolutionary optimum given a certain set of selective circumstances, and once an optimum is found under the constraints assumed, one simply implies that the genetic machinery allows the organisms to achieve that optimum. Admittedly, the process of splitting is genetically much more complicated than converging to an optimal trait value. Nevertheless, in the perspective taken here splitting is a solution to a problem posed by frequency-dependent interactions, and just as evolution is likely to find an optimal solution, evolution is also likely to find a splitting solution, at least some of the time. The basic ecological question is: What are the ecological environments in which adaptive diversification becomes a solution?

This book is aimed at theoreticians, as well as theoretically inclined empirical researchers, starting at the graduate student level. Technical prerequisites for making the most of this book are a good understanding of calculus and of some basic concepts from dynamical systems theory. The appendix introduces some of the basic concepts from adaptive dynamics theory and hopefully

provides a useful theoretical backdrop. Throughout the book, I have included a number of problems and exercises, which are set apart from the main text as Challenges. Many of these require a fair amount of work, and some of them, marked by a superscript *, are difficult and open ended, and may have the scope of a scientific publication. I hope that graduate students in particular will find these challenges useful, as only practice makes perfect.