

3 High-Dimensional Fitness Landscapes and Speciation

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The Modern Evolutionary Synthesis of the 1930s and 1940s remains the paradigm of evolutionary biology (Futuyma 1998; Gould 2002; Pigliucci 2007; Ridley 1993). The progress in understanding the process of evolution made during that period had been a direct result of the development of theoretical population genetics by Fisher, Wright, and Haldane, who built a series of mathematical models, approaches, and techniques showing how natural selection, mutation, drift, migration, and other evolutionary factors are expected to shape the genetic and phenotypic characteristics of biological populations. These theoretical advances provided “a great impetus to experimental work on the genetics of populations” (Sheppard 1954) and a “guiding light for rigorous quantitative experimentation and observation” (Dobzhansky 1955), and had many other far-reaching implications.

According to Provine (1978), the work of Fisher, Wright, and Haldane had significant influence on evolutionary thinking in at least four ways. First, their models showed that the processes of selection, mutation, drift, and migration were largely sufficient to account for microevolution. Second, they showed that some directions explored by biologists were not fruitful. Third, the models complemented and lent greater significance to particular results of field and laboratory research. Fourth, they stimulated and provided framework for later empirical research. Since the time of the Modern Synthesis, evolutionary biology has arguably remained one of the most mathematized branches of the life sciences, in which mathematical models and methods continuously guide empirical research, provide tools for testing hypotheses, explain complex interactions between multiple evolutionary factors, train biological intuition, identify crucial parameters and factors, evaluate relevant temporal and spatial scales, and point to the gaps in biological knowledge, as well as provide simple and intuitive tools and metaphors for thinking about complex phenomena.

In this chapter, I discuss two particular areas of theoretical evolutionary biology that have experienced significant progress since the late 1980s: a theory of fitness landscapes and a theory of speciation. I also outline two particular directions for theoretical studies on the origins of biodiversity which are especially important, in my opinion, for unification of different branches of the life sciences. One is the development of a theory of large-scale evolutionary diversification and adaptive radiation. The other is a quantitative theory of the origins of our own species.

Classical Fitness Landscapes

The theoretical notion of fitness landscapes (also known as “adaptive landscapes,” “adaptive topographies,” and “surfaces of selective value”), which emerged at the onset of the Modern Synthesis, has become a standard tool both for formal mathematical modeling and for the intuitive metaphorical visualizing of biological evolution, adaptation, and speciation. This notion was first introduced by Sewall Wright in a classic paper delivered at the 1932 International Congress of Genetics. Wright wanted to illustrate his ideas and mathematical results on the interaction of selection, random drift, mutation, and migration during adaptation in a nontechnical way accessible to biologists lacking quantitative skills (Wright 1932, 1988). Wright’s metaphor of fitness landscapes is widely viewed as one of his most important contributions to evolutionary biology (Coyne et al. 1997; Pigliucci and Kaplan 2006; Provine 1986). Over the ensuing 70 years, the notion of fitness landscapes has been substantially expanded and has found numerous applications well outside of evolutionary biology (e.g., in computer science, engineering, economics, and biochemistry).

A key idea of evolutionary biology is that individuals in a population differ in fitness (due to the differences in genes and/or environments experienced). Differences in fitness that have genetic bases are the most important ones because it is the changes in genes that make innovations and adaptation permanent. The relationship between genes and fitness (direct or mediated via phenotype) is obviously of fundamental importance. In the most common modern interpretation, a fitness landscape specifies a particular fitness component (e.g., viability, that is, the probability to survive to the age of reproduction) as a function defined on a particular set of genotypes or phenotypes.

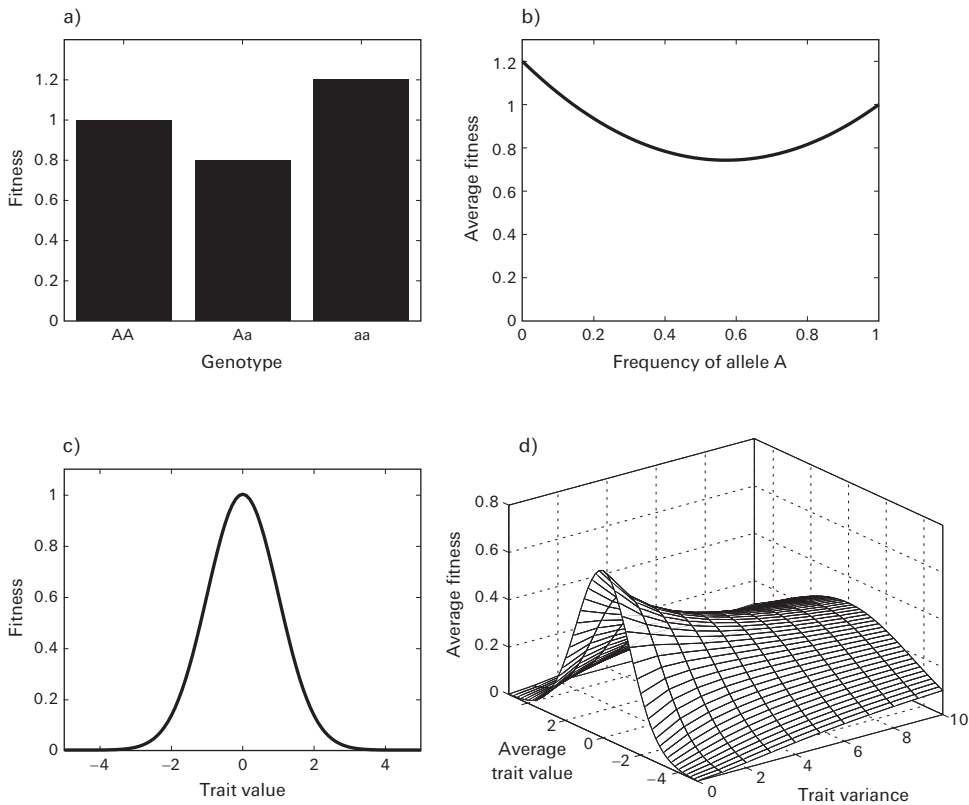


Figure 3.1

Examples of fitness landscapes. (a) Fitness landscape in a one-locus, two-allele model. (b) The average fitness landscape in a one-locus, two-allele model. (c) Fitness landscape for a quantitative trait model. (d) The average fitness landscape for a quantitative trait model.

For example, consider a very large, randomly mating diploid population under constant viability selection. Let us focus on a particular locus with two alleles, A and a , controlling fitness (viability). Then there are three different genotypes: two homozygotes, AA and aa , and a heterozygote, Aa . An example of a fitness landscape for this simple model is given in figure 3.1a. The fitness landscape illustrated in this figure corresponds to disruptive selection, that is, selection acting against intermediate genotypes (here, heterozygotes Aa). One may imagine an individual as a point on a fitness landscape and a population as a cloud of points which changes both its structure and its position as a result of action of different evolutionary factors (e.g, natural selection and sexual selection, mutation, recombination, drift, migration). The peaks and

valleys of the landscape represent high-fitness and low-fitness combinations of genes (or phenotypic values), respectively; natural selection is imagined as a force pushing the population uphill, and adaptive evolution is visualized as hill-climbing.

In his original 1932 paper, Wright introduced two versions of fitness landscapes. The first corresponds to a relationship between a set of genes and individual fitness as illustrated in figure 3.1a. The second describes a relationship between variables characterizing the population's genetic state (e.g., allele frequencies) and the average fitness of the population. The fitness landscape for the average fitness can be derived from a fitness landscape for individual fitness in a straightforward way. For example, figure 3.1b illustrates the fitness landscape for the average fitness corresponding to the fitness landscape for individual fitness shown in figure 3.1a. In fitness landscapes for the average fitness, it is the population (rather than an individual) that is imagined as a point climbing the slope toward a nearby peak. The attractive feature of this interpretation of fitness landscapes is the fact that in some simple models, the change in allele frequencies induced by selection is directly proportional to the gradient of the average fitness (Wright 1931). In this case one can intuit the general features of the evolutionary change just from the shape of the corresponding fitness landscape, without the need to solve the underlying dynamic equations.

The generalization of the notion of fitness landscapes for the case of continuously varying traits (such as size, weight, or a concentration of a particular gene product) was introduced by Simpson (1953). An example of a fitness landscape for a single quantitative character is shown in figure 3.1c. The fitness landscape illustrated in this figure describes stabilizing selection, that is, selection favoring an intermediate optimum (here, at trait value 0). Figure 3.1d illustrates the average fitness landscape corresponding to the individual fitness landscape shown in figure 3.1c. In figure 3.1d the independent variables are the average and variance of the trait values in the population which jointly control the average fitness. Lande (1976, 1980) showed that the change in the average trait value induced by selection is proportional to the gradient of the average fitness. The theoretical work of Lande (1976, 1980), Barton (e.g., 1989a; Barton and Rouhani 1987; Barton and Turelli 1987), and others in the 1970s and 1980s made such landscapes an indispensable part of the theoretical toolbox of evolutionary biology.

In the original formulation and in most of the latter work, the fitness component under consideration was viability and, as such, it was a prop-

erty of an individual. Later the notion of fitness landscapes was generalized to other fitness components, such as fertility (i.e., the number of offspring) or mating success (i.e., the probability of mating), which can be a property of a mating pair rather than of an individual (Gavrilets 2004). In most interpretations, fitness landscapes are static, that is, they do not change over time. However, models also exist in which landscapes change over time as a result of changes in the external environment. Frequency-dependent selection (e.g., Asmussen and Basnayake 1990; Cockerham et al. 1972; Dieckmann et al. 2004; Waxman and Gavrilets 2005), under which fitness continuously changes as the population evolves, can also be interpreted in terms of landscapes (or seasapes). Overall, fitness landscapes are an inherent and most crucial feature of all mathematical models dealing with natural or sexual selection. (Note that in many modeling papers, a technical term for specifying the relationship between genotype (or phenotype) and fitness is “fitness function” rather than “fitness landscape.”)

In general, biological organisms have thousands of genes and/or gene products that can potentially affect fitness. This means that fitness landscapes are inherently multidimensional, as was already well realized by Wright himself. Unfortunately, the relationships between genotype (or phenotype) and fitness for real biological organisms are still poorly understood. Therefore, the dominant strategy for using fitness landscapes in theoretical evolutionary biology has been to make simplifying assumptions about their structure in an attempt to get a tractable model which, it is hoped, will capture some essential properties of the process under consideration. But are there any generic features of multidimensional fitness landscapes? Although we still miss precise and broad empirical evidence, some general features of fitness landscapes can be identified from available data, biological intuition, and mathematical reasoning.

To Sewall Wright, who used three-dimensional geographic landscapes as a metaphor for multidimensional relationships between genotype and fitness, the most prominent feature was the existence of many peaks of different height separated by many valleys of different depth. Different peaks can be viewed as alternative solutions to the problem of survival, which all biological organisms face. In Darwin's words, “the multifarious means for gaining the same end” (see Beatty 2008). Wright reasoned that nonlinear interactions of the effects of different loci and alleles on fitness coming from pleiotropy and epistasis will make the existence of multiple fitness peaks unavoidable. This picture of fitness landscapes (illustrated

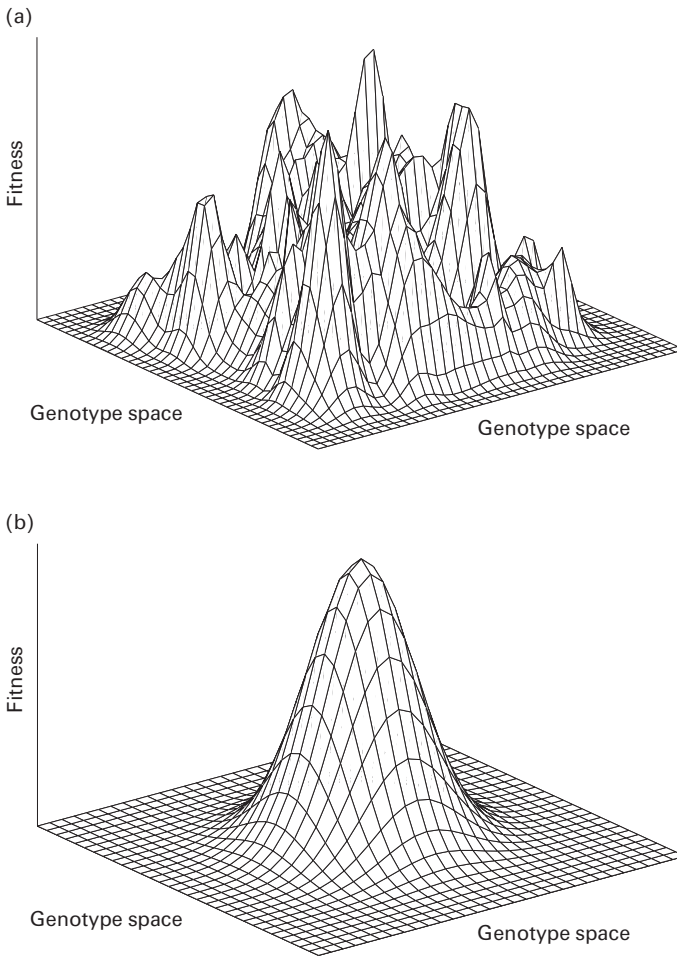


Figure 3.2 Two types of classical fitness landscapes. (a) A rugged landscape. (b) A single-peak landscape.

in figure 3.2a) is now known as that of rugged fitness landscapes (Kauffman 1993). Fitness peaks are important because of the expectation that natural selection will drive populations toward them. However, as soon as the population reaches a neighborhood of a local peak, any movement away from the peak will be prevented by selection.

It is important to realize that the peak reached by the population does not necessarily have the highest fitness. On the contrary, it is much more plausible that this peak has an intermediate height and that (much)

higher fitness peaks exist nearby (Kauffman 1993; Kauffman and Levin 1987). Without some additional forces, a population evolving on a rugged landscape will stop changing after a relatively short, transient time. Selection is a force pushing the population uphill and thus preventing it from going downhill. Therefore, within the framework of rugged fitness landscapes, the problem of crossing fitness valleys, which is necessary for moving toward other peaks (and that would result in increased adaptation and/or evolutionary divergence), becomes of major importance.

There are two possible solutions to this problem. First, additional factors opposing selection and overcoming it, at least occasionally, can drive the population across a fitness valley. The factor that has received most attention in this regard is random genetic drift, which is particularly important in small populations (Kimura 1983; Lynch 2007). Second, temporal changes in the fitness landscape itself can result in temporary disappearance of fitness valleys. Sewall Wright's own solution was his shifting balance theory (Wright 1931, 1982), which relies on complex interactions of multiple evolutionary factors (selection, mutation, migration, and random drift).

The shifting balance theory focuses on a population spatially subdivided into a large number of small subpopulations (demes) exchanging migrants. Because demes are small and there are many of them, it is likely that one of them will make a transition by genetic drift across the fitness valley to an alternative (perhaps higher) peak. Wright separated the process of peak shift (i.e., evolution from one peak to another) in a deme into two steps: stochastic transition by random genetic drift from a neighborhood of an old fitness peak into the domain of attraction of a new peak (Wright's phase I), and deterministic movement toward the new peak once the deme is within its domain of attraction (Wright's phase II). Wright reasoned that once a new adaptive combination of genes realizing the new higher peak is established in a deme, the deme will have a higher population density. Then, as a result of higher emigration from such demes, the higher fitness peak will take over the whole system (Wright's phase III). Wright's argument was mainly verbal. However, the conclusions of later formal analyses did not support Wright's intuition. Recent formal modeling has shown that although the mechanisms underlying Wright's theory can, in principle, work, the conditions are rather strict (Coyne et al. 1997, 2000; Gavrillets 1996). Therefore, the mechanisms implied in the shifting balance theory can hardly provide a general route for adaptation and diversification (for a

dissenting opinion see, e.g., Goodnight and Wade 2000; Wade and Goodnight 1998).

In contrast to Wright, another founder of theoretical population genetics, R.A. Fisher (see Provine 1986: 274–275; Ridley 1993: 206–207), believed that as the number of dimensions in a fitness landscape increases, local peaks in lower dimensions will tend to become saddle points in higher dimensions. In this case, according to Fisher's intuition, natural selection will be able to move the population to the global peak. A typical fitness landscape implied by Fisher's views has a single peak (see figure 3.2b). Fisher's scenario is based on a belief that (1) there is one perfect combination of genes (rather than a series of more or less similar alternative combinations), and that (2) this gene combination (fitness peak) can be "found" by selection without the need for any additional factors such as genetic drift. Fisher's beliefs were already reflected in his earlier work (Fisher 1930), in which he suggested a simple model (now known as "Fisher's geometric model") postulating the existence of a single global peak which can be reached by a sequence of advantageous mutations. More recent work has shown that Fisher's criticism of Wright's arguments is not warranted: the peaks that get transformed to saddle points by increasing the dimensionality of genotype space are well outnumbered by new local peaks brought about by the same process (Kauffman and Levin 1987). This means that a typical fitness landscape has an enormous number of local peaks, and finding the global peak by selection only is, in general, impossible. (I note that this is a well appreciated feature of numerical optimization techniques used across many areas of science and engineering.) In spite of this, Fisher's geometric model remains an important tool for studying adaptation in the neighborhood of a fitness peak (Orr 2002, 2006a, 2006b; Waxman 2006; Waxman and Welch 2005).

Classical Population Genetics and Speciation

Overall, the focus of earlier modeling work in evolutionary biology performed by Fisher, Wright, and Haldane was on adaptation and on showing how biological populations evolve, diversify, and adapt under the joint action of selection and other factors. Another question of paramount importance in the Modern Synthesis—the origin of species (Dobzhansky 1937; Mayr 1942)—had only a peripheral place in the earlier mathematical theory. Fisher, Wright, and Haldane published but a handful of modeling papers on some aspects of speciation (see Gavrilets

2004 for a discussion). This probably was one of the justifications for Mayr's attempt to diminish the role of mathematical modeling in the Modern Synthesis, which he undertook several decades later (Haldane 1964; Mayr 1959).

In spite of the limited amount of concrete models and results, the impact of earlier theoretical work and ideas on our understanding of speciation has been significant. In particular, Fisher's verbal theory of sexual selection (Fisher 1930) has provided a theoretical foundation for studies of the effects of sexual selection performed since the 1970s and 1980s (Andersson 1994). Fisher's discussion of the expected negative consequences of hybridization may have affected Dobzhansky's thinking, which later led to a hugely influential theory of reinforcement of premating reproductive isolation (Butlin 1987, 1995; Dobzhansky 1940; Howard 1993; Noor 1999; Servedio et al. 2003). Wright's shifting balance theory is popular among some evolutionary biologists, who invoke it to explain speciation in some genera (e.g., Levin 1993; Mallet and Joron 1999).

Since the early 1960s, modeling of speciation has become a flourishing part of theoretical evolutionary biology (Gavrilets 2003a, 2004). Interestingly, a significant part of this work was done by generations of theoreticians trying to prove wrong Mayr and Dobzhansky's intuition on the importance of sympatric speciation (more precisely, the lack of it). In particular, as Maynard Smith told me once, a significant part of his motivation for writing his classical 1966 paper on sympatric speciation was to annoy Mayr, whose 1963 book was very critical of this mode of speciation. Although sympatric speciation still remains a controversial topic (Coyne and Orr 2004; Dieckmann et al. 2004; Gavrilets 2004), most researchers tend to agree with Mayr's intuition, as conditions for sympatric speciation appear to be very restrictive (Bolnick and Fitzpatrick 2007; Coyne and Orr 2004; Gavrilets 2004, 2005; Waxman and Gavrilets 2005).

Ironically, in spite of his expressed disregard for theoretical work, Mayr himself was apparently strongly influenced by Wright's ideas on the importance of random drift for evolution in rugged fitness landscapes. In the theory of founder effect speciation, which he proposed in 1942 (and was elaborated later by Carson 1968; Carson and Templeton 1984; Kaneshiro 1980; Mayr 1954; Templeton 1980; see also Provine 1989 for a history of this theory), a few individuals found a new population which rapidly grows in size. A new adaptive combination of genes is formed by random genetic drift during a short time interval when the

size of the expanding population is still small. An inherent feature of the shifting balance that severely constrains this process is the necessity to spread the new adaptive combination of genes from a local deme to the rest of the population. During this stage (i.e., phase III) new combinations of genes have to compete with the old ones, which outnumber them. Founder effect speciation avoids this difficulty by simply removing the need for the new combination of genes to compete with the old one: a local subpopulation grows to become a new species without interacting with the ancestral one. For several decades, buoyed by Mayr's authority, founder effect speciation (in various forms) was the dominant explanation of at least island speciation (Provine 1989).

The proponents of these theories offered only verbal schemes without trying to formalize them. Formal analyses of founder effect speciation using analytical models and numerical simulation were undertaken only in the 1980s and later (Barton 1989b; Barton and Charlesworth 1984; Charlesworth and Rouhani 1988; Charlesworth and Smith 1982; Gavrilets 2004; Lande 1980; Rouhani and Barton 1987). Contrary to prevailing wisdom at that time, the general conclusion of these analyses was that a founder event cannot result in a sufficiently high degree of reproductive isolation with a high enough probability to be a reasonable explanation for speciation. Convincing empirical evolutionary biologists that Mayr's theory cannot work was a very important contribution of theoreticians to our understanding of speciation.

As the preceding discussion shows, a number of beliefs and ideas held by the architects of the Modern Synthesis were later proven wrong or of limited biological significance and importance. Mathematical modeling played an important role in this continuous process of refining, extending, generalizing, and pruning evolutionary thought.

Properties of Multidimensional Landscapes Not Captured by Classical Theories

Both Wright and Fisher, along with other researchers utilizing the notion of fitness landscapes in their work, well realized that the dimensionality of biologically relevant fitness landscapes is extremely high (in thousands and millions). Still, they believed that the properties of three-dimensional "geographic" landscapes well captured those of multidimensional landscapes. However, the theoretical work of the past two decades (discussed below) has led to understanding that these expectations were not quite justified.

The extremely large dimensionality of fitness landscapes implies that the number of possible genotypes is astronomically high. (For example, with 1,000 genes, each of which can have only two alleles, the number of possible sequences is $2^{1000} \approx 10^{300}$.) Therefore, one should not expect them all to have different fitnesses—there should be a lot of redundancy in the genotype-to-fitness relationship, so that different genotypes must have similar fitnesses. The question is how these genotypes with similar fitnesses are distributed in the genotype space and whether high fitness genotypes may form connected networks expanding through the genotype space. As far as I am aware, it was Maynard Smith (1962, 1970) who was the first to suggest such a possibility. He explained such networks by an analogy with a word game where the goal is to transform one word into another by changing one letter at a time, with the requirement that all intermediate words are meaningful (as in the sequence WORD-WORE-GORE-GONE-GENE). More recent work has shown that connected networks of genotypes with similar fitnesses represent a generic property of multidimensional landscapes.

To illustrate these ideas, let us consider a two-dimensional lattice of square sites in which sites are independently painted black or white with probabilities P and $1 - P$, respectively (see figure 3.3). We will interpret black sites as viable genotypes and white sites as inviable genotypes. For each site, let its one-step neighbors be the four adjacent sites (directly above, below, on the left, and on the right). Let us say that two black sites are connected if there exists a sequence of black sites starting at one of them and going to another, such that subsequent sites in the sequence are neighbors. For any black site, let us define a *connected component* as the set of all black sites connected to the site under consideration. A simple numerical experiment shows that the number and the structure of connected components depend on the probability P . For small values of P there are many connected components of small size (see figure 3.3a). As P increases, the size of the largest connected component increases (see figure 3.3b). As P exceeds a certain threshold P_c known as the *percolation threshold*, the largest connected component (known as the *giant component*) emerges, which extends (percolates) through the whole system and includes a significant proportion of all black sites (see figure 3.3c). In this model, describing a so-called site percolation on an infinite two-dimensional lattice, the percolation threshold is $P_c \approx 0.593$ (e.g., Grimmett 1989).

Consider next a different model. Assume that there is a very large number L of diallelic loci. Now each genotype has L one-step neighbors

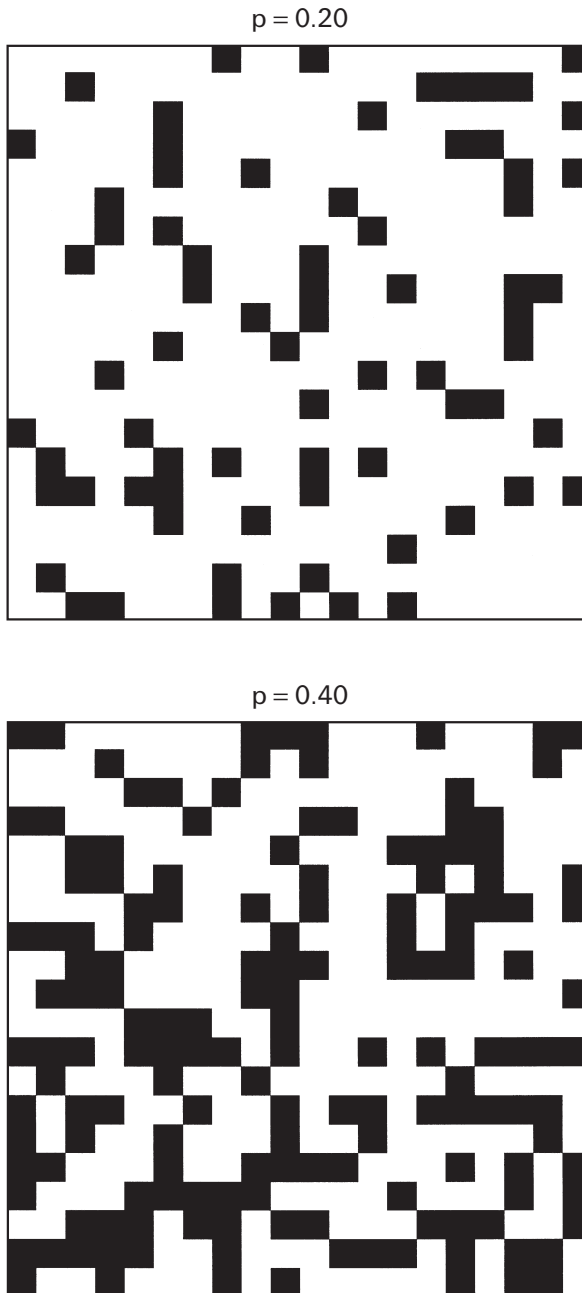


Figure 3.3
Percolation in two dimensions for three different values of P .

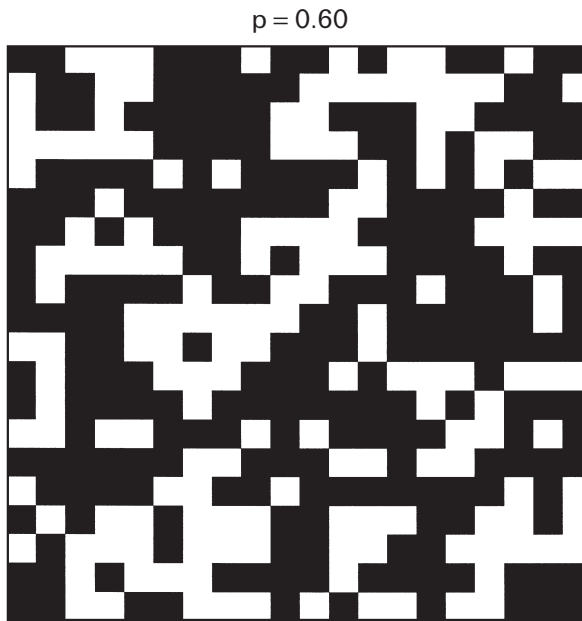


Figure 3.3
(Continued)

(single mutants). Let us assign fitnesses in exactly the same way as in the previous paragraph, that is, fitnesses are generated randomly and independently and are equal only to 1 (viable genotype) or 0 (inviable genotype), with probabilities P and $1 - P$, respectively. Similarly to the previous model (figure 3.3), viable genotypes will tend to form neutral networks. In this model, for small values of P , there are two qualitatively different regimes: subcritical, in which all connected components are relatively small (which takes place when $P < P_c$, where P_c is the percolation threshold), and supercritical, in which the majority of viable genotypes are connected in a single giant component, which takes place when $P > P_c$ (Gavrilets and Gravner 1997). A very important, though counterintuitive, feature of this model is that the percolation threshold is approximately the reciprocal of the dimensionality of the genotype space: $P_c \approx 1/L$, and thus P_c is very small if L is large (see Gavrilets 2004; Gavrilets and Gravner 1997). Therefore, increasing the dimensionality of the genotype space L , while keeping the probability of being viable P -constant, makes the formation of the giant component unavoidable.

The assumption that fitness can take only two values, 0 and 1, might be viewed as a serious limitation. To show that this is not so, let us consider the same genotype space as in the previous section (i.e., the set of L diallelic loci), but now assume that fitness, w , is a realization of a random variable having a uniform distribution between 0 and 1 (Gavrilets and Gravner 1997). Let us introduce threshold values w_1 and w_2 , which differ by a small value, ϵ . Let us say that a genotype belongs to the (w_1, w_2) -fitness band if its fitness w satisfies the conditions $w_1 < w \leq w_2$. Parameter ϵ can be viewed as the probability that a randomly chosen genotype belongs to the (w_1, w_2) -fitness band. One should be able to see that being a member of the (w_1, w_2) -fitness band is analogous to being viable in the previous model, with parameter ϵ playing the role of P in the previous model. Therefore, if the dimensionality of genotype space L is very large and $\epsilon > 1/L$, there exists a giant component (i.e., a percolating nearly neutral network) of genotypes in the (w_1, w_2) -fitness band. Its members can be connected by a chain of single-gene substitutions resulting in genotypes that also belong to the network. If ϵ is small, the fitnesses of the genotypes in the (w_1, w_2) -fitness band will be very similar. Thus, with large L , extensive evolutionary changes can occur in a nearly neutral fashion via single substitutions along the corresponding nearly neutral network of genotypes belonging to a percolating cluster. Note that if one chooses $w_2 = 1$ and $w_1 = 1 - \epsilon$, it follows that fitness landscapes have very high ridges (with genotype fitnesses between $1 - \epsilon$ and 1) that continuously extend throughout the genotype space. In a similar way, if one chooses $w_2 = \epsilon$ and $w_1 = 0$, it follows that the landscapes have very deep gorges (with genotype fitnesses between 0 and ϵ) that also continuously extend throughout the genotype space. I stress that the above conclusions apply not only for the uniform distribution of fitness values but also for any random distribution of fitnesses, provided the overall frequency of genotypes that belong to a (w_1, w_2) -fitness band is larger than $1/L$.

The above discussion illustrates two general points about scientific metaphors which one should keep in mind. The first is that specific metaphors (as well as mathematical models) are good for specific purposes only. The second is that accepting a specific metaphor necessarily influences and defines the questions that are considered to be important. The metaphor of “rugged adaptive landscapes” is very useful for thinking about local adaptation. However, its utility for understanding large-scale genetic and phenotypic diversification and speciation is questionable. The metaphor of rugged adaptive landscapes, with its emphasis on adap-

tive peaks and valleys, is to a large degree a reflection of the three-dimensional world we live in. However, genotypes and phenotypes of biological organisms differ in numerous characteristics, and thus the dimensionality of biologically realistic fitness landscapes is much larger than 3. Properties of multidimensional fitness landscapes are very different from those of low dimension. Consequently, it may be misleading to use three-dimensional analogies implicit in the metaphor of rugged adaptive landscapes in a multidimensional context. In particular, the problem of crossing fitness valleys may be nonexistent.

The networks of genotypes with similar fitnesses expanding throughout the genotype space can be graphically illustrated using a metaphor of holey fitness landscapes (Gavrilets 1997a, 2004; Gavrilets and Gravner 1997). A holey fitness landscape is a fitness landscape where relatively infrequent well-fit (or, as Wright put it, “harmonious”) genotypes form a contiguous set that expands (“percolates”) throughout the genotype space. An appropriate three-dimensional image of such a fitness landscape is an approximately flat surface with many holes representing genotypes that do not belong to the percolating network (see figure 3.4). Within the metaphor of holey landscapes, local adaptation and microevolution can be viewed as climbing from a hole toward a nearly neutral network of genotypes with fitnesses at a level determined by mutation-

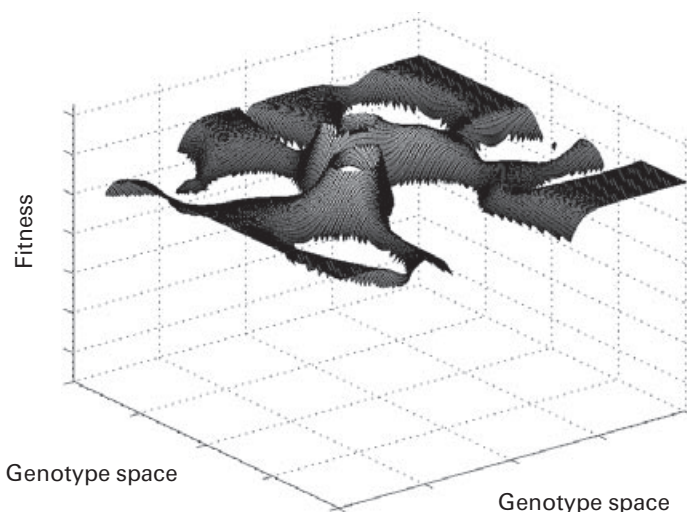


Figure 3.4
A holey fitness landscape.

selection-random drift balance. The process of climbing occurs on a shorter time scale than that necessary for speciation, clade diversification, and macroevolution. Once a corresponding fitness level is reached, the population will be prevented by selection from slipping off of this level to lower fitnesses, and by mutation, recombination, and gene flow from climbing to higher fitnesses. Speciation occurs when a population evolves to a genetic state separated from its initial state by a hole.

The earlier work on neutral and nearly neutral networks in multi-dimensional fitness landscapes concentrated exclusively on genotype spaces in which each individual is characterized by a discrete set of genes. However, many features of biological organisms that are actually observable and/or measurable are described by continuously varying variables such as size, weight, color, or concentration. A question of particular biological interest is whether (nearly) neutral networks are as prominent in a continuous phenotype space as they are in the discrete genotype space. Recent results provide an affirmative answer to this question. Specifically, Gravner et al. (2007) have shown that in a simple model of random fitness assignment, viable phenotypes are likely to form a large connected cluster even if their overall frequency is very low, provided the dimensionality of the phenotype space L (i.e., the number of phenotypic characters) is sufficiently large. In fact, the percolation threshold P_c for the probability of being viable scales with L as $1/2^L$ and thus decreases much faster than $1/L$, which is characteristic of the analogous discrete genotype space model.

Earlier work on nearly neutral networks was also limited to consideration of the direct relationship between genotype and fitness. Any phenotypic properties that usually mediate this relationship in real biological organisms were neglected. Gravner et al. (2007) studied a novel model in which phenotype is introduced explicitly. In their model, the relationships both between genotype and phenotype, and between phenotype and fitness, are of the many-to-one type, so that neutrality is present at both the phenotype and the fitness levels. Moreover, their model results in a correlated fitness landscape in which similar genotypes are more likely to have similar fitnesses. Gravner et al. (2007) showed that phenotypic neutrality and correlation between fitnesses can reduce the percolation threshold, making the formation of percolating networks easier.

Overall, the results of Gravner et al. reinforce the previous conclusion (Gavrilets 1997b, 2004; Gavrilets and Gravner 1997; Reidys et al. 1997; Reidys and Stadler 2001, 2002) that percolating networks of genotypes

with approximately similar fitnesses (holey landscapes) is a general feature of multidimensional fitness landscapes (both uncorrelated and correlated, and in both genotype and phenotype spaces). To date, most empirical information on fitness landscapes in biological applications has come from studies of RNA (e.g., Fontana and Schuster 1998; Huynen et al. 1996; Schuster 1995), proteins (e.g., Lipman and Wilbur 1991; Martinez et al. 1996; Rost 1997), viruses (e.g., Burch and Chao 1999, 2004), bacteria (e.g., Elena and Lenski 2003; Woods et al. 2006), and artificial life (e.g., Lenski et al. 1999; Wilke et al. 2001). Although limited, these data provide support for the biological relevance of holey fitness landscapes.

The realization that biologically realistic fitness landscapes have properties fundamentally different from those implied during the Modern Synthesis represents a significant theoretical advance that took place relatively recently. The biological implications of this result concern a number of areas (Gavrilets 2004), including the dynamics of adaptation, maintenance of genetic variation, the role of genetic drift, genetic robustness, evolvability, the importance of chance and contingency in evolution, and speciation.

Modern Speciation Theory

As I have already mentioned, systematic attempts to lay foundations of a quantitative theory of speciation did not start until the 1960s and 1970s. The pioneering work of Balkau and Feldman (1973), Bazykin (1969), Crosby (1970), Dickinson and Antonovics (1973), and Maynard Smith (1966) laid foundations for future modeling efforts. Recent years have seen significant advances in speciation research (e.g., Coyne and Orr 2004; Dieckmann et al. 2004; Gavrilets 2003a, 2004; Howard and Berlocher 1998), and by now we have solid understanding of the factors promoting and restricting speciation, shaping its dynamics, as well as its characteristic time scales and patterns. As our understanding of the processes leading to the origin of new species increases, we appreciate more and more the importance of the insight of the founders of the Modern Synthesis that “speciation can occur in different ways” (Dobzhansky et al. 1977), and that “there are multiple answers to every aspect of speciation” (Mayr 1982).

Given a variety of speciation mechanisms, the question of their classification is of importance. Theoretical population genetics has identified a number of factors controlling evolutionary dynamics, such as mutation,

random genetic drift, recombination, and natural and sexual selection. A straightforward approach for classifying different mechanisms and modes of speciation is according to the type and strength of the factors controlling or driving genetic divergence. In principle, any of the factors listed above can be used at any level of classification. However, traditionally the discussions of speciation in evolutionary biology are framed in terms of a classification in which the primary division is according to the level of migration between the diverging (sub)populations (Mayr 1942). In this classification the three basic (geographic) modes of speciation are allopatric, parapatric, and sympatric. The traditional stress on the spatial structure of (sub)populations as the primary factor of classification (rather than, say, on selection) reflects both the fact that it is most easily observed (relative to the difficulties in inferring the type and/or strength of selection acting in natural populations) and the growing realization that the spatial structure of populations is very important. Alternatively, it has been suggested to use a classification based on types of selection (Via 2001) or on a continuum of “geography/prezygotic isolating mechanisms” (Kirkpatrick and Ravigné 2002).

Sometimes very different biological mechanisms can be described by very similar mathematical models. Therefore, classifying mechanisms of speciation on the basis of similarity of the corresponding models may be of some use. Three general, partially overlapping sets of models can be identified. In the first set, which I will call “spontaneous clusterization” models, an initially random mating population accumulates a substantial amount of genetic variation by mutation, recombination, and random drift, and then splits into two or more partially or completely reproductively isolated clusters. Spontaneous clusterization models include those describing the accumulation of Dobzhansky-Muller genetic incompatibilities, speciation by hybridization, divergence in mating preferences, or allochronic speciation via divergence in the timing of mating (reviewed by Coyne and Orr 2004; Gavrilets 2004). Spontaneous clusterization can happen in any geographic context (i.e., allopatric, parapatric, or sympatric). This type of speciation can be imagined as population fragmentation on ridges in a holey fitness landscape with different clusters becoming reproductively isolated because they happen to be on opposite sides of a hole in the landscape. The fitness differences between genotypes which may be present are not of particular importance. This set of models is most advanced analytically.

In the second set of models, which can be called “adaptation with reproductive isolation as a by-product” models, the population is pulled

genetically apart by some kind of selection (natural or sexual) for adaptation to a local abiotic or biotic environment. Reproductive isolation between diverging parts of the population emerges as a by-product of genetic or phenotypic divergence. This type of speciation can happen in any geographic context (i.e., allopatric, parapatric, or sympatric), but migration (gene flow) between the subpopulations actively opposes their genetic divergence and the evolution of reproductive isolation. Speciation again can be imagined as population fragmentation on ridges in a holey fitness landscape, but now fitness differences between genotypes along the ridge and at local fitness peaks are important. By now there is a variety of analytical models for this type of speciation.

The third set of models is similar to the second, but now there is an explicitly considered trait (or traits) that can evolve to directly decrease the probability of mating (and the level of gene flow) between diverging subpopulations. These are “reinforcement-type models” related to the classical idea of reinforcement (Dobzhansky 1940; Fisher 1930). These also are the most complex models, which are difficult to study analytically, and so far their analyses have been limited to numerical simulations. Imagining this kind of speciation in terms of fitness landscapes is very difficult (and not particularly useful), as there are several fitness components which are relevant simultaneously.

The most controversial scenario of speciation has traditionally been sympatric speciation. These controversies have attracted the attention of many theoreticians, and by now the great majority of theoretical work on speciation concerns speciation in the presence of gene flow between diverging populations driven by ecological selection (Gavrilets 2004; Kirkpatrick and Ravigné 2002). Most of this work is represented by numerical studies, but there now exist a number of simple analytical models of sympatric speciation (Gavrilets 2003b, 2004, 2006; Gavrilets and Waxman 2002). The theory of sympatric speciation is arguably the most developed part of theoretical speciation research. The general conditions for sympatric speciation as identified by recent theoretical research are (1) strong combined effects of disruptive selection and nonrandom mating, (2) strong association of the genes controlling traits subject to selection and those underlying nonrandom mating, (3) high levels of genetic variation, and (4) the absence of costs on being choosy in mate choice (Gavrilets 2004). Two most straightforward ways for sympatric speciation are provided by a “magic trait” mechanism and a habitat selection mechanism. The former describes situations in which there is a trait that is both subject to disruptive/divergent

selection and simultaneously controls nonrandom mating (such as size in stickleback fish or color in *Heliconius* butterflies). The latter corresponds to situations in which organisms evolve stronger and stronger preferences for specific habitats where they form mating pairs and/or mate.

Mathematical models clearly show that, under certain biologically reasonable conditions, sympatric speciation is possible (Gavrilets 2004). However, in spite of the enormous interest in sympatric speciation and strong motivation to find examples, there are only a few cases (reviewed in Coyne and Orr 2004) where sympatric speciation is strongly implicated. One explanation for this discrepancy is that sympatric speciation is difficult to prove or it is difficult to rule out alternative scenarios. Another possibility is that conditions for sympatric speciation as identified by mathematical models are rarely satisfied in natural populations. Incorporating theoretical insights into empirical work and applying mathematical models to particular case studies (e.g., Gavrilets and Vose 2007; Gavrilets, Vose, et al. 2007) are crucial steps toward assessing the importance of sympatric speciation in nature.

Not surprisingly, there have been a number of theoretical developments that were not appreciated, predicted, or emphasized during the time of the Modern Synthesis. For example, from the theoretical point of view, the power of the phenomenon of spontaneous clusterization became apparent only recently. Although the recent theory of the reinforcement-type speciation provides some support for the verbal arguments made during the Modern Synthesis, it also identifies a number of limitations and weaknesses in these arguments (Servedio and Noor 2003). Mayr was very skeptical of the generality of ecological speciation and sympatric speciation, but recent work has shown that under certain conditions, both can be important. The potential role of sexual selection in speciation (Andersson 1994) is stressed by many modern theoretical studies, whereas it was almost completely neglected in the early discussions. Many models show that speciation can happen very rapidly after a long period of relative stability (stasis), while the earlier work emphasized continuity and small changes in evolution and speciation. The importance of conflicts (e.g., genomic or sexual) or coevolutionary interactions was not realized, while now models show that these factors can be a very powerful engine of speciation (Gavrilets and Waxman 2002). Overall, a diversity of new mechanisms for generating biodiversity are known now, but were unknown or underappreciated at the onset of the Modern Synthesis.

Two Focal Areas for Future Research on the Origins of Biodiversity

There are many exciting directions for empirical and theoretical research on the origins of biodiversity. Here I want to touch on two of them which are particularly important, in my opinion, for unification of different branches of life sciences. One is the development of a theory of large-scale evolutionary diversification. Ideally such a theory would link microevolutionary processes (e.g., selection, mutation, random drift, adaptation, coevolution, competition, etc.), studied by evolutionary biologists and ecologists, with macroevolutionary patterns (e.g., stasis, punctuation, dynamics of diversity and disparity, species selection), studied by paleontologists (Eldredge et al. 2005). The initial step in building such a theory would be a development of a theoretical framework for modeling adaptive radiation. The second question concerns the origins of our own species. Arguably, no area of evolutionary biology is more compelling to general audiences than those related to human origins; the topic underpins discussions of our place in the universe, of morality and cognition, and of our fate as a species. It is now recognized that many features of modern human behavior, psychology, and culture may be explainable to a certain extent in terms of selective factors that operated during the Pleistocene. Developing a modeling formalism for describing the action and effects of genetic, ecological, environmental, social, and cultural factors operating during the process of human origin would be a major breakthrough in (theoretical) evolutionary biology.

A Theory of Adaptive Radiation

Adaptive radiation is defined as the evolution of ecological and phenotypic diversity within a rapidly multiplying lineage (Schluter 2000; Simpson 1953). Classical examples include the diversification of Darwin's finches on the Galápagos islands, *Anolis* lizards on Caribbean islands, Hawaiian silverswords, and cichlids of the East African Great Lakes, among many others (Gillespie 2004; Givnish and Sytsma 1997; Losos 1998; Salzburger and Meyer 2004; Schluter 2000; Seehausen 2007; Simpson 1953). Adaptive radiation typically follows the colonization of a new environment or the establishment of a "key innovation" (e.g., nectar spurs in columbines, Hodges 1997) which opens new ecological niches and/or new paths for evolution.

Adaptive radiation is both a spectacular and a remarkably complex process, which is affected by many different factors (genetical, ecological, developmental, environmental, etc.) interweaving in non-linear ways.

Different, sometimes contradictory, scenarios explaining adaptive radiation have been offered (Mayr 1963; Schluter 2000; Simpson 1953). Some authors emphasize random genetic drift in small founder populations (Mayr 1963), while others focus on strong directional selection in small founder populations (Eldredge 2003; Eldredge et al. 2005), strong diversifying selection (Schluter 2000), or relaxed selection (Mayr 1963). Which of these scenarios is more general is controversial. The large time scale involved and the lack of precise data on its initial and intermediate stages make identifying general patterns of adaptive radiation very difficult (Gillespie 2004; Losos 1998; Salzburger and Meyer 2004; Schluter 2000; Seehausen 2007; Simpson 1953). Further, it is generally unknown if the patterns identified in specific case studies apply to other systems.

The difficulties in empirical studies of general patterns of adaptive radiation, its time scales, driving forces, and consequences for the formation of biodiversity make theoretical approaches important. However, the phenomenon of adaptive radiation remains largely unexplored from a theoretical modeling perspective. Adaptive radiation can be viewed as an extension of the process of speciation (driven by ecological factors and subject to certain initial conditions) to larger temporal and spatial scales. As I already stated, a recent explosion in empirical speciation work (reviewed by Coyne and Orr 2004) was accompanied by the emergence of a quantitative theory of speciation (Gavrilets 2004). In contrast, there have been only few attempts to build genetically based models of large-scale evolutionary diversification.

Some recent work in my lab has begun to lay the foundations of a quantitative theory of adaptive radiation. Some of them are based on a model of adaptive radiation which is intended to be more abstract and general (Gavrilets and Vose 2005, 2009). Other attempts use models tailored for particular case studies such as cichlids in a crater lake (Barluenga et al. 2006; Gavrilets, Vose, et al. 2007), palms on an oceanic island (Gavrilets and Vose 2007; Savolainen et al. 2006), snails on seashores (Hollander et al. 2005, 2006; Sadedin et al. 2008), and butterflies in jungles (Duenez-Guzman et al. 2009; Mavárez et al. 2006). The general setup in all these models is similar. We typically start with a few individuals of a sexual diploid species colonizing a new environment (e.g., an island or a lake) in which a number of spatially structured empty ecological niches are available. Although the founders have low fitness, the abundant resources and the lack of competitors allow them to seed a population that is able to survive throughout the environment at low densities. The founders have no particular preference for the ecological

niches available in the new environment. However, as selection acts on the new genetic variation supplied by mutation, different lineages can become adapted to and simultaneously develop genetic preferences for different ecological niches. The process of ecological and phenotypic diversification and speciation driven by selection for local adaptation is accompanied by the growth in the densities of emerging species. Eventually species utilizing different ecological niches evolve differences in mating preferences by a process analogous to reinforcement. In some models, rather than starting the simulations with a population of low-fitness individuals, we assumed that the initial population is represented by specialists perfectly adapted for one of the available niches. Our main interest is to develop a better understanding of the dynamics of invasion of empty ecological niches and subsequent diversification.

Although these efforts are still at very initial stages, some patterns do emerge across different models. The following summarizes these patterns:

- Traits controlling adaptation to ecological niches evolve faster, approach their optimum values closer, and maintain less genetic variation at (stochastic) equilibrium than traits controlling habitat preferences;
- Mating preference traits evolve at a slower pace than the ecological and habitat preference traits, maintain more genetic variation, and can fluctuate dramatically in time;
- Mating preferences can diverge both between and within species utilizing different ecological niches;
- Area effect: empty ecological niches get filled only on islands and in lakes of sufficiently large size;
- Effect of the number of loci: rapid and extensive diversification is most likely if the number of loci controlling ecological traits and habitat and mating preference traits is small;
- Timing of speciation: typically, there is a burst of speciation soon after colonization rather than a more or less continuous process of speciation;
- Overshooting effect: the diversity (i.e., the number of species) peaks early in the radiation;
- Hybridization and neutral gene flow: species can stably maintain their divergence in a large number of selected loci for very long periods of time in spite of substantial hybridization and gene flow that removes differentiation in neutral markers;

- Least action effect: speciation occurring after the initial burst usually involves a minimum phenotypic change;
- Differentiation in mating characters is often of a continuous nature without clearly defined, discrete morphs;
- Parallel diversification when new mating characters get shared across different ecological niches and/or when new ecological characters get shared across different “sexual morphs” is expected;
- While the characters controlling local adaptation and habitat preferences remain close to the optimum values, mating characters can change continuously in a neutral fashion;
- Given everything else the same, the typical stages of adaptive radiation are (1) divergence with respect to macrohabitat, (2) evolution of microhabitat choice and divergence with respect to microhabitat, (3) divergence with respect to “magic traits” (i.e., traits that simultaneously control the degree of local adaptation and nonrandom mating), and (4) divergence with respect to other traits controlling survival and reproduction.

Although some of these predictions are supported by empirical data (Gavrilets and Losos 2009), much more work (both theoretical and empirical) is necessary to really evaluate their biological and evolutionary significance. In evolutionary biology, comprehensive studies of a few model organisms have been very successful in identifying and understanding general evolutionary mechanisms and principles. In a similar way, comprehensive numerical studies of a few models of adaptive radiation will greatly benefit our understanding of large-scale diversification.

The Ultimate Speciation Event: The Origin of Our Own Species

Decades of intensive work by generations of evolutionary biologists have led to a dramatic increase in our understanding of how new species arise (Coyne and Orr 2004; Dieckmann et al. 2004; Gavrilets 2004; Howard and Berlocher 1998)—the central theme of Darwin’s revolutionary book (Darwin 1859). I believe that the time is ripe for attacking the ultimate speciation event—the origin of our own species (Darwin 1871). Any general theory of the origin of humans will include a significant quantitative/mathematical component that will have to deal with a complex combination of ecological, genetic, cultural, and social factors, processes, and changes. Here, I want to illustrate one possible theoretical approach for

modeling factors that likely were important during the earlier evolution of humans.

There are many features that make humans a “uniquely unique species,” but the most crucial of them are related to the size and complexity of our brain (Geary 2004; Roth and Dicke 2005; Striedter 2005). Brain size in *Homo sapiens* increased in a runaway fashion over a period of a few hundred thousand years, but then stabilized or even slightly declined in the last 35,000–50,000 years (Geary 2004; Ruff et al. 1997; Striedter 2005). In humans, the brain is very expensive metabolically: it represents about 2% of the body’s weight but utilizes about 20% of total body metabolism at rest (Holloway 1996). The burning question is what factors drove the evolution of human brain size and intelligence? A number of potential answers focusing on the effects of climatic (Vrba 1995), ecological factors (Russon and Begun 2004), and social factors have been hotly debated. One widely discussed set of ideas (Alexander 1990; Byrne and Whiten 1988; Dunbar 1998, 2003; Flinn et al. 2005; Geary 2004; Humphrey 1976; Roth and Dicke 2005; Striedter 2004; Whiten and Byrne 1997), coming under the rubric of the “social brain” hypothesis (sometimes also called the “Machiavellian intelligence” hypothesis), considers selective forces coming from social competitive interactions as the most important factor in the evolution of hominids, who at some point in the past became an ecologically dominant species (Alexander 1990; Flinn et al. 2005). These forces selected for more and more effective strategies of achieving social success (including deception, manipulation, alliance formation, exploitation of the expertise of others) and for the ability to learn and use them. In this scenario, the social success is translated into reproductive success (Betzig 1986, 1993; Zerjal et al. 2003) selecting for larger and more complex brains. Once a tool for inventing, learning, and using these strategies (i.e., a complex brain) was in place, it could be used for a variety of other purposes, including coping with environmental, ecological, technological, linguistic, and other challenges.

Modeling these processes requires one to build complex models that would include genes, memes (i.e., socially learned strategies), and competition for mating success. In an attempt to shed some light on the interaction of these processes, Gavrilets and Vose (2005) introduced an explicit genetic, individual-based, stochastic mathematical model of the coevolution of genes, memes, and mating behavior. In their model, genes control two properties of the brain: a learning ability characterizing the probability to learn a particular meme, and a cerebral capacity

characterizing the number of memes a brain can learn. Both of these characteristics were treated as additive quantitative traits subject to stabilizing selection in order to capture the energetic costs of having a large brain. In turn, memes were characterized by their complexity (i.e., difficulty) and their “Machiavellian fitness” quantifying the advantage to an individual who has this meme. Meme complexity and fitness were negatively correlated, so that more efficient memes were more difficult to learn. The model also assumed that the effects of memes known to both competing individuals cancel each other. This assumption results in a need to continuously invent or learn new memes to be able to stay in the competition for mating success.

Due to its complexity, the model had to be studied numerically. Overall, the results of Gavrilets and Vose suggest that the mechanisms underlying this hypothesis can indeed result in a significant increase in the brain size and in the evolution of significant cognitive abilities on the time scale of 10,000–20,000 generations. Interestingly, Gavrilets and Vose show that in their model the dynamics of intelligence has three distinct phases. During the dormant phase only newly invented memes are present in the population. These memes are not learned by other individuals. During the cognitive explosion phase the population’s meme count and the learning ability, cerebral capacity, and Machiavellian fitness of individuals rapidly increase in a runaway fashion. During the saturation phase natural selection resulting from the costs of having large brains checks further increases in cognitive abilities.

Both the learning ability and the cerebral capacity are selected against due to costs of having large brains, but having nonzero values of both traits is necessary for learning and using different memes. The process of transition from the dormant phase to the cognitive explosion phase is somewhat similar to that of a peak shift on a rugged landscape. As in the case of stochastic peak shifts on a rugged landscape, the transition from the dormant phase to the cognitive explosion phase is mostly limited by new genetic variation. The levels of cognitive abilities achieved during the cognitive explosion phase increase with the intensity of competition for mates among males and decrease with the number of loci controlling the brain size. The latter effect is explained by the fact that a larger number of loci implies weaker selection on each individual locus.

In the model, evolutionary processes occur at two different time scales: fast for memes and slow for genes. More complex memes provide more fitness benefits to individuals. However, during the cognitive explosion

phase the complexity of memes present in the population does not increase but, on the contrary, decreases in time. This happens as a result of intense competition among memes: while complex memes give advantage to individuals on a slow (biological) time scale, they lose competition to simpler memes on a fast (social) time scale because they are more difficult to learn. Intriguingly, the model suggests that there may be a tendency toward a reduction in cognitive abilities (driven by the costs of having a large brain) as the reproductive advantage of having a large brain decreases and the exposure to memes increases in modern societies.

Much more effort is needed for building a comprehensive theory of the coevolution of genes, memes, groups, behaviors, and social networks that would be applicable to earlier human evolution. These efforts should include both the development of simple models that can be studied analytically and the performing of large-scale individual-based simulation studies of more complex and realistic models.

Conclusion

The emergence of a quantitative/mathematical theory of biological evolution was crucial for the success of the Modern Synthesis. The steady progress of empirical evolutionary research observed since the 1930s and 1940s was accompanied by many theoretical developments, including the theory of multidimensional fitness landscapes and the emergence of a dynamical theory of speciation and diversification on which I have focused in this chapter. We now have a much better understanding of evolutionary processes. Not unexpectedly, many of the new theoretical results show that certain expectations and intuitions prevalent earlier are wrong or have a limited scope. This is part of the scientific process. The development of adequate mathematical theories will remain crucial in the future for better understanding of other evolutionary processes. The common wisdom is that a picture is worth a thousand words. In the exact sciences, an equation is worth a thousand pictures. Two areas of theoretical research are, in my opinion, particularly important and poised for significant advances, as I attempted to illustrate above. The first is a theory of evolutionary diversification across multiple spatial and temporal scales that would link microevolutionary processes with macroevolutionary patterns. The second is a theory of human origins and factors shaping our behavior, social interactions, and history. In 2009 we celebrate the 150th anniversary of the publication of *The Origin*

of *Species*. In 2021 we will celebrate the 150th anniversary of Darwin's other groundbreaking book, *The Descent of Man*. Significant theoretical progress can be achieved in the twelve years separating those two years.

Some Thoughts on an Extended Evolutionary Synthesis

The synthesis of several biological disciplines that occurred in the 1930s and 1940s and became known as the Modern Synthesis marked the beginning of the still ongoing process of unification of biological sciences. As our knowledge and understanding of particular areas of biology increases, the connections among them become clearer, resulting in a stronger and broader synthesis. Many developments in biology that have occurred since the 1970s and 1980s were not (and could not be) anticipated by Darwin or during the time of the Modern Synthesis. Many patterns and processes that were unknown or not viewed as particularly important and/or relevant earlier have become crucial for our understanding of the evolution of life on Earth in general, and of the place of our own species in this process in particular. All this is a normal process in the development of any scientific discipline. Do new developments and knowledge really challenge the ideas central at the time of the Modern Synthesis and require a dramatic reevaluation of the basics? Definitely not. Declaring the Modern Synthesis or the Darwinian theory dead, wrong, or in crisis because some of the beliefs or views held previously are not supported by newer data or theories, or because there are still gaps in our knowledge, means being ignorant of how the science develops. Do new developments and new knowledge in different areas of biology justify the need for something that can be called an Extended Evolutionary Synthesis? I think the answer to this question is a very subjective matter.

To me, many recent advances of evolutionary biology that are sometimes presented as focal points of a future Extended Evolutionary Synthesis (e.g., Pigliucci 2007) fit well in the grand scheme of variation, selection, and inheritance within the populational context laid down during the Modern Synthesis. Moreover, from the theoretical point of view, the general rules and patterns of evolutionary dynamics will not be dramatically different if, say, the contribution of large mutations to variation were more significant, or if inheritance via epigenetic effects were more common, or if group selection and autocatalytic selection mediated via niche construction were more powerful or widespread than currently thought. I expect the underlying dynamic equations to be

similar to those describing more “mainstream” types of variation (via small mutation), selection (individual or pair selection), and inheritance (via “classical” genes). This implies that general evolutionary patterns as we already understand them will not be significantly altered. Finally, great advances having significant implications both for our understanding of evolution and for many practical questions concerning our lives have happened across many different areas of biology, so that singling out just a few for defining an extended synthesis does not seem justified. The unification of biological sciences will be achieved via continuous extension of evolutionary thinking into various branches of the life sciences and social sciences.

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