CHAPTER 1

Introduction

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1.1 A gradualist history

Our knowledge of evolutionary rates is as old as evolutionary theory itself. Gradualism—or slow and steady change—has been one of the most important defining characteristics of the theory of evolution since its inception (Darwin 1859). Along with variation and adaptation, gradual evolution quickly became integrated into evolutionary theory for a variety of reasons. First, we hardly observe discernible evolutionary changes during our own lifetimes and we do not expect to since the environment, while fluctuating wildly back and forth, does not appear to change in any net (i.e. predictable) direction in any significant way. Second, evolutionary change requires excess death (of less fit individuals) and/or excess fertility. While some species possess high fertility and hence can afford strong selection on short timescales, it is not true for all organisms, especially those with low reproductive rates, high parental investments, and/or small population sizes such as those found in many large mammals. Third, the immensity of the evolutionary timescale as perceived from the geological and fossil records seemed in favor of slow and constant evolutionary change. Finally, some argue that Darwin promoted the idea of gradual evolution in order to make the theory more palatable to a conservative Victorian society that believed in social stability and had little room for fluctuations of any kind—revolutionary, evolutionary, or otherwise.

Although this paradigm of slow and steady change became generally accepted, an active debate on rates prevailed after Darwin's Origins. Alfred Russell Wallace wrote:

Mr. Darwin was rather inclined to exaggerate the necessary slowness of the action of natural selection; but with the knowledge we now possess of the great amount and range of individual variation, there seems no difficulty in an amount of change, quite equivalent to that which usually distinguishes allied species, sometimes taking place in less than a century, should any rapid change of conditions necessitate an equally rapid adaptation (Wallace 1889, p. 125).

Even Thomas Huxley, a strong advocate of Darwin's new theory, warned Darwin about his insistence on gradual evolution when he wrote 'you have loaded yourself with an unnecessary difficulty in adopting natura non facit saltum so unreservedly' (quoted in Gould 2002, p. 151).

In the early years of the 20th century, gradualism found its way into the mechanistic underpinnings of evolutionary models, thus making the bold leap from phenotypes to their underlying genotypes. Ronald Fisher provided theoretical support for gradual evolution on the basis that micromutations would allow evolutionary changes to occur smoothly without destroying existing adaptations through major mutations (Fisher 1918). Much of this was a response to the saltationist mutational theories of Hugo DeVries and William Bateson at the beginning of the century and later espoused by Richard Goldschmidt (1940). Early population geneticists built on a paradigm of small gradual change and evolution by micromutations and this paradigm has become the cornerstone of population genetics theory (Fisher 1930; Wright 1931; Haldane 1932; Mayr and Provine 1980).

However, there remained an obvious gap between the continuous microevolutionary patterns found in population genetic models and the episodic macroevolutionary patterns observed in systematics and paleontology. The Modern Evolutionary Synthesis attempted to fill this void by integrating population genetic theory with systematics...
and paleontological views (Dobzhansky 1937/1951; Simpson 1944). Using gradualist mechanisms of microevolutionary change, it became possible to explain the discontinuities found in the fossil record. Thus, within this framework, gradualism conforms, on one hand, to the immensity of the geological timescale and, on the other hand, to the imperceptible changes in the environment requiring adaptive modifications. Under this model and in the short term, most changes in nature would be of a stabilizing nature and the changes in the environment, biotic or abiotic, would generally be of a very slow and gradual nature. Thus, evolutionary rates were seen in concordance with the geological timescale.

In addition, population genetic theory suggested that most lineages might not be able to sustain rapid evolution for long, continuous periods of time. Sooner or later, the lack of adequate genetic variation and/or the lack of opportunity would eventually slow the pace of change. Over longer periods of time, evolutionary rates would likely average out to increasingly slower rates. Therefore, it is expected that any rapid evolution will be of an intermittent nature—few and far between geologic time points, much like Gould’s punctuated equilibria (see Section 1.3)—and, therefore, in terms of overall long-term evolution, the law of diminishing average returns will prevail. Thus, gradual evolution would appear to be a geologic reality.

Gradualism found its greatest ally in the grand neutral theory of molecular evolution, formalized during the latter part of the last century. Motoo Kimura’s neutral theory (1968) posits the regularity of evolutionary change, observed previously in proteins by biochemists such as Emile Zuckerkandl and Linus Pauling (1962) and Emanuel Margoliash (1963), as the basic product of fixed substitutions on neutral mutations. Neutral theory made three important contributions. First, and most importantly, to this discussion, neutral theory suggested a clock-like mechanism of evolutionary change at the molecular level. Using this clock, neutral theory offers us the ability to infer historical patterns and estimate rates of molecular evolution on varying timescales across a range of genes and species. Second, it provided a null hypothesis to measure selection and adaptation at the gene level. Without the null model, it would be impossible to evaluate whether an allele is directly under selection, is being hitch-hiked, or has low functional constraints. Finally, neutral theory showed that, even in the face of adaptive evolution, much existing genetic variation can remain standing because of neutral fitness effects, and such mutations can drift to fixation over time. Together, these three contributions made us realize, for the first time, that while populations may be under selective pressures (stabilizing or directional) on a regular basis, this does not necessarily mean that surviving organisms are genetically optimized. It also reinforced the idea that rates of change—whether slow, moderate, or fast—are a constant force of nature and provide a seemingly linear rate of evolution over long periods of time.

1.2 Mechanisms of rapid and episodic change

Yet, this tradition of evolutionary regularity does not mean that all evolutionary biologists have always accepted gradual evolution as dogma. In fact, far from it. Debates of one kind or another and arguments have been made in support of rapid, and often episodic, modes of evolutionary change. These arguments have been largely based on non-equilibrium situations such as changes in the neutral landscape, sudden demographic shifts in populations, and adaptive radiations. In the following sections, we highlight representative mechanisms in which non-granual, and in particular, rapid evolution, occurs from molecular to population level perspectives.

1.2.1 Unconstrained neutral space

Marathon runners dream of running free, unencumbered by other runners or by any other factors. At the start, their pace may be constrained due to an abundance of fellow runners, but soon the crowds thin out and they run in relative autonomy. Neutral mutations are like marathon runners—their evolution may also be constrained at the start line due to neighboring mutations that are armed with selective advantages or disadvantages. However, they may ultimately evolve at rates free of constraint and that are solely governed by neutral mutation
rates (Kimura 1968). Depending on the degree of functional constraints, different genes or genetic elements will also evolve at different rates. Third codon positions, intergenic regions, gene duplications, multigene families, satellite DNA, and pseudogenes are examples of genetic elements that evolve at faster rates due to lower selective constraints (Kreitman 1983; Lynch 2007).

Yet a model of strict neutrality does not fit most genetic data. For example, Gillespie (1984) observed that molecular evolution generally did not follow a Poisson model of constant rate change. He used the term ‘episodic clock’ to directly contrast its behavior to the regularity of the molecular clock, as originally proposed by Kimura (1968). Context-dependent fitness effects offer a mechanism to explain how molecules, which are usually evolving neutrally, can possess different evolutionary rates over time. In particular, landscape models that were originally developed by Sewall Wright have recently begun to be used to incorporate the role of epistasis in the evolution of proteins (e.g. Kulathinal et al. 2004; Weinreich et al. 2006), providing a mechanism to rapidly change the pace of evolution.

1.2.2 Horizontal gene transfer

In complex eukaryotes, mating and sexual reproduction between individuals of the same species is a common feature of reproduction. This mode of reproduction allows genetic exchange and recombination to take place but also at the same time provides a means to safeguard the genome integrities of populations and species from invasions by foreign genetic elements. However, such a mechanism is not present in prokaryotes. Instead, genetic exchange can occur among distantly related organisms through transformation, transduction, and conjugation. Indeed, genomic sequence analyses of bacteria and archaea over the last decade have shown that horizontal gene transfer is a major force in shaping prokaryotic genome size, and gene content, and plays an important role in the adaptation and long-term survival of these organisms. Horizontal gene transfer allows for the fast acquisition of novel genes; if these genes enhance the host cell’s survival and reproduction, they will be retained by the host genome. However, if the newly acquired genetic elements are not beneficial, they degenerate quickly and are often rapidly removed from the genomes (Hao and Golding 2006). Different from genetic exchanges in sexual eukaryotes, horizontal gene transfer is generally localized to a small genomic region, and does not involve whole genome shuffling typical of sexual recombination in eukaryotes.

1.2.3 Developmental macromutations

Developmental biology, more often than not, has been at odds with population genetics particularly during their early histories. The most famous example is that of Richard Goldschmidt who proposed the idea of rate genes, i.e. genes controlling molecular and physiological steps, which he envisioned could accelerate rates of evolution. In simple terms, rate genes were macromutations with the capacity to make major phenotypic changes (Goldschmidt 1940). As a first-rate experimental biologist who studied variation and evolution in moths, Goldschmidt accepted microevolution within species. However, he did not believe that microevolution gave rise, or was the natural precursor, to macroevolution, i.e. speciation. As a result, he supported the role of macromutations in speciation. It is important to note that the argument has never been whether macromutations can create rapid change but whether such mutations play a major role in long-term evolution (Singh 2003). The argument, however, has been more about the mode rather than the tempo of evolution. The occasional role of macromutations, especially in a new environment, has been an accepted component of modern population genetics theory (Wright 1982).

The field of evolutionary developmental biology (‘evo-devo’) has provided many examples of such large evolutionary jumps caused by mutations in developmental genes, gene clusters, and sometimes even whole genomes (e.g. genome duplication and polyploidization events). These events can place these individuals at a selective advantage resulting in saltational leaps in both genotype and phenotype.

1.2.4 Evolution by gene regulation

Changes in gene regulation—the variation in amount and time of gene expression, and in tis-
sue distribution—have always been seen as a source of rapid phenotypic change. A landmark study by Mary-Claire King and Allan Wilson (King and Wilson 1975) based on comparative molecular studies of genetic differences between humans and chimpanzees, highlighted the importance of gene regulation evolution in species differences. King and Wilson observed that the level of protein electrophoretic divergence between humans and chimps was no greater than that found between indistinguishable sibling species of *Drosophila*. However, based on their results, what they proposed was truly shocking at that time: that humans and chimpanzees diverged from a common ancestor 5–7 million years ago (mya), and not 30 mya, as was commonly believed at the time based on anthropological studies. How can humans and chimps be so different, yet share a very recent common ancestor? Thus, the great debate on evolution by gene regulation began.

Gene regulatory changes have the potential to make rapid phenotypic changes but only if the organism-environment circumstances allow for it to happen. For example, it is generally believed that the hominid lineage has evolved faster in cognitive, behavioral, and social characters but it is not evident if gene regulation has played a greater role. Considering that the supply of extant genetic variation is a universal feature of all sexually reproducing organisms, a relatively rapid rate of evolution can be sustained by changes in gene regulation as well (Hoekstra and Coyne 2007). Nevertheless, rapid gene-regulation-driven evolution, especially through cis-acting elements, has been taken as not just a possibility, but the norm, by some authors (e.g. Carroll 2005).

1.2.5 Coevolutionary forces

Aside from abiotic factors, biotic factors such as the activities of other species can exert significant influence on rates of evolution. The influence is stronger if the organisms are more closely linked to each other in their respective life cycles. This is precisely what occurs in coevolution involving interacting partners such as host–parasite, predator–prey, and pollinator–plants. In coupled systems such as these, rates of evolution can, in principle, be slower or faster. And if faster, these rates can accelerate extremely rapidly. For example, the generation and maintenance of disease resistance and immune-response genes in humans are direct reflections of the hosts' responses to the diversity of infectious agents. Similarly, interactions between predators and prey (e.g. Brodie et al. 2002) and between pollinators and flowering plants (Farrell 1998) have been hypothesized as the main mechanism responsible for the rapid evolution of genes and genetic systems in such biological communities.

1.2.6 Sexual selection and sexual arms races

Secondary sexual traits provide some of the most spectacular displays of diversity, especially in birds, insects, and mammals (Andersson 1994). Darwin proposed his sexual selection theory to explain the evolution of secondary sexual traits. These traits are more common in males and are often exaggerated in appearance and look maladaptive from a survival point of view. Darwin surmised that the evolution of these traits is driven by mate choice as females use these traits as a basis for choosing mates. As demonstrated by Fisher’s ‘runaway selection’ model of sexual selection (Fisher 1930), secondary sexual traits, including genes affecting secondary sexual traits in the male and choosiness in females, are expected to evolve at faster rates: the mutual reinforcement between increasing female choice and male traits can lead to a cycle of accelerated evolution of secondary sexual traits in males and rapid speciation (Fisher 1930; Lande 1981).

Other sexual selection mechanisms also incorporate rapid evolution into their models. Although female choice is primarily female-driven, we can imagine the two sexes interacting in many ways to increase their own fitness by what is now called a sexual arms race (Arnvist and Rowe 2005; Rice 1996). Sexual arms races can quickly lead to the rapid evolution of traits associated with sex and reproduction. Such arms races resemble predator–prey or host–parasite models except that in the case of the former, the effects of response and its counterresponse is felt by traits affecting sex and reproduction of interacting partners within the same species. Sexual selection has been a driving force in the
evolution of sex- and reproduction-related genes in general (Civetta and Singh 1998) and mating system and egg-sperm fertilization proteins in particular (Swanson and Vacquier 1998).

1.2.7 Population demography and genetic revolutions

Major demographic and geographical shifts in populations can also lead to very rapid, and episodic, evolutionary change. Peripatric speciation (Mayr 1954) is a popular extension of the allopatric model of speciation, involving smaller subpopulations located at the periphery of its species' distribution. The combination of small population size and more extreme environmental variation makes rapid genetic changes more likely in what Mayr called speciation by genetic revolution (Mayr 1963). A variation on the same theme was proposed by Hampton Carson when studying Hawaiian Drosophila (Carson 1971). For their size and age (molecular evidence demonstrates that the Hawaiian Drosophila lineage is quite old), Hawaiian Islands have a disproportionately high number of Drosophila species that are morphologically and behaviorally very diverse. Geologic evidence reveals that the Hawaiian Islands form a chain of islands of which the newest ones have arisen through the most recent volcanic eruptions, giving rise to opportunities for new species, while the oldest ones are re-submerged. The founder-effect speciation model was proposed to fit the observation of rapid and diversified speciation in Hawaiian Drosophila. Carson (1971) extended the founder-effect speciation model to involve populations going through repeated rounds of increase (flush) and decrease (crash) in size giving rise to rapid evolution. Carson envisioned these population cycles as a result of volcanic eruptions and decimation of populations followed again by exponential population growth between eruptions with dramatic effects on the constancy of evolutionary rates.

1.2.8 Adaptive radiation

For decades, evolutionary biologists have been describing the widespread variation found in rates of evolution and in levels of diversity among different taxonomic groups. Niche expansion, or the availability of new niches, has the potential to initiate rapid evolution. For example, Gaylord Simpson (1949) described the relatively rapid evolution of mammals after the demise of the dinosaurs: within a span of just 60 million years, a remarkable diversity of mammals evolved. Other recent examples of adaptive radiations include anole lizards, cichlids, and the Hawaiian Drosophila.

Since Darwinian evolution is usually taken to mean both adaptive and gradual, do radiations such as the ones listed here fit Darwin's notion of gradualism? Non-gradual or rapid evolution is not necessarily anti-Darwinian. The nature of genetic variation in combination with various evolutionary forces has the potential to produce gradual or non-gradual response. Biologists expounding rapid evolution have historically raised an eyebrow or two among their peers. However, they have traditionally been focusing on the role of either unusual genetic variation (such as macromutations) or dramatic demographic shifts. Niche expansion-associated rapid evolution works fully within the framework of Darwinian evolution. In fact, one of Darwin's favorite evolutionary examples is the rapid radiation of finches found on different island habitats in the Galapagos (Grant 1999).

1.3 Punctuated equilibrium within a microevolution framework

As shown earlier, a wide range of mechanisms, from molecular to population and community, can generate rapid episodic rates of change. All these mechanisms fit within a population genetics framework that can be explained by mutation, selection, drift, and gene flow. In contrast, paleontology examines the changes in fauna and flora as well as their anatomical and morphological features through the geological record. The remarkable breadth and depth of fossil record evidence have provided some of the most direct support for the theory of evolution. With respect to mechanisms of evolution, paleontology has traditionally dealt with macroevolution while population genetics stays within the domain of microevolution. The combinations of the two fields were essen-
tial in forging the 'Modern Synthesis' in the 1940s (Simpson 1944). However, these same two fields have often shown divergent views on the mechanisms of macroevolution. Stephen J. Gould and Nile Eldredge's punctuated evolution is a prominent case in point (Gould and Eldredge 1977).

There are many instances of the fossil series where geological records provide distinct and unequivocal evidence of non-gradual evolution, i.e. long periods of stasis followed by brief bursts of diversity and speciation. For example, new species often appear suddenly in the fossil record. While it has been argued that such findings are fortuitous, e.g. that these new species may have originated elsewhere and migrated to the fossilized locale, the idea that speciation can occur through physiological and behavioral changes, with morphological differentiation following later, did not hold ground against Gould's persistent and eloquent arguments to the contrary. Since large populations are more likely to leave fossils than small populations, Gould appealed to Mayr's sympatric model of speciation. This appeal was later extended to sympatric models of speciation, to Goldschmidt's rate genes, and to any theory that would make speciation go faster. While sympatric speciation fully fits in the realms of population genetics theory, as time went on, Gould became more convinced that the rapid rate of speciation was the property of the speciating lineage itself rather than the property of the speciation process.

A careful reading of Gould's writing on punctuated speciation reveals that he was using the term, speciation, in a geological sense and not in a population genetics sense. Based on fossil records, Gould suggested that the punctuation or evolutionary burst period accounted for only about 1–2% of the length of the stasis period, implying a punctuation period of about 1–2 million years (my) in a lineage undergoing a stasis period of ~100 my. In population genetics terms, 1–2 my is an exceedingly long time for gradual evolution, even though it represents a very short time on the geological scale. One would think that there shouldn't be a disagreement between geologically-inspired punctuated speciation and gradual speciation in population genetics (for a discussion, see Jagdeeshan et al. 2011) but Gould, looking for a mechanistic explanation, kept the two views connected and interchanged them back and forth. Gould treated species as individuals with a propensity to speciate—a characteristic that could not be reduced to the characteristics of the comprising individual organisms and thus not to be explained by natural selection. In fact, Gould went so far as to initially maintain that all significant evolutionary changes occur during speciation (Gould 1982) but later relented. As seen in the previous sections (1.2.1–1.2.8), it is now clear that there are ample microevolutionary mechanisms that could generate such extreme patterns of variable evolutionary rate.

1.4 Tempo, mode, and the genomic landscape

In Tempo and Mode in Evolution, Gaylord Simpson (1944) promoted the Modern Evolutionary Synthesis by interconnecting the disparate fields of genetics, systematics, and paleontology within a gradualist framework. Since then, researchers have been finding more and more examples of non-gradual change, as either an episodic phase or a rapid and continual process in a species' evolutionary trajectory. All known cases of rapid evolution, whether in the wild or in the lab, are directly or indirectly associated with high selective pressure or sudden changes in the direction of selection. For example, the high diversity of Hawaiian Drosophila and island fauna and flora in general are associated with geographic isolation, environmental variation, and population dynamics. The spectacular diversity of cultivated plants and animals during the last few thousand years is the result of not new genetic variation but strong man-made selection pressure. The famous long-term University of Illinois selection experiment for increased oil content in corn from 4% to nearly 20% over 90 generations is a classic case of selection and human-driven rapid change (Dudley and Lambert 1992). More recent cases of very rapid evolution include sexual selection-driven changes in color spots in male guppies within months (Endler 1986), the evolution of new carbon sources in bacteria (Lenski and Travisano 1994), the domestication of silver foxes within 35 generations (Trut 1999), and the evolution of diet (from insectivore to herbivore) and associated
changes in head shape and muscles in the lizard, *Podarcis sicula*, on two Adriatic islands off the coast of Croatia within a span of a mere 30 years (Herrel et al. 2008).

The field of evolutionary biology has also expanded in tools, resources, and scope, and we now can readily evaluate the tempo and mode of molecular evolution at the genomic level, and to relate it to the tempo and mode observed at the phenotypic level. The super-exponential increase of genomic information has propelled the field into exciting new domains. Evolutionary genomics allows large-scale comparisons of sequence and gene expression changes in both closely and widely separated taxa and thus provides relevant data for comparing rates of evolution between different genetic elements as well as in different evolutionary lineages over any desired length of time. In a very short period of time, evolutionary genomics has revised our view of almost all aspects of genetic variation: the nature of point mutation, nucleotide repetition, insertion-deletions, copy number polymorphism and gene duplication, retrotransposition, gene families, and structural and functional redundancies (Lynch 2007). The rate of progress in sequencing technologies and downstream informatics is indeed breathtaking. Comparative genomics is allowing researchers to study rates of evolution from single nucleotides to whole genomes and is thus providing in-depth views on how the various components of the genome have changed over time.

In microorganisms, unique genetic mechanisms (e.g. horizontal gene transfer) and/or rapid changes in the environment, such as the use of antibiotics, provides opportunities for rapid change. In prokaryotes, rapid changes as seen in eukaryotic sexual system genes and immune response genes are more likely due to responses to changes in the environment as has likely been the case in the Hawaiian *Drosophila* and the cichlids of Lake Victoria. Common sense dictates that in the long term, genetic and phenotypic evolution would necessarily be coupled and the law of gradualism would apply as a result of a rolling average of rates. However, in the short term, evolutionarily speaking, and in different organisms and at different times, this need not be the case: different genetic elements and lineages can evolve faster or slower than the average rates.

During much of the last 150 years, evolutionary biology has preoccupied itself with the study of phenotypic evolution. Such studies have greatly enriched our perception and appreciation of organismal diversity from molecules to humans. Now, the arrival of the genomics era promises not only to unravel the structure of molecular machinery, but also to provide us with an unprecedented knowledge of the rates and limits of evolutionary change. Such knowledge would be needed as we embark on manipulating genomes for food, medicinal, and commercial purposes. Just as comparative genomics has helped settle the debate between neutralist and adaptationist views of molecular variation by supplying evidence that supports both views (Kimura 1983; Kreitman 1983; Andolfatto 2005), functional and developmental genomics will progressively reveal the diverse rates of evolution, unravel the complex relationships between genotypes and phenotypes (Lewontin 1974; Artieri et al. 2009; Artieri and Singh 2010) and provide the material basis for understanding the tempo and mode of both molecular and phenotypic evolution.

1.5 'Rapidly evolving genes and genetic systems': a brief overview

The objective of this book is to provide an advanced, comprehensive, and topical overview of evolutionary rates in biological systems by drawing upon evidence for the rapid evolution of genes and genetic systems from diverse perspectives. The 27 chapters, together, describe a fantastic array of rapidly evolving systems: from individual phenotypes to sets of related traits and developmental pathways; from natural populations to experimental evolutionary studies; from bacteria to fungi; from plants to animals; from simple genetic elements to a complex of species. These chapters are placed into the following five parts.

The first part, ‘From Theory to Experiment’, contains four chapters and provides readers with a theoretical, and experimental foundation on the rate of evolution. Otto introduces the concept in Chapter 2 from a historical and theory-driven perspective. In Chapter 3, Albu et al. model the effects of
recombination on the rate of selective change while Kumagai and Uyenoyama, in Chapter 4, explore how sex-specific hybrid incompatibilities can drive the distribution of evolutionary rates across the genome. Xu (Chapter 5) provides a review of the experimental evolution field. Together, this first part shows how such parameters as population size, recombination, and intensity of selection, impact the rate of evolution for a variety of genotypic and phenotypic traits in natural, experimental, and in silico biological systems.

The second part, 'Rapidly Evolving Genetic Elements', contains seven chapters that showcase a variety of genetic and genomic examples for variable and often rapid rates of DNA sequence change. Chapter 6 by Haerty and Golding, focuses on the rapid evolution of a specific category of coding sequences, the low complexity sequences, and amino acid repeat regions. Hao (Chapter 7) describes the ubiquitous signature of horizontal gene transfer in bacteria and how these transfers impact bacterial genome evolution, including those related to virulence properties. Xia (Chapter 8) describes the patterns of animal mitochondrial genome evolution and discusses the mechanisms for its rapid evolution. Roach et al. highlight the rapid evolution of centromere and centromeric/kinetochores in Chapter 9. Rogers and Hartl (Chapter 10) discuss the rapid origin and evolution of novel genes and gene functions through the formation of chimeric genes. In Chapter 11, Long et al. highlight the interactions between sex chromosomes and autosomes. Torgerson and Hernandez discuss, in the last chapter of this part, the general patterns of non-coding DNA sequence variation, with a special focus on the human genome (Chapter 12).

The third part, 'Sex- and Reproduction-Related Genetic Systems', presents seven chapters highlighting the rapid evolution of sex and reproduction-related genes. The chapter topics include Palmer and Swanson's review on sperm-egg interactions (Chapter 13), Lessios and Zigler's analysis of evolutionary rates in the sea urchin bindin protein (Chapter 14), fast evolving Drosophila seminal proteins and their networks by Wong and Wolfner (Chapter 15), the evolution of the sperm proteome in Drosophila by Karr and Dorus (Chapter 16), Civetta's essay on natural selection versus sexual selection of reproductive systems (Chapter 17), O'Grady and Markow's chapter on behavioral traits involved in mating and host use (Chapter 18) and, finally, fungal mating systems and mating type genes by James (Chapter 19).

The fourth part, 'Pathogens and their Hosts', contains three chapters that highlight the evolution of pathogens and the impacts of pathogen genomic changes on their hosts, from Drosophila to humans. Lazzaro and Clark (Chapter 20) provide a review of the evolution of the Drosophila innate immunity system. Yang et al. (Chapter 21) focus on the rapid evolution of the human plague pathogen, Yersinia pestis. Lastly, an excellent example of how the human genome responds to the evolution of the malaria parasite is covered by Ko et al. (Chapter 22).

The fifth and final part, 'From Gene Expression to Development to Speciation' comprises five chapters that highlight above species-level consequences of rapidly evolving processes. Artieri (Chapter 23) discusses the rapid changes in gene expression across closely related species and focuses on the roles that these changes often bring to dramatic phenotypic divergence between these species. Kopp (Chapter 24) utilizes an evo-devo approach to understanding the consequences of rapidly evolving genes. Arnold et al. (Chapter 25) and Moe et al. (Chapter 26) explore how, respectively, species hybridization and coevolutionary processes, can drive the rapid evolution of traits and lineages. Finally, Kulathinal and Singh (Chapter 27) provide a synthesis in speciation theory, based on the consequences of rapidly evolving reproductive genetic systems.

1.6 Future prospects

Exciting new developments in evolutionary research are providing an opportunity to study genetic systems in unprecedented detail with the promise of learning not only about genic rates of evolution but about the mechanisms as well. A comprehensive understanding of evolutionary rates across lineages would allow us, for the first time, to infer from rates of genic changes, the rates of environmental changes—both abiotic and biotic—that have generated the diversity of life
on our planet. While a post-genomic synthesis awaits us, the exceptional chapters in this book, together, provide an exciting step to understanding the important evolutionary forces that have shaped our world.

References


