
Contents

Foreword	xiv
<i>Richard Lewontin</i>	
Preface	xvi
List of Contributors	xvii
1 Introduction	1
<i>Rama S. Singh, Jianping Xu, and Rob J. Kulathinal</i>	
1.1 A gradualist history	1
1.2 Mechanisms of rapid and episodic change	2
1.2.1 Unconstrained neutral space	2
1.2.2 Horizontal gene transfer	3
1.2.3 Developmental macromutations	3
1.2.4 Evolution by gene regulation	3
1.2.5 Coevolutionary forces	4
1.2.6 Sexual selection and sexual arms races	4
1.2.7 Population demography and genetic revolutions	5
1.2.8 Adaptive radiation	5
1.3 Punctuated equilibrium within a microevolution framework	5
1.4 Tempo, mode, and the genomic landscape	6
1.5 'Rapidly evolving genes and genetic systems': a brief overview	7
1.6 Future prospects	8
Part I From Theory to Experiment	
2 Theoretical perspectives on rapid evolutionary change	13
<i>Sarah P. Otto</i>	
2.1 Introduction	13
2.2 When is strong selection strong?	13
2.3 Does strong selection differ in kind from weak selection?	16
2.4 Concluding thoughts	20
3 Recombination reshuffles the genotypic deck, thus accelerating the rate of evolution	23
<i>Mihai Albu, Amir R. Kermany, and Donal A. Hickey</i>	
3.1 Introduction	23
3.2 Simulating selection on multilocus genotypes	24
3.3 Discussion	27
3.4 Conclusions	29

4 Heterogeneity in neutral divergence across genomic regions induced by sex-specific hybrid incompatibility	31
<i>Seiji Kumagai and Marcy K. Uyenoyama</i>	
4.1 Introduction	31
4.1.1 Detecting incompatibility factors	31
4.1.2 Within-species polymorphisms for incompatibility factors with sex-limited transmission	31
4.2 Genealogical migration rate	32
4.2.1 Definition	32
4.2.2 Non-sex-specific incompatibility	33
4.2.3 Sex-specific incompatibility	33
4.3 Applications	33
4.3.1 Mitochondrial introgression	33
4.3.2 Interpreting region-specific F_{ST}	35
4.4 Conclusions	37
5 Rapid evolution in experimental populations of major life forms	40
<i>Jianping Xu</i>	
5.1 Introduction	40
5.2 Features of experimental evolution	41
5.3 Types of experimental evolution	42
5.3.1 Directional selection	42
5.3.2 Adaptation	42
5.3.3 Mutation accumulation	42
5.4 Rapid change and divergence among mutation accumulation population lines	43
5.4.1 Microbial growth rate	43
5.4.2 Other microbial traits	45
5.4.3 Plants and animals	45
5.5 Adaptation and directional selection experiments	47
5.5.1 Adaptation of <i>E. coli</i> populations	47
5.5.2 Adaptation of viral populations	47
5.5.3 Adaptation and directional selection in fruit flies	48
5.5.4 Adaptation in yeast	48
5.5.5 Directional selection in mammals	48
5.5.6 Correlated changes between traits	49
5.5.7 Acquisition of novel phenotypes	49
5.6 Genomic analysis of experimental evolution populations	50
5.7 Conclusions and perspectives	50

Part II Rapidly Evolving Genetic Elements

6 Rapid evolution of low complexity sequences and single amino acid repeats across eukaryotes	55
<i>Wilfried Haerty and G. Brian Golding</i>	
6.1 Introduction	55
6.2 Rapid evolution of low complexity sequences	55
6.2.1 Mutational processes	56

6.3	Rapid divergence of LCRs and their impact on surrounding sequences	57
6.3.1	LCRs as indicators of regions of lowered purifying selective pressures	57
6.3.2	Mutagenic effect of LCRs	58
6.4	Low complexity sequences under selection	59
6.4.1	Deleterious effects of LCR size variation	59
6.4.2	DNA composition	59
6.4.3	LCR distribution	60
6.4.4	Phenotypic effects of LCR size variation	60
6.4.5	Selection for low information content	61
6.5	Perspectives	61
7	Fast rates of evolution in bacteria due to horizontal gene transfer	64
	<i>Weilong Hao</i>	
7.1	Introduction	64
7.2	Quantifying horizontal gene transfer	65
7.3	Understanding the variation of gene gain and loss	66
7.4	Horizontal gene transfer in duplicated genes	67
7.5	Pseudogenization of horizontally transferred genes	67
7.6	Mobile sequences and gene movement	68
7.7	Gene exchange goes fine-scale	69
7.8	Conclusions	69
8	Rapid evolution of animal mitochondrial DNA	73
	<i>Xuhua Xia</i>	
8.1	Introduction	73
8.2	Mitochondrial replication, strand bias, and evolutionary rates	74
8.3	The change in genetic code and evolutionary rate	77
8.4	The change in tRNA genes and evolutionary rate	79
8.5	Conclusions	81
9	Rapid evolution of centromeres and centromeric/kinetochore proteins	83
	<i>Kevin C. Roach, Benjamin D. Ross, and Harmit S. Malik</i>	
9.1	Centromeres in 'the fast lane'	83
9.2	Rapidly evolving centromeric histones	83
9.3	Bewildering centromeric DNA complexity and evolution	85
9.4	The 'centromere paradox': conflict, not coevolution	87
9.5	Support for the centromere drive model	89
9.6	Taxonomic differences in susceptibility to centromere drive	89
9.7	Rapid evolution of other centromeric proteins	90
9.8	Centromere drive and postzygotic isolation between species	91
9.9	Future directions	91
10	Rapid evolution via chimeric genes	94
	<i>Rebekah L. Rogers and Daniel L. Hartl</i>	
10.1	Introduction	94
10.2	Mechanisms of formation	94
10.3	Selection	96

10.4 Genomic stability	96
10.5 Function	97
10.6 Non-coding DNA	98
10.7 Future directions	99
11 Evolutionary interactions between sex chromosomes and autosomes	101
<i>Manyuan Long, Maria D. Vibranovski, and Yong E. Zhang</i>	
11.1 Introduction	101
11.2 Gene traffic between sex chromosome and autosomes	102
11.2.1 Gene traffic in <i>Drosophila</i>	102
11.2.2 Gene traffic in mammals	103
11.2.3 The cause and consequence of gene traffic	104
11.3 The generality of gene traffic out of the X in the genus <i>Drosophila</i>	105
11.3.1 Gene traffic in Drosophilidae and RNA-based and DNA-based duplication	105
11.3.2 Independent tests of gene traffic	105
11.4 Mechanisms underlying gene traffic out of the X: the detection of meiotic sex chromosome inactivation	107
11.4.1 Evolutionary genetic models	107
11.4.2 Molecular mechanistic models	107
11.5 The X-recruitment of young male-biased genes and gene traffic out of the X chromosome	108
11.5.1 Age-dependence in <i>Drosophila</i>	109
11.5.2 Age-dependence in mammals	110
11.5.3 The slow enrichment of X-linked female genes	110
11.6 Concluding remarks	111
12 Evolutionary signatures in non-coding DNA	115
<i>Dara G. Torgerson and Ryan D. Hernandez</i>	
12.1 Introduction	115
12.2 Challenges to studying the evolution of non-coding DNA	116
12.2.1 Identifying functional non-coding DNA	116
12.2.2 Estimating the neutral evolutionary rate	117
12.2.3 Limitations of identifying rapid evolution in non-coding DNA	117
12.3 Patterns of evolution in non-coding DNA	117
12.3.1 Selection in conserved non-coding sequences?	118
12.3.2 Detecting selection in promoters and TFBSs	120
12.3.3 Emerging trends in microRNA binding sites	121
12.3.4 Coding versus non-coding	121
12.4 Future prospects	122
Part III Sex- and Reproduction-Related Genetic Systems	
13 Evolution of sperm-egg interaction	127
<i>Melody R. Palmer and Willie J. Swanson</i>	
13.1 Introduction	127
13.2 Evolution at each step of sperm-egg interaction	127

13.3 Causes of rapid evolution	130
13.4 Methods to identify interacting proteins	132
13.5 Conclusions	132
14 Rates of sea urchin bindin evolution	136
<i>H. A. Lessios and Kirk S. Zigler</i>	
14.1 Introduction	136
14.2 Function and structure of bindin	136
14.3 Rate of bindin evolution	137
14.4 Possible reasons for different evolutionary rates in bindin	139
14.5 Conclusions and future prospects	141
15 Evolution of <i>Drosophila</i> seminal proteins and their networks	144
<i>Alex Wong and Mariana F. Wolfner</i>	
15.1 Introduction	144
15.2 <i>Drosophila</i> seminal fluid as a model system for rapidly evolving proteins	144
15.3 Extensive variation in rates of SFP evolution	147
15.4 Selection on a network?	149
15.5 Conclusions	150
16 Evolutionary genomics of the sperm proteome	153
<i>Timothy L. Karr and Steve Dorus</i>	
16.1 Introduction	153
16.2 Characterization of the <i>Drosophila</i> sperm proteome	154
16.3 Molecular evolution of the <i>Drosophila</i> sperm proteome	154
16.4 Evolution of novel <i>Drosophila</i> sperm components	155
16.4.1 Novel genes in the sperm proteome	156
16.4.2 Expansion and diversification of S-LAP gene family	157
16.5 The mouse sperm proteome: intensified selection on sperm membrane and acrosome genes	157
16.6 Rapid evolution of immunity-related genes in mammalian sperm	160
16.7 Sexual selection and compartmentalized adaptation in reproductive genetic systems	161
16.8 Future perspectives	162
17 Fast evolution of reproductive genes: when is selection sexual?	165
<i>Alberto Civetta</i>	
17.1 Introduction	165
17.2 What has been the role of selection during the evolution of male reproductive genes?	167
17.3 When is selection sexual? The phylogenetic approach	168
17.4 Testing sexual selection in the era of genomes	168
17.5 The need for association studies and functional assays	171
17.6 Conclusions	172

18 Rapid morphological, behavioral, and ecological evolution in <i>Drosophila</i>: comparisons between the endemic Hawaiian <i>Drosophila</i> and the cactophilic <i>repleta</i> species group	176
<i>Patrick M. O'Grady and Therese Ann Markow</i>	
18.1 Introduction	176
18.1.1 Ecological adaptations	177
18.1.2 Morphological adaptations	177
18.1.3 Behavioral adaptations	178
18.2 Hawaiian <i>Drosophila</i> radiation	179
18.2.1 Phylogenetic relationships	179
18.2.2 Sexual adaptations to morphology and behavior	179
18.2.3 Ecological adaptations to morphology and behavior	179
18.3 Cactophilic <i>Drosophila</i> radiation in the New World	180
18.3.1 Phylogenetic relationships	180
18.3.2 Rapid evolution of ecological adaptations	180
18.3.3 Rapid evolution of behavioral traits	182
18.4 Conclusions: adaptive radiation versus adaptive infiltration	183
19 Ancient yet fast: rapid evolution of mating genes and mating systems in fungi	187
<i>Timothy Y. James</i>	
19.1 Introduction	187
19.2 Incompatibility systems in fungi	189
19.3 Fungal reproductive proteins show evidence for positive and balancing selection	190
19.4 Evidence for rapid evolution of fungal incompatibility genes and systems	193
19.4.1 Sequence evolution	194
19.4.2 Mating systems and loci	194
19.5 Evidence for ancient alleles and mating systems	196
19.6 Conclusions	198
Part IV Pathogens and their Hosts	
20 Rapid evolution of innate immune response genes	203
<i>Brian P. Lazzaro and Andrew G. Clark</i>	
20.1 The evolution of immunity	203
20.2 Orthology and gene family evolution in antimicrobial immunity	204
20.3 Molecular evolution of the antimicrobial immune system	205
20.4 The evolution of defense against viruses and transposable elements	206
20.5 Concluding remarks	208
21 Rapid evolution of the plague pathogen	211
<i>Ruifu Yang, Yujun Cui, and Dongsheng Zhou</i>	
21.1 Introduction	211
21.2 Plasmid acquisition in <i>Y. pestis</i>	212
21.3 The impact of phages on genome structure	213

21.4	Prophages in the <i>Y. pestis</i> genome	213
21.5	CRISPRs diversity and the battle between phage and <i>Y. pestis</i>	214
21.6	Gene acquisition, loss, and inactivation	216
21.7	Rearrangements and copy number variants	217
21.8	Neutral versus adaptive evolution	219
21.9	Conclusions	220
22	Evolution of human erythrocyte-specific genes involved in malaria susceptibility	223
	<i>Wen-Ya Ko, Felicia Gomez, and Sarah A. Tishkoff</i>	
22.1	Introduction	223
22.2	Adaptive evolution in erythrocyte-specific genes	224
22.2.1	Genetic variants causing erythrocytic structural, regulatory, or enzymatic deficiency: candidates for heterozygote advantage	224
22.2.2	Positive selection on erythrocyte-surface receptors	226
22.3	Evolutionary response of the human genome to malaria infection	227
22.3.1	Maintenance of deleterious mutations due to selective pressure of malaria	227
22.3.2	Effects of population substructure on genetic variation in malaria-endemic human populations	230
22.3.3	Effects of gene conversion between homologous sequences on genetic variation at loci associated with malarial susceptibility	232
22.4	Future perspectives	232
Part V	From Gene Expression to Development to Speciation	
23	The rapid evolution of gene expression	237
	<i>Carlo G. Artieri</i>	
23.1	Introduction	237
23.2	One genome harbors many transcriptomes	238
23.3	Transcriptome divergence is complex	239
23.4	Factors affecting the rate of evolution of gene expression	240
23.4.1	Spatial heterogeneity	240
23.4.2	Temporal heterogeneity	241
23.5	Beyond comparisons of expression levels	242
23.6	Open questions and future directions	243
24	Rate variation in the evolution of development: a phylogenetic perspective	246
	<i>Artyom Kopp</i>	
24.1	Introduction	246
24.2	Examples of rate variation in the evolution of development	247
24.2.1	Same clade, different pathways: evolution of vulval development in rhabditid nematodes	247
24.2.2	Same pathway, different clades: evolution of sex combs and pigmentation in <i>Drosophila</i>	248

24.2.3	Same clade, same pathway, different genes: evolution of embryonic development and sex determination in insects	251
24.3	Technical and conceptual challenges to quantifying the evolution of development	252
24.4	Future directions: the promise of phylogenetic approaches to the evolution of development	253
25	Natural hybridization as a catalyst of rapid evolutionary change	256
	<i>Michael L. Arnold, Jennafer A.P. Hamlin, Amanda N. Brothers, and Evangeline S. Ballerini</i>	
25.1	Introduction	256
25.2	Adaptive trait introgression: when strange is really good	256
25.2.1	Adaptive trait transfer in <i>Canis</i> : wolves in dogs' clothing	257
25.2.2	Adaptive trait origin in <i>Saccharomyces cerevisiae</i> : hybrids make the best wine	258
25.3	Hybrid speciation: when opposites attract	259
25.3.1	Homoploid hybrid speciation: hybrid butterflies (quickly) change their spots	259
25.3.2	Allopolyploid speciation: <i>Tragopogon</i> hybrid polyploids form again, and again, and again... in less than 100 years...	260
25.4	Natural hybridization and adaptive radiations: hybrid speciation on steroids	261
25.4.1	Hybridization and adaptive radiations of Lake Malawi cichlids: from hybrid swarm to 800 species, in one lake?!	261
25.4.2	Hybridization and adaptive radiations in Alpine lake whitefish: Swiss fish diversify after the last big thaw	262
25.4.3	Hybridization and adaptive radiations in Hawaiian silverswords: allopolyploids in an island paradise	263
25.5	Conclusions and future prospects	264
26	Rapid evolution of pollinator-mediated plant reproductive isolation	266
	<i>Annika M. Moe, Wendy L. Clement, and George D. Weiblen</i>	
26.1	Plant-insect diversification	266
26.2	Pollination and reproductive isolation	266
26.3	<i>Ficus</i> versus <i>Castilleja</i>	267
26.4	A pollinator-mediated model for fig speciation	269
26.5	Future directions: plant-pollinator interactions and rapid evolution	271
27	Sexual system genomics and speciation	274
	<i>Rob J. Kulathinal and Rama S. Singh</i>	
27.1	In the beginning: Darwin and Wallace on sexual selection and speciation	274
27.2	The Modern Synthesis and the development of speciation theory	275
27.3	A new paradigm: the genomics of sexual systems and the origin of species	276
27.3.1	Functional genomics: organization into sexual and non-sexual systems	277
27.3.2	Higher variation among reproductive systems	277

27.3.3 Strength of sexual selection	278
27.3.4 Sexual systems interaction, coevolution, and rapid change	279
27.3.5 Rapid breakdown of sexual systems in species hybrids	280
27.4 Towards a post-genomics synthesis of speciation	280
27.5 Future prospects: sex as a major force in evolution	281
Index	285