

# Contents

Preface	xiii
Mathematical symbols	xv
Common abbreviations	xviii
1. Introduction	1
1.1. General structure of the book	7
1.2. Some biological ideas and notions	9
1.2.1. <i>Species definition and the nature of reproductive isolation</i>	9
1.2.2. <i>Geographic modes of speciation</i>	10
1.2.3. <i>Some speciation scenarios and patterns</i>	14
PART I FITNESS LANDSCAPES	
2. Fitness landscapes	21
2.1. Working example: one-locus, two-allele model of viability selection	22
2.2. Fitness landscape as fitness of gene combinations	25
2.3. Fitness landscape as the mean fitness of populations	30
2.4. The metaphor of fitness landscapes	33
2.4.1. <i>Wright's rugged fitness landscapes</i>	34
2.4.2. <i>Fisher's single-peak fitness landscapes</i>	36
2.4.3. <i>Kimura's flat fitness landscapes</i>	38
2.5. Fitness landscapes for mating pairs	40
2.6. Fitness landscapes for quantitative traits	41
2.6.1. <i>Fitness landscape as fitness of trait combinations</i>	41
2.6.2. <i>Fitness landscape as the mean fitness of populations</i>	42
2.6.3. <i>Fitness landscapes for mating pairs</i>	45
2.7. General comment on fitness landscapes	46
2.8. Summary	47

2.9. Conclusions	48
<i>Box 2.1. Dynamics of allele frequencies in one-locus, multiallele population</i>	49
<i>Box 2.2. Hill climbing on a rugged fitness landscape</i>	50
<i>Box 2.3. Evolution on flat landscapes</i>	51
3. Steps toward speciation on rugged fitness landscapes	53
3.1. Stochastic transitions between isolated fitness peaks	53
3.1.1. Fixation of an underdominant mutation	54
3.1.2. Peak shift in a quantitative character	60
3.1.3. Fixation of compensatory mutations in a two-locus haploid population	62
3.2. Some consequences of spatial subdivision and density fluctuations	66
3.2.1. Spatial subdivision	66
3.2.2. Stochastic transitions in a growing population	71
3.3. Peak shifts by selection	75
3.4. Summary	76
3.5. Conclusions	77
<i>Box 3.1. Diffusion theory: the probability of fixation</i>	78
<i>Box 3.2. Diffusion theory: the time to fixation</i>	79
<i>Box 3.3. Diffusion theory: the duration of transition</i>	80
4. Nearly neutral networks and holey fitness landscapes	81
4.1. Simple models	82
4.1.1. Russian roulette model in two dimensions	83
4.1.2. Russian roulette model on hypercubes	86
4.1.3. Generalized Russian roulette model	89
4.1.4. Multiplicative fitnesses	90
4.1.5. Stabilizing selection on an additive trait	91
4.1.6. Models based on the Nk-model	92
4.2. Neutral networks in RNA landscapes	95
4.3. Neutral networks in protein landscapes	97
4.4. Other evidence for nearly neutral networks	99
4.5. The metaphor of holey fitness landscapes	100
4.6. Deterministic evolution on a holey landscape	105
4.6.1. Error threshold	105
4.6.2. Genetic canalization	106
4.7. Stochastic evolution on a holey landscape	108

4.7.1. <i>Random walks</i>	108
4.7.2. <i>Dynamics of haploid populations</i>	112
4.8. <i>Summary</i>	113
4.9. <i>Conclusions</i>	114

## PART II

## THE BATESON-DOBZHANSKY-MULLER MODEL

5. <i>Speciation in the BDM model</i>	117
5.1. <i>The BDM model of reproductive isolation</i>	117
5.1.1. <i>Fitness landscapes in the BDM model</i>	119
5.1.2. <i>The mechanisms of reproductive isolation in the BDM model</i>	121
5.2. <i>Population genetics in the BDM model</i>	124
5.2.1. <i>Haploid population</i>	125
5.2.2. <i>Diploid population</i>	128
5.3. <i>Dynamics of speciation in the BDM model</i>	130
5.3.1. <i>Allopatric speciation</i>	131
5.3.2. <i>Parapatric speciation</i>	137
5.4. <i>Summary</i>	143
5.5. <i>Conclusions</i>	145
Box 5.1. <i>Hitting probability and hitting time in discrete-time Markov chains</i>	146
Box 5.2. <i>Genetic barrier to gene flow</i>	147
6. <i>Multidimensional generalizations of the BDM model</i>	149
6.1. <i>One- and two-locus, multiallele models</i>	149
6.2. <i>Multilocus models</i>	151
6.2.1. <i>The Walsh model</i>	152
6.2.2. <i>Divergent degeneration of duplicated genes</i>	154
6.2.3. <i>Three- and four-locus models</i>	155
6.2.4. <i>Accumulation of genetic incompatibilities</i>	158
6.2.5. <i>Allopatric speciation</i>	174
6.2.6. <i>Parapatric speciation</i>	185
6.3. <i>Summary</i>	192
6.4. <i>Conclusions</i>	194
7. <i>Spatial patterns in the BDM model</i>	195
7.1. <i>Individual-based models: spread of mutually incompatible neutral genes</i>	197

7.1.1. <i>Model</i>	197
7.1.2. <i>Parameters</i>	198
7.1.3. <i>Numerical procedure</i>	199
7.1.4. <i>Results</i>	200
7.1.5. <i>Interpretations</i>	205
7.2. Deme-based models: spread of mutually incompatible neutral genes	207
7.2.1. <i>Model</i>	207
7.2.2. <i>Parameters and dynamic characteristics</i>	210
7.2.3. <i>Results</i>	211
7.2.4. <i>Interpretations</i>	219
7.3. Deme-based models: spread of mutually incompatible advantageous genes	221
7.4. Comment on adaptive radiation	228
7.5. Summary	229
7.6. Conclusions	230

### PART III

## SPECIATION VIA THE JOINT ACTION OF DISRUPTIVE NATURAL SELECTION AND NONRANDOM MATING

8. Maintenance of genetic variation under disruptive natural selection	233
8.1. Spatially heterogeneous selection	235
8.1.1. <i>The Levene model</i>	235
8.1.2. <i>Two-locus, two-allele haploid version of the Levene model</i>	238
8.1.3. <i>Restricted migration between two niches</i>	240
8.1.4. <i>Spatial gradients in selection</i>	242
8.1.5. <i>Coevolutionary clines</i>	249
8.2. Spatially uniform disruptive selection	251
8.2.1. <i>Migration-selection balance: the Karlin-McGregor model</i>	251
8.2.2. <i>Migration-selection balance: the Bazykin model</i>	252
8.3. Temporal variation in selection	254
8.4. Frequency-dependent selection in a single population	255
8.4.1. <i>Phenomenological approach</i>	256
8.4.2. <i>Intraspecific competition</i>	257
8.4.3. <i>Spatially heterogeneous selection and competition</i>	263
8.4.4. <i>Adaptive dynamics approach</i>	265

8.5. Summary	277
8.6. Conclusions	278
9. Evolution of nonrandom mating and fertilization	279
9.1. A general framework for modeling nonrandom mating and fertilization	280
9.1.1. <i>Random mating within mating pools joined preferentially</i>	282
9.1.2. <i>Preferential mating within mating pools joined randomly</i>	284
9.2. Similarity-based nonrandom mating	287
9.2.1. <i>Single locus</i>	287
9.2.2. <i>Multiple loci</i>	299
9.2.3. <i>General conclusions on similarity-based nonrandom mating</i>	309
9.3. Matching-based nonrandom mating	309
9.3.1. <i>Two loci</i>	311
9.3.2. <i>Two polygenic characters</i>	321
9.3.3. <i>One locus, one character</i>	325
9.3.4. <i>General conclusions on matching-based nonrandom mating</i>	327
9.4. Nonrandom mating controlled by a culturally transmitted trait	327
9.5. Summary	328
9.6. Conclusions	330
10. Interaction of disruptive selection and nonrandom mating	331
10.1. Disruptive selection and similarity-based nonrandom mating	332
10.1.1. <i>Single locus</i>	333
10.1.2. <i>Single quantitative character</i>	352
10.1.3. <i>Sympatric speciation with culturally transmitted mating preferences</i>	356
10.2. Disruptive selection and matching-based nonrandom mating	359
10.2.1. <i>Two loci</i>	359
10.2.2. <i>Two polygenic characters</i>	364
10.3. "Magic trait" models	368
10.3.1. <i>Single locus</i>	369
10.3.2. <i>Two loci: speciation by sexual conflict</i>	370
10.3.3. <i>Single polygenic character</i>	374
10.3.4. <i>Two polygenic characters: speciation by sexual selection</i>	384
10.4. Disruptive selection and modifiers of mating	387

10.5. Summary 396

10.6. Conclusions 398

11. General conclusions 399

11.1. The structure of fitness landscapes and speciation 399

11.2. Allopatric speciation 401

11.3. Parapatric speciation 401

11.4. Sympatric speciation 403

11.5. Some speciation scenarios and patterns 406

11.6. General rules of evolutionary diversification 412

11.7. Why species? 414

11.8. Some open theoretical questions 416

11.9. Final thoughts 417

References 419

Index 457

PART III

10. Evolution of nonrandom mating and fertilization

10.1. Disruptive selection and similarity-based nonrandom mating

10.1.1. Single locus

10.1.2. Single-phenotype character shift-out

10.1.3. Sympatric speciation with similarity-based nonrandom mating

10.1.4. Spatial selection

10.2. Disruptive selection and matching-based nonrandom mating

10.2.1. Spatially uniform disruptive selection

10.2.2. Migration-selection

10.3. "Magic trait" models

10.4. Disruptive selection and modifiers of recombination

10.5. Frequency-dependent selection

10.6. The loci of speciation

10.7. Single-phenotype character shift-out

10.8. The polygenic character shift-out