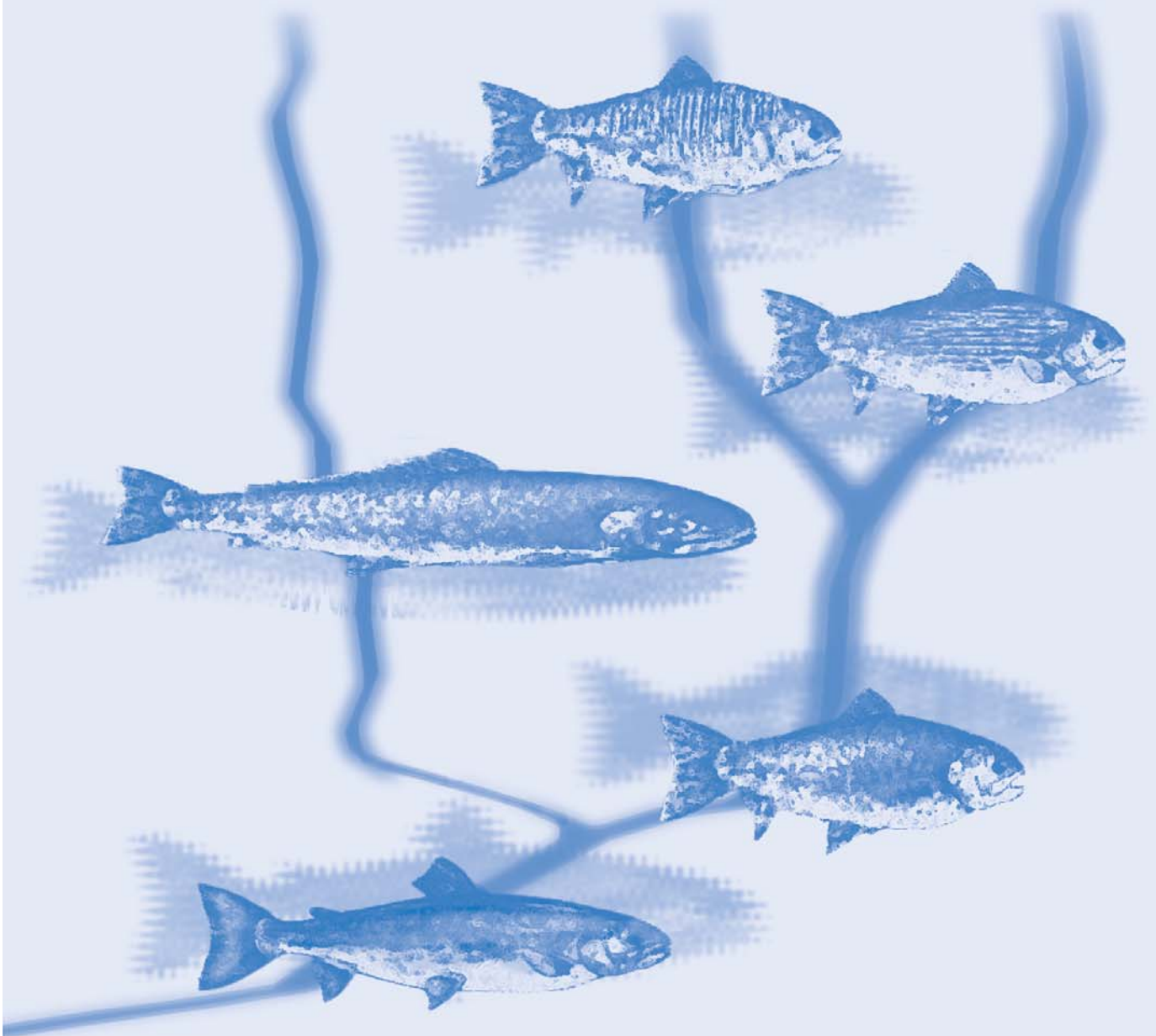


Cambridge Studies in Adaptive Dynamics

Adaptive Speciation



Edited by

U. Dieckmann, M. Doebeli, J.A.J. Metz, and D. Tautz

Adaptive Speciation

Edited by

Ulf Dieckmann, Michael Doebeli, Johan A.J. Metz,
and Diethard Tautz



PUBLISHED BY THE PRESS SYNDICATE OF THE UNIVERSITY OF CAMBRIDGE
The Pitt Building, Trumpington Street, Cambridge, United Kingdom

CAMBRIDGE UNIVERSITY PRESS
The Edinburgh Building, Cambridge CB2 2RU, UK
40 West 20th Street, New York, NY 10011-4211, USA
477 Williamstown Road, Port Melbourne, VIC 3207, Australia
Ruiz de Alarcón 13, 28014 Madrid, Spain
Dock House, The Waterfront, Cape Town 8001, South Africa

<http://www.cambridge.org>

© International Institute for Applied Systems Analysis 2004

This book is in copyright. Subject to statutory exception
and to the provisions of relevant collective licensing agreements,
no reproduction of any part may take place without
the written permission of the
International Institute for Applied Systems Analysis.

<http://www.iiasa.ac.at>

First published 2004

Printed in the United Kingdom at the University Press, Cambridge

Typefaces Times; Zapf Humanist 601 (Bitstream Inc.) *System* L^AT_EX

A catalog record for this book is available from the British Library

ISBN 0 521 82842 2 hardback

Contents

Contributing Authors	xi
Acknowledgments	xiii
Notational Standards	xiv
1 Introduction	1
Ulf Dieckmann, Johan A.J. Metz, Michael Doebeli, and Diethard Tautz	
1.1 A Shift in Focus	1
1.2 Adaptive Speciation	2
1.3 Adaptive Speciation in Context	6
1.4 Species Criteria	9
1.5 Routes of Adaptive Speciation	11
1.6 Pattern and Process in Adaptive Speciation	13
1.7 Structure of this Book	14
2 Speciation in Historical Perspective	17
Will Provine	
2.1 Introduction	17
2.2 Darwin on Species and Speciation	18
2.3 Mayr on Species and Speciation	20
2.4 Species Now	22
2.5 Speciation Now	24
A Theories of Speciation	31
Introduction to Part A	32
3 Genetic Theories of Sympatric Speciation	36
Tadeusz J. Kawecki	
3.1 Introduction	36
3.2 Sustained Disruptive Selection	38
3.3 Evolution of Divergent Mate Choice	42
3.4 Evolution of Divergent Habitat or Host Preference	49
3.5 Concluding Comments: Synergism Between Processes	52
4 Adaptive Dynamics of Speciation: Ecological Underpinnings	54
Stefan A.H. Geritz, Éva Kisdi, Géza Meszéna, and Johan A.J. Metz	
4.1 Introduction	54
4.2 Invasion Fitness	56
4.3 Phenotypic Evolution by Trait Substitution	58
4.4 The Emergence of Diversity: Evolutionary Branching	61
4.5 Evolutionary Branching and Speciation	70
4.6 Adaptive Dynamics: Alternative Approaches	72
4.7 Concluding Comments	73

5 Adaptive Dynamics of Speciation: Sexual Populations	76
Ulf Dieckmann and Michael Doebeli	
5.1 Introduction	76
5.2 Adaptive Speciation in Sexual Populations	78
5.3 Coevolutionary Adaptive Speciation in Sexual Populations	94
5.4 Adaptive Speciation through Sexual Selection	98
5.5 Concluding Comments	107
6 Genetic Theories of Allopatric and Parapatric Speciation	112
Sergey Gavrilets	
6.1 Introduction	112
6.2 Modes of Speciation	113
6.3 Adaptive Landscapes	115
6.4 Rugged Adaptive Landscapes	118
6.5 Bateson–Dobzhansky–Muller Adaptive Landscapes	123
6.6 Holey Adaptive Landscapes	127
6.7 Concluding Comments	137
7 Adaptive Dynamics of Speciation: Spatial Structure	140
Michael Doebeli and Ulf Dieckmann	
7.1 Introduction	140
7.2 Classic Models of Parapatric Speciation	141
7.3 Evolutionary Branching in Spatially Structured Populations	143
7.4 Extension to Sexual Populations: Parapatric Speciation	155
7.5 A Note on Species–Area Relationships	161
7.6 Concluding Comments	165
B Ecological Mechanisms of Speciation	169
Introduction to Part B	170
8 Speciation and Radiation in African Haplochromine Cichlids	173
Jacques J.M. van Alphen, Ole Seehausen, and Fretson Galis	
8.1 Introduction	173
8.2 Sexual Selection and Speciation in Cichlids	175
8.3 Sexual Selection in <i>Pundamilia</i>	177
8.4 Sexual Selection in <i>Neochromis omnicaeruleus</i>	179
8.5 Pharyngeal Jaw Versatility and Feeding Diversification	186
8.6 Concluding Comments	190
9 Natural Selection and Ecological Speciation in Sticklebacks	192
Howard D. Rundle and Dolph Schluter	
9.1 Introduction	192
9.2 Natural History of the Sympatric Sticklebacks	196
9.3 Parallel Speciation of Limnetics and Benthics	199
9.4 Premating Isolation Strengthened in Sympatry	203
9.5 Concluding Comments	208
10 Adaptive Speciation in Northern Freshwater Fishes	210
Sigurður S. Snorrason and Skúli Skúlason	
10.1 Introduction	210
10.2 Ecological Factors that Promote Diversification	211
10.3 Factors that Facilitate Assortative Mating	213
10.4 Nature and Basis of Phenotypic Variation	214

10.5	Ecological Determinants of Diversity Patterns	218
10.6	Concluding Comments	222
11	Sympatric Speciation in Insects	229
	Guy L. Bush and Roger K. Butlin	
11.1	Insect Diversity, Body Size, Specialization, and Speciation	229
11.2	Cospeciation	231
11.3	Allopatric Speciation on the Same Host	232
11.4	Allopatric Speciation with a Host Shift	233
11.5	Sympatric Speciation with a Host Shift	235
11.6	Conditions Needed for Sympatric Shifts	243
11.7	Concluding Comments	247
12	Adaptive Speciation in Agricultural Pests	249
	Martijn Egas, Maurice W. Sabelis, Filipa Vala, and Iza Lesna	
12.1	Introduction	249
12.2	Crops as Ecological Niches	252
12.3	Adaptive Learning of Host Preference	253
12.4	Adaptive Mate Choice	256
12.5	Symbiont-induced Reproductive Incompatibility	259
12.6	Concluding Comments	262
13	Ecological Speciation in Flowering Plants	264
	Nickolas M. Waser and Diane R. Campbell	
13.1	Introduction	264
13.2	Ecological Speciation Driven by Animal Pollinators	265
13.3	Adaptation and Speciation in Different Environments	272
13.4	Combined Speciation Mechanisms	273
13.5	Concluding Comments	277
14	Experiments on Adaptation and Divergence in Bacterial Populations	278
	Michael Travisano	
14.1	Introduction	278
14.2	Allopatric Divergence	279
14.3	Sympatric Divergence	288
14.4	Concluding Comments	298
C	Patterns of Speciation	301
	Introduction to Part C	302
15	Phylogeography and Patterns of Incipient Speciation	305
	Diethard Tautz	
15.1	Introduction	305
15.2	Molecules, Morphology, and Time Frames	308
15.3	Assortative Mating and Patterns of Subdivision	311
15.4	Natural Populations	314
15.5	Concluding Comments	320
16	Evolutionary Diversification of Caribbean <i>Anolis</i> Lizards	322
16.1	Introduction (J.B. Losos and R.S. Thorpe)	322
16.2	Adaptation and Speciation in Lesser Antillean Anoles (R.S. Thorpe, A. Malhotra, A. Stenson, and J.T. Reardon)	324

16.3	Adaptation and Speciation in Greater Antillean Anoles (J.B. Losos)	335
16.4	Concluding Comments (R.S. Thorpe and J.B. Losos)	343
17	Adaptive Radiation of African Montane Plants	345
	Eric B. Knox	
17.1	Introduction	345
17.2	Vegetation Zones on African Mountains	349
17.3	The Giant Senecios and Giant Lobelias	351
17.4	Phylogenetic Patterns and Biogeographic Interpretation	353
17.5	Adaptive Speciation	357
17.6	Concluding Comments	359
18	Diversity and Speciation of Semionotid Fishes in Mesozoic Rift Lakes	362
	Amy R. McCune	
18.1	Introduction	362
18.2	Semionotid Fishes	363
18.3	Newark Lake Paleolimnology	364
18.4	<i>Semionotus</i> Radiations in the Newark Supergroup	366
18.5	Ecological Context of Evolutionary Novelty and Speciation	368
18.6	Time Required for Speciation	374
18.7	Concluding Comments	379
19	Epilogue	380
	Ulf Dieckmann, Diethard Tautz, Michael Doebeli, and Johan A.J. Metz	
19.1	The Allopatric Dogma	380
19.2	Adaptive Speciation	381
19.3	Diversity of Speciation Processes	383
19.4	Empirical Studies of Speciation	384
19.5	Continuous Splitting and Radiations	388
19.6	Future Directions	389
	References	395
	Index	445

Contributing Authors

- Guy L. Bush* (bushfly@pilot.msu.edu) Department of Zoology, Michigan State University, 336 Natural Sciences Building, East Lansing, MI 48824, USA
- Roger K. Butlin* (r.k.butlin@leeds.ac.uk) School of Biology, University of Leeds, Leeds LS2 9JT, United Kingdom
- Diane R. Campbell* (drcampbe@uci.edu) Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92697, USA
- David Claessen* (david.claessen@bbsrc.ac.uk) Biomathematics Unit, Institute of Arable Crops Research, Rothamsted, Harpenden, Hertfordshire AL5 2JQ, United Kingdom
- Ulf Dieckmann* (dieckman@iiasa.ac.at) Adaptive Dynamics Network, International Institute for Applied Systems Analysis, A-2361 Laxenburg, Austria
- Michael Doebeli* (doebeli@zoology.ubc.ca) Departments of Mathematics and Zoology, University of British Columbia, 6270 University Boulevard, Vancouver, BC V6T 1Z4, Canada
- Martijn Egas* (egas@science.uva.nl) Population Biology Section, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Kruislaan 320, NL-1090 GB Amsterdam, The Netherlands
- Frietsen Galis* (galis@rulsfb.leidenuniv.nl) Institute of Evolutionary and Ecological Sciences, University of Leiden, P.O.Box 9516, NL-2300 RA Leiden, The Netherlands
- Sergey Gavrilets* (gavrila@tiem.utk.edu) Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN 37996, USA
- Stefan A.H. Geritz* (stefan.geritz@utu.fi) Department of Mathematical Sciences, University of Turku, FIN-20014 Turku, Finland
- Tadeusz J. Kawecki* (tadeusz.kawecki@unifr.ch) Unit for Ecology and Evolution, Department of Biology, University of Fribourg, Chemin du Musée 10, CH-1700 Fribourg, Switzerland
- Éva Kisdi* (eva.kisdi@utu.fi) Department of Mathematical Sciences, University of Turku, FIN-20014 Turku, Finland & Department of Genetics, Eötvös University, Múzeum krt 4/A, H-1088 Budapest, Hungary
- Eric B. Knox* (eknox@bio.indiana.edu) Department of Biology, Indiana University, 1001 E. Third Street, Bloomington, IN 47405, USA
- Iza Lesna* (lesna@science.uva.nl) Population Biology Section, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Kruislaan 320, NL-1090 GB Amsterdam, The Netherlands
- Jonathan B. Losos* (losos@biology2.wustl.edu) Department of Biology, Washington University, Campus Box 1137, St Louis, MO 63130, USA
- Anita Malhotra* (a.malhotra@bangor.ac.uk) School of Biological Sciences, University of Wales, Bangor, Gwynedd LL57 2UW, United Kingdom
- Amy R. McCune* (arm2@cornell.edu) Department of Ecology and Evolutionary Biology, Cornell University, E249 Corson Hall, Ithaca, NY 14853, USA
- Géza Meszéna* (geza.meszena@elte.hu) Department of Biological Physics, Eötvös University, Pázmány Péter sétány 1A, H-1117 Budapest, Hungary
- Johan A.J. Metz* (metz@rulsfb.leidenuniv.nl) Institute of Biology, Leiden University, Van der Klaauw Laboratory, P.O.Box 9516, NL-2300 RA Leiden, The Netherlands & Adaptive Dynamics Network, International Institute for Applied Systems Analysis, A-2361 Laxenburg, Austria
- Ferenc Mizera* (mizera@colbud.hu) Department of Biological Physics, Eötvös University, Pázmány Péter sétány 1A, H-1117 Budapest, Hungary
- Will Provine* (wbp2@cornell.edu) Department of Ecology and Evolutionary Biology, Corson Hall, Cornell University, Ithaca, NY 14853, USA

- James T. Reardon* (ReardonJ@LandcareResearch.co.nz) Landcare Research, P.O.Box 282, Alexandra, New Zealand
- Howard D. Rundle* (hrundle@sfa.ca) Department of Biological Sciences, Simon Fraser University, Burnaby, BC V5A 1S6, Canada
- Maurice W. Sabelis* (sabelis@science.uva.nl) Population Biology Section, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, NL-1090 GB Amsterdam, The Netherlands
- Dolph Schluter* (schluter@zoology.ubc.ca) Department of Zoology, University of British Columbia, Vancouver, BC V6T 1Z4, Canada
- Ole Seehausen* (o.seehausen@hull.ac.uk) Department of Biological Sciences, University of Hull, Hull HU6 7RX, United Kingdom
- Skúli Skúlason* (skuli@holar.is) Hólar College, Hólarí Hjaltadal, 551 Sauðkrókur, Iceland
- Sigurður S. Snorrason* (sigsnor@hi.is) Institute of Biology, University of Iceland, Grensásvegur 12, Reykjavík 108, Iceland
- Andrew Stenson* (a.g.stenson@bangor.ac.uk) School of Biological Sciences, University of Wales, Bangor, Gwynedd LL57 2UW, United Kingdom
- Diethard Tautz* (tautz@uni-koeln.de) Institut für Genetik, Universität zu Köln, Weyertal 121, D-50931 Köln, Germany
- Roger S. Thorpe* (r.s.thorpe@bangor.ac.uk) School of Biological Sciences, University of Wales, Bangor, Gwynedd LL57 2UW, United Kingdom
- Michael Travisano* (mtrav@uh.edu) Department of Biology and Biochemistry, University of Houston, Houston, TX 77204, USA
- Filipa Vala* (f.vala@ucl.ac.uk) Department of Biology, University College London, Wolfson House, London NW1 2HE, United Kingdom
- Jacques J.M. van Alphen* (alphen@rulsfb.leidenuniv.nl) Section of Animal Ecology, Institute of Evolutionary and Ecological Sciences, University of Leiden, P.O. Box 9516, NL-2300 RA Leiden, The Netherlands
- Nickolas M. Waser* (waser@citrus.ucr.edu) Department of Biology, University of California, Riverside, CA 92521, USA

Acknowledgments

Development of this book took place at the International Institute of Applied Systems Analysis (IIASA), Laxenburg, Austria, where IIASA's former directors Gordon J. MacDonald and Arne B. Jernelöv, and current director Leen Hordijk provided critical support. A workshop at IIASA brought together all authors to discuss their contributions and thus served as an important element in the strategy of achieving as much continuity across the subject areas as possible.

Financial support toward this workshop by the European Science Foundation's Theoretical Biology of Adaptation Programme is gratefully acknowledged. Michael Doebeli and Ulf Dieckmann received support from the Natural Sciences and Engineering Research Council of Canada. Ulf Dieckmann and Hans Metz received support from the European Research Training Network *ModLife* (Modern Life-History Theory and its Application to the Management of Natural Resources), funded through the Human Potential Programme of the European Commission.

The success of any edited volume aspiring to textbook standards very much depends on the cooperation of the contributors in dealing with the many points the editors are bound to raise. We are indebted to all our authors for their cooperativeness and patience throughout the resultant rounds of revision. The book has benefited greatly from the support of the Publications Department at IIASA; we are especially grateful to Ewa Delpos, Anka James, Martina Jöstl, Eryl Maedel, John Ormiston, and Lieselotte Roggenland for the excellent work they have put into preparing the camera-ready copy of this volume. Any mistakes that remain are our responsibility.

*Ulf Dieckmann
Michael Doebeli
Johan A.J. Metz
Diethard Tautz*

Notational Standards

To allow for a better focus on the content of chapters and to highlight their interconnections, we have encouraged all the authors of this volume to adhere to the following notational standards:

A, B, C	Locus, with alleles A, a; B, b; C, c
M	Modifier or mating locus, with alleles M, m
<hr/>	
p, q	Gene frequency
n	Population density (potentially a vector)
N	Population size (in number of individuals) or Total population density (sum of components of n)
E	Condition of the environment
a	Ecological interaction coefficient
r	Per capita growth rate
K	Carrying capacity
m	Migration/movement rate
D	Diffusion coefficient, or dilution rate
<hr/>	
x	Phenotypic or allelic trait value
<hr/>	
u	Per locus mutation probability or Probability of a mutational step in a quantitative trait
U	Gametic mutation probability
<hr/>	
f	Fitness in continuous time ($f = 0$ is neutral)
W	Fitness in discrete time ($W = 1$ is neutral)
w	Relative fitness
s	Selection coefficient
h	Heterozygote advantage
<hr/>	
D_M	Mahalanobis' (morphological) distance
D_N	Nei's genetic distance (between populations)
d	Genetic distance (between individuals) = number of allele changes
<hr/>	
z, z_1, z_2	Spatial coordinates
t	Time
T	Duration
τ	Waiting time
<hr/>	
p, q	Probability or relative frequency (subscript indicates type)
σ^2	Variance (subscript indicates type)
i, j	Index
\dots'	Invader
$\hat{\dots}$	Equilibrium value
\dots^*	Evolutionarily singular value (of a trait)
$\bar{\dots}$	Average

1

Introduction

Ulf Dieckmann, Johan A.J. Metz, Michael Doebeli, and Diethard Tautz

1.1 A Shift in Focus

Millions of species currently exist on earth, and to secure an understanding of how all this magnificent variety arose is no small task. Biologists have long accepted Darwinian selection as the central explanation of adaptation and evolutionary change; yet, to date, no similar agreement has emerged about evolutionary processes that can create two species out of one. Almost 150 years after Darwin's seminal work *On the Origin of Species* (1859), conditions for and mechanisms of biological speciation are still debated vigorously.

The traditional “standard model” of speciation rests on the assumption of geographic isolation. After a population has become subdivided by external causes – like fragmentation through environmental change or colonization of a new, disconnected habitat – and after the resultant subpopulations have remained separated for sufficiently long, genetic drift and pleiotropic effects of local adaptation are supposed to lead to partial reproductive incompatibility. When the two incipient species come into secondary contact, individuals from one species cannot mate with those of the other – even if they try – or, if mating is still possible, their hybrid offspring are inferior. Further evolution of premating isolation (like assortative mate choice or seasonal isolation) and/or postmating isolation (like gametic incompatibility) eventually ensures that the two species continue to steer separate evolutionary courses.

The trigger for speciation in this standard model is geographic isolation. It is for this reason that the distinction between allopatric speciation (occurring under geographic isolation) and sympatric speciation (without geographic isolation) has taken center stage in the speciation debate. Strictly speaking, this dichotomy characterizes no more than the spatial structure of populations that undergo speciation, as has been pointed out by the originator of the classification, Ernst Mayr:

[E]ven today some authors confound the mechanisms of speciation – genes, chromosomes, and so forth – with the location of the populations involved in speciation (that is, whether the populations are sympatric or allopatric), not realizing that the two aspects are independent of each other and both are by necessity involved simultaneously. (Mayr 1982, p. 565)

Yet, the common understanding of this classification, widespread in the scientific literature, does not properly distinguish between its biogeographic (or pattern-oriented) and mechanistic (or process-oriented) aspects. Indeed, the term allopatric

speciation has come to imply that the primary cause for a speciation event is geographic isolation and its primary mechanism is the emergence of reproductive incompatibility as a by-product of the interrupted gene flow – both implications being in accordance with the standard model. By contrast, the notion of sympatric speciation has become associated with speciation via other causes and different mechanisms. In short, pattern and process have become mixed up.

This confusion has not arisen by chance. Pattern and process are correlated so clearly in the standard model of speciation that no harm seemed to arise from a little conceptual sloppiness. In turn, mechanisms other than genetic drift or pleiotropic effects of local adaptation must be invoked to explain why species can be expected to arise without geographic isolation. Such mechanisms would most likely involve natural or sexual selection and for this reason the notion of sympatric speciation has become almost synonymous with speciation driven by ecological interactions or mate choice.

In this book our focus is on processes of speciation and, in particular, on their causes and mechanisms. To avoid misunderstandings and futile semantic debate, we suggest the terms allopatric and sympatric speciation be used, as far possible, in their original and precise meaning when classifying the biogeography of speciation events. To characterize causes and mechanisms beyond this classic dichotomy, a different terminology is required.

1.2 Adaptive Speciation

Speciation is a splitting process – an ancestral lineage splits into descendant lineages that are differentiated genetically and isolated reproductively. The split may be a consequence of geographic isolation, in which case the chain of cause and effect cannot, in general, be traced further: geographic factors that interrupt the gene flow between populations generally are the result of some coincidental environmental change, for example, in temperature, topography, or in the ranges of other species; or else are linked to chance events, like the incident of a rare colonization.

By contrast, splitting may be an evolutionary consequence of interactions within the speciating population. That is, the splitting itself may be an adaptation. As so often, this idea was foreshadowed in Darwin's work, as the following two quotes illustrate:

Consequently, I cannot doubt that in the course of many thousands of generations, the most distinct varieties of any one species [...] would always have the best chance of succeeding and of increasing in numbers, and thus of supplanting the less distinct varieties; and varieties, when rendered very distinct from each other, take the rank of species. (Darwin 1859, p. 155)

Natural selection, also, leads to divergence of character; for more living beings can be supported on the same area the more they diverge in structure, habits, and constitution [...]. Therefore during the modification of the descendants of any one species, and during the incessant struggle of all species to increase in numbers, the more

diversified these descendants become, the better will be their chance of succeeding in the battle of life. Thus the small differences distinguishing varieties of the same species, will steadily tend to increase till they come to equal the greater differences between species of the same genus, or even of distinct genera. (Darwin 1859, p. 169)

Given this precedence, discussions in this book may be seen as contributing to a much-belated renaissance of Darwinian ideas about speciation (Kondrashov 2001; Mallet 2001; Section 2.5). Such a development could have occurred earlier, had it not been for the commitment of major proponents of the Modern Synthesis to reproductive isolation for defining species and to geographic isolation to explain speciation. In a similar vein, the main part of the past century has seen the ubiquity of frequency-dependent selection – which played a key role in Darwin's ideas about speciation – unduly downplayed.

For splitting to be adaptive, a population must be under disruptive selection. Disruptive selection imposed purely by external causes is extremely unlikely, because this implies, as in allopatric speciation, a sudden, and very precisely aimed, change in the environment: otherwise the population would never come to occupy an externally imposed fitness minimum. Therefore, the only realistic scenario for splitting to be adaptive occurs when intraspecific interactions generate disruptive selection. This, in turn, can only happen if such interactions are frequency dependent. That is, these interactions must have the consequence that the fitness of a phenotype (i.e., its expected contribution to future generations) depends on the phenotypic composition of the population in which it occurs.

Obviously, for selection to be frequency dependent ecological contact must occur between the individuals involved. Conversely, it is also true that ecological contact almost invariably leads to frequency-dependent selection: under conditions of ecological contact, other individuals are part of the environment that determines the fitness of a given individual. For the particular phenotypes of these other individuals to be irrelevant in this determination, special, highly nongeneric circumstances would be required (notwithstanding that such circumstances are regularly assumed in simplified evolutionary models). In summary, for all practical purposes ecological contact and frequency-dependent selection are two sides of the same coin.

Strong frequency dependence can generate disruptive selection. If it does, the stage is set for adaptive diversification: a lineage split becomes selectively advantageous, as do adaptations that result in diminished gene flow between the emerging lineages. Under these conditions, the cause for the development of reproductive segregation rests within the species – therefore, such speciation scenarios are more amenable to further investigation. It is this perspective that makes it attractive to view some speciation processes as particular forms of adaptation, driven by selection pressures similar in origin to those that underlie directional evolution. We therefore propose to concentrate on distinguishing speciation processes that are adaptive from those that are nonadaptive and introduce the following definition:

“Adaptive speciation” refers to speciation processes in which the splitting is an adaptive response to disruptive selection caused by frequency-dependent biological interactions.

Naturally, the question of how often and under which circumstances frequency-dependent interactions are likely to induce disruptive selection is of central importance in the study of adaptive speciation. Traditionally, it is thought that such internally generated disruptive selection can only arise under rather special circumstances. In particular, in classic models of adaptive speciation (Chapter 3), disruptive selection through frequency-dependent interactions typically occurs only for a very restricted range of parameters. However, recent theoretical advances, based on a more dynamic view of the interplay between a population’s evolution and its environment, have led to a different picture (Chapter 4).

The basic (and, by itself, well known) observation underlying these new insights is that when selection is frequency dependent, fitness landscapes change dynamically during the evolutionary process, because the phenotypic composition of the population changes. Thus, a population that starts out in a regime of directional selection may, nevertheless, evolve to a state in which it experiences disruptive selection. Indeed, this is not as unlikely as it appears at first sight, as the following metaphor of a gold rush may help to illustrate. Before a gold rush, very few people lived where the gold was found. As news of the gold reached a major city many people moved to the location of the gold find; this corresponds to a regime of directional selection. However, once everybody had ventured to the gold find, things quickly deteriorated, because soon too many people were looking for gold. What initially was an advantageous strategy became severely deleterious, simply because the same strategy was adopted by a plethora of competitors. After the initial regime of directional selection, being caught in the gold rush became the worst option, and resulted in the population of prospectors occupying a “fitness minimum”.

If the gold-rush metaphor suggests that the basic cause of diversification is competitive interaction, it should be borne in mind that in any ecology that keeps populations bounded the individuals are necessarily subject to apparent or direct competition. If, moreover, the ecological roles of individuals vary continuously with their traits, similar individuals necessarily compete more strongly than less similar ones. Therefore, all that matters for diversification to be profitable is whether there exists something akin to the location of the gold, and whether at that location competition acts sufficiently narrowly that by behaving differently individuals can temporarily escape from it.

The gold-rush scenario corresponds to an adaptive process during which a trait value gradually converges to a point at which selection turns disruptive. This is illustrated schematically in Figure 1.1, which shows the evolutionary dynamics of the population mean of an arbitrary quantitative trait (thick curve). The figure also shows snapshots of the fitness profiles that generate this dynamics. While selection initially is merely directional, the fitness profiles, because of the adaptation of the mean trait value, soon feature a minimum (thin curve in Figure 1.1).

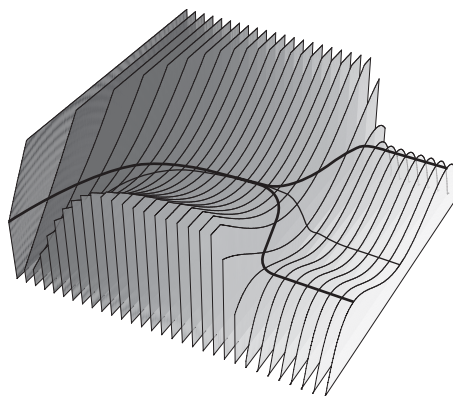


Figure 1.1 Adaptive speciation unfolding. A fitness landscape's shape changes jointly with a population's mean trait value (thick curve; the initial snapshot of the landscape is colored dark gray and the final one white). While the population undergoes directional selection by ascending the fitness landscape, the landscape itself changes because of frequency-dependent selection in such a way that a fitness minimum (thin curve) catches up with the population. Once trapped at the minimum, the population experiences disruptive selection and (under certain conditions) splits into two branches. In the figure, this divergence continues until the two branches arrive at local fitness maxima, at which selection becomes stabilizing.

As long as the mean trait value lies to one side of this minimum, the population still experiences directional selection and accordingly evolves away from the fitness minimum. However, as the evolutionary process unfolds, the fitness landscape continues to change in such a way that the distance between the mean trait value and the fitness minimum decreases. In other words, the fitness minimum catches up with the evolving population. Once the distance has shrunk to zero, the monomorphic population finds itself caught at a fitness minimum: through directional selection it has converged to a state in which it continuously experiences disruptive selection.

In this situation, a splitting of the population becomes adaptive. Adaptive speciation occurs provided the population possesses (or can evolve) a capacity for splitting into two reproductively isolated descendant species, as illustrated in Figure 1.1. Note that splitting induces further changes in the fitness landscape, so that eventually the two descendant species may come to occupy local fitness maxima. Such an outcome underscores that the splitting process itself is adaptive and that the eventually observed two niches do not pre-exist, but instead are generated by the very process of adaptive speciation. In asexual populations, splitting is the immediate consequence of disruptive selection operating at the fitness minimum (Chapter 4). In sexual populations, however, the splitting process is more complicated and requires some mechanism for assortative mating (Chapter 5).

The type of evolutionary dynamics illustrated in Figure 1.1, which comprises gradual convergence to a fitness minimum and subsequent adaptive splitting, has

been termed evolutionary branching (Metz *et al.* 1996; Geritz *et al.* 1998). In principle, any continuous trait can undergo evolutionary branching, but despite the intuitive appeal of the gold-rush metaphor, it is not clear *a priori* how ubiquitous evolutionary branching is expected to be. In fact, later chapters in this book show that many different evolutionary models that incorporate frequency-dependent interactions contain the seed for evolutionary branching (Chapters 4, 5, and 7; see also Boxes 9.5, 10.3, 13.3, and 14.3). Moreover, in these models evolutionary branching does not require fine-tuning of the parameters, but instead typically occurs for wide ranges of the parameters. Thus, evolutionary branching appears to correspond to a general process that can occur under a great variety of circumstances.

1.3 Adaptive Speciation in Context

In this book, evolutionary branching is probed as the main theoretical paradigm for adaptive speciation. In sexual populations, evolutionary branching, and hence adaptive speciation, can only occur if assortative mating can latch on to the trait under disruptive selection. In principle, this can happen in a number of different ways, either through direct selection for assortative mating or because assortativeness is linked to the diverging trait as a result of behavioral or physiological constraints. Such linkages can also occur if disruptive selection acts on mating traits themselves, for example through sexual selection or sexual conflict (Chapter 5). Once a population has converged to a fitness minimum, it often experiences selection for nonrandom mating.

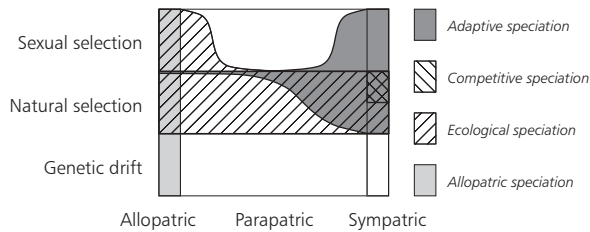
In the definition of adaptive speciation given above, the notion of selection encompasses both natural and sexual selection. In the literature, sexual selection is often pitted against natural selection. This convention goes back to Darwin and is meant to highlight a distinction between those causes of selection that exist without mate choice (natural selection) and those that only arise from its presence (sexual selection). We think that, in a general context, this division can mislead: mating traits under sexual selection are special life-history characters and are therefore subject to selection, like any other adaptive trait. In particular, the process of adaptive splitting is not restricted to ecological traits. Instead, adaptive speciation can involve different mixtures of ecological and mating differentiation: on the one extreme are asexual organisms in which speciation results only in ecological differentiation, and on the other extreme are sexual species with very pronounced assortative mating and only minimal ecological differentiation.

It is also worth noting that the scenario of adaptive speciation envisaged in this book contrasts sharply with traditional models for allopatric speciation. Even though selection may lead to divergence between allopatric subpopulations, selection is not disruptive in allopatric scenarios. Thus, in allopatric speciation the splitting may be a by-product of adaptations, but it is not an adaptation itself. This means that reproductive isolation does not evolve through selection for isolating mating mechanisms. Even though it is intuitively appealing to assume that genetic

incompatibilities leading to reproductive isolation are an inevitable consequence of prolonged evolution in allopatry, the mechanisms that underlie such incompatibilities are actually poorly understood (as are the ecological and genetic factors that determine the rates at which incompatibilities are expected to accumulate). The same conclusions, in essence, also hold for classic parapatric scenarios with limited gene flow. For example, in speciation models in which sexual selection generates evolutionary runaway processes with directions that differ between populations inhabiting different geographic locations, thus leading to speciation, at no point in time do the speciating populations experience disruptive selection. Thus, even though adaptation obviously plays an important role in such speciation processes, this scenario does not fall in the category of adaptive speciation as defined above, because it does not involve disruptive selection, and thus the splitting itself is not adaptive. Likewise, ecological speciation (Chapter 9) is defined as the consequence of adaptation to different resources or environments, without making explicit the role of frequency dependence in creating disruptive selection. Box 1.1 provides a systematic overview of the relations between adaptive speciation and other speciation concepts prevalent in the literature.

A final question with regard to the definition of adaptive speciation concerns the amount of ecological contact required for a speciation process to be considered adaptive. Since the definition is meant to distinguish speciation by natural and sexual selection from coincidental speciation as a by-product of, for example, spatial segregation, the minimal ecological contact needed for adaptive speciation should prevent, at the considered time scale, speciation by genetic drift and by pleiotropic effects of local adaptation. This also clarifies the relation between adaptive and parapatric speciation. Parapatric speciation occurs under conditions of spatial adjacency between two incipient species. Such a pattern, while it allows for some gene flow and mixing between individuals, may restrict these homogenizing forces to an extent that genetic drift or local adaptation may engender speciation. Alternatively, the spatial proximity in a parapatric setting may preserve the genetic cohesion within a species, and thus only allow for speciation by adaptive mechanisms. In consequence, parapatric speciation can be either adaptive or occur as a by-product of other processes.

The concept of adaptive speciation, of course, does not challenge the need to explain how speciating sexual populations overcome their genetic cohesion. It stresses, however, that there can be internally driven adaptive mechanisms that induce splitting and lead to the cessation of genetic exchange and interbreeding. This is in contrast to the external factors that are assumed to initiate allopatric speciation (although even in this it is believed to be relatively rare that the speciation process achieves completion without some internally driven adaptive mechanisms, such as reinforcement on secondary contact). We may therefore expect to gain a deeper understanding of the biological diversity that surrounds us by careful examination of the relevant forces of frequency- and density-dependent selection as they result from the biological interactions between individuals and their environment. In this

Box 1.1 Notions of speciation

Speciation processes can be broadly categorized by the patterns and mechanisms that underlie the diversification. While the schematic figure above is too coarse to accommodate all the subtleties and multiple stages that may be involved (Box 19.1), it conveniently highlights several basic distinctions. The horizontal axis discriminates between the pattern at the onset of the speciation process being allopatric, parapatric, or sympatric. It can be argued that speciation under fully allopatric or sympatric conditions (left and right columns, respectively) are limiting cases, which, in particular in the case of sympatric speciation, are probably encountered rarely in nature. Although most speciation processes may thus be parapatric (at least initially), they can differ greatly in the level of possible gene flow and ecological contact between the incipient species (from nearly allopatric cases on the left, to nearly sympatric cases on the right). The figure's vertically stacked rows discriminate between the three main mechanisms potentially involved in speciation: genetic drift, natural selection on ecological characters, and sexual selection on mating traits [mixed or layered cases (see Box 19.1) are not represented in the figure].

How can the various notions of speciation suggested in the literature be accommodated on this grid? Within the figure's horizontal rows, the curves describe the propensity for the alternative speciation processes to happen when the assumption about the underlying pattern passes from allopatric, through parapatric, to sympatric.

Adaptive speciation (dark gray region) occurs when frequency dependence causes disruptive selection and subsequent diversification, either in ecological characters (middle row) or in mating traits (top row). Adaptive speciation requires sympatry or parapatry and becomes increasingly unlikely when gene flow and ecological contact diminish toward the allopatric case. Yet, for adaptive speciation in ecological characters to proceed, sufficient ecological contact can, in principle, arise in allopatry, given that such contact is established by other more mobile species that interact with the two incipient species.

Allopatric speciation (light gray region; see Chapter 6) occurs in geographically isolated populations, through genetic drift (bottom row), pleiotropic consequences of local adaptation in ecological characters (middle row), or divergent Fisherian runaway processes in mating traits (top row). When isolation by distance is sufficiently strong (nearly allopatric cases), parapatric speciation can be driven by the same mechanisms as allopatric speciation.

continued

Box 1.1 *continued*

Ecological speciation (large hatched region; see Chapter 9) occurs when adaptation to different resources or environments induces divergent or disruptive selection. Ecological speciation can (a) proceed in allopatry, parapatry, or sympatry, (b) result from adaptations to different environments as well as from intraspecific competition for resources, (c) involve by-product reproductive isolation as well as reinforcement, and (d) include speciation through sexual selection. While this definition is meant to encompass all speciation processes driven by natural selection (middle row), ecological speciation by sexual selection (top row) requires the divergence of mating traits to be driven by adaptation to different environments [e.g., by sensory drive (Boughman 2002)], which becomes increasingly unlikely toward the sympatric case. The broad definition of ecological speciation means that such processes can occur through a wide variety of qualitatively different mechanisms.

Competitive speciation (small hatched region; Rosenzweig 1978) results from intraspecific competition in sympatry and leads to the establishment of a stable dimorphism of ecological characters involved in resource utilization. While competitive speciation is a special case of evolutionary branching and thus of adaptive speciation, the latter can also arise from noncompetitive interactions, in parapatry, and through disruptive selection on mating traits.

sense the time-honored debate as to the relative importance of allopatric and sympatric speciation may relax in its fervor as discussions shift to elucidate the roles of nonadaptive and adaptive speciation.

1.4 Species Criteria

So far, we have used the notion of species without the usual elaborate qualifications and definitions that tend to be attached to it. There have been so many controversies and misunderstandings about what species “are” that some biologists have become reluctant to engage in or even follow these debates. Also, the purpose of this book – to illuminate the role of selection, driven by intraspecific interactions, in speciation processes – does not seem to benefit too much from refined arguments about the underlying concepts of species. Yet, given the substantial literature that exists on this topic, a few clarifying remarks are in order.

The naive species concept of old refers to a group of individuals, the members of which are relatively similar to each other in terms of their morphology (interpreted in the broadest sense) and clearly dissimilar from the members of any other species that exist at the same time. Species defined in this way are nowadays called morphospecies. A different, though related, perspective is stressed in the concept of ecospecies, defined as groups of ecologically similar individuals that differ in their ecological features from other such groups (Van Valen 1976). As any change in the ecological role of an individual has to be caused by its morphological make-up (in the aforementioned broad sense), we may expect an almost one-to-one correspondence between morpho- and ecospecies.

Sexual populations that differ morphologically or ecologically, but in which the individuals do not differ in their abilities to mate with one another, will hybridize when they share the same habitat. This consideration led Mayr (1963) to replace the naive species definition with the concept of “biological” species: the gene flow of a “biological” species is isolated from that of other species by the existence of intrinsic reproductive barriers. However, consideration of the reverse case reveals a drawback of this species definition: it elevates to the species rank sexual populations that differ in their abilities to mate with one another, but otherwise do not differ morphologically and ecologically. Such ecological sibling species usually are unable to coexist stably when they share the same habitat. So, to adhere to the biological species concept may lead to numerous distinctions that are relevant when addressing very specific questions only. Other, more important, difficulties with the biological species concept arise from the practical problems of testing for interbreeding capacity under “natural conditions” and because the fossil record does not offer direct evidence of reproductive isolation. In addition, the definition of “biological” species does not readily apply to asexual organisms, such as bacteria or imperfect fungi, or to organisms that reproduce clonally, like some plants.

As the concept of biological species attracted increasing criticism, other ideas emerged concerning the specific features of species that could be singled out to define them. The genotypic-cluster species concept, introduced by Mallet (1995) as a direct genetic counterpart to the morphospecies concept, requires that gene flow between species be low enough and disruptive selection strong enough to keep the genotypic clusters separate from one another. The recognition species concept of Paterson (1985) defines species as groups of individuals that share a common fertilization system. The cohesion species concept of Templeton (1989) stresses the gene flow between individuals of a species and their ecological equivalence as characteristic features. Species concepts qualified by attributes like genealogical, phylogenetic, or evolutionary emphasize that individuals of a species share a common evolutionary fate through time, and thus form an evolutionary lineage.

This broad and, as it seems, rather persistent variety of perspectives suggests that some pluralism in species concepts is inevitable and must be regarded as being scientifically justified. The salient criteria championed – variously – by phylogenetic taxonomists, experimental plant systematists, population geneticists, ecologists, molecular biologists, and others legitimately coexist: there are many features in which species can differ and the choice of particular definitions has to be appropriate to the actual research questions and priorities of each circumstance.

For the discussions in this book, perhaps the genotypic-cluster species concept may be most illuminating. It clearly highlights the need for adaptation to counteract gene flow if speciation is to occur outside rigorously allopatric settings. Also, the emphasis of the cohesion species concept on ecological interactions in addition to conditions of reproductive isolation is a welcome contribution to a debate about the prevalence of processes of adaptive speciation. Yet, we believe that biologists can discuss fruitfully causes and mechanisms of speciation processes without reaching, beforehand, a full consensus about their pet species criteria. As pointed

out by de Queiroz (1998), such criteria often tend to differ in practice only in where precisely they draw the line between the one-species and the two-species phases of a particular speciation process. In this book we are interested in investigating how processes of speciation advance through time; drawing such lines is therefore not our primary concern.

1.5 Routes of Adaptive Speciation

We now outline some main adaptive speciation routes. As is well known, the ubiquity of frequency-dependent selection prevents the portrayal of evolution as a process of simple optimization. A trait combination that is best in an empty environment may become worst in an environment in which all individuals share that same trait combination. Similarly, directional selection can lead to trait combinations that, once adopted by a whole population, become the worst possible choice, so that selection turns disruptive. As explained above, this self-organized convergence to disruptive selection is the hallmark of evolutionary branching. It allows a phenotypically unimodal asexual population to become bimodal. According to the generally adopted criteria for asexual species, evolutionary branching can thus explain speciation in asexual populations.

In sexual populations, frequency-dependent selection can send evolving populations toward fitness minima. But in this scenario the genetic cohesion of sexual populations prevents their departure from such fitness minima – the continual creation of intermediate types by recombination usually makes it impossible for a randomly mating sexual population to respond to disruptive selection by becoming phenotypically bimodal. However, once individuals start to mate assortatively, the population can escape the trap. If individuals on each side of the fitness minimum happen to choose their partners from the same side, evolutionary branching also becomes possible in sexual populations.

Such assortative mating can come about in a number of ways; here we mention three different possibilities only. In the first scenario, assortative mating comes for free. Such a situation occurs when the ecological setting directly causes increased relative mating rates between partners on the same side of the fitness minimum. An example is the famous apple maggot fly. As a result of the strong spatial and temporal correlations between feeding preferences and mating opportunities, flies that have a slight preference for feeding on apples tend to mate more with partners of the same preference. The situation is analogous for flies with a slight preference for feeding on the traditional host plant, the hawthorn. In the second scenario, assortative mating may already be present, but may be based on traits other than those that vary across the fitness minimum. In such circumstances, the system for mate recognition and preference is already in place; it only has to be latched on to the right trait by the evolution of a genetic correlation. A third scenario is that the population is still mating perfectly randomly when it arrives at the fitness minimum. It can then be shown that such situations tend to give rise to positive selection pressures for the emergence of mate-choice mechanisms. Until assortative mating develops, frequency-dependent selection prevents departure of

the population from the fitness minimum, and thus keeps it under a regime of disruptive selection: there is thus ample time for any one out of the plethora of possible mechanisms of assortative mating to develop.

It seems possible that the actual prevalence of nonrandom mating is underrated currently, perhaps because of the widespread dominance of assumptions of panmixia in genetics teaching and modeling, and because of the practical difficulties in empirically testing for assortativeness driven by yet unknown cues. However, independent of any consideration of speciation, choosing a good healthy partner is never a bad idea. Moreover, animals in general have well-developed cognitive abilities, not the least because they often have to cope with interference competition from conspecifics. The need to recognize conspecifics and, even more so, the requirements of social and territorial behavior may easily jump-start the development of mate-recognition systems. Also, if in a group of sexual taxa the processes of adaptive speciation are not uncommon, some mate-recognition mechanisms will have evolved already during preceding speciation events.

The evolution of assortative mating in a population situated at a fitness minimum has some aspects in common with the reinforcement of postmating barriers by the evolution of premating barriers. Yet, concerns about the likelihood of reinforcement do not carry over to the evolution of assortativeness under evolutionary branching. When two only partially isolated species come into secondary contact after allopatric divergence, the time scale at which the underlying bimodal phenotypic distribution again becomes unimodal through the formation of hybrids may be far too short for the relatively slow evolution of premating barriers to take hold. Worse, in the absence of frequency-dependent selection, hybrids may not even experience a selection pressure toward reinforcement. By contrast, in an adaptive-speciation scenario, ecological differentiation between incipient species is regulated dynamically to arise on the same time scale as mate choice emerges. This means that the ecological traits and mating traits evolve in-step: at any moment of the diverging evolutionary process, the current degree of ecological differentiation is sustainable given the current degree of mating differentiation, while – and this is critical – increasing degrees of mating differentiation continue to be selected for.

Although the persistent coexistence of ecological sibling species in sympatry is not expected, under certain conditions processes of adaptive speciation may be driven mainly by sexual selection. In particular, in sexual populations that already have in place a refined system for mate recognition and for which the costs of assortative mating are low, the generation of ecological sibling species by evolutionary branching in mating traits is likely. Here assortativeness comes for free as the differentiating characters are the mate-choice traits themselves. After the initial convergence of a population toward those preferences that would guarantee maximal reproductive success in the absence of mate competition, disruptive selection may favor individuals that avoid this competition by expressing slightly different preferences (Chapter 5). If this occurs in both sexes, the diversity of sympatric sibling species that results from multiple evolutionary branching is only limited by the maximal resolution of mate recognition and the maximal variability

of mating signals. This diversity, however, is ephemeral if not accompanied by ecological differentiation or anchored on pronounced spatial heterogeneity in the habitat. And yet, for populations of sufficiently large size, a balance between rates of sibling speciation and extinction through ecological equivalence may lead to the persistence of sizable sympatric flocks of ecological sibling species. In such a situation the appearance of even relatively weak opportunities for ecological differentiation can lead, through evolutionary branching by natural selection, to a fast and bushy adaptive radiation.

1.6 Pattern and Process in Adaptive Speciation

At first sight it seems clear that adaptive speciation always occurs in sympatry and nonadaptive speciation in allopatry. This correlation between pattern and process can probably be expected to hold for a wide range of speciation events. Yet, there are exceptions. Clearly, chromosomal doubling and the emergence of polyploidy are processes of nonadaptive speciation that can take place in sympatry.

There may also be instances of adaptive allopatric speciation, as illustrated by the following hypothetical example. Imagine two disconnected populations of a clonal plant species that can defend itself against herbivory by the metabolism of secondary compounds, like alkaloids or tannins. In the absence of herbivores, both plant populations do not invest in defense. When, however, a mobile herbivore exploits the two plant populations, it pays for the plants to step up their defense. If plant populations in both patches do this by producing the same cocktail of secondary compounds, the herbivore may continue to exploit the two populations, albeit at a reduced level. If, however, one population presents the herbivore with a mixture of defense substances that differs from that adopted by the other population, that deviation will be favored by selection. This leads to the evolution of two different plant ecospecies by a process of adaptive allopatric speciation. The example shows that, in principle, ecological contact, although indirect, can occur in allopatry.

Keeping pattern and process clearly separated is also critical when considering speciation processes that progress via different phases, some of which occur in sympatry, and some in allopatry (Chapter 9; Box 19.1). Indeed, the traditional standard model of speciation, when combined with reinforcement, is already of such a type: postmating barriers emerge in allopatry and could be reinforced by the evolution of premating barriers in sympatry. Simply referring to such a two-stage process as allopatric speciation can be misleading. It is also possible that evolutionary branching in sympatry, followed by further phases of the same speciation process, leads to a biogeographic pattern of parapatry, or even allopatry. For example, we can think of a process in which ecologically differentiated sympatric populations start to latch on to those regions of a habitat with spatial variation to which they are adapted marginally better by a reduction in migration, which thus increases the assortativeness of mate choice. The segregated pattern that results from such a process may be misconstrued easily as evidence for nonadaptive speciation (Chapter 7).

As a last point it should be mentioned that present-day patterns may differ widely from those that occurred during the speciation process, which further complicates the task of inferring back from pattern to process.

1.7 Structure of this Book

The above discussion indicates that the interplay between pattern and process of speciation is potentially much more intricate (and interesting) than the common wisdom seems to suggest. This book is devoted to exploring adaptive speciation in theory and practice; we mean to investigate how far we can push the alternative paradigm. This means that, throughout the empirical parts of the volume, we as editors have strived to highlight the extent to which reported observations are compatible with scenarios of adaptive speciation. This effort must not be misconstrued as implying that in each of the analyzed systems adaptive speciation has been identified as the most likely scenario: such quantitative assessments are mostly still out of reach. Under these circumstances, we have encouraged the authors of this volume to bring out, as sharply as possible, the actual and potential links between their work and the notion of adaptive speciation. This is meant to enable our readers and colleagues to challenge the hypotheses championed in this book, and thus ideally encourage all of us to move forward toward a situation in which the espousal of alternative speciation mechanisms gradually ceases to be largely a matter of tradition and belief.

The book is divided into three parts. Part A outlines the existing theory of adaptive speciation. Part B confronts this theory with reality by exploring the extent to which the mechanisms implicated in models of adaptive speciation have been observed in natural systems. Finally, Part C moves to larger scales in space and time and examines how patterns of speciation inferred from phylogeographic or paleontological data can give insight into the underlying mechanisms of speciation. As we try to show in this book, adaptive speciation is not only an entirely plausible theoretical scenario, but the underlying theory also offers intriguing new perspectives on speciation processes. To make this explicit we start the book with an outline of the theory of adaptive speciation, and thus set the stage for the remainder of the book.

In Part A, recent theoretical developments on adaptive speciation, based on the framework of adaptive dynamics, are discussed in detail. To put matters into perspective, Part A also contains overviews of the classic approaches to modeling sympatric, parapatric, and allopatric speciation. The part ends with Chapter 7, which attempts to synthesize pattern-oriented and process-oriented approaches to understanding speciation through the study of adaptive speciation in geographically structured populations. Chapter 7 shows that parapatric patterns of species distributions may result from intrinsically sympatric ecological processes and provides new perspectives on the role of geographic structure in shaping speciation processes.

Empirical investigations of speciation are often hampered by the problem of long generation times in the organisms under study. Indeed, speciation theory has

too often succumbed to speculation, partly because of the paucity of direct empirical tests of hypotheses about mechanisms of speciation. It is therefore imperative to strive for empirical, and in particular experimental, tests of the hypothetical driving forces behind speciation processes. Part B provides an array of examples of natural systems in which mechanisms of frequency-dependent disruptive selection and/or mechanisms of assortative mating are likely to operate. Such systems include fish flocks in young lake systems, insects in the process of host switching or increased specialization, and plants interacting with their pollinators. Perhaps microbes are the class of organisms most amenable to direct observation of the whole process of adaptive diversification originating from a single ancestor. Part B thus ends with an outlook on the great promise that experimental evolution in microorganisms holds for direct empirical tests of hypotheses on adaptive diversification.

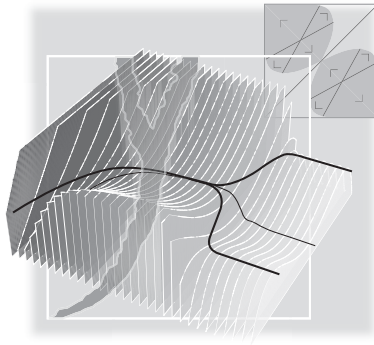
Since direct empirical tests are laborious and time consuming, processes of speciation are often inferred from data gleaned from natural speciation experiments, as reflected in phylogeographic patterns and in time series pried from the fossil record. In particular, many closely related species show little overlap in their ranges, which suggests, at first sight, their allopatric origin. However, models of adaptive speciation in geographically structured populations indicate that things may not be that simple, because processes of adaptive speciation under conditions of ecological contact may result in parapatric (and, in the longer run, even allopatric) patterns of species abundance. Thus, extant patterns are not necessarily good indicators of the past processes that brought them about. Moreover, since processes of adaptive speciation are expected to unfold relatively fast on a paleontological time scale (Chapter 18), the conditions under which a phylogenetic split actually occurred may have changed drastically after long periods of subsequent divergence. It is therefore important to interpret phylogeographic patterns in light of the dynamic, and potentially multilayered, nature of speciation processes, and to pay attention to the appropriate time scales. The chapters in Part C examine what phylogeographic or paleontological patterns can tell us about processes of speciation. These chapters show that many of the patterns that arise in a diverse array of taxa are consistent with adaptive speciation processes, and that in many cases adaptive speciation may provide a more parsimonious interpretation of the phylogeographic patterns than does allopatric speciation.

This book has an agenda. We hope to convince the reader that adaptive speciation through frequency-dependent interactions under conditions of ecological contact is a plausible, and perhaps even ubiquitous, evolutionary process. This view is supported both by detailed theories of adaptive diversification and by a growing body of empirical data on patterns and processes of speciation. In our view, the time has come to do away with the notion that allopatric speciation is true until proved wrong, an idea that may prevail mainly because of the deceptive simplicity of allopatric scenarios and the towering scientific stature of its initial proponents. However, how well a mechanistic theory describes reality has little to do with its mathematical complexity; if anything, more detailed theories would appear to be more reliable. On this basis, we think that adaptive speciation should

be viewed as an equally valid null hypothesis. Once the bias toward detecting allopatric speciation in empirical data is removed, the data may actually suggest adaptive speciation as the more likely explanation of many speciation events. We hope that the perspectives put forward in this book will spark new empirical work specifically designed to test hypotheses of adaptive speciation. Overall, we hope to contribute to an intellectual process, vaguely akin to adaptive diversification itself, by freeing research on species formation from the constraint of always having to view speciation processes through the allopatric lens. The formation of new species appears to be more complex, and also more fascinating, than the traditional view suggests. Thus, a plea for pluralism: an open mind and a diverse array of perspectives will ultimately be required to understand speciation, the source of our planet's biodiversity.

Acknowledgments We are indebted to Agusti Galiana for drawing our attention to the quote by Mayr (1982, p. 565) and to Menno Schilthuizen for highlighting the relation between adaptive speciation and the quote by Darwin (1859, p. 155). Franjo Weissing and Sander van Doorn provided valuable assistance in improving the clarity of this chapter.

Part A
Theories of Speciation



Introduction to Part A

Theories of speciation, in the past often couched in verbal terms, should explain how ecological divergence and genetically determined reproductive isolation evolve between lineages that originate from single, genetically homogeneous ancestral populations. As Will Provine highlights in Chapter 2, the predominant perspective for a long time was that reproductive isolation emerges as a by-product of other evolutionary processes, through the incidental accumulation of genotypic incompatibility between related species. It is easiest to imagine that such incompatibilities arise when subpopulations become geographically isolated and henceforth evolve independently: genetic distance between them is then expected to increase with time. Thus, “given enough time, speciation is an inevitable consequence of populations evolving in allopatry” (Turelli *et al.* 2001). On a verbal level this theory of allopatric speciation appears both simple and convincing. This apparent theoretical simplicity has contributed to the view that the allopatric mode of speciation is the prevalent one – a perspective that has found its most prominent advocate in Ernst Mayr (Chapter 2).

Unfortunately, not only is the simplicity of the usual accounts of allopatric speciation based on the poorly understood concept of genetic incompatibility, but simplicity in itself is no guarantee for ubiquitous validity. Other plausible, but theoretically more intricate, mechanisms for the evolution of reproductive isolation in the absence of geographic isolation have been proposed. Recent approaches have focused attention on adaptive processes that lead to ecological and reproductive divergence as an underlying mechanism for speciation processes – a change in emphasis that occurred concomitantly with a shift in biogeographic focus from allopatric scenarios to parapatric speciation between adjacent populations or fully sympatric speciation. This was foreshadowed by the idea of reinforcement (the evolution of prezygotic isolation through selection against hybrids) and has culminated in theories of sympatric speciation, in which the emergence and divergence of new lineages result from frequency-dependent ecological interactions. Such interactions can induce disruptive selection, which in turn generates indirect selection for a proper choice of mates and thus leads to prezygotic isolation. While these theories of adaptive speciation can also be described verbally, the involved mechanisms are more intricate than those of the basic allopatric scenario. This does not imply that adaptive speciation is an unlikely evolutionary process: it can even be argued that the explicit and detailed inclusion of ecological interactions as driving forces of evolutionary change renders these speciation models more convincing than the purely verbal models.

Part A of this book outlines the existing theory of adaptive speciation. Overviews of the classic approaches to modeling sympatric, parapatric, and allopatric speciation are added for perspective. The material in this part shows that

adaptive speciation is a theoretically plausible scenario, and thus sets the stage for the remainder of the book. The most recent theoretical developments on adaptive speciation, based on the framework of adaptive dynamics, are discussed in detail. In these models, evolutionary dynamics are derived explicitly from ecological interactions between individuals. These interactions often result in frequency dependence, and the populations evolve such that they end up at fitness minima, even though they are continually climbing the fitness landscape. During such processes disruptive selection on metric characters emerges gradually and dynamically. This extends traditional ecological theories of sympatric speciation, which descend from the early models of Maynard Smith (1966) and deal with small numbers of alleles and discrete resources or habitat types. To put matters into context, Part A begins with an overview of this classic work on sympatric speciation.

In Chapter 3, Kawecki first reviews models in which protected polymorphisms can arise from density-dependent competition for two discrete resource niches. In some special scenarios, divergent sexual selection alone can lead to reproductive isolation under sympatric conditions, even in the absence of disruptive ecological selection. Disruptive selection creates the conditions for the evolution of assortative mating, which can be based directly on the ecological character under disruptive selection or on selectively neutral traits that enter into linkage disequilibrium with the ecological trait. In the former case the evolution of assortative mating is more likely than in the latter, a line of thought that is taken up again in Chapter 5. Chapter 3 concludes by discussing divergent mate choice that evolves as a by-product of habitat preference, which may be an important mechanism for sympatric speciation through the evolution of divergent host races in insects. The theoretical work discussed in this chapter “will hopefully change the still prevailing attitude that speciation is allopatric until proved sympatric” (Chapter 3, Concluding Comments). This hope is fostered further by recent developments discussed in the subsequent chapters, which take a dynamic perspective on the emergence of disruptive selection and show that a wide range of circumstances makes adaptive speciation a likely event.

In Chapter 4, Geritz, Kisdi, Meszéna, and Metz discuss implications of the recently developed adaptive dynamics framework for the study of speciation mechanisms. In contrast to traditional models of sympatric speciation, adaptive dynamics typically describes the evolution of continuously varying traits or metric characters. For speciation to occur, a population must retain genetic variation under the sustained action of disruptive selection. Without frequency-dependent selection such variation is rapidly lost. By starting at the ecological end, adaptive dynamics models highlight that frequency dependence is not only ubiquitous, but often drives evolving populations to trait combinations at which selection turns disruptive. Frequency dependence can continually reshape the fitness landscape in ways that, after a persistent uphill climb toward so-called evolutionary branching points, the population finds itself at a fitness minimum. Under such conditions clonal populations become dimorphic, with the trait values in the resultant phenotypic branches diverging. This provides a basic paradigm for evolutionary diversification.

In randomly mating Mendelian populations, divergence through evolutionary branching is prevented by recombination: abundance gaps between incipient phenotypic branches are jammed by hybrids. This prevents populations from becoming phenotypically bimodal and instead stabilizes them at the branching point. Chapter 5 by Dieckmann and Doebeli explains how Mendelian populations can undergo evolutionary branching despite this apparent obstacle: at the branching point assortative mating is selected for and, once this has become sufficiently strong, evolutionary branching can proceed. The chapter also presents an overview of the ecological interactions between species that have been shown to cause evolutionary branching. By exploiting an analogy between evolutionary branching driven by natural versus sexual selection, how frequency-dependent disruptive selection can originate either from competition for resources or from competition for mates is explained. The chapter closes with an assessment of the strengths and weaknesses of current models of adaptive speciation through sexual selection and sexual conflict.

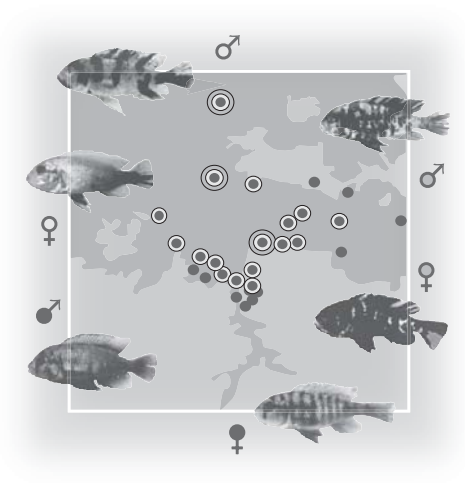
Chapter 6 reviews theories of allopatric and parapatric speciation and thus helps to contrast models of these speciation modes, predominantly based on the effects of presumed genetic incompatibilities, with models of adaptive speciation occurring under fully sympatric conditions. By describing how processes of gradual evolution and speciation unfold on adaptive landscapes, Gavrilets provides a unifying account of existing approaches to explain the emergence of reproductive isolation between geographically segregated subpopulations. While evolution on rugged adaptive landscapes would appear to result readily in subpopulations that occupy different adaptive peaks and thus become genetically isolated, selection against descent into adaptive valleys renders such outcomes unlikely. This problem is overcome on adaptive landscapes that feature extended networks of selectively neutral ridges along which evolution by genetic drift proceeds unimpeded. After extending the classic model by Bateson, Dobzhansky, and Muller to genetic architectures with multiple alleles or loci, the chapter ends with a discussion of how different spatial population structures affect evolutionary waiting times for reproductive isolation.

Chapter 7 establishes a link between two important aspects of speciation theory: biogeographic patterns of species distributions and frequency-dependent ecological processes that induce disruptive selection. Linking pattern and process in such a manner, Doebeli and Dieckmann investigate conditions for evolutionary branching in spatially structured populations. Under localized competitive interactions, evolutionary branching occurs much more easily than in nonspatial models, because local adaptations along environmental gradients lead to increased frequency dependence. The chapter also highlights how sympatric evolutionary branching often generates patterns of species abutment, reminiscent of parapatric or allopatric speciation scenarios. This suggests that the classic controversy between allopatric and sympatric speciation may often be ill posed: what eventually appears to be an allopatric (or parapatric) pattern of species distribution may well

have been generated by an intrinsically sympatric evolutionary process that results from frequency-dependent ecological interactions. The model presented also suggests an explanation as to why larger areas have higher speciation rates: the likelihood for adaptive speciation increases when ecological interactions are more localized relative to the spatial scale of environmental heterogeneities.

Parts B and C of this book show that, already, a respectable body of empirical work indicates that adaptive speciation occurs in natural systems. Understanding the theoretical underpinnings of speciation, to which Part A contributes, is indispensable for carrying out and interpreting these empirical studies.

Part B
Ecological Mechanisms of Speciation



Introduction to Part B

The theoretical studies reviewed in Part A give credence to the expectation that processes of adaptive speciation will be encountered in nature, under a wide range of circumstances. Part B confronts these ideas with reality and explores the extent to which the mechanisms implicated in models of adaptive speciation have been observed:

- What mechanisms of frequency-dependent disruptive selection operate in particular systems?
- What mechanisms for the development of assortative mating are available in principle, and which ones have been recognized operating in actual systems?

To observe these mechanisms in action requires systems with two crucial features: they must be sufficiently accessible in all their parts, and they must be caught at suitable stages of speciation. The latter is only effectively possible when speciation is happening in the wake of recent environmental change.

This combination of prerequisites leads one immediately to think of bacteria as the only group of organisms for which the full processes of speciation can be studied in the laboratory in ways that allow all the subprocesses involved to be discerned (Chapter 14). Somewhat unfortunately, however, bacteria have a rather different kind of sex than higher organisms, and hence are not the ideal test bed for those theories of speciation targeted at the latter. Chapters on higher organisms – reproducing sexually and showing all the intricate behavior that appeals to watchers of nature documentaries – are therefore the primary focus of Part B. Only a few such systems conform to the requirements laid out above: the immediate candidates include fish flocks in young lake systems (Chapters 8, 9, and 10) and insects in the process of host switching, or increased specialization, as a result of recent changes in agricultural landscapes (Chapters 11 and 12). For plants, with their intricate relationships between flowers and pollinators, no studies have yet found systems in the process of adaptive speciation. Nevertheless, the mechanisms that drive such processes are present in principle, although they can only be documented indirectly (Chapter 13). The following chapters impart our taste buds with a healthy mix of the expected and the weird, as only nature can provide.

Part B begins with a discussion of the haplochromine cichlids in the African Great Lakes, well known for their extremely fast adaptive radiation. In Chapter 8, van Alphen, Seehausen, and Galis discuss the mechanisms that are believed to have caused this spectacular diversity. They argue that the primary reason for the speed and extent of the radiation is the potential for fast speciation through sexual selection. Two possible mechanisms are identified: local heterogeneity in ambient lighting that interacts with mate choice based on color patterns, and continual need for rescue from a sex-ratio distorter that operates in a complicated genetic

interaction with some color-pattern genes. The resultant high degrees of assortative mating provide a fertile substrate for repeated adaptive radiation driven by resource competition and facilitated by the versatility of the cichlid jaw apparatus.

Whereas the tropics are interesting for their great riches in biodiversity and in mechanisms for niche separation and ensuing speciation processes, the far north has the advantage that it provides an abundance of near replicas of young lakes with relatively simple ecologies. This abundance is explored in Chapters 9 and 10.

Chapter 9 describes one of the cornerstones of empirical research on adaptive divergence and speciation: the three-spined sticklebacks in postglacial lakes of British Columbia. Rundle and Schluter investigate the role of selection and divergent adaptation for the evolution of reproductive isolation between limnetic and benthic species pairs. They envisage a scenario in which a phase of allopatric divergence between lacustrine and marine forms is followed by secondary invasion of the marine form, after which divergence and reproductive isolation evolve in sympatry because of ecological and reproductive character displacement. Evidence for a role of natural selection in this process comes from experiments that show premating isolation to be determined by phenotypic rather than geographic distance. Additional experiments have shown that benthic females in coexistence with limnetics demonstrate a higher degree of preference for benthic males than do solitary benthic females. These findings indicate that disruptive selection on ecological and mating traits was important for the evolution of reproductive isolation in lake sticklebacks, and thus provides evidence of processes thought to occur during adaptive speciation.

In Chapter 10, Snorrason and Skúlason take a wider view on the adaptive speciation of northern lake fish, with an emphasis on charr. Molecular evidence suggests that similar radiations have occurred on various occasions and at more than one locality. Ecologically, these radiations can be seen as genetic assimilations of resource polymorphisms. The great variety in lake types and ages allows replications of equivalent processes with regard to time and ecological conditions, the latter described by habitat diversity and environmental stability. From this, a scenario emerges in which developmental plasticity dominates in unstable environments and is replaced by genetic differentiation in stable environments. How the latter is aided by assortative mating through differentiation in spawning grounds or spawning time turns out to depend on the opportunities offered by the lake topography; where these options are not available, size-dependent mate choice has evolved.

Insects comprise the largest number of described species. In Chapter 11, Bush and Butlin suggest that resource specialization, in particular among phytophagous insects, is a major pathway for adaptive speciation in insects. Reproductive isolation can arise from co-speciation with the host, from allopatric speciation with or without host shift, or from sympatric speciation. The best-studied case of the latter class is sympatric speciation in the fruit fly *Rhagoletis pomonella*. The host shift in this case occurred very recently and reproductive isolation was achieved by assortative mating on the different host plants. The new host races maintain

distinct gene pools, in spite of a considerable amount of ongoing gene flow, which indicates strong selection against hybrids. The authors use this example to discuss major general issues of sympatric speciation, such as preference and performance, negative trade-offs, and reinforcement.

Adaptations of phytophagous pests to agricultural plants provide other excellent opportunities to study mechanisms of incipient differentiation and adaptation. In Chapter 12, Egas, Sabelis, Vala, and Lesna highlight aspects of such systems that facilitate adaptive speciation. Herbivorous arthropods display preferences toward hosts, which translate into mate-choice preferences. Learning can play an important role, as it retards stabilizing selection and enhances disruptive selection. Also, infection by *Wolbachia* bacteria, which results in cytoplasmic incompatibilities for certain mating combinations, can ease speciation. Taken together, this complex of factors promotes adaptive speciation in phytophagous pests, which may be one of the explanations for the observed fast emergence of new pest species.

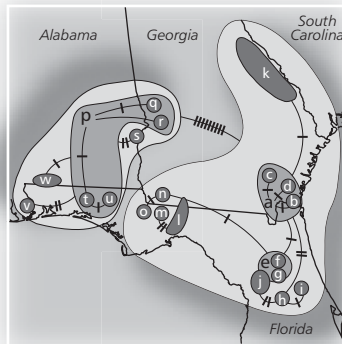
Processes of speciation in plants, and in particular in angiosperms, are influenced by their interaction with pollinators. In Chapter 13, Waser and Campbell discuss various relevant mechanisms. First, flower morphology can adapt to locally available pollinators, a process that could lead to reproductive isolation and character displacement upon secondary contact. Second, when the distribution of pollinator phenotypes acts as a resource-availability spectrum, frequency-dependent competition for pollinators could drive evolutionary branching according to an adaptive speciation scenario. Alternatively, reproductive isolation may arise as a pleiotropic by-product of local plant adaptation, which could occur under conditions of close spatial proximity and would also depend on the behavior of the pollinators. Reciprocal plant-transplantation experiments are expected to better elucidate and discriminate between these mechanisms.

To study experimental evolution in microorganisms may be the only viable approach to observing entire processes of speciation. In Chapter 14, Travisano reviews evolution experiments in bacteria that study the emergence of diversity out of genetically homogeneous ancestral populations. Allopatric divergence is investigated in experiments in which replicate populations are reared separately under identical environmental conditions. This reveals parallel evolution in traits that are highly correlated with fitness, whereas divergence in other traits is driven by genetic drift and historical contingency. Sympatric divergence is observed in experiments in which trade-offs in glucose metabolism result in specialization on either glucose or its breakdown products. Sympatric divergence is also observed when frequency-dependent selection for differential resource utilization leads to the evolution of three novel bacterial types from a single ancestral strain. These results underscore the role of experimental evolution as a promising tool in the study of adaptive diversification.

The chapters in this part highlight that there clearly is more to adaptive speciation than theorists could imagine, even in their wildest dreams.

Part C

Patterns of Speciation



Introduction to Part C

Part A presents the theory of adaptive speciation and Part B describes natural systems for which speciation mechanisms can be assessed. Part C goes one step further and looks at the distribution patterns of populations and species that have the potential to shed light on the underlying mechanisms. At first sight it may seem counterintuitive to examine phylogeographic patterns as evidence for adaptive speciation under sympatric conditions, since such patterns are usually taken to prove the prevalence of allopatric speciation mechanisms. However, when interpreting observed distribution patterns it is necessary to account for the dynamic nature of the speciation process: as shown in Chapter 7, adaptive speciation along an environmental gradient can lead to species abutment. It is also critical to pay attention to the appropriate time scales: most phylogeographic studies deal with time horizons of millions of generations after the initial splits, while the theory of adaptive speciation suggests that the split of populations may occur within thousands of generations. The ecological and spatial conditions under which the split actually occurred are very likely to be eradicated after such long divergence times.

There is a further argument for the study of distribution patterns. Although speciation can occur relatively fast, it is still too slow to be replicated easily in the laboratory, at least for sexually reproducing populations. Similarly, experimental interference in natural settings is problematic, since such action is likely to alter the prevailing ecological conditions and thus disturb those processes that drive the split. This can only be avoided by studying natural experiments of recent speciation that started some time ago and are now waiting to be analyzed by comparing model predictions with observed patterns. While phylogenetic history and time frames of population divisions can be studied by molecular techniques, trends in morphology and population distribution have to be assessed through paleontological analysis.

Part C features four chapters that deal with different aspects of phylogeographic patterns and their analysis. The first chapter highlights the connection between speciation pattern and process, with particular emphasis on the relevant time frames (Chapter 15); the other three chapters focus, respectively, on examples in animals, plants, and paleontology (Chapters 16 to 18). Example systems were chosen so as to discuss the relevant patterns in conjunction with insights into ecological settings. It must be stressed, however, that research on these systems has, so far, not been carried out to test adaptive speciation theory. We therefore much appreciate that all these authors discuss their findings in the light of adaptive speciation theory, although clear distinctions between alternative speciation scenarios cannot be drawn until more detailed data have been collected.

Chapter 15 by Tautz discusses a framework in which to apply molecular techniques to the study of phylogeographic patterns. A four-phase model is suggested to characterize the processes of population subdivision that result from adaptive

speciation; each such phase is defined by a combination of morphological and molecular characteristics. This analysis highlights that differential predictions for different speciation scenarios arise for the earliest phases of subdivision, which should therefore become a preferred target of analysis in future studies. Distinctions between the four phases are illustrated for specific natural examples and a point is made that even the phylogeographic patterns found for late phases of population subdivision may sometimes be explained more easily by adaptive speciation.

An excellent example of differential adaptation and speciation are the *Anolis* lizards on Caribbean islands. Chapter 16 by Thorpe and Losos discusses these systems. Between them, Thorpe, Malhotra, Stenson, and Reardon describe the situations found on the small islands of the Lesser Antilles. Few within-island speciation events have occurred, but often very different ecotypes of the same species have adapted to different habitats. Translocation experiments and common-garden experiments show that these ecotypes are determined genetically and do not result from phenotypic plasticity. Some of the adaptations correlate with molecular differentiation, while ongoing gene flow is found for other pairs of types. Losos examines the situation on the larger islands of the Greater Antilles, which is characterized by evidence for many within-island speciation events. Intriguingly, highly visible signals for assortative mating have evolved in these lizard species (which include differently colored dewlaps, as well as display behaviors) that are not found on the Lesser Antilles. A joint conclusion section reflects ongoing discussions by the experts. While some discrepancies in interpretation may result from different approaches and criteria, it is clear that the *Anolis* system lends itself to tests of adaptive speciation scenarios that will have to be carried out in the future.

Stunning patterns of convergent adaptation and speciation in plants have been observed for giant senecios and lobelias on African mountains; these are described by Knox in Chapter 17. High mountains scattered across Central and East Africa have been compared to “islands in the sky”. Molecular and morphological analysis of the colonization and speciation history has revealed that more than half of the speciation events occurred on individual mountains. More than a dozen species and subspecies are known for each taxon – these must have evolved within only one million years in the senecios and within only a few million years in the lobelias, which suggests that differential adaptation and speciation can be fast, even for perennial plants. Different species of the same taxon abut each other in altitudinal steps, a spatial pattern reminiscent of that described in Chapter 7.

The application of paleontological methods to infer the history of evolutionary diversification is described by McCune in Chapter 18. Straddling the Triassic–Jurassic boundary, the Newark rift lakes in eastern North America underwent repeated cycles of dessication and refilling over a period of 20 000 years. This resulted in a fossil record with an exquisite time resolution down to single years and provides replicas of adaptive radiation in Semionotid fish. Semionotids were encased by heavy scales that fossilized well, and the record reveals a large variety of body shapes, suggestive of ecological diversification. Studies of the lake

with the best fossil record showed that the radiation was extremely fast initially, comparable to that of Lake Victoria cichlids, and slowed down substantially later on. For the initial radiation phase, some fairly wild variations in the dorsal ridge scales have also been documented. Both patterns are best explained by a scenario of adaptive sympatric speciation.

Chapters in this part look at adaptive speciation with different experimental and conceptual approaches and emphasize different and sometimes conflicting points of view. It becomes clear that in future studies data acquisition and analysis must be geared toward testing alternative speciation scenarios, much more than is possible with the data currently available. Analyses of the phylogeographic patterns shaped by natural experiments promise a high potential in the study of dynamic processes and ecological mechanisms that lead to population subdivision.

19

Epilogue

Ulf Dieckmann, Diethard Tautz, Michael Doebeli,
and Johan A.J. Metz

When Terry Erwin from the Smithsonian National Museum of Natural History examined the diversity of beetles that lived on a single species of tropical trees, he found 682 different beetle species, 163 of which he classified as specialist species that lived exclusively on the particular tree species used in his study. Since there are around 50 000 tropical trees species, Erwin extrapolated that there must be on the order of 7 million specialist beetle species (Erwin 1982). Using similar extrapolations, Erwin (1982) also estimated the total number of tropical arthropod species as about 30 000 000. While these estimates may be too high (Schilthuizen 2000; Ødegaard 2000; Novotny *et al.* 2002), they are mind-boggling nevertheless and serve as an illustration of the incredible amount of species diversity that exists on our planet: estimates for the total number of extant species of plants and animals range from 10 million to 100 million (May 1990; Schilthuizen 2000). It is also estimated that the number of extant species represents only about 1% of the total number of species that ever existed during the history of life on earth. Together with the common phylogenetic ancestry usually inferred for the tree of life for higher organisms, this implies that speciation must have been truly rampant during the creation and evolution of our biosphere.

Indeed, there was ample space and time for the evolutionary generation of diversity. After all, the past 3.5 billion years, during which life presumably evolved from some self-replicating molecules, has seen large-scale geographic changes, including the rise, shift, and disappearance of continents and oceans. For example, the fauna and flora of Australia is in many ways very different from that of any other place in the world, presumably because of the long-lasting geographic isolation of this continent from other landmasses.

19.1 The Allopatric Dogma

By scaling down to smaller geographic areas, one arrives at the allopatric speciation model. According to this perspective, speciation occurs when subpopulations of a single ancestral population become geographically isolated and embark on different evolutionary trajectories. During separate long-term evolution in geographic isolation, reproductive isolation evolves as a by-product of divergence in other aspects of an organism's phenotype or genotype. When, at some later point in time,

secondary contact occurs between the diverging species, so that their ranges overlap again, hybrid inferiority may reinforce reproductive isolation, but the primary cause of speciation in this scenario remains long-term geographic isolation.

Prominent evolutionary biologists, such as Theodosius Dobzhansky and Ernst Mayr, strongly promoted this type of speciation as the main mode of evolutionary diversification, to the point of ridiculing alternative scenarios, as evidenced by Dobzhansky's remark that sympatric speciation, that is, speciation unfolding in the absence of geographic isolation, "is like the measles; everyone gets it and we all get over it" (Bush 1998). Indeed, it is now the widely accepted common wisdom that most evolutionary diversification occurred according to the allopatric speciation scenario.

However, even though allopatric speciation, with its apparent simplicity, is an intuitively appealing idea, a number of problems reveal themselves upon closer inspection. For one thing, allopatric speciation is not really simple conceptually, because the mechanisms that underlie the evolution of reproductive isolation as a by-product of divergence in other traits are understood only poorly, both empirically and theoretically. In particular, some closely related species (e.g., North American and European buffaloes) have evolved in allopatry for millions of years, but readily interbreed when brought into contact. Moreover, other species, such as oak, have long evolved in sympatric ranges and clearly maintained their phenotypic and genetic identity, yet they can interbreed easily. It seems, then, that by-product reproductive isolation is a far more complicated concept than implied by allopatric speciation theories. It is also commonly acknowledged that – except when driven by sexual arms races (Schilthuizen 2001) – allopatric speciation is a very slow process, because it involves neither inherent selection for differentiation, nor selection for isolating mating mechanisms. This, combined with need to postulate billions of geographic events to create the isolation between subpopulations of ancestral species, casts serious doubts on the ubiquity of allopatric speciation.

19.2 Adaptive Speciation

Perhaps the most convincing counterarguments against the supreme rule of allopatric mechanisms come from theoretical developments which show that speciation in sympatry, that is, under conditions of ecological contact, is an entirely plausible evolutionary scenario. Models of adaptive speciation show that many types of frequency-dependent biological interactions can readily cause the dynamic emergence of disruptive selection in an evolving population, and disruptive selection can in turn readily induce adaptations that result in diminished gene flow between sympatrically diverging subpopulations. Part A of this book is devoted to explaining the theory of adaptive speciation in some detail. The theory is developed within the framework of adaptive dynamics, and is based on the phenomenon of evolutionary branching. The basic notions used in this theoretical framework for the study of evolutionary dynamics in phenotype space are explained in Chapter 4, which focuses on asexual populations. Combining this with population genetic

modeling leads to a fully fledged theory of adaptive speciation in sexual populations, both under completely sympatric conditions (Chapter 5) and in geographically structured populations with spatially localized gene flow (Chapter 7). The models presented in Part A of this book show that adaptive speciation under sympatric conditions can no longer be dismissed on theoretical grounds.

The theory of adaptive speciation advanced here arises from a confluence of earlier developments. In particular, the notion that frequency-dependent selection can induce sympatric speciation has been highlighted already in previous models, based on the assumption that reproductive isolation can be pleiotropically induced by adaptation to different local habitats. These Levene-type models are reviewed in Chapter 3, and many of them are, in turn, based on one of the early paradigms of sympatric speciation: host shifts and host-race formation in insects (Bush 1969; Feder 1998). The theory of adaptive speciation extends these early models by showing that disruptive selection does not occur only under rather special assumptions about pleiotropic fitness interactions in two different habitats. Rather, the dynamic emergence of disruptive selection during the course of gradual evolution is a robust consequence of frequency-dependent interactions of many different kinds, including all the basic types of ecological interactions, as well as interactions that lead to sexual selection and sexual conflict (Chapter 5). That frequency-dependent ecological interactions can often lead to the dynamic emergence of fitness minima has been foreshadowed in earlier work (Rosenzweig 1978; Eshel 1983; Taylor 1989; Christiansen 1991; Brown and Pavlovic 1992; Abrams *et al.* 1993a), but until recently neither its ubiquity nor its significance for the theory of speciation had been appreciated fully.

This may, in part, arise from the focus on studying the mean and variance of quantitative genetic traits (Lande 1979b), an approach that makes it difficult to model evolutionary processes through which the trait's frequency distribution can become bimodal. Also, when approaching the problem from the population genetics' aspect, the simplifying assumptions turn out to be restrictive. Study of the evolution of isolating mating mechanisms in Levene-type models with deterministic dynamics that involved at most a few loci had initially cast doubt on the feasibility of sympatric speciation (Felsenstein 1981; Seger 1985a), and thus reinvigorated the case for allopatric speciation. In rather stark contrast, individual-based stochastic models of adaptive dynamics that incorporate multilocus genetics reveal that the evolution of various types of isolating mating mechanisms occurs generically and with relative ease once disruptive selection has emerged dynamically in a sexual population.

We thus see the theory of adaptive speciation as an extension of this earlier work, based on a less restrictive genetic modeling of reproductive processes, as well as on advances in our understanding of the ecological causes of evolutionary diversification that result from an integrated approach to phenotypic evolution under frequency-dependent selection. These developments have led to a unifying framework for theoretical investigations of adaptive diversification, which may challenge the perception of allopatric speciation as the only viable scenario.

19.3 Diversity of Speciation Processes

Freeing research on species formation from the straitjacket imposed by considering such processes allopatric unless unequivocally proved otherwise refocuses our attention onto the great richness and exciting complexity of speciation processes. To appreciate this richness it must be recognized that speciation processes – far from being the single events they present themselves as to the evolutionary taxonomist – have a temporal and spatial extension that allows them to involve multiple phases in time and/or multiple domains in space. In particular, species may originate against a background of allopatric, parapatric, and sympatric distribution patterns, and the results of such a pattern-oriented classification may differ when applied to successive stages of the speciation process. The same holds for the process-oriented distinction between adaptive and nonadaptive mechanisms of speciation: here, too, the classification may differ between stages, or possibly even between domains, of unfolding speciation dynamics. In general, the perception of speciation as a potentially multilayered process offers a healthy antidote against becoming caught up in semantic controversies about rigid dichotomies.

We are thus compelled to be more pragmatic about the classification of speciation processes, because it is unlikely that the complexity of these processes can be captured in a single binary distinction. The long-standing debate as to the prevailing mode of speciation focused primarily on spatial patterns of population distributions and championed nonadaptive mechanisms of speciation (genetic drift, or separate local adaptation to disconnected habitats with pleiotropic implications for reproductive isolation). In this traditional view, reproductive isolation emerges as a by-product of other factors and is not by itself adaptive. By contrast, many chapters in this book illustrate how reproductive isolation can be selected for directly through natural and sexual selection. This alternative view incorporates processes of reinforcement as special cases that can occur after a primary allopatric phase has already created a situation of partial reproductive isolation, which is brought to completion through selection against hybrids and for assortative mating. Discussions in this volume highlight that a primary allopatric phase is entirely dispensable: reproductive isolation can also be selected for in continual sympatry.

This leads to the conclusion that we can characterize speciation processes adequately only by utilizing various dichotomies complementarily: allopatric versus sympatric, nonadaptive versus adaptive, speciation driven by natural versus sexual selection, speciation with and without ecological character displacement, etc. It is also clear that, sometimes, these distinctions can be attributed meaningfully to individual process phases only and not necessarily to the speciation process as a whole. At first sight, this may seem like a plea for unwieldy conceptual intricacy. Instead, we suggest that this recognition provides a fascinating opportunity to achieve a greater (and more encompassing) unity in our description of speciation processes. Aspects of spatial structure and pattern formation, of ecological character displacement and limiting similarity, and of reproductive isolation and assortative mating are often dynamically and inextricably linked when speciation

processes run their course. Based on this recognition, we propose to unfold the resultant continuum of possible speciation scenarios along three fundamental axes: spatial differentiation, ecological differentiation, and mating differentiation. As explained in more detail in Box 19.1, this allows us to look at alternative evolutionary pathways of species formation within a common conceptual framework. All traditionally acknowledged speciation mechanisms, as well as those described in this book, are accommodated readily in this broadened classification scheme.

19.4 Empirical Studies of Speciation

The natural diversity of speciation patterns and processes is captured in the empirical chapters of Parts B and C. These deal with examples from very different systems and perspectives, and reflect the broadness of the speciation scenarios encountered in nature. None of these studies were conducted with the theory of adaptive speciation in mind, but they can be seen as starting points to disentangle the diversity of processes into the basic components depicted in Box 19.1.

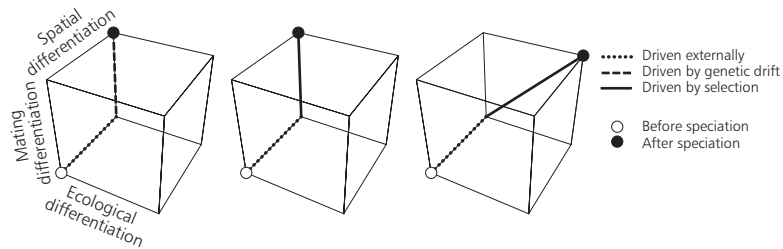
The chapters in Part B deal with cases of recent or ongoing genetic divergence under conditions of contact, which is where one can hope to find the best evidence for the adaptive speciation scenario. However, each of the chapters deals with settings in which alternative or additional components must be considered. For example, although the three chapters on fish systems deal with very recent splitting events, they come to different conclusions with respect to the primacy of the process that causes speciation. While sexual selection is suggested as the primary driving force for the haplochromine cichlids in African lakes (Chapter 8), the plasticity of the pharyngeal jaw apparatus is also implicated as an additional factor that facilitates quick adaptation to new ecological niches. The stickleback study (Chapter 9) is an excellent example of the interplay between primary allopatric divergence and secondary contact that leads to niche partitioning. And in the arctic charr (Chapter 10), the complexity of the available niches after the postglacial reinvasion of volcanic lakes provides a level of resource polymorphism that is expected to promote the fast generation of newly adapted morphs. Adaptive speciation mechanisms are likely to play a role in all three of these cases, but the actual natural settings will inevitably always be more complex than the idealized world of theoretical abstractions.

The chapters in Part C look at the natural patterns of speciation, including those from phylogeography and paleontology. To infer past processes from extant pattern is an old exercise in speciation research, but to use the knowledge of processes to interpret patterns may be equally enlightening. For example, the paleontological analysis of the repeated radiations of semionotid fish in mesozoic rift lakes (Chapter 18) shows that most evolutionary novelties arose very quickly after the colonization of the lake. This is difficult to explain with a conventional allopatric model, but it is perfectly in line with predictions from the theory of adaptive speciation. Niche partitioning under conditions of disruptive selection is expected to be most efficient during an initial colonization phase, when ecological opportunities abound and evolutionary pathways are less constrained.

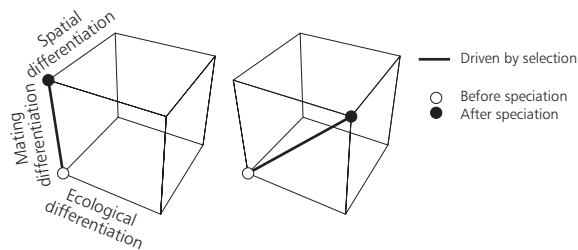
Box 19.1 A process-based classification of speciation routes

Realizing that the dichotomies traditionally applied to describe speciation processes are too coarse, here we propose an extended classification scheme. It encompasses that speciation, in general, can be driven by or lead to differentiation between the incipient species in terms of their spatial distributions, their ecological role, and their mating and interbreeding options.

The graphs below therefore simultaneously utilize continuous axes for spatial differentiation (front to back), ecological differentiation (left to right), and mating differentiation (bottom to top). At the onset of speciation, populations are undifferentiated, which corresponds to a starting point at the origin (i.e., in the lower left front corner) of each panel (open circles).



In classic allopatric speciation scenarios, external causes first result in geographic isolation between two incipient species, and thus introduce a high degree of spatial differentiation (dotted lines). After that, either genetic drift (dashed line in left panel above; Sections 6.2 and 6.6, and Box 6.5) or sexual selection and/or conflict (continuous line in middle panel above; Section 6.6, and Box 6.5) can increase mating differentiation. Alternatively, local adaptation with pleiotropic effects on mating can increase ecological and mating differentiation concomitantly (continuous line in right panel above; Sections 7.2, 8.4, 10.4, 11.6, and 13.2 to 13.3, and Box 13.1). In all three cases, the incipient species become reproductively isolated at the end of these speciation trajectories (filled circles).

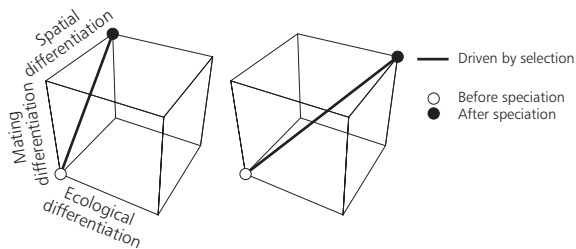


Sympatric speciation scenarios, in contrast, do not require that external causes, as a first step, lead to geographic isolation. For populations that lack any spatial structure, two scenarios have been suggested: either evolution driven by sexual selection and/or conflict induces reproductive isolation in the absence of concomitant ecological differentiation (left panel above; Sections 3.3, 5.4, and 8.2 to 8.4) or such

continued

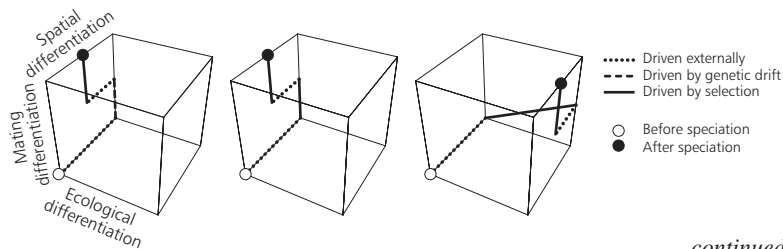
Box 19.1 *continued*

ecological differentiation is accompanied by the evolution of assortative mating (right panel above; Sections 3.3, 5.2, and 5.3). While the first of these cases draws its motivation from the explosive radiation of cichlid color morphs in African lakes, it is doubtful that morphs differentiated only with respect to their mating characteristics, and not ecologically or spatially, can coexist on an ecological time scale: a large proportion of the resultant species are thus likely to be ephemeral only.



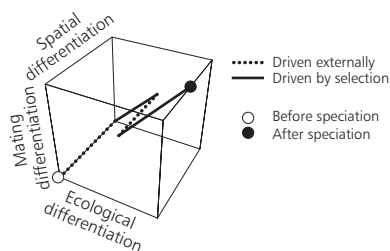
Introducing a spatial extension, and thus the opportunity for populations to differentiate spatially, extends models of sympatric speciation. If the resultant models are classified according to where the speciation mechanism operates, they can still be called sympatric, whereas judged from the spatial pattern that the speciation process generates they might be termed parapatric. This ambiguity underscores that features like allopatric, parapatric, and sympatric can be attributed meaningfully only to particular stages of speciation processes. Again, we have to consider two cases: either evolution driven by sexual selection and/or conflict induces reproductive isolation and spatial differentiation by giving rise to mating domains (left panel above; Section 15.3; Boxes 7.5 and 15.1), or ecological differentiation is accompanied by the evolution of assortative mating and the emergence of spatial differentiation (right panel above). The latter type of speciation process can occur at least in two guises: first, in the course of host-race formation (Sections 3.4, 11.5 to 11.6, 12.2 to 12.4, and Box 11.1) and, second, through local adaptation and speciation along environmental gradients (Sections 7.3 and 7.4).

The speciation processes considered so far are all examples of one-phase processes (provided we do not count the imposition of geographic isolation in allopatric scenarios as a separate phase). Given these process “atoms”, as the next step we can classify those slightly more complex speciation processes in which two phases are involved. This is accomplished easily, as the examples below illustrate.

*continued*

Box 19.1 *continued*

The three panels above show alternative scenarios in which allopatric speciation is brought to completion by reinforcement (Sections 7.2, 9.4, and 11.6). In the wake of geographic isolation (dotted long lines), the incipient species develop partial reproductive isolation, through genetic drift (left panel above), through sexual selection and/or conflict (middle panel above), or through local ecological adaptation (right panel above). This first phase is followed by the establishment of secondary contact (dotted short lines) and subsequent reinforcement (upper continuous lines).



The panel above shows another two-phase speciation process. This time, evolution during a first phase after geographic isolation results in partial ecological differentiation and partial mating differentiation (lower continuous line). In a second phase, contact between the incipient species is reestablished, and further ecological and mating differentiation ensues (upper continuous line); the second phase may also involve an increase in spatial differentiation. A process of this type is favored currently to explain the sympatric occurrence of limnetic and benthic forms of sticklebacks in some Canadian lakes (Sections 9.3 to 9.4, and Boxes 9.1, 9.2, 9.4, and 9.5).

It is evident that the classification scheme proposed here can accommodate even more complex types of speciation processes that involve, for example, three consecutive phases until speciation is completed. Speciation in asexual organisms is another special case: since no mating differentiation evolves, speciation trajectories are restricted to the bottom plane in the graphs above.

Phylogeography based on the analysis of DNA sequences from spatially distributed populations is another source of patterns that can be used to evaluate alternative models of speciation. These patterns enable us to estimate the time scale of divergence events, as well as vicariance patterns and population histories. Such studies often show that closely related species or populations do not occupy the same spatial area (i.e., do not occur in sympatry). This is interpreted habitually as the strongest evidence for the ubiquity of allopatric speciation. However, distinct spatial segregation is often maintained in spite of species ranges that shift in response to environmental fluctuations, such as ice-age cycles (Chapter 15). In such situations segregation must be maintained actively and cannot be considered as a simple by-product of previous allopatry. Such active separation mechanisms are

more likely to evolve during an initial sympatric phase under the adaptive speciation scenario, in which assortative mating builds up and results in discrimination between the differently adapted forms. Chapter 7 explains how such sympatric processes of local adaptive diversification can result in patterns of spatial segregation of newly forming species.

The empirical studies in this book were chosen as examples in which adaptive speciation might play an important role, but none of them provides unequivocal proof for the mechanism. Of all the possible empirical approaches, the experiments that involve microorganisms (Chapter 14) will probably enable the most careful control of the conditions required for adaptive speciation. However, we think that adaptive speciation will also be a satisfying explanation for the results of many other studies, even when alternatives cannot be ruled out completely. Future investigations will benefit highly from an intensified interplay between theoretical and empirical work, in particular because this will diminish the risk of biased data acquisition and interpretation that results from self-imposed conceptual restrictions.

19.5 Continuous Splitting and Radiations

The adaptive speciation process has an inherent tendency to lead to the continuous splitting of populations. The reason is that, when a population has reached a new adaptive peak, it may well again come into a situation in which intraspecific competition causes disruptive selection. This can lead to a further split, and also the resultant new populations may go through a new cycle. This tendency for continuous splitting will be limited only by the ecological opportunities initially available or becoming available through changes in the biotic environment caused by the diversification process itself. However, once such saturation is attained, many of the then extant lineages are likely to be highly specialized. Since these lineages will be sensitive to even mild environmental perturbations, they can be lost again easily. On this basis, we should expect a pattern of lineage splitting as depicted in Figure 19.1: while a large diversity of lineages can exist at any given time, only a few of these will survive to form deeper splits.

At first sight, it might appear that such a continuous-splitting process is not compatible with the phylogenetic patterns found in nature. At least in the official taxonomy, species are well defined and clearly delimited. But for almost any species it is possible to identify subspecies, or races, that differ in certain characters. Some species appear so variable that they are officially even called “polytypic”. We suggest that this inherent variability can be explained by the continuous-splitting scenario outlined here.

If an environment offers completely new ecological opportunities, the expectation is that newly split lineages are less likely to be lost. Going beyond the small changes that occur under relatively stable conditions, these initial lineages could, rather, be the basis for further specific adaptations. Such cases would become manifest as radiations in the evolutionary history and in the fossil record. Paleontological patterns have been described as punctuated equilibria with periods of

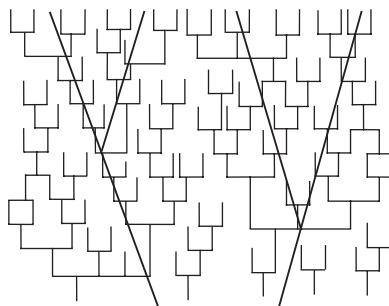


Figure 19.1 The continuous-splitting scenario. If populations have a continuous tendency to split, closely related sister groups are present at any time. However, because of environmental fluctuations, many of these splits are either lost or merge again. Hence, only a relatively few deeper splits persist in the long run. For example, at the top of the tree, we would count 18 genetically different populations, subspecies, or species (thin lines), but only four taxonomically distinguished species that have descended from deeper splits (thick lines).

fast radiation and generation of morphological diversity, followed by relative stasis with little morphological change. If one envisages evolution and speciation as a continuous process of divergence, this would seem like a paradox. However, this is the expected pattern under the adaptive speciation scenario: when new ecological opportunities open up – for example, when a species colonizes a new area (see Boxes 4.8 and 18.2) – it quickly adapts to the new condition and starts cycles of adaptive speciation that lead to a fast succession of splits until all the available ecological opportunities are taken. Since each cycle of splitting may take less than a thousand generations, such radiation will seem very sudden in the fossil record. As long as there is no further ecological change, new adaptations cannot happen and relative morphological stasis is expected. Moreover, as discussed in Box 4.8, adaptively driven punctuation events also can be triggered by quantitatively minor changes in the geometry of the fitness landscape, which occur in the wake of slow changes in the overall environment. Thus, there is no need to invoke a special macro-evolutionary mechanism, or divergence in peripheral isolates, to explain the pattern of punctuated equilibria encountered in the fossil record.

19.6 Future Directions

It is evident that new, dedicated studies are required to better explore the applicability of the adaptive speciation process to a wide range of natural systems. The preceding chapters also highlight a suite of unanswered questions that need to be tackled. Advances are needed with regard to both theoretical and empirical approaches.

Speciation models have come a long way over the past five decades – yet major challenges still remain. The ultimate goal of theoretical endeavors is to catalog the relationship between potential mechanisms and potential phenomena. In the

Box 19.2 Future theoretical research

In this book we survey a number of processes that can lead to adaptive speciation, and discuss the patterns such processes are expected to generate. We clearly are in the initial phases of this endeavor, and most of the models put forward still require further investigation. Below we outline some of the most interesting options for further theoretical research.

Many questions below extend to sympatric, parapatric, and allopatric speciation and address the following two fundamental issues. First, what genetic, ecological, mating, and spatial structures are particularly conducive to speciation that progresses along certain routes? Second, what are the phylogenetic and biogeographic consequences of such speciation? Answers to these questions will help us evaluate the probabilities of past speciation routes from present observations.

Speciation genetics. Responses of alternative genetic architectures to the selection pressures encountered at evolutionary branching points should be analyzed. Forays in this direction have been made by Kawecki (Chapter 3), and by Geritz and Kisdi (2000), who considered adaptive dynamics in allele space in Levene-type models (see Box 4.7). Corresponding multilocus models, comparable to those considered by Dieckmann and Doebeli (Chapter 5), should also be investigated. In this context departures from additive genetics have to be explored and their implications for the potential and pace of adaptive speciation analyzed. In addition, we need better insight into the potential of sex-ratio distorters and selfish elements to promote or prevent adaptive speciation (Chapter 12).

Evolving mate choice. Models in which mate choice is based on separate loci for mating signals, mating preferences, and the strength of these preferences need to be integrated with ecological models of adaptive speciation. Also, mate finding and mate recognition could be modeled separately from mate choice. In the real world, the space of phenotypes potentially involved in such processes is often very highly dimensional. The implications of such high dimensionality for the speed at which fitness minima can be escaped need to be analyzed (e.g., Van Doorn *et al.* 2001). Also, general models for speciation based on sexual selection alone have to be developed and studied in greater detail (Van Doorn and Weissing 2001); such models should start to incorporate the frequency dependence that often arises from mate choice. Sexual arms races are one potential mechanism that enables fast allopatric speciation [Schilthuizen 2001; see also Gavrillets (2000b) and Section 5.4]; more mechanistic models that underpin this idea are needed, as well as parapatric and sympatric variants of these models to assess the amount of gene flow under which pairs of arms races can still diverge.

Speciation, learning, and plasticity. Models that combine genetic evolution with learning of the ecological role, or with plasticity in an ecologically relevant trait, should be developed and studied. In this context, links with optimal foraging theory should be explored. The same applies to models that combine ecological branching with learned mate selection (e.g., through song learning in birds, or parental imprinting). In general, under what conditions does plasticity or learning help speciation to take off, by allowing species to enter a wider variety of niches, and when does it actually preclude speciation by broadening resource specialization (Chapter 12)? The answer necessarily depends on details of the fitness landscape: plasticity can make a bumpy landscape smoother and so more conducive to evolutionary change (as species do not become stuck on any little hill), but plasticity can also just supply the phenotypic variation otherwise provided by genetic diversification (Chapter 10).

continued

Box 19.2 *continued*

Patterns, biogeographic and other. Predictions are needed about the spatial patterns of genetic variation of and linkage disequilibria between ecological and mating characters expected from adaptive speciation. These patterns are likely to depend on the speciation route followed by the process (Chapter 7; Box 19.1); therefore, mechanisms need to be grouped according to the patterns they engender. Predictions that can distinguish ongoing sympatric speciation from secondary contact after incomplete allopatric speciation would be particularly valuable. Also, conditions for the evolution of spatial mosaics through adaptive speciation have to be better understood; these should refer to the ecological mechanism that causes divergence, the movement pattern of individuals, and the underlying environmental heterogeneity. At the temporal end, in allopatric speciation as envisaged in Chapter 6, the average number of speciation events per time unit will probably decrease only slowly over evolutionary time, while the arguments put forward in Box 18.2 suggest that speciation rates decrease very rapidly in sympatric adaptive speciation scenarios. In general, certain phylogenetic features may indicate certain speciation processes – exactly how remains to be determined.

Speciation time scales. We need better insight into the time scales of speciation processes as they unfold along different routes. How robust are the salient numerical results, that is, to what extent do they depend on particular model assumptions? For example, how predictions from the models discussed in Chapter 6 depend on the specific assumptions made about the dependence of genetic incompatibility on genetic distance should be resolved. When considering alternative mechanisms – like dominance, sexual dimorphisms, or step-like phenotypic plasticity (Van Dooren 1999; Matessi *et al.* 2001) – that could accomplish splitting a population into a number of discrete morphs, we have to assess how these mechanisms fare when raced against each other in more elaborate ecological models.

Long-term phylogenetic implications. It will also be interesting to understand how patterns caused by the various speciation routes considered in this book can themselves act as historical constraints on later developments. This can involve ecological processes (speciation events change the community and may thus prepare the way for further speciation events, either in the descendant species or in other parts of the community), spatial patterns (particular distributions may be more conducive to further speciation than others), and genetic architectures affected by earlier speciation (some such architectures may allow escapes from fitness minima more readily than others, as, for example, when earlier mechanisms for assortative mating help new sorts of assortativeness to start).

More complex speciation models. Integration of the various speciation mechanisms into more general models is required. In particular, models for the generation of ecological sister species through sexual selection, like that discussed in Chapter 8, should be combined with models for adaptive speciation caused by ecological factors, to better understand how the processes may interact (Van Doorn and Weissing 2001). Also, with regard to the underlying ecology it is of great importance to assess the robustness of predictions within more extended model families. An interesting development in this direction is that for very large classes of ecological models the local form of invasion fitness is the same (up to second-order terms) as that of a Lotka–Volterra system (Durinx *et al.*, unpublished). This suggests that for particular theoretical problems we can restrict our attention to such approximations of more complex ecologies.

Box 19.3 Future empirical research

The chapters in this book make clear that, to gain access to more conclusive evidence for particular speciation scenarios, much more attention has to be paid to the earliest phases of the splitting process, which are confined to a few hundred generations after the conditions for splitting have been established. Identifying such situations will be a challenge, but the continuous-splitting scenario (Figure 19.1) suggests that they are not rare. Studying newly colonized habitats will probably provide the best entry point to such situations in nature. Furthermore, because the splitting process is expected to be relatively quick, it will be possible to set up laboratory experiments with rapidly reproducing species that may allow the full speciation process to be followed. Several aspects should be at the top of the agenda for such future empirical research.

Assortative mating. For sexually reproducing species, the emergence of assortative mating is a prerequisite for the splitting process. Although assortativeness is a well-known phenomenon in nature, it must now be studied in much more detail and with new conceptual approaches. The simplest assumption would be that signals for assortative mating are coupled pleiotropically to the ecological trait under selection. However, this is not a strict requirement since Dieckmann and Doebeli (1999) showed that such coupling between the ecological trait and specific mating signals can also evolve from scratch. A further alternative is that an assortative mating system is already present, because it evolved in the previous round of speciation. Only minor modifications may be necessary to achieve a further differentiation. It should thus be rewarding to identify situations in which successive speciation events have taken place within a short time and compare the signaling and recognition mechanisms in each of the sister groups. Ethologists know that animals are generally rather choosy when it comes to mating, for good reasons. The choice of the right partner has a direct fitness consequence because it determines the genetic quality of the offspring. The optimal partner for an organism is one that is most compatible with its own genotype, in the sense that the joint offspring are able to compete effectively for the ecological niche that was also used by the parents. This leads to “genotypic assortativeness”, which needs to be coupled to specific signals. Thus, genetic assortativeness can be considered as something that is already built into the system of a sexually reproducing species, and that does not have to evolve newly during a speciation process. In general, a better understanding of the genetics of recognition and signaling is required to investigate ongoing processes of adaptive speciation.

Genetic incompatibilities. Although the initial splitting may only involve prezygotic mechanisms and the sorting of pre-existing alleles, it is clear that postzygotic genetic incompatibility evolves at some point. There is increasing evidence that such postzygotic effects are not simply a consequence of the random accumulation of differences, but can be driven by specific genes. One of these, the Odysseus locus in *Drosophila*, is particularly well studied and there is evidence for continuous strong positive selection at this locus, which suggests an active role in the separation process (Ting *et al.* 1998). In future studies, it will be very important to trace the role of such “speciation genes” during the separation process. Can they act as selfish elements that drive separation on its own, such as *Wolbachia* bacteria in insects? Are they part of the assortative mating process by affecting signaling or recognition? Or are they only recruited during a later phase of the separation process?

continued

Box 19.3 *continued*

Spatial context. One of the largest challenges for the future is to understand the connection between the splitting processes under conditions of ecological contact and subsequent spatial separation. Clearly, most closely related species do not occur in sympatry and there must therefore be a mechanism that leads to these spatial splits. Modeling efforts in this direction are already well underway (Chapter 7; Doebeli and Dieckmann 2003; M. Rost and M. Lässig, personal communication). For empirical studies, it is particularly important to apply refined molecular markers in the phylogeographic reconstruction of existing patterns of species and population distribution. This will enable situations to be identified at different stages of the separation, or secondary contact process, which can then be studied in detail. In particular, a number of interesting differences in the gene flow patterns for mitochondrial and nuclear markers have now been documented (Shaw 2002; Ogden and Thorpe 2002). These findings might provide vital clues about the role of male and female migration in establishing or obliterating spatial patterns of genetic differentiation.

Experimental systems. To study the full process of separation in the laboratory, one will have to resort to organisms with short generation times. The first choice would be viruses, bacteria, or unicellular eukaryotes, such as yeast or algae. They potentially allow each generation to be retained by freezing samples, to carry out replicate experiments under controlled conditions, and possibly to study genetic changes at the genome level. Chapter 14 provides salient examples of how such studies can be used to investigate adaptive speciation and radiation. However, while experimental systems of microorganisms have many advantages for the study of ecological mechanisms of diversification, they have some obvious disadvantages when it comes to the study of assortative mating mechanisms – if only because many microorganisms have irregular and often quite complicated modes of sexual reproduction. It should therefore be attractive to further develop short-lived, sexually reproducing organisms of higher taxa into laboratory models for speciation experiments. *Drosophila* has already been used often for speciation studies, but not in the context of explicit scenarios for adaptive speciation processes. With the availability of the *Drosophila* genome sequence, this system might offer an attractive alternative to studies that focus on unicellular organisms.

best of all worlds we would thus be able to write down and analyze a single, all encompassing family of eco-evolutionary speciation models. This family's parameter space would be parceled up into different regions that correspond to different speciation routes and mechanisms. In practice, however, speciation processes at present appear far too complex and diverse for such an exercise to be feasible yet. At best we can analyze small subsets of the larger family in which we stress some mechanisms at the cost of neglecting others. In a next stage, we may tentatively combine two, or sometimes even more, mechanisms to explore their interactions. Box 19.2 gives an overview of the present and future challenges offered by such a research program.

Future empirical studies will benefit from the analysis of carefully controlled laboratory populations, as well as from the identification of natural situations of ongoing splitting. We need to better understand the specific biological mechanisms that underlie evolutionary branching and the evolution of assortative mating. Although assortative mating and specific mate choice are well known as such, their genetic basis and evolutionary origins now have to be explored in the context of speciation. As discussed in Chapter 1, there are many possibilities as to how assortativeness can come about, so the empirical studies should pay particular attention to these mechanisms. The implied challenges for further empirical research are summarized in Box 19.3.

A key issue for both theory and empirical studies is the inclusion of spatial context. After all, parapatric or allopatric patterns of species distribution are prevalent in nature and need to be explained. The model discussed in Chapter 7 shows that gradients of environmental resource distribution lead to spatial splits under the adaptive speciation scenario (Doebeli and Dieckmann 2003). This line of investigation bears further exploration, and there is a need for empirical studies that analyze the ecological settings prone to such spatial splitting.

The study of speciation mechanisms can be freed finally from the conceptual chains that external causes always have to be invoked as the driving forces of speciation processes. Instead, frequency-dependent selection and evolutionary branching emerge as plausible mechanisms of lineage splits that are adaptive and immanently arise in speciating populations. When the conditions for adaptive speciation are met, the splitting of a population becomes an inescapable consequence of its interacting and reproducing constituents. Speciation is thus a law of nature, rather than an accident.