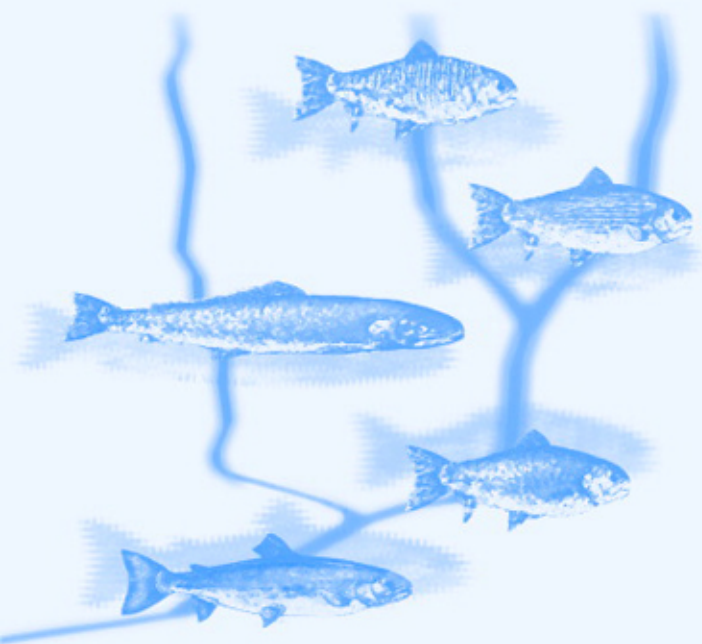


Cambridge Studies in Adaptive Dynamics

Adaptive Speciation



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

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Adaptive Speciation

Unraveling how biological diversity originates through speciation is fundamental to understanding the past, present, and future of life on earth. Promoting an ongoing paradigm shift, *Adaptive Speciation* elucidates how selection driven by biological interactions can trigger the adaptive splitting of lineages. Recent advances in speciation theory are carefully explained and confronted with celebrated empirical examples of speciation under natural selection. With an emphasis on the potentially intricate interplay between geographic patterns and ecological processes of speciation, this book seeks to overcome the default perception of speciation as a mere side effect of geographic isolation. The consequent richer perspective enables adaptive speciation to be appreciated as a major force in the generation of biological diversity. Written for students and researchers alike, this book provides a thorough treatment of the newest developments in speciation science.

ULF DIECKMANN is Project Leader of the Adaptive Dynamics Network at the International Institute for Applied Systems Analysis (IIASA) in Laxenburg, Austria. He is coeditor of *The Geometry of Ecological Interactions: Simplifying Spatial Complexity*, of *Adaptive Dynamics of Infectious Diseases: In Pursuit of Virulence Management*, and of *Evolutionary Conservation Biology*.

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Cambridge Studies in Adaptive Dynamics

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The modern synthesis of the first half of the twentieth century reconciled Darwinian selection with Mendelian genetics. However, it largely failed to incorporate ecology and hence did not develop into a predictive theory of long-term evolution. It was only in the 1970s that evolutionary game theory put the consequences of frequency-dependent ecological interactions into proper perspective. Adaptive Dynamics extends evolutionary game theory by describing the dynamics of adaptive trait substitutions and by analyzing the evolutionary implications of complex ecological settings.

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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
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
x	Phenotypic or allelic trait value
u	Per locus mutation probability or Probability of a mutational step in a quantitative trait
U	Gametic mutation probability
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
D_M	Mahalanobis' (morphological) distance
D_N	Nei's genetic distance (between populations)
d	Genetic distance (between individuals) = number of allele changes
z, z_1, z_2	Spatial coordinates
t	Time
T	Duration
τ	Waiting time
p, q	Probability or relative frequency (subscript indicates type)
σ^2	Variance (subscript indicates type)
i, j	Index
\dots'	Invader
$\hat{}$	Equilibrium value
\dots^*	Evolutionarily singular value (of a trait)
$\bar{}$	Average

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).

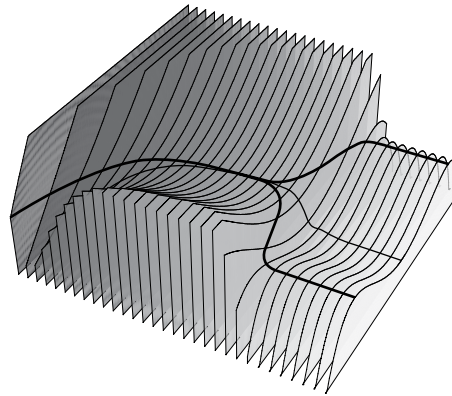


Figure 1.1 Adaptive speciation unfolding. A fitness landscape's shape changes jointly with a population's mean trait value (thick curve; the initial snapshot of the landscape is colored dark gray and the final one white). While the population undergoes directional selection by ascending the fitness landscape, 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.

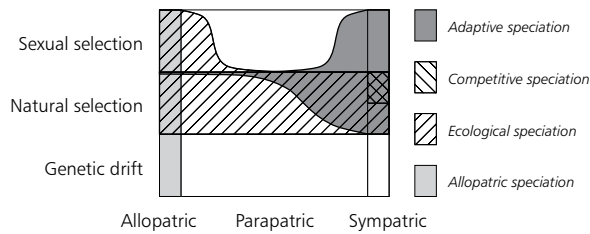
In the definition of adaptive speciation given above, the notion of selection encompasses both natural and sexual selection. In the literature, sexual selection is often pitted against natural selection. This convention goes back to Darwin and is meant to highlight a distinction between those causes 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.

2

Speciation in Historical Perspective

Will Provine

2.1 Introduction

By the time Darwin died in 1882, evolution by descent was widely hailed, never again to be challenged by the vast majority of biologists. His theory of natural selection as the key to understanding adaptation, however, was less successful. Alfred Russel Wallace's *Darwinism*, which strongly defended natural selection, appeared soon after Darwin's death (Wallace 1889). Detractors of natural selection increased in strength during the 1890s; indeed, historian Peter Bowler termed the period close around the turn of the century as "the eclipse of Darwinism" (Bowler 1983). A contemporary biologist billed this period, more graphically as, "the deathbed of Darwinism" (Dennert 1903). Even Wallace, in his old age, began to backpedal from natural selection toward belief in god-designed organisms (Wallace 1910). Beginning with the "evolutionary synthesis" of the 1930s and 1940s, Darwin's natural selection enjoyed a rebirth, and became known as "Twentieth Century Darwinism," the name made famous by the 1959 Cold Spring Harbor Symposium *Genetics and Twentieth Century Darwinism* (Mayr 1959a).

Evolution produces two major results: adaptations and biodiversity. Natural selection loomed large in the mid-20th century as the explanation of adaptive design, but Darwin's ideas about species and speciation simultaneously were driven to obscurity, where they have remained. The argument here is that "21st Century Darwinian Speciation" is emerging from the darkness of the past half-century.

Study of speciation today addresses most of the same issues debated so intensely by Charles Darwin, Alfred Russel Wallace, Joseph D. Hooker, Henry Walter Bates, Fritz Müller, Moritz Wagner, or Asa Gray:

- What is a species?
- What causes determine the divergence of species from a single ancestral species?
- What is the role of sterility in speciation?
- Why do some kinds of organisms speciate readily and others speciate rarely?
- Is geographic separation required for speciation, or can species form in the same geographic area?
- Do population structure, sexual selection, and recognition of mates play important roles in speciation?
- Are chance factors important in speciation? Is speciation enhanced when open ecological niches are available?

For most of the world's population, gods or purposive forces design adaptations. For biologists, however, adaptation has only one naturalistic explanation: natural selection. Thus, natural selection is a great unifying concept in the study of evolution. Although very few examples of natural selection in nature were revealed in the first century after publication of *On the Origin of Species* (Darwin 1859), they have grown in number since then and a whole book (Endler 1986) devoted to their analysis. Even critics of neo-Darwinism (alias panselectionism), such as Motoo Kimura (1983) and Masatoshi Nei (1989), both advocates of neutral molecular evolution, or Eldredge and Gould (1972), advocates of punctuated equilibrium, nevertheless agree that adaptations are produced by the causes of natural selection.

Diversity, in the form of speciation, has no book such as Endler's, and the examples so far are hardly robust. In theory and practice, speciation is a much more difficult problem than adaptation and far less unified. In this brief chapter only four topics are addressed:

- Charles Darwin's ideas about species and speciation.
- Evolutionary synthesis (1930s–1950s) and the work of Ernst Mayr on species and speciation in his *Animal Species and Evolution* (1963).
- Changes in evolutionary biology and their effects on theories of speciation since 1963.
- Greater openness of contemporary biologists, by focusing upon Dolph Schluter's book *The Ecology of Adaptive Radiation* (2000) and the review by John Avise (2000b) of species concepts.

2.2 Darwin on Species and Speciation

Darwin's views on species and speciation fare well in comparison with other approaches adopted over the past 150 years.

Darwin on species

Darwin's contemporaries could agree on no clear definition of species, and in the *On the Origin of Species* (1859) and elsewhere Darwin declined to offer one of his own ["No one definition has yet satisfied all naturalists, but every naturalist knows vaguely what he means when he speaks of a species" (Darwin 1859, p. 44)]. This hardly reassuring definition of a species was buttressed by other declarations of vague and arbitrary attributes of species:

Many years ago, when comparing, and seeing others compare, the birds from the closely neighbouring islands of the Galapagos Archipelago, one with another, and with those from the American mainland, I was much struck how entirely vague and arbitrary is the distinction between species and varieties. (Darwin 1859, p. 48)

Certainly no clear line of demarcation has as yet been drawn between species and subspecies – that is, the forms which in the opinion of some naturalists come very near to, but do not quite arrive at, the rank of species; or, again, between sub-species and well-marked varieties, or between lesser varieties and individual differences. (Darwin 1859, p. 51)

Darwin, of course, wanted above all to convince his audience that evolution by shared descent had occurred. To have no clear distinctions between species and subspecies, subspecies and well-marked varieties, and lesser varieties and individual differences was crucial to his argument: “These differences blend into each other by an insensible series; and a series impresses the mind with the idea of an actual passage” (Darwin 1859, p. 51).

P. Chalmers Mitchell, who wrote the article on “species” for the 11th edition of the *Encyclopedia Britannica* (1911), argued that Darwin and evolutionists after him had destroyed all possibility of a clear notion of species: “... Systematists no longer regard species as more than an artificial rank in classification to be applied for reasons of convenience A species, in short, is a subjective conception” (Mitchell 1911, pp. 616–617).

Darwin, however, was sure species existed. “I believe that species come to be tolerably well-defined objects, and do not at any one period present an inextricable chaos of varying and intermediate links ...” (Darwin 1859, p. 177). Only when viewed across time, or across geography, did species depart from “tolerably well-defined objects”. Thus, Darwin did not torture himself on the species question – he just accepted the assessments of systematists who knew their species, as he trusted his own work on the systematics of barnacles. He used, as would most naturalists of his day, a morphological approach to the differences between species. He would not have accepted the assessment of “species” given by Mr. P. Chalmers Mitchell.

Darwin on speciation

All editions of Darwin’s *On the Origin of Species* carried as the first subtitle, “By Means of Natural Selection”. Darwin was fascinated by the different ways species were adapted to their ecology:

The face of Nature may be compared to a yielding surface, with ten thousand sharp wedges placed close together and driven inwards by incessant blows, sometimes one wedge being struck, and then another with greater force. (Darwin 1859, p. 67)

What counted about the species of a genus was how the species (“wedges”) differed, and to what extent their fit into to the ecology could be understood by means of natural selection.

Darwin’s attempt to understand how closely related species were adapted to their environments presented him with questions about natural selection and the production of species. When Darwin speaks of “sterility,” he includes all forms of reproductive isolation:

Why should the degree of sterility be innately variable in the individuals of the same species? Why should some species cross with facility, and yet produce very sterile hybrids; and other species cross with extreme difficulty, and yet produce fairly fertile hybrids? Why should there often be so great a difference in the result of a reciprocal cross between the same species? Why, it may even be asked, has the production of hybrids been permitted? To grant to species the special power of producing hybrids, and then to stop their further propagation by different degrees of sterility ... seems to be a strange arrangement. (Darwin 1859, p. 260)

These bothersome questions could be answered, however, by attributing the results to something other than natural selection, a process that seemed to have no direct answers to questions about sterility between closely related species:

On the theory of natural selection the case is especially important, inasmuch as the sterility of hybrids could not possibly be of advantage to them, and therefore could not have been acquired by the continued preservation of successive profitable degrees of sterility. I hope, however, to be able to show that sterility is not a specially acquired or endowed quality, but is incidental on other acquired characters. (Darwin 1859, p. 245)

There is no more reason to think that species have been specially endowed with various degrees of sterility to prevent their crossing and blending in nature, than to think that trees have been specially endowed with various and somewhat analogous degrees of difficulty in being grafted together in order to prevent them inarching in our forests. (Darwin 1859, p. 276)

Subspecies showed the same range of sterility as species themselves, but with a higher frequency of fertility than in species. So for Darwin it was possible to have two subspecies that were totally sterile when crossed, and two species that were totally fertile when crossed, although neither scenario was a frequent occurrence.

2.3 Mayr on Species and Speciation

In 1964 Mayr published a facsimile edition of Darwin's *On the Origin of Species*, with his own introduction. Population thinking and natural selection, Mayr said, were Darwin's great contributions to evolutionary thought. In other respects, however, Mayr said Darwin was sadly mistaken:

Though Darwin was wrong in his discussions of inheritance and the origin of variation, confused about varieties and species, and unable to elucidate the problem of the multiplication of species, he was successful in discovering the basic mechanism of evolutionary change. (Mayr 1964, p. viii)

Darwin could hardly be faulted for his lack of appreciation of Mendelian inheritance, but why did he fare so poorly on species and speciation?

Mayr on species

By the mid-1930s, dissatisfaction with the morphological definitions of species was growing. Theodosius Dobzhansky, Ernst Mayr, Sewall Wright, and others pushed for what they called a more "scientific" definition of species, upon which all could agree. The outcome was what Mayr termed the "biological species concept", which defines species by the isolating mechanisms that guarantee the purity of the gene pools of the species. To determine if two populations were two species, morphological differences were useless and ignored in the biological species concept. At last, a satisfyingly universal, *scientific* concept of species had been invented:

The general adoption of the biological species concept has done away with a bewildering variety of “standards” followed by the taxonomists of the past. One taxonomist would call every polymorph variant a species, a second would call every morphologically different population a species, and a third would call every geographically isolated population a species. This lack of a universally accepted standard confused not only the general biologists who wanted to use the work of the taxonomist, but the taxonomists themselves. Agreement on a single yardstick, the biologically defined category species, to be applied by everybody, has been a great advance toward mutual understanding. (Mayr 1963, p. 21)

The quickest way to return to “a bewildering variety of standards” is, according to Mayr, to think about subspecies. Citing the classic paper of Wilson and Brown (1953) on the difficulties of the subspecies category, Mayr declared: “... the subspecies, which conceals so much of the inter- and intrapopulation variation, is an altogether unsuitable category for evolutionary discussions; the subspecies as such is not one of the units of evolution” (Mayr 1963, p. 348). When the subspecies reaches the level of a species (i.e., has an independent gene pool), then it becomes a genuine evolutionary unit, one that anyone can recognize. In a long section on gene pools and homeostasis, he argued that a gene pool was coadapted and resistant to change: “Genetic homeostasis determines to what extent a gene pool can respond to selection” (Mayr 1963, p. 289). With Mayr’s great influence, the biological species concept became the most widely accepted definition of species ever, including the present, though now more dissension exists than in the 1960s.

Mayr on speciation

Once the biological species concept is accepted, speciation is easy to envision: one gene pool becomes two separate gene pools. In his 1963 book Mayr addresses the obvious question of how one gene pool with homeostasis becomes two. “The mechanisms that isolate one species reproductively from others are perhaps the most important set of attributes a species has, because they are, by definition, the species criteria” (Mayr 1963, p. 89):

Reproductive isolation refers to the protective devices of a harmoniously coadapted gene pool against destruction by genotypes from other gene pools. These protective devices are known under the term isolating mechanisms. Speciation is characterized by the acquisition of these devices. (Mayr 1963, pp. 546–547)

Calling isolating mechanisms “protective devices” sounds like these devices are primary outcomes of natural selection, but this impression is false as Mayr explains.

In a section of Chapter 17 (The genetics of speciation) entitled “The origin of isolation mechanisms”, Mayr (1963) clarifies how these protective devices originate. In the first place, the evolution of isolating mechanisms required geographic separation, perhaps Mayr’s most famous and lasting postulate of speciation. After geographic separation,

The most indispensable step in speciation is the acquisition of isolating mechanisms. Isolating mechanisms have no selective value as such until they are reasonably efficient and can prevent the breaking up of the gene complexes. They are *ad hoc* mechanisms. (Mayr 1963, p. 548)

However, isolating mechanisms are very important for the cohesion of species. How could they have “no selective value” and be merely “*ad hoc*” mechanisms?

Mayr was thinking here about the controversy between Darwin and Wallace (and many later evolutionists) over the evolution of sterility between species. In a major article, Mayr (1959b) had evaluated their positions carefully, and stated his strong support for Darwin’s views. As Mayr points out, Darwin used “sterility” to refer mostly to what we now call isolating mechanisms, not mere physiological sterility. So as populations diverge from each other, the isolating mechanisms arise as “an incidental by-product of genetic divergence in isolated populations” or as a “by-product of the total genetic reconstitution of the speciating population” (Mayr 1963, p. 551). For Mayr, the genetic divergence related to morphological differences in adaptive characters had nothing to do with the speciation, which depended upon only the incidental by-products, the isolating mechanisms. Rates of acquisition of isolating mechanisms varied from case to case and “there is no standard rate of speciation. Each case is different and the range between the possible extremes is enormous” (Mayr 1963, p. 581). Even within a genus with only a few several species, one case of speciation might give no good indication of speciation in another case.

So the question is, what kind of “by-products” are these isolating mechanisms? According to Mayr, they comprised by-products of the “genetic divergence” of the populations. There, unfortunately, the story ended and ignorance prevailed. Speciation had become inscrutable, and nothing but vague “correlations” with factors produced by natural selection and observable differences at morphological to genetic levels. However, Darwin at least had not failed Mayr completely on the issue of speciation – they agreed deeply on the issue of sterility factors (or isolating mechanisms) being merely incidental.

2.4 Species Now

A sea change in evolutionary biology has occurred since the 1960s (Provine 2001, Afterword). Thoughts about species and speciation, in particular, have begun to change during the past 40 years. The rise of cladism, DNA sequencing, protein sequencing and analysis of function in proteins, theories of neutral molecular evolution, and other factors have challenged the hope that evolutionary biology is unified across all levels of organization. The evolutionary synthesis has been unraveled since 1980. Now the unity of evolutionary biology in the “synthesis” has given way to a much more intriguing complex of different levels, each with a particular complex of causes. To argue that the DNA-sequence level marches to the same beat as the adaptive-trait level, which seemed natural in the 1960s, seems hopeless at the present.

We have seen how Mayr centralized the ideas of the “gene pool” and “genetic homeostasis” in his biological species concept, but now we can see in hindsight that both concepts are nearly useless. “Gene pool” now appears to be one of the most artificial concepts of population genetics. What exists in the “gene pool” is vague, but perhaps most often either “genes” or “alleles”. Other candidates for the gene pool are chromosomes, gametes, and whole organisms. Neither genes nor alleles float free, but are on chromosomes, and do not cleave every generation. To talk about the cohesion, coadaptation, and homeostasis of the gene pool means attributing fancy characteristics to a nonexistent entity.

In small populations, invocation of the gene pool as the intuitive source of the binomial sampling for genetic drift leads to mathematical models that look robust, but are not. The basic problem is that recombination is far too weak to make random binomial sampling of individual genes (or DNA bases) possible over tens or hundreds of generations (Gillespie 1999, 2000a, 2000b).

Genetic homeostasis is an attractive idea, but sadly lacks substance. We hear no more about it these days; instead, we hear about DNA repair mechanisms at the level of the individual genome and nothing about homeostasis at the “gene pool” or population level. For Mayr, the homeostasis of the gene pool held the species together, but now this says nothing biological about species.

In the 1960s, the definition of “species” was mercifully clear. Now, let us try an assignment to a new graduate student in evolutionary biology. Our hypothetical student had a fine background in natural history with undergraduate research in *Drosophila* in the field and in the laboratory, read Doug Futuyma’s *Evolutionary Biology* (1979) in her evolution course, and then took a reading course on Mayr’s *Animal Species and Evolution* (1963). Untroubled by doubt about either species or speciation, she looks forward to our reading course. In sequence, she reads: Slobodchikoff (1976), Barigozzi (1982), Otte and Endler (1989), Howard and Berlocher (1998), Wheeler and Meier (2000), Schluter (2000), and this volume. At the end of the reading course, species and speciation are discussed. The first question is, “Using your extensive background reading, would you please give your most precise general definition of a species?” She gives, probably, one of two answers. “How do you expect me to give you an answer to this question when the world experts can’t agree at all?” or “The only concept that seems general and scientific is the biological species concept.” On the one hand, the drive is back to poor P. Chalmers Mitchell and his “artificial” species, but on the other to Mayr’s biological species concept with the baggage that it has to focus on the “by-product” isolating mechanisms and ignore the adaptive radiations that grab our attention as natural historians.

As a historian, I am struck by the continuing struggle of biologists to derive a robust, single, best concept of species. Nearly every book on species read by the hypothetical student expresses over and over the hope of finding *the* definition of species.

John Avise, whose field work and analysis of species and speciation in a wide variety of organisms is well known and erudition wide, has recently written a review of Wheeler and Meier (2000), with the great title, “Cladists in wonderland” (Avise 2000b). Educated in the biological species concept, Avise finds that the four distinctive cladist concepts of species lack biological realism, but at the same time believes that the biological species concept needs revision. Perhaps he should have taken the line that to worry so much about the correct and scientific concept of species was a mistake, but no, he wants that robust concept, a synthesis of the concepts of biological species and phylogenetic species through unification with phylogeographic and coalescent principles:

Perhaps the ongoing phylogeographic synthesis that tries to wed (rather than divorce) phylogenetic and reproductive concepts in species recognition will yet prove to be only another fantasy. But I doubt it. Instead, I have great hope that the peculiar tea-party banter between the Aliceians and the Mad Hatters over species concepts will eventually clarify, and that a more intelligent dialogue and eventual synthesis will emerge. If so, the 20-year quarrel between proponents of the BSC [biological species concept] and the PSC [phylogenetic species concept], so cogently encapsulated in the Wheeler and Meier volume, will someday be remembered as little more than a “tempest in a teapot”. (Avise 2000b)

Perhaps the most insightful single article to deal with species concepts and speciation is Richard G. Harrison’s “Linking evolutionary pattern and process: The relevance of species concepts for the study of speciation” (Harrison 1998). Harrison concludes that the BSC remains the only major species concept to escape the withering objections of all phylogenetic and species-recognition concepts. In his review of Howard and Berlocher (1998), Schemske (2000) agrees with Harrison, as do many others; Coyne (1992, 1994), especially, has similar views.

If I were asked the same question posed to the hypothetical student above, and forced to answer, I would probably agree with Harrison. I am not, however, faced with such an unattractive pair of choices. Instead, I can see excellent uses of the wide variety of species concepts, and the crucial mistake is biologists’ obsessive search for the best species concept, however limited. As soon as we feel the onus that one species concept has to be chosen for all purposes, from constructing phylogenies to speciation, then we are in a needlessly poor situation. Even armed with a species concept well-suited to its particular use, a biologist might want to carry it lightly.

2.5 Speciation Now

Is, as Harrison suggests, the biological species concept the best species concept for understanding speciation? One place to look is Dolph Schluter’s *The Ecology of Adaptive Radiation* (2000), because Schluter focuses upon the same problem as Darwin: how does adaptive radiation take place? Speciation, according to Schluter, is central to adaptive radiation, so he has to address the problem of species concepts and does so early in the book:

Speciation refers to the evolution of reproductive isolation, defined as the complete absence of interbreeding between individuals from different populations (should they encounter one another), or the strong restriction of gene flow sufficient to prevent collapse of genetically distinct populations that continue to interbreed at a low rate. This is basically the biological species concept (Mayr 1942), but accommodates the fact that a great many sexual species hybridize [many pertinent citations] yet existing levels of assortative mating do not decay. (Schluter 2000, p. 13)

Mention of species' concepts then ceases, and the rest of the book flows along with little attention paid to "isolating mechanisms" or, in Harrison's more neutral language, "barriers to gene exchange". Here is a whole book about speciation and the emphasis is upon adaptive radiations and natural selection. Schluter (2000) does admit that "not everyone's definition of adaptive radiation includes speciation", but that he is happier to focus upon the preponderance of cases in which speciation has occurred.

Compare this book with the many papers published within the past ten years that analyze isolating mechanisms, the key to species and speciation. Although this work is great, I do worry about those doing the labor, because no general theory of speciation will ever come from it, as both Mayr and Harrison emphasize. If J.F.W. Herschel was happy to describe natural selection as the "law of higgeldy, piggeldy", then speciation is best described as "the law of super higgeldy, piggeldy". I now discuss two examples, one famous and one not.

Speciation in cichlids

Tijs Goldschmidt went to Lake Victoria in 1985 to study speciation in the cichlid fish. He wrote about his adventures in his book, *Darwin's Dream Pond: Drama in Lake Victoria* (Goldschmidt 1996), the perfect book for a course on evolution for nonmajors in biology. Indeed, Lake Victoria looked like the place to study speciation. In less than 13 000 years (Goldschmidt thought it was older in 1985), an amazing adaptive radiation of cichlid fish happened. Probably a single introduction of a small number of fish (perhaps only one pregnant female) resulted in from 400 to 800 species by the beginning of the 20th century. The differentiations between species include body size, color patterns, skull shapes, and mouth and jaw parts, along with many differences in feeding habits and adaptations to different ecological niches. Many rift lakes in northern Africa and many other places in the world now and in the fossil record show similar radiations of cichlid fish.

However, "Darwin's dream pond" is hardly that. Goldschmidt himself, after careful collecting and attempts to study speciation of the cichlids, says, "I decided that nothing beat poetic truth and abandoned science" (Goldschmidt 1996, pp. 244b–244c). He became a wonderful writer about the science of studying speciation, but stopped doing it. The most recent survey, "New markers for new species: microsatellite loci and the East African cichlids" (Markert *et al.* 2001), suggests that use of allozymes, nuclear DNA, and mitochondrial DNA (mtDNA) has not been very helpful in the study of speciation in cichlids:

The brief periods between speciation events cause what little variation exists at these markers to be shared among taxa. These types of marker are not definitive in studies of assortative mating, only mildly informative for population studies, and are phylogenetically informative in only the oldest lineages. (Markert *et al.* 2001)

Although using microsatellite DNA gives hints about estimates of divergence, to deduce robust phylogenies for the cichlids in Lake Victoria is still impossible. Nor is it yet possible to examine two closely related species and deduce whether their speciation was “microallopatric” or sympatric. Darwin’s dream pond is a tough place to study speciation in cichlids.

Still, what is so interesting about these fishes? Is it the details of the isolating mechanisms? Or is it the adaptive radiation? The recent ecological disturbances of Lake Victoria, especially the introduction of the Nile perch, have so muddled and changed the lake that many of the species of cichlids have disappeared and crossbreeding between remaining ones has occurred. Does this mean that the fish are quickly reverted to the nonbiological category of unscientific “subspecies” and their worth for understanding speciation nothing? To me, the adaptive radiation was no less interesting whether the final “species” had doubtful or certain status as biological species.

North American rat snakes

The other, less famous, example comes from my favorite childhood (and perhaps adult) animal, rat snakes of the USA, and concerns the mtDNA phylogeography of the polytypic North American rat snake *Elaphe obsoleta* (Burbrink *et al.* 2000).

One general pattern in rat snakes was obvious: gray versions occurred in the south, and black versions in the north. Striped versions, north from Florida and up the eastern coast, go from pink to yellow to olive green to black. I have caught black rat snakes from New York State west to Illinois (Pennsylvania, Ohio, Indiana, Illinois), gray in Tennessee, Kentucky, Alabama, and Mississippi, and the striped rat snakes from coastal North Carolina south to Kissimee Lake in central Florida. The map of Burbrink *et al.* (Figure 2.1) fits perfectly my own observations. For a very long time, black rat snakes have been considered to be a single subspecies. The different gray patterns were sometimes given species status.

Into this picture, Burbrink *et al.* (2000) introduced a real surprise, based directly upon their analysis of the phylogeography of mtDNA over the distribution of *E. obsoleta*. Their results show that black rat snakes in North America have descended from three different adaptive radiations, as shown in Figure 2.2.

What a delightful surprise this was. The experts had been completely misled by the apparent similarity of black rat snakes and not even suspected that they could have come from three different radiations. What is the conclusion of the authors regarding species and speciation? The subtitle of the paper (“A critique of the subspecies concept”) and its first paragraph both criticize the validity of the subspecies rank. The authors favorably quote Mayr’s assessment that “the subspecies was not a concept of evolutionary biology ...” and add: “subspecies

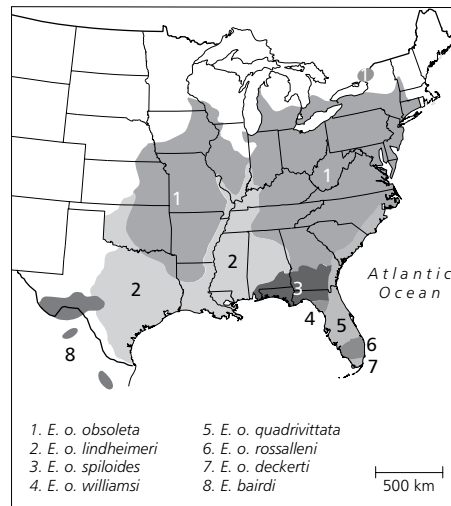


Figure 2.1 Map of the eastern United States showing the geographic range of the subspecies of *E. obsoleta* and *E. bairdi*. Source: Burbrink *et al.* (2000).

have no real taxonomic meaning if they are used to represent arbitrary pattern classes or incipient species” (Burbrink *et al.* 2000).

I find these conclusions perplexing. These authors have resoundingly rejected the long-standing and well-accepted subspecies of *E. obsoleta* with the warning, so clearly expressed in the conclusion:

This study has demonstrated that the subspecies of *E. obsoleta* do not represent distinct evolutionary lineages and underscores the danger of recognizing subspecies based on few characters, especially coloration. These poorly defined subspecies actually mask the evolutionary history of the group. Therefore, describing or recognizing subspecies from a few characters may not simply be a harmless handle of convenience for museum curators, but may be detrimental to understanding evolutionary history. (Burbrink *et al.* 2000)

The authors suggest that the three clades may possibly be lineages that have evolved independently, or “evolutionary” species. I agree that the previous subspecies were defined poorly, and that the three clades revealed by their studies give a much more accurate taxonomy and evolutionary picture. Giving up upon the entire concept of subspecies from the data given seems unnecessary to me. Whether one calls the clades well-characterized “subspecies” or pre-“evolutionary species” seems a minor issue to me.

Is this article a throwaway if, indeed, these clades are not true “evolutionary species” or true “biological species”, but only incipient species? Of course not, the article is equally important whether the clades are full species (evolutionary or biological), or three incipient species of either kind. The phylogenetic order that

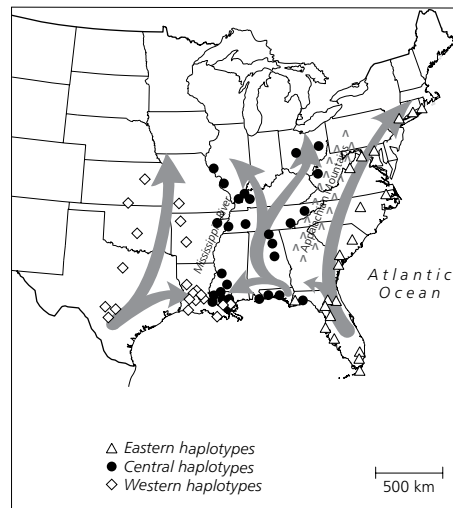


Figure 2.2 Map showing northern dispersal patterns of *E. obsoleta* mitochondrial clades from southern refugia following glacial retreat. *Source:* Burbrink *et al.* (2000).

emerges in this study provides a basis for real investigation of the three adaptive radiations and the differentiation in each clade. The authors mention this possibility.

The rat snake speciation (or subspeciation) problem thus has progressed beyond the case of the Lake Victoria cichlids, for which the entire panoply of molecular evidence has been unable to produce robust phylogenies. However, we know next to nothing about the speciation of the three clades, except that they were probably separate during the last full glaciation. Whether they were separate after the previous glaciation, or the one before that, we have no clue as yet.

Returning to Harrison's belief that the biological species concept is best for understanding speciation, I plead skepticism. If the usual implications of the biological species concept hold true, then to focus upon isolating characters, demotion of subspecies, and dismissal of "incipient species" tends to turn attention away from understanding processes of adaptive speciation. Many chapters in this volume address precisely crucial steps during the incipient divergence of new lineages through adaptive mechanisms.

Our hypothetical student returns to the discussion. She now wants to study speciation as her major interest. She has some requirements for her study. First, she wants complete sequences for nuclear DNA, mtDNA, microsatellite DNA, and any other genetic material for her study organism and its close relatives. She will then see if she can obtain robust phylogenies and, if not, choose another organism for study (but even a perfect, robust phylogeny does not by itself explain speciation). Next, she wants to know about the biology of the study organism, from genes and development to adult morphology and behavior, including sexual selection. She wants to understand the ecological setting not just now, but in recent history. She must, in short, be a natural historian who understands the organism. Finally, she

wants a study organism that has recent speciation and incipient species. (A ten-year generous grant from a suitable source would help her project along.)

This volume

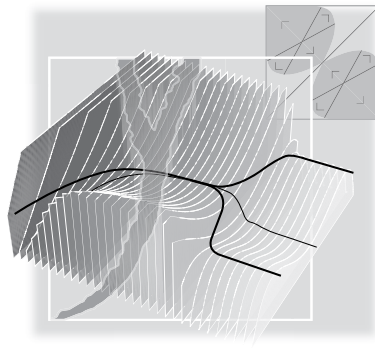
The present volume started with a three-day workshop at which the authors outlined their contributions. All the results of previous conferences on speciation that I have read were much involved with species concepts. This conference, refreshingly, was in no way dominated by discussions of “what is a species?” Instead, the processes of adaptive speciation are the main focus of this book. Adaptive speciation, as defined in the Introduction (Chapter 1), occurs when divergence is an adaptive response to interactions within ancestral populations. Isolating mechanisms may then be either a by-product of divergence, or they may be favored by natural selection. In either case, adaptive speciation typically requires some degree of sympatry between the emerging lineages.

Indeed, many participants did talk about adaptive speciation as a kind of code word for sympatric speciation. Even allopatric speciation is tied deeply to adaptive evolution, since isolation factors often move to fixation because of close linkage relationships with parts of the genome that evolve by natural selection. But the emphasis in this volume is on the adaptive significance of divergence *per se*, rather than just upon isolating mechanisms and the biological species concept. As a corollary, the book does not dwell so much on the pattern-oriented debate about allopatric versus sympatric speciation: it is the process of diversification that is at center stage, and biogeographic patterns are of secondary interest.

The book discusses evidence for adaptive speciation from theory (Part A), experiments (Part B), and phylogenetic patterns (Part C). I tend to view the growing trend toward studying speciation and diversification as adaptive processes, a trend that is represented in this volume, as providing a period of “Darwinian speciation” in the 21st century.

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