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Introduction

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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).
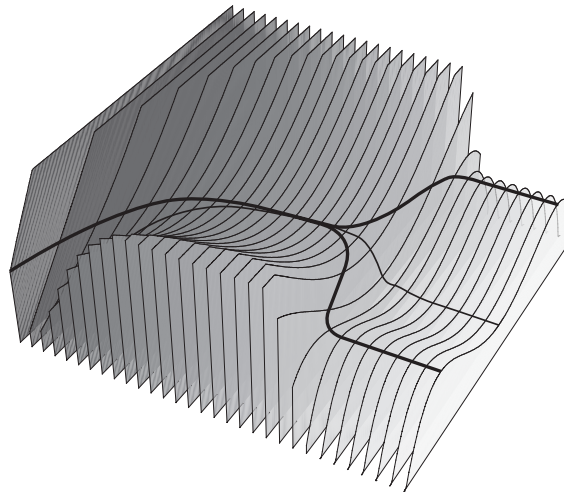
Figure 1.1 Adaptive speciation unfolding. A fitness landscape's shape changes jointly with a population's mean trait value (thick curve; the initial snapshot of the landscape is colored dark gray and the final one white). While the population undergoes directional selection by ascending the fitness landscape, 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.
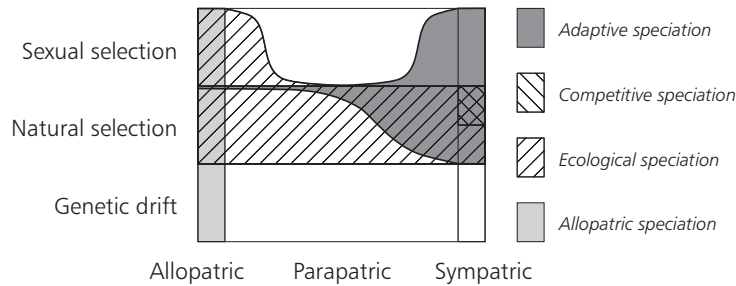
In the definition of adaptive speciation given above, the notion of selection encompasses both natural and sexual selection. In the literature, sexual selection is often pitted against natural selection. This convention goes back to Darwin and is meant to highlight a distinction between those causes 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.

References

References in the book in which this chapter is published are integrated in a single list, which appears on pp. 395–444. For the purpose of this reprint, references cited in the chapter have been assembled below.

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